

**Handbook of  
ENVIRONMENTAL  
PHYSIOLOGY  
of FRUIT CROPS**

**Volume I  
Temperate Crops**

**Edited by  
Bruce Schaffer  
Peter C. Andersen**

**HANDBOOK OF ENVIRONMENTAL  
PHYSIOLOGY OF FRUIT CROPS**

**VOLUME I:  
TEMPERATE CROPS**



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# **Handbook of Environmental Physiology of Fruit Crops**

## **Volume I: Temperate Crops**

*Edited by*

**Bruce Schaffer**

*University of Florida*

*Tropical Research and Education Center*

**Peter C. Andersen**

*University of Florida*

*North Florida Research and Education Center*



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## THE EDITORS

**Bruce Schaffer, Ph.D.**, is Professor of Plant Physiology at the University of Florida, Tropical Research and Education Center in Homestead.

Dr. Schaffer received his B.Sc. degree in Entomology and Zoology in 1978 and his M.S. degree in Forest Biology in 1981, both from Colorado State University in Fort Collins. He obtained a Ph.D. degree in Horticulture in 1985 from Virginia Polytechnic Institute and State University in Blacksburg. After working as a Post-doctoral Associate in Plant Physiology at the University of Heidelberg, Germany, he was appointed Assistant Professor of Plant Physiology at the University of Florida, Tropical Research and Education Center in 1985. He became an Associate Professor in 1990, and Professor in 1994.

Dr. Schaffer is a member of the International and American Societies for Horticultural Science and the honor societies Sigma Xi, Gamma Sigma Delta, Phi Sigma, and Chi Sigma Xi. He has been an Associate Editor of *HortScience*, is currently an Associate Editor of the *Journal of the American Society for Horticultural Sciences*, and is on the Editorial Review Board of *Tree Physiology*.

Dr. Schaffer has been a recipient of research grants from several organizations, including the United States Department of Agriculture and the Charles A. Lindbergh Fund. He has published more than 60 research papers, primarily focusing on whole-plant physiology. His major research interests are environmental physiology of tropical fruit and vegetable crops and sustainable tropical horticulture.

**Peter C. Andersen, Ph.D.**, is Professor at the University of Florida, North Florida Research and Education Center in Monticello.

Dr. Anderson obtained a B.Sc. degree (cum laude) in Biology from Florida State University in 1974, an M.S. degree in Horticultural Sciences from the University of Florida in 1978, and a Ph.D. degree in Horticultural Sciences from Oregon State University in 1982. From 1982 to 1984 he was employed as Assistant Research Professor of Plant Physiology at the Southwest Missouri State University Experiment Station in Mountain Grove. In 1984 he accepted a position as Assistant Professor of Horticulture at the University of Florida, North Florida Research and Education Center in Monticello. He was promoted to Associate Professor in 1989, and Professor in 1994.

Dr. Andersen is a member of the American Society for Horticultural Sciences and the Scandinavian Society for Plant Physiology. He has published more than 100 research articles, the majority of which deal with aspects of environmental physiology. His current research interests include topics in environmental physiology and plant-insect-disease interactions of horticultural crops.

## CONTRIBUTORS

**Peter C. Andersen**

University of Florida  
North Florida Research and Education Center  
Monticello, FL 32344

**Guido Bongi**

National Research Council  
Istituto Ricerche Olivicoltura  
Perugia 06128, Italy

**James G. Buwalda**

The Horticulture and Food Research Institute  
of New Zealand Ltd.  
Ruakura Research Centre  
Hamilton, New Zealand

**Rebecca L. Darnell**

Department of Horticultural Sciences  
University of Florida  
Gainesville, FL 32611

**Frederick S. Davies**

Department of Horticultural Sciences  
University of Florida  
Gainesville, FL 32611

**Nick K. Dokoozlian**

Department of Viticulture and Enology  
University of California, Davis  
and Kearney Agricultural Center  
Parlier, CA 93648

**James A. Flore**

Department of Horticulture  
Michigan State University  
East Lansing, MI 48829

**Alan P. George**

Department of Primary Industries  
Maroochy Horticultural Research Station  
Nambour 4560, Queensland, Australia

**Ian Goodwin**

Institute of Sustainable Irrigated Agriculture  
Tatura 3616, Victoria, Australia

**Peter H. Jerie**

Institute of Sustainable Irrigated Agriculture  
Tatura 3616, Victoria, Australia

**Alan N. Lakso**

Department of Horticultural Sciences  
Cornell University  
New York State Agricultural Experiment Station  
Geneva, NY 14456

**Kirk D. Larson**

South Coast Research and Extension Center  
University of California  
Irvine, CA 92718

**Peter D. Mitchell**

Institute of Sustainable Irrigated Agriculture  
Tatura 3616, Victoria, Australia

**Alistair D. Mowat**

The Horticulture and Food Research Institute  
of New Zealand Ltd.  
Ruakura Agricultural Centre  
Hamilton, New Zealand

**Alberto Palliotti**

National Research Council  
Istituto Ricerche Olivicoltura  
Perugia 06128, Italy

**Bruce Schaffer**

University of Florida  
Tropical Research and Education Center  
Homestead, FL 33031

**Garth S. Smith**

The Horticulture and Food Research Institute of  
New Zealand Ltd.  
Hamilton, New Zealand

**Robert L. Wample**

Department of Horticulture and  
Landscape Architecture  
Washington State University  
Irrigated Agriculture Research and  
Extension Center  
Prosser, WA 99350

**Larry E. Williams**

Department of Viticulture and Enology  
University of California, Davis  
and Kearney Agricultural Center  
Parlier, CA 93648

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## Introduction

**Bruce Schaffer and Peter C. Andersen**

Environmental variables modulate virtually all aspects of plant growth and development. The sum of the interactions between plant genotype and the environment determines plant phenotype and plant productivity. An understanding of environmental physiology is crucial in selecting optimum sites for a given species or cultivar, to minimize the deleterious impacts of suboptimal environmental conditions and to modify or create microenvironments that are conducive to maximum productivity. Moreover, the establishment of a database on environmental physiology is essential in an era of agricultural sustainability where agricultural inputs are becoming increasingly scrutinized.

Previous review articles concerning physiological, and growth and developmental responses of fruit crops to the environment have typically addressed a specific or multiple plant response to a single environmental factor, or alternatively, a specific plant response to multiple environmental variables. In addition, few articles integrate environmental physiology with plant growth and development. Often a large volume of literature from many sources must be compiled to obtain a comprehensive coverage of the environmental physiology of a specific crop.

The purpose of this volume of *The Handbook of Environmental Physiology of Fruit Crops* is to provide a comprehensive reference source on the responses of temperate fruit crops to the environment. This book addresses plant responses to abiotic variables (light, temperature, water, wind, salinity, and air pollution) and when possible integrates whole plant physiology with production horticulture. The volume was designed to appeal to a wide audience of researchers, extension workers, and students interested in fruit crop physiology and is written on a level that is commensurate with a general understanding of plant physiology.

We have relied on the broad horticultural definition of fruit crops to include woody or herbaceous perennial trees, shrubs, or vines with the edible portion (fruit) an expanded and ripened ovary with attached and subtending reproductive structures.<sup>1,2</sup> At times we have strayed from this definition. For example, we have included strawberry, which is often grown as an annual. Most of the commercially-important temperate fruit crops are contained in this volume. However, some crops were omitted due to either the lack of available information and/or the inability to locate a qualified author. A few “warm temperate” crops, such as persimmon, are discussed in this volume although they can be cultivated in subtropical and tropical regions. Although an attempt was made to solicit chapters from highly qualified individuals, clearly there are many more individuals who would have been eminently qualified as authorities on certain crop species.

This book is generally divided according to fruit crops species or related species of fruit crops. In one chapter, “Temperate Nut Species”, many species have been combined in the discussion because of the limited available database. Crop origin, genetic diversity, botany, and ecology were often included to facilitate a discussion of environmental physiology. There is a great deal of flexibility in the orientation, content, and style of each chapter. The terminology and abbreviations used to define physiological variables are consistent within each chapter. However, there are some differences in terminology among chapters, reflecting the lack of a commonly accepted terminology among plant physiologists. Although the authors attempted to comprehensively discuss plant responses to abiotic factors, to some extent chapters reflect the authors’ particular research specialty. For certain crops such as grape, apple, and stone fruit there has been much research on environmental physiology focusing on leaf gas exchange, water relations, and carbon partitioning. The extensive database for those crops presented the authors with much flexibility to determine the scope and content of their material and allowed for an integration of several physiological responses. In contrast, little information was available for some of the fruit and nut species, and consequently, the discussion often relied more heavily on growth and developmental responses.

In addition to serving as a useful reference source, this volume of *The Handbook of Environmental Physiology of Fruit Crops* will underscore the limitations of our knowledge in this area and will help delineate areas in need of further research.

The physiological, growth and developmental responses in relation to the interaction among multiple environmental stresses is a topic that warrants increasing emphasis. For most fruit and nut species the database concerning the influences of environmental variables must be expanded to allow for the development of models that maximize plant productivity and resource use efficiency.

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## Chapter 2

# Apple

Alan N. Lakso

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## I. INTRODUCTION

The environmental physiology of the apple (*Malus domestica* Borkh.) has been extensively researched compared to many other fruit crop species. Since a comprehensive review of this entire knowledge base is beyond the scope of a review of this size, this chapter will be interpretive rather than comprehensive, emphasizing (1) knowledge developed primarily since the last major reviews on radiation, water, temperature, etc. (mostly work in the 1980s), (2) integration of knowledge with a view toward whole-plant and crop physiology, (3) interactions of physiological responses to multiple environmental factors in the field, and (4) identification of remaining roadblocks and new opportunities to apply this knowledge to solve problems of apple production.

The reader is referred to several excellent reviews of apple physiology and morphology on which this chapter is based<sup>1-9</sup> as well as general reviews and books that are applicable.<sup>10-13</sup> The reader is referred to several useful books and reviews and references therein for methods and techniques.<sup>14-18</sup> This review will emphasize carbon and water relations of apple trees growing in temperate zones. Since the apple is grown for fruit production, the discussions will primarily concern the range of conditions normally occurring in a producing orchard rather than in extreme conditions.

### A. LIMITING FACTORS

Before discussing individual environmental factors that affect productivity, it is worthwhile to consider the concepts of limiting factors. Monteith<sup>19</sup> has emphasized that each resource (light, CO<sub>2</sub>, water, nitrogen, phosphorus, boron, etc.) and each process (light interception, photosynthesis, respiration, leaf area development, translocation, nutrient uptake, nitrogen reduction, protein synthesis, hormone transport, ion exchange processes, etc.) is *essential* for productivity. However, that does not mean that any one resource or process is necessarily *controlling the variations* in crop productivity. It is important to understand that many processes can be essential without ever being important to the variations in crop productivity (for example, water is essential, but accounts for little of the variations in productivity in irrigated orchards). The primary role of the crop physiologist is to determine which resources or processes are limiting crop performance at any given time and ideally determine a feasible way to overcome the limitation.

There is no *a priori* reason to believe that any one resource or process is always limiting to a crop. It is much more likely that there are periods of differing resource or process limitations during the developmental stages of the crop. Environmental resources (light, water, etc.) or conditions (temperature, humidity) may limit crop development at certain times depending on the crop sensitivity and how extreme the environment may be. Additionally, plant status, such as crop load, may greatly change the relative sensitivity of the plant to an environmental stress or resource limitation.

Interactions of plant development and the environment should be kept in mind when evaluating the plant's response to any particular environmental factor. A useful analogy is that of pulling at any one connection point in a net. Other nearby connection points will react similarly, while those further away will react less. The entire net, however, will adjust to the new set of forces. The plant is a network of processes that must be considered together. We must consider the whole when considering any one part. As Jules Henri Poincaré reportedly said: "Science is built up with facts, as a house is built up with stones. But a collection of facts is no more a science than a heap of stones is a house."

This review will attempt to address not only the physiological "stones" that have been studied for many years, but also the physiological "house" we call an apple tree.

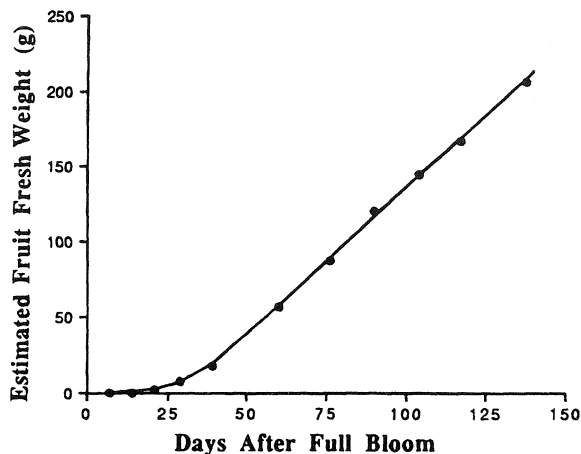
## B. GROWTH AND DEVELOPMENT

Before considering specifics of physiological responses of the apple to the environment, a brief overview of the inherent growth and development patterns can provide a context with which to evaluate the physiological information (see review by Forshey and Elfving<sup>2</sup> for review of general growth relationships in the apple).

The apple is a hardy, deciduous, temperate fruit crop species that is very adaptable to different climates, growing commercially from the tropics<sup>20</sup> to the high latitudes in Norway.<sup>21</sup> A perennial structure with carbon and nutrient reserves allows very rapid leaf area development in the spring compared to annual crops (see Oliveira and Priestley<sup>22</sup> for a general review of carbon reserves). Early development, combined with slow leaf aging for apple,<sup>23</sup> translates to a long duration of photosynthetically-active leaf area. This is the basis of high yield potential since dry matter production by crops is generally positively related to the amount of total radiation intercepted per hectare per season.<sup>24</sup> In general, apple is considered day neutral for most processes. The few reports of light quality effects indicate that fruit set may be stimulated by night breaks with red light,<sup>25</sup> and that UV light may be important in anthocyanin development in the fruit.<sup>26</sup> Leaf retention appears to be due in part to the lack of photoperiodism. Leaf senescence and abscission in the autumn are apparently regulated by the advent of cool temperatures, not daylength.<sup>27,28</sup> The growth and productivity of apple trees are largely limited by the length of the growing season at each location, perhaps one reason why apple is so widely adaptable.

The structure of the apple canopy is varied, containing shoots of differing lengths. Short rosette-type shoot complexes, referred to here as the "spurs", and longer single shoots with leaves spaced with long internodes, referred to as the "extension shoots", develop concurrently in the spring.<sup>8</sup> The spurs develop with a rosette of primary leaves unfolding by bloom, followed by the development of generally one lateral shoot, the "bourse" shoot, after bloom. The bourse shoots are typically also quite short and terminate within a few weeks of bloom; however, in high-vigor situations they may grow to be quite long, similar to the extension shoots. Extension shoots typically develop from terminal or lateral buds of the extension shoots of the previous year. These shoots may terminate early (sometimes called "lateral or terminal short shoots") and become the spurs of the following year or they may extend as described above. Depending on the age of the tree, spur versus standard growth habit, pruning, vigor, and growing conditions, the distribution of shoot length and the spur:shoot ratio will vary dramatically.<sup>2,29-31</sup> The balance of the types of growth habit has implications for the type of canopy and for the penetration of light within the canopy (see Radiation section).

The apple bears many more flowers compared to fruits at harvest. A dwarf tree with heavy bloom may have up to 800 flower clusters of an average of 6 flowers per cluster, a total of up to about 5000 flowers. The same tree will typically retain perhaps 200 fruits to harvest, only 4–10% of the potential fruits. There are many potential reasons why the abscission rate is so high, but nonetheless, the apple has a great variability in the numbers of sinks that can be retained on the tree. Under near-ideal conditions fruit yields can be extremely high, reaching record sustained yields approaching 180 tons per hectare in New Zealand.<sup>32</sup> Converted to dry matter of about 30 tons per hectare, apple is comparable with potato, having the highest  $C_3$  crop productivity.<sup>33</sup> The high dry matter yield is also due in part to the very inexpensive energetic costs for the primarily carbohydrate apple fruit compared to other crops, such as nut crops and avocado, that accumulate energetically expensive proteins or oils.<sup>34,35</sup> Heavily cropping apple trees can exhibit very high harvest indices (percentage of total dry weight gain partitioned into the fruit). Palmer<sup>36</sup> reported a harvest index of about 65%, including root mass, with young, dwarf Mutsu/M27 trees. In mature heavy-cropping 'Jonamac'/M26 trees, the estimated harvest index exceeded 80% including roots.<sup>37</sup> These high harvest indices are largely due to the very low investment of carbon required for the perennial structure in established dwarf trees.



**Figure 1** Seasonal growth of 'Empire' apples with early thinning to light crop in New York and fitted "expolinear" model based on the expolinear growth function (Equation 1) described by Goudriaan and Monteith.<sup>40</sup> Regression parameter estimates were  $C_m = 1.95 \text{ g day}^{-1}$ ,  $R_m = 0.167 \text{ g g}^{-1} \text{ day}^{-1}$ ,  $t_b = 30 \text{ days}$ .

The growth of the apple fruit has been described in textbooks and reviews as being sigmoid.<sup>1,10,12,38</sup> It is not clear, however, if the sigmoid pattern is that inherent to the fruit (i.e., the growth pattern if the fruit was not limited by any resource) or whether it reflects a variety of late-season limitations of resources or temperature. When 'Empire' apple fruits were allowed to grow on very light cropping trees with early thinning and apparently optimal water and nutrients, fruit weight increased exponentially during the cell division period, typically the first 3–6 weeks after bloom, then increased linearly until normal harvest (Figure 1). This pattern was shown by Blanpied in 1966.<sup>39</sup> Cold temperatures in the last weeks before harvest slowed growth, but plotting growth against growing degree days during the last portion of the season linearized the growth. This growth pattern has been described well with a growth equation developed by Goudriaan and Monteith<sup>40</sup> called the "expolinear" function:

$$W = (C_m/R_m)\ln\{1 + \exp[R_m(t - t_b)]\} \quad (1)$$

where  $W$  = crop (or fruit) weight,  $C_m$  = maximum absolute growth rate (in weight gain per day in the linear phase),  $R_m$  = maximum relative growth rate (in weight gain per unit weight per day),  $t$  = time in days,  $t_b$  = x axis intercept of the linear growth phase (termed the "lost time").

The implications of this growth habit suggest that: (1) after the cell division period is over, the growth rate or demand of the fruit (i.e., the slope of the weight vs. time curve) remains essentially constant until harvest; and (2) the slope of the linear portion of the growth curve depends on accumulation of cell numbers during the exponential period. This emphasizes resources needed to support good fruit growth during cell division in order to provide good potential for the rest of the season.

### C. AN ECOPHYSIOLOGY VIEWPOINT

When considering the environmental physiology of the apple, it is useful to consider two factors. First, clonal propagation stops the natural selection process (except for breeders' selection for fruit color and quality factors and uniformity of bearing), thus little selection for physiological responses has occurred in commercial cultivars. Few physiological differences in environmental responses can be found between a 200-year-old cultivar such as 'McIntosh' and a newly released cultivar. This suggests that an understanding of the physiological behavior of apple may be enhanced by considering natural selection pressures during evolution.

Although not entirely clear, the center of origin of the apple is probably in southern China or Georgia and Armenia. The descriptions of Vavilov<sup>41</sup> in the Caucasus Mountains suggest that the apple evolved in exposed wooded canyons reasonably close to sources of water, but in competition with other grasses, shrubs, and trees in a temperate climate with occasional droughts. Under such conditions it might be expected that overall strategies of productivity may be based on the need for initial vegetative develop-

ment of the shoot system in competition for sunlight and of the root system to reach a relatively large, deep water supply found below the dense rooting zone of grasses and other annuals. Since the production of fruits is detrimental to shoot growth and especially to root growth,<sup>42,43</sup> the extended juvenility period of apple seedlings would appear advantageous to competitiveness. Once an adequately exposed canopy and a deep, extensive root system have developed, the tree may be expected to be able to produce fruit without harming the competitive status of the tree for water, nutrients, or radiation.

Therefore, it may be reasonable that early season stresses such as water deficits, shade, or nutrient deficiencies would induce fruit abscission to allow for a vegetative response to compete for the limited resource. The general concept from ecology that the reproductive development is the first priority of the plant needs to be viewed in a multi-year perspective for perennials like apple. In this case, survival for many years and successful competition against other plants for limited resources afforded by good vegetative growth may lead to the maximization of reproduction over the life of the tree. In each individual year, however, the drop of fruit may, ironically, be the method by which the apple maximizes lifetime fruit production.

This may explain to some extent the variability of fruit set and yield that is the bane of agricultural practitioners and marketers. It may be helpful to consider that the fruits may not be programmed to set, but rather to abscise. Only under conditions of adequate resources (nutrients, water, radiation, etc.) that do not threaten the survival of the tree will the fruit be able to continue to grow and mature. Zucconi<sup>44</sup> has proposed that fruit retention is a function of maintenance of fruit growth rate and that limitation of growth from any source will lead to the reduction of auxin transport from the fruit to the abscission zone<sup>45</sup> and thus cause abscission. This view is consistent with the great range of conditions or stresses observed to cause fruit abscission and yield variation. Lang<sup>46</sup> has suggested similarly that the study of dormancy should be founded in an understanding of the ecophysiology of the species and the range of environmental stresses under which it evolved. Perhaps an ecophysiological view may provide some insights to apple physiology that are not as apparent when tree behavior is viewed from the agricultural perspective alone.

## II. RADIATION

Of all the environmental factors, solar radiation should be considered first due to its primary role as the source of energy that drives the biological production of dry matter that ultimately limits fruit yield. First, we should consider the quantitative aspects of yield and how they are regulated by light availability and utilization. It is helpful to break yield into several components: biological yield, fruit yield, and economic yield (i.e., total dry matter, dry matter in fruit, and the economic return from the fruit, respectively).

### A. BASES OF ORCHARD PRODUCTIVITY

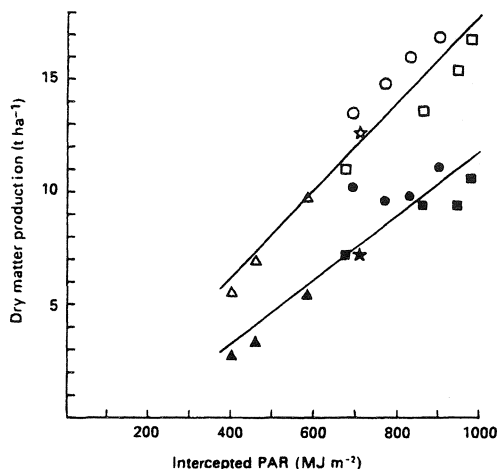
As illustrated in Equation 2, biological yield of dry matter has as primary components: the amount of incident light, the fraction of light intercepted, the photosynthetic transduction of light energy into fixed carbon minus the carbon lost to respiration.<sup>47</sup>

$$\text{Bio Yield} = (\text{Light Available})(\% \text{ Intercepted})(\text{Photosynthesis}) - \text{Respiration} \quad (2)$$

Inducing variation in specific components via management can be, and has been, used to cause desired effects on yields. The light available to an orchard is a function of the climate of a given location and year, thus is not amenable to manipulation, although the variations among locations and years on yield can be great. The amount of radiation intercepted by an orchard, however, is an important regulator of potential productivity of apple orchards, although total light interception is often sacrificed due to specific localized needs for exposure for fruit yield and fruit quality (see Section II.D).

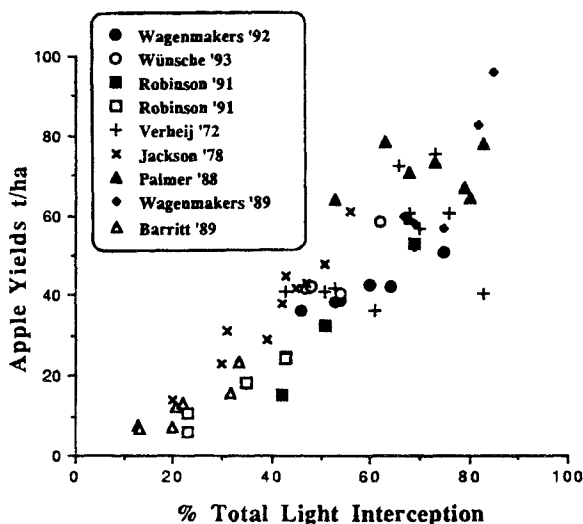
### B. ORCHARD LIGHT INTERCEPTION

Crop physiologists, led by Monteith,<sup>19,24</sup> have demonstrated a fundamental relationship between crop dry matter production and seasonal integrated light interception. The slope of the relationship (dry matter produced per unit of light intercepted) has been called radiation use efficiency or conversion efficiency. Palmer<sup>6</sup> has reported in two different studies that apple production systems conform well to



**Figure 2** The relationship between seasonal intercepted PAR and dry matter accumulation in the fruit (solid symbols) and total tree (open symbols) in 'Golden Delicious'/M9 spindle and 'Crispin'/M27 bed plantings in England. (From Palmer,<sup>6</sup> reproduced with permission)

this relationship (Figure 2). Caution should be used, however, when interpreting the dry matter to accumulated light interception correlations. A good linear correlation may imply that different productivities are caused only by differences in light interception, reasonable considering the essential role of light as the energy source for crops. Yet, to show a stronger causal relationship, short-term (e.g., weekly) dry matter gains and light interception should be plotted against each other rather than plotting the accumulated values over a season.<sup>48,49</sup> Nonetheless, this concern does not diminish the importance of light interception and manipulation of light for comparisons of potential, if not actual, productivity of different apple training systems with similar management.<sup>6,50</sup> If the canopies are managed to be open for good light penetration, differences among systems are commonly due to differences in total light interception. From the literature, fruit yields versus mid-season percent of light interception in well-managed orchards show a generally good relationship (Figure 3). The data from the low interception/low yield portion of the plot show a linear correlation, while at interceptions over 50% the yields vary more, indicating that factors other than light may be limiting. Interestingly, although poor yields



**Figure 3** The relationship between apple training system yields and percent of total light interception from several reports from the literature. (References 36, 52, 57, 60, 119, 274–276)

in dense orchards with high light interception are often observed, those situations rarely appear in the literature.

### 1. Factors Affecting Light Interception

A great deal of progress has been made in the last 25 years in understanding the factors related to light interception by orchards. A variety of light interception models have been developed based on radiation geometry and canopy characteristics such as height, width, spacing, orientation, and leaf area density. Initially, these were “solid” models that assumed no transmission through the canopy, so that they predicted the maximum possible interception for each orchard design (see reviews by Jackson,<sup>3</sup> Palmer,<sup>6</sup> Johnson and Lakso,<sup>51</sup> and Wagenmakers<sup>52</sup>). Palmer extended the models by incorporating leaf area to estimate patterns of exposure on the canopy surfaces and within canopies.

The classic assumption for annual crops of full cover with leaf area distributed randomly in space could not be utilized for discontinuous canopies as in orchards.<sup>53</sup> Consequently, Jackson and Palmer<sup>54</sup> proposed a simplified approach (Equations 3 and 4) for orchards in which they distinguished the light that was transmitted directly to the orchard floor between the rows from the light that was transmitted through the tree canopies.

$$T = T_r + T_c \quad (3)$$

and

$$T_c = (1 - T_r) e^{-KL'} \quad (4)$$

where  $T$  = fractional transmission of light by the orchard;  $T_r$  = fractional transmission of light passing *between* the trees;  $T_c$  = fractional transmission of light passing *through* the canopies;  $K$  = extinction coefficient (amount of light intercepted per unit LA) and is the slope of the  $\ln$  light transmission vs. leaf area index (LAI);  $L'$  = adjusted leaf area index ( $LAI/1 - T_r$ ) which expresses leaf area on the basis of mean ground area shaded by the tree.

The fraction of light that was transmitted directly to the floor was estimated with solid models, either mathematical or physical,<sup>3,55</sup> allowing the relationship of light transmission to leaf area to be determined for radiation incident upon the canopy. Light transmission through the canopy was then related to the light actually incident on the volume allotted to the canopy. The LAI was divided by the fraction of light incident to the canopy (i.e., essentially the mean daily shadow area) to be more representative of actual LA density. This approach has recently also been utilized for a simplified canopy photosynthesis model of the apple where the assumption of LA being distributed over the whole orchard area was not appropriate.<sup>56</sup>

In most species there is typically one extinction coefficient,  $K$ , given for that type of canopy. However, Jackson<sup>3,57</sup> has summarized the estimates of  $K$  to vary between 0.33 in more mature trees, and 0.77 for young trees with primarily extension shoots. With the variation in the balance of spurs versus shoots in different apple canopies, extinction coefficients should not be expected to be constant. In mature trees having a spur-type habit and relatively few extension shoots,  $K$  values of 0.3–0.4 are reasonable since the clumped foliage of the rosette-type spurs would be expected to intercept less light per unit leaf area than the more uniformly displayed leaves on extension shoots. Clearly, this variation in canopy  $K$  should be taken into account when modeling light interception and distribution patterns in apple trees.

### 2. Value of Orchard Models

Orchard light utilization models have helped guide apple crop physiology. First, the models were helpful to understand the implications of the changing canopy sizes and spacing patterns that became prevalent in the 1970s with higher density plantings that emphasized earlier bearing. From the solid models it became apparent that even though the newer plantings were of higher density and intercepted light earlier in their life; at maturity light interception actually declined compared to older larger tree orchards. This decline was primarily due to restricting tree height to 2–2.5 m, while maintaining alleyways of about 2.5 m or more for equipment. The older, taller standard trees could grow over the alleyways and intercept light, allowing equipment to pass under the canopy. The solid models have demonstrated that modern dwarf pyramid from orchards limit light interception to a potential maximum of about 60%.<sup>54</sup>

**Table 1 Simulation of comparable light interception (all approximately 62%) by orchards of different canopy dimensions, spacings, leaf area indices, and common indirect canopy indices for truncated triangular hedgerows listed below**

| Canopy Dimensions (m) |             |                 | Indirect Canopy Indices |                                       |  |
|-----------------------|-------------|-----------------|-------------------------|---------------------------------------|--|
| Height                | Basal Width | Clear Alley (m) | LAI                     | Volume ( $\text{m}^3 \text{m}^{-2}$ ) | Surface ( $\text{m}^2 \text{m}^{-2}$ ) |
| 3.0                   | 1.2         | 2.5             | 4.3                     | 0.73                                  | 1.79                                   |
| 3.0                   | 1.5         | 1.0             | 2.4                     | 1.35                                  | 2.72                                   |
| 1.5                   | 0.3         | 0.5             | 2.5                     | 0.42                                  | 3.94                                   |

Adapted from Jackson, J.E. and Palmer, J.W., *Sci. Hortic.*, 13, 1, 1990.

In actual orchards, modern plantings of Slender Spindle forms typically intercept between 40 and 50% of the incident light in mid-season because the rows are not complete hedgerows and a relatively porous canopy is required for maximum yield and quality.<sup>58,59</sup>

Understanding the limits to high density plantings led, in part, to attempts to increase productivity by reducing the amount of alleyway relative to tree size with double, multiple rows, and full fields of single rows with very narrow between-row spacing. Although successful in increasing light interception, and in some cases total yields, generally these approaches have generally failed due to the difficulties of management and to poor fruit quality caused by poor light exposure in dense plantings. A different approach has been to move from the pyramid tree either to taller, less sloped hedgerow forms (i.e., Italian palmette, French l'axis centrale) or to Y- or V-shaped hedgerows that grow over the alleyway above the equipment. In a comparison of three similar pyramid forms of differing sizes versus a Y-shaped trellis hedgerow, Robinson et al.<sup>58</sup> and Robinson and Lakso<sup>60</sup> found that all pyramid form systems had similar light interception values at about 45–50%, but that the Y-trellis form had 60–70% interception, and higher yields, while allowing equivalent or better equipment access.

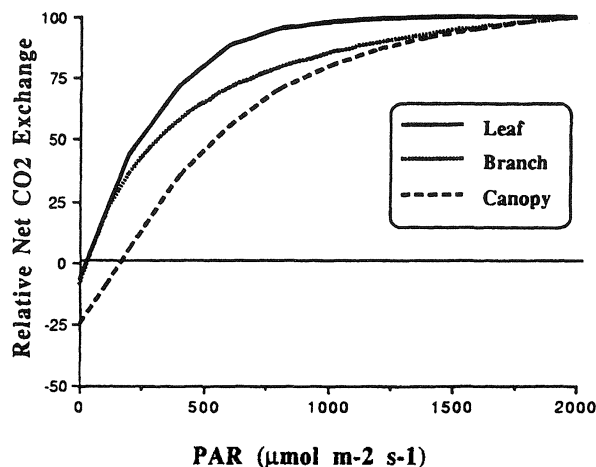
Row orientation effects on orchard light interception and distribution have been elucidated. A north-south (N-S) orientation of a solid hedgerow distributes the light on both sides of an orchard row and latitude will not have much effect on light interception or distribution. For individual trees at higher latitudes with lower solar altitudes, more tree-to-tree shading within the row will occur at mid-day than at lower latitudes with high solar altitudes (on the summer solstices for each hemisphere the sun at noon is perpendicular to the earth at 23° from the equator). Similarly, it seems logical that east-west (E-W) rows should have less light interception than N-S rows since the solar track runs E-W. Modeling has shown, however, that this last assumption is not necessarily true,<sup>61</sup> since E-W rows intercept significantly less light than N-S rows only at lower latitudes, 10–25° from the equator, where the solar track is almost parallel to the E-W row. At higher latitudes the solar track is relatively flat so that in the morning and afternoon the sun shines on the north side of an E-W hedgerow.

It should be noted that the effects discussed above are primarily relevant to more vertical tree forms. The flatter the tree form, the less the effects of row orientation. The light interception of a flat horizontal surface is independent of orientation. It is important when measuring light interception to understand that measurements taken at one time during a day may be representative of the daily integral for horizontal canopies, but not for more vertical canopies. The light interception of a tall, very thin tree wall at noon will be low, but clearly not true for the rest of the day.

In a particularly useful analysis, Jackson and Palmer<sup>54</sup> simulated orchard light interception with families of curves useful to estimate light interception by hedgerow shapes with varying row spacing, tree height, tree thicknesses, clear alley width, and leaf area densities. A good example (Table 1) is given that demonstrates that light interception can be equal with greatly varying combinations of the above factors, pointing out that none of these factors alone (nor other indirect terms such as tree volume or surface area) can predict light interception or potential yields.

### C. SHORT-TERM RESPONSES TO RADIATION

The light interception of an orchard is the maximum energy supply that determines the *potential* dry matter yield. But the energy must be efficiently converted to dry matter by the process of photosynthesis (and is partially utilized by respiration) to produce the *actual* dry matter yield.



**Figure 4** Light response curves of CO<sub>2</sub> exchange for a single apple leaf, a branch (from data of Proctor et al.<sup>64</sup>) and for a whole canopy (data from Corelli Grappadelli and Magnanini<sup>62</sup>).

## 1. Photosynthesis

Although incident light is not controllable, the light responses of apple leaves and whole canopies need to be known to understand the effects of different light levels since light is the single most important factor controlling tree carbon fixation of healthy trees. A large number of studies have shown that the apple leaf photosynthesis is a C<sub>3</sub> type with a hyperbolic light response that typically saturates at 25–50% of full sunlight (500–1000  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ), with a light compensation at about 20–60  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  photosynthetic photon flux (PPF) (Figure 4). Good rates of photosynthesis per unit leaf area for healthy, exposed leaves are approximately 15  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf area s}^{-1}$ , which is comparable to the *Prunus* species and grapes, but higher than citrus.<sup>13</sup>

The photosynthetic response of branches or the whole canopy to light intensity, however, is much more gradual than that of individual leaves, and may not saturate even at full sunlight levels<sup>62–65</sup> (Figure 4). The lack of clear light saturation in the whole canopy is due primarily to the variation in leaf angles and exposures such that in a full canopy only a portion of the leaves are exposed to saturating light levels at any time. Other leaves are exposed to sun, but at low angles of incidence so the light intensity is low, while the remaining leaves are shaded and dependent on diffuse light only. Canopy structure may be expected to affect the light response as well. Horizontal canopies with leaves that have adapted to the light orientation by displaying more horizontally would be expected to have a clearer mid-day light saturation than a vertical canopy. Note also that the dark respiration is much greater in whole-canopy measurements than for single leaf measurements due to the inclusion of non-photosynthetic organs in the whole canopy chamber (Figure 4).

For a whole canopy, the distribution of light between direct and diffuse components may be important as well as the total light since many leaves may be dependent only on diffuse light. Under very clear conditions with only 10–15% diffuse light, the shaded leaves may be at much lower light intensities than under bright, hazy conditions even though the total light intensities are not very different (easily seen as the darkness of shadows under different conditions). Allen et al.<sup>66</sup> suggested that for C<sub>3</sub> plants whole-canopy photosynthesis may actually be higher under bright, hazy conditions than under clear conditions due to higher light levels on the shaded leaves. Although it is expected that this may be the case also for apple trees, it has not been documented. If true, climates with lower light, but higher diffuse components, may not have less whole-tree photosynthesis compared to clear climates. Fortunately, relatively simple, inexpensive methods have been developed to measure whole-tree gas exchange under close-to-ambient conditions in clear plastic film “balloon” chambers.<sup>62</sup> These methods should be increasingly useful in fruit crop physiology.

Estimating whole-canopy responses of trees is not straightforward, however. Measured CO<sub>2</sub> exchange of whole canopies is *not* strictly photosynthesis in that respiration of non-photosynthetic organs is included in the measurements. Additionally, light response curves for a whole tree should not be estimated by plotting diurnal changes in whole-canopy gas exchange against diurnal changes in incident

light. First, the amount of light intercepted by the canopy may change during the day, especially in the case of vertical canopies. Second, there may be changes with time, temperature, or humidity during the day that may modify the apparent light response if these factors are ignored. It is more appropriate to do short-term measurements with shade materials to avoid many of these problems, although shading may reduce canopy temperatures, possibly reducing respiration rates (see Section II.B.1).

## 2. Short-Term Carbon and Water Balance Effects

Since many aspects of apple tree growth and physiology are affected by the photosynthetic rates, there will be many indirect, thus somewhat delayed, effects related to the carbohydrate availability. One recently documented effect is that of a reduction in root respiration rate and proportion of the total root length (white in color) following a reduction in shoot irradiance.<sup>67</sup> Similarly, growth rates of young apple fruitlets during the fruit drop period have been found to decline with shading of the canopy, but increase with short-term CO<sub>2</sub> enrichment, implicating carbon supply limitations.<sup>5,68</sup> Reductions in fruit growth rates have been found in our studies to be an indicator of impending fruit abscission in young fruitlets as reported earlier.<sup>44,69</sup> Short-term shading has been shown to reduce cell division rates in young fruits<sup>70</sup> as well as to cause significant abscission if imposed during the cell division period prior to the final fruit drop.<sup>68,71–75</sup>

The exposure of leaves to high radiation loads also induces higher rates of transpiration (E) and water use. In a tree such as the apple that has a relatively high resistance to water flow, short-term high E rates induce low leaf water potentials ( $\Psi_l$ ) in exposed leaves.<sup>4,11,76</sup> Although this may be expected to lower the leaf turgor, osmotic adjustment has been found to occur in relation to exposure so that mean daily turgor was essentially unchanged with exposure.<sup>5</sup> Water relations will be covered in detail later.

## D. LONG-TERM RESPONSES OF EXPOSURE TO RADIATION

### 1. Photosynthesis

Long-term exposure of leaves to sunlight has significant effects on both the development and the “aging” of mature leaves. As with most plants, apple leaves that develop in the sun develop into “sun” leaves that are thicker, denser, contain more nitrogen, and exhibit higher photosynthetic rates than those developing in the shade.<sup>13,77,78</sup> Later in the season the decline of light-saturated photosynthesis rates appears to be remarkably slow compared to many fruit crops, with exposed leaves maintaining relatively constant rates until harvest in cropping field trees<sup>23</sup> (also see Flore and Lakso<sup>13</sup> for a discussion of methods of determining photosynthetic “aging”). Leaves that are shaded, however, show more rapid declines in light-saturated photosynthesis rates, apparently related to the time-shade integral, with little recovery if re-exposed by summer pruning.<sup>23,79</sup> It is thought that the very slow aging of apple leaves compared to other temperate deciduous species may be an important mechanism that allows the apple to adapt to long growing seasons with high productivity. This would be especially advantageous since most new leaf production usually stops in mid-summer, and productivity depends on the existing leaves.

#### a. Fruiting

In addition to the short-term instantaneous responses to light, many important processes in the production of apple fruit are strongly modulated by the amount of light exposure over long periods.<sup>3,6,59,80,81</sup> The initiation and differentiation of floral buds is strongly stimulated by good exposure of the spurs to light. Little or no bloom develops on spurs with less than about 15% exposure to light, while flowering is maximal at exposures above about 60%. Similarly, the leaf areas and productive potential of spurs require good light exposure, and may be the actual basis of the apparent correlation between spur age and declining spur vigor or fruit quality.<sup>82</sup> Yet, this author has observed vigorous spurs with large leaf areas and large fruits on spur complexes greater than 20 years old if the spurs were very well exposed throughout their life. In the fruiting season, fruit set, size, dry matter, soluble solids, and color are positively related to exposure, although the effects are probably a combination of carry-over and short-term processes (e.g., good exposure the previous year may give high leaf area/spur which can provide the short-term supply of carbohydrates needed for fruit growth).

#### b. Potential Mechanisms of Light Exposure Effects

The mechanisms of physiological responses to light exposure have not been elucidated. Several possibilities are worthy of discussion.

First, the natural shade/exposure effects may be due to changes in light quality with filtration of the light through the leaves of the canopy. The light spectrum changes within the canopy, especially the red:far red ratio<sup>83</sup> that is of importance to phytochrome-mediated morphogenesis. It does not appear, however, that important exposure effects (such as flowering, leaf photosynthetic characteristics, fruit growth rates, fruit size, and fruit color) are phytochrome-mediated since studies with artificial, neutral density shade cloths are able to reproduce the exposure effects with only changes in light intensity.<sup>3</sup>

Second is the direct effect of light striking the organ of interest. Outside of the direct effect of light on the development of red color in fruit, there is little evidence of morphogenetic mechanisms requiring high light intensities. However, the effects of light on temperature, photosynthesis, and carbon balance may be important. The proximity or the specific type of the photosynthesizing organ may be important to flowering or fruit development. In the case of fruit growth and fruit set, it appears that much of the early fruit growth after bloom is dependent on photosynthates from spur leaves. Leaves on growing shoots primarily export to the shoot tip until the shoots develop at least 10–12 leaves, and many more leaves are required if the shoot is in the shade.<sup>5,68,84–87</sup> Increases of available photosynthates due to light exposure of spur leaves at that time could explain the exposure effects on fruit growth and set.

Since apple fruits contain chlorophyll, direct exposure of the fruits allows some photosynthetic activity that should help the carbon balance of the fruit. A series of studies at the Institut für Obstbau und Gemüsebau, University of Bonn, and by others have shown that exposure to light can significantly reduce the loss of carbon via respiration by the fruit, and that the fruit may be able to respond to light throughout the season.<sup>88–93</sup> The relative importance of the direct effects of carbon balance as affected by light exposure of the fruit needs to be better documented, especially the potential role for fruit set.

A third alternative mechanism of exposure effects is not related to visible or photosynthetically active light, but to radiation-induced differences in foliage temperature, E, and the resultant allocation patterns of root-supplied hormones and/or nutrients.<sup>94,95</sup> Within the canopy, the exposed foliage receives much higher radiant energy loads that induce higher transpirative rates as the energy is dissipated (see Nobel<sup>96</sup> to review energy balances). The higher E rates are expected to partition a greater portion of the xylem sap and its contents into the more exposed sites in the canopy. Although there is evidence that root-derived regulators or nutrients may be important to flowering, the potential direct importance for fruit growth and set is not as clear except possibly for the general role of cytokinins as stimulators of cell division. In apple as well as other fruit crops, nitrogen contents of leaves have been found to increase with light exposure, and leaf photosynthetic rates were related to the nitrogen contents as well.<sup>97–102</sup> Partitioning of xylem-derived solutes may provide a better nutrient supply in general to exposed foliage and fruits. Additionally, the direct exposure of the fruit has been shown to increase fruit temperatures<sup>103</sup> and would be expected to increase fruit transpirational flux as well. Higher fruit temperatures may stimulate the translocation of nutrients and hormones to the fruit sink, thus increasing sink strength.

### *c. Flower Bud Development*

Flower bud development is a difficult process to understand, despite considerable research previously reviewed.<sup>104–106</sup> The regulation of flowering in general has been accepted to be a hormonal mechanism, specifically diffusible gibberellins from apple fruits inhibiting flower bud development on that spur. Unfortunately, the research on hormonal regulation of flowering has not thoroughly addressed the problem of the light exposure requirement for flowering.<sup>3,6</sup> Recent reports suggest that root-supplied xylar cytokinins or nitrogenous regulators such as arginine or putrescine can induce flowering, but the results have not been consistent.<sup>107–111</sup> Although carbohydrate availability has been disregarded as a primary regulator of flowering, Hansen and Grausland<sup>112</sup> reported that CO<sub>2</sub> enrichment of young trees increased bloom, and in preliminary studies in our lab we have found increases in return bloom in heavily cropping ‘Empire’ apple trees injected with sorbitol solutions four times during the month after bloom.<sup>113</sup>

As discussed in the introduction, there is no reason to assume any one resource or regulator is always limiting. For example, light exposure-induced partitioning of xylar cytokinin or other regulators may induce flower bud development, while increased availability of photosynthates produced by the leaves of the spur and the nitrogen from reserves or current uptake may provide quantitative support for flower bud differentiation. Thus, any of these regulators may limit the process under a particular set of conditions. Regardless of the merit of this example, progress is more likely to be made if the various physiological mechanisms are integrated rather than isolated. It is clear that there is much to do before we will understand this complex, but critical process.

#### *d. Fruit Growth and Set*

Fruit growth and fruit set are more amenable to study than the microscopic processes of flower bud development, thus we have a somewhat better information base. As with flowering, there is a debate between hormone vs. nutrient (i.e., carbon or nitrogen) mechanisms of regulation. The hormone hypotheses have been based on correlations of endogenous hormones or exogenous growth regulators to the observed processes. Due to complexity of measuring endogenous hormones and/or the interests of the investigators, these studies have not typically included treatments of environmental factors such as light, temperature, CO<sub>2</sub>, etc. So it is difficult to make clear conclusions as to hormonal interactions with the environment. The reviews of Dennis<sup>1</sup> and Browning<sup>14</sup> are suggested reading for understanding the hormonal approach. Although there are many methodological difficulties and inconsistencies in the literature, hormones are surely involved in environmental responses and cannot be either ignored or accepted as autonomous controllers of fruit growth and set.

#### *e. An Example of Utilization of Physiology*

The accumulation of research on carbon partitioning in relation to fruit growth, set, and yield provides a useful example of how such physiological knowledge may be integrated to address orchard management questions. An example is offered addressing the physiological bases of variation in productivity per hectare of different apple planting designs, training systems, and pruning regimes.

Clearly, total radiation is an ultimate limitation to yield, but at maturity, many orchards have declining productivity due to excessively dense canopies<sup>3,6</sup> (Figure 3). As discussed earlier, apple fruit development during the cell division period appears to be supported with carbon initially from spur leaves. The extension shoot leaves support the growth of the shoot tip until there are at least 10–12 unfolded leaves in full sun, later if in low light conditions. It is hypothesized that a basis of the low yields in orchards with dense canopies (assuming otherwise healthy trees with appropriate flowering, fertility, etc.) is a combination of two potential factors: (1) the total light interception may be low, limiting potential productivity, and/or (2) limitation of carbon availability to the fruit when final fruit numbers and yield potential are being set, normally about 4 weeks after bloom. This limitation of carbon to the fruit is viewed as a supply/demand balance that depends on the numbers of fruits versus actively growing shoots, the amount of spur leaf area, and the relative exposure of the spur canopy that supports early fruit development. Combining all these considerations, it is proposed that the yield of different orchard systems depends on the total radiation intercepted by the spur canopy per hectare at about 3–4 weeks after bloom.

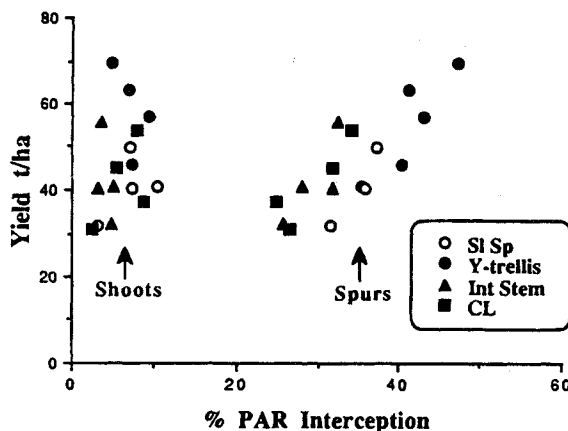
A modification of the classic point quadrat method for canopy analysis in which metal needles, simulating sunbeams, are pushed into a canopy<sup>115–117</sup> was used to test this hypothesis. The laser modification of Vanderbilt et al.<sup>118</sup> and a new solar tracking device to move a laser over apple trees was used to estimate which types of leaves or organs intercepted light.<sup>119</sup> Combined with measurements of total light interception, estimates of light interception/hectare by spur canopy and shoot canopy were made in several orchard systems with different productivities. Dry matter yield of fruit was positively correlated with the spur light interception/hectare and negatively correlated with shoot light interception at one month after bloom (Figure 5), supporting the hypothesis.<sup>119</sup> The relationships at full canopy were not as strong, especially if pruning that season led to differences in spur versus shoot light interception at full canopy that were not developed at one month after bloom. In mature canopies that do not change dramatically from year to year, spur canopy light interception/hectare may be a useful indicator of not only current carbon balances for the fruit development, but also the longer-term exposure effects on the reproductive behavior.

### III. TEMPERATURE

#### A. GENERAL EFFECTS

The effect of temperature on growth and productivity is the most complex topic in environmental physiology, since it integrates all processes. Since comprehensive coverage of this topic is beyond the scope of this chapter, only selected examples will be examined (see Jones<sup>17</sup> for a general review of temperature effects). Before addressing high and low temperature extremes, some general effects in the intermediate range of temperatures will be discussed.

The growth of apple fruits and other organs such as shoots are positively related to temperatures below about 25–30°C, but at higher temperatures growth may be limited by other factors. In the lower



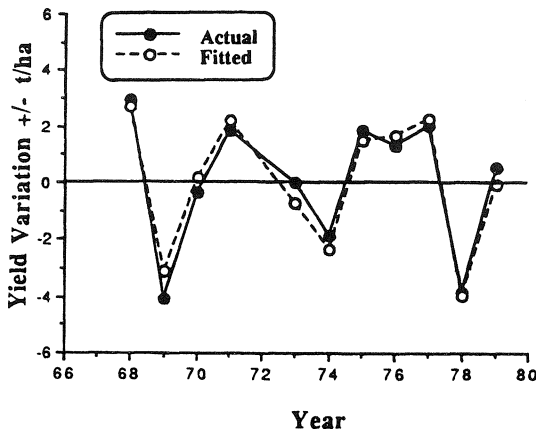
**Figure 5** Relationships between yield per hectare of representative 'Empire' apple trees of different training systems and the light interception by the shoot canopy and by the spur canopy. (From Wünsche et al.<sup>119</sup> with permission)

range of temperatures, active growth of organs during periods of variable temperatures can be related or normalized by expressing growth rates against degree-days (normally the accumulation of daily temperature means minus a base temperature) instead of time. This is particularly useful as an index of development in the spring when growth in a perennial plant, with carbon and nutrient reserves, is probably more limited by temperatures than by resource availability. Mid-summer development tends to be less tightly regulated by temperature, suggesting that resource availability may be more limiting.

### 1. Effects of Yearly Patterns of Temperature

Long-term temperature effects on apple may be integrated over many months or years. The length of the growing season has clear effects on apple productivity as longer growing seasons typically produce larger crops (as long as there is adequate chilling in the winter). For example, the long, mild growing season in New Zealand can produce apple fruit yields almost twice that achievable in the shorter growing season in New York State. Although climatic differences in temperature have great effects on apple productivity, unfortunately, little is known concerning the physiological bases of such effects. Short-term temperature effects may cause long-term manifestations (e.g., the long-term effects of a single crop-destroying freeze are obvious). Subtle temperature effects generally require many years of observation of natural systems in a range of climates, either year to year or geographically, or by statistical correlation studies (called "fishing for correlations" by some).

A good example of "statistical fishing" has been that of correlations of apple yields to temperature periods. As early as 1927, Mattice,<sup>120</sup> a statistician for the U.S. National Weather Service, had begun to note correlations of apple yields to spring temperatures. This work was followed in more detail by scientists in England who found that in addition to the expected value of warm temperatures before and during pollination, variation in yearly yields of Cox's 'Orange Pippin' in England was negatively related to temperatures in February–April.<sup>121–123</sup> Similar results were found for regional yields of different cultivars of apples in New York State.<sup>124</sup> Though the relationships are purely correlations, these statistical approaches have been useful in pointing out effects not obvious otherwise. The effects can be reproduced in potted trees and the results also apply to fruit set data from apple breeders.<sup>123</sup> This regression approach has been extended in New York to relate regional yield variation to the temperatures during three periods with differing signs of correlation with temperature: previous year harvest to leaf fall period (positive), mid-winter to budbreak (negative), and budbreak to bloom (positive) (Figure 6). Heim et al.<sup>125</sup> compared tree growth with a consistent group of young trees grown in England versus in southern France. Seasonal dry matter accumulation differed little up to harvest, but post-harvest growth accounted for about 5% of the seasonal total in England, but more than 20% in France. Observations made while observing apple production in various years and climates lead this author to conclude that the post-harvest period may be important in the ability of the tree to recover from a crop that season, and to allow vegetative buds to develop into reproductive buds. Researchers working on biennial bearing have noted that following an "on" year, the subsequent year "off" yield depends on the warmth and radiation



**Figure 6** Yield variation over years of Western New York regional apple yields and fitted regression values with regression using temperatures during 3 periods: previous year harvest–leaf fall, January 1–budbreak, and budbreak–bloom. (From Lakso<sup>113</sup>)

during the “on” year postharvest period.<sup>126,127</sup> In the spring Tromp and Penders<sup>128</sup> have found that rapid spring development to bloom led to higher final fruit set compared to slow development in cool temperatures.

It is most striking that a large amount of the variation in regional yields appears to be related to environmental conditions during times in which there are no leaves or fruit on the tree!

## 2. Growing Season Temperature Effects

After bloom there is much growth occurring, both vegetative and reproductive, that is driven by respiration as well as the supportive processes of photosynthesis, E, and nutrient uptake. All of these processes are affected by temperature, but not with the same sensitivity.

*Respiration* is unavoidable since it is required as the energy conversion process for growth and for the maintenance of tissues.<sup>129</sup> Consequently, when there are high growth rates there will be high respiration rates. For example, DeJong and Goudriaan<sup>130</sup> found a very high correlation between the relative growth rate of peach fruits and the respiration rates. Similar work needs to be done with apple to not only confirm the relationship, but also to allow broader modeling of respiratory costs from growth rate measurements that are much easier to take than respiration measurements.<sup>130–132</sup>

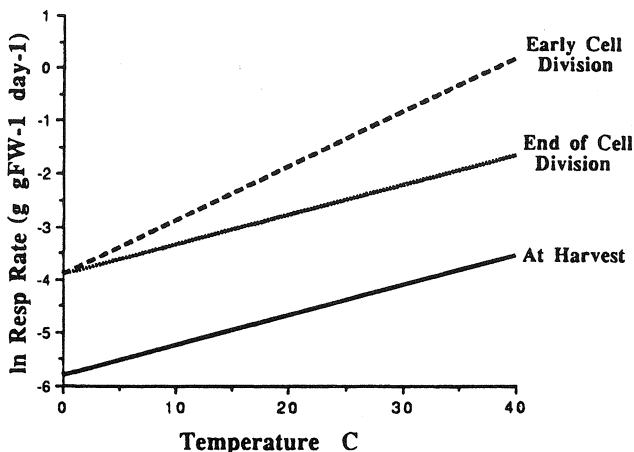
In general, respiration responds to temperature logarithmically over the normal range of temperatures encountered during the season, 0–42°C. The general form of the response is

$$R = a e^{kT} \quad (5)$$

where  $R$  = respiration rate;  $a$  =  $R$  at  $T = 0^\circ\text{C}$  (the intercept of  $\ln R$  versus  $T$ );  $k$  = temperature coefficient of  $R$  (the slope of  $\ln R$  versus  $T$ );  $T$  = temperature in  $^\circ\text{C}$ .

The temperature coefficients of respiration varies with the type of tissue and with the time of the year.<sup>64,78,90,133,134</sup> Generally, respiration rates for leaves are based on surface areas ( $\text{g m}^{-2}$  leaf area  $\text{s}^{-1}$ ), while fruit respiration is typically based on fruit fresh weight ( $\text{g g}^{-1}$  fresh weight  $\text{s}^{-1}$  or  $\text{day}^{-1}$ ). It has been found that respiration rates of different ages of the structural wood of the tree vary if expressed on a weight or volume basis, but they are essentially the same if expressed on a wood surface area basis.<sup>133</sup> We have confirmed this with winter respiration rate measurements. The primary activity, i.e., active living cells, of the stems of the tree are in the cambium and phloem which represent the surface wrapped around the xylem. Although helpful, there is little information on the surface area of apple tree structures,<sup>30</sup> though correlations of surface area to weight of branch and trunk diameters should be derivable.

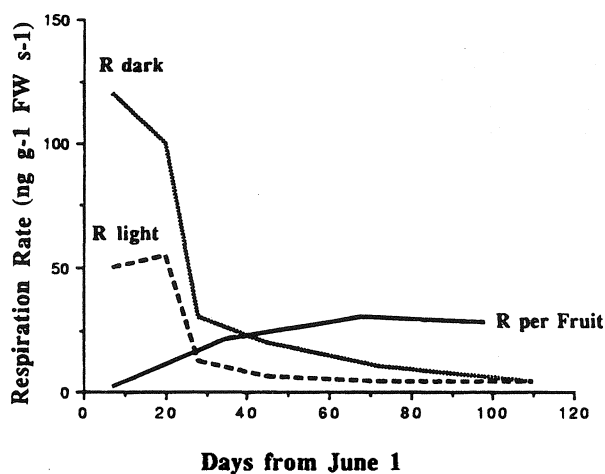
Leaf dark respiration rates ( $\text{g m}^{-2}$  leaf area  $\text{s}^{-1}$ ) tend to have a relatively constant temperature coefficient  $k$  of about 0.09 while the intercept,  $a$ , varies seasonally from 0.025 to 0.080.<sup>64,78,134</sup> With many crops the leaf dark respiration rate has been found to be increased in proportion to the photosynthetic rate of the leaf during the previous light period.<sup>53,129</sup>



**Figure 7** Apple fruit respiration responses to temperature at different stages of fruit development. (Data adapted from Jones<sup>90</sup> and Lakso and Johnson<sup>143</sup>)

Fruit respiration rates have been of great interest to postharvest physiologists for many years, but fruit respiration while on the tree has received less attention. Respiration temperature coefficients  $a$  and  $k$  (the intercept and slope of  $\ln R$  versus  $T$ ) both vary seasonally. During the cell division period,  $k$  begins at 0.100 then falls to 0.055 during the cell expansion phase in mid and late summer<sup>90</sup> (Figure 7). The intercept  $a$  began at 0.020 and fell to 0.003 by late season. This suggests that the respiration rate response to temperature changes significantly during the seasonal development of the fruit. Although the respiration rate declines over the season, the increase in fruit weight leads to a relatively stable total respiration rate per fruit (Figure 8). A significant effect of light on decreasing apparent respiration via re-fixation of  $\text{CO}_2$  in the light has been found<sup>90,92,93,135,136</sup> and may be very significant to the carbon balance of fruits in the first half of the season. Pruning to provide good exposure for fruit might be expected to improve the carbon balance, but increased fruit temperatures may counterbalance this effect by increasing respiration compared to shaded fruits.

Wood respiration ( $\text{g m}^{-2}$  surface area  $\text{s}^{-1}$  basis) for apple was reported by Butler and Landsberg<sup>133</sup> to have a constant  $k$  slope coefficient at 0.085 throughout the year. In preliminary experiments the author has found similar results during the dormant period. The  $a$  intercept coefficient varied from 0.004 at harvest to 0.010 near bloom, then declined during the remainder of the season.



**Figure 8** Apple fruit respiration rates in the dark, in the light and per fruit ( $\text{ng s}^{-1}$  per fruit) over a season. (Data adapted from Jones<sup>90</sup>)

A significant gap in the knowledge of respiration of the apple tree is the respiration of the root system. Recent initial studies by Ebert et al.<sup>137-139</sup> have shown that root respiration rates tend to increase linearly with temperature, the slope of the response to temperature was higher in the summer than in the winter, respiration was inhibited by low oxygen concentrations, and phosphorus or potassium deficiencies reduced respiration, but mostly via reduced root growth. A transfer of nitrogen source from nitrate to ammonium gave a rapid increase in root respiration that lasted for many days. A particularly interesting finding was that the diurnal pattern of root respiration lagged behind that of leaf photosynthesis by about 4–6 hours, peaking at 10–12 and 14–16 hours, respectively.<sup>138</sup>

### 3. Seasonal Respiratory Costs

Even though respiration rates are reported in the literature, there have been few attempts to quantify the total respiratory costs of the tree or any particular organ. Jones<sup>90</sup> measured fruit respiration over the season in England and estimated that about 15% of the carbon imported seasonally by an exposed fruit was used for fruit respiration while the other 85% was accumulated as dry matter in the fruit. This value was reasonably similar to Walton and DeJong's estimate of about 23% of imported carbon used for respiration for the development of the kiwifruit in the much warmer Central Valley of California.<sup>140</sup> Blanke and Lenz<sup>93</sup> estimated a much lower value of about 6%. It is difficult to compare the estimates since the basis of calculations and temperatures used were not explained.

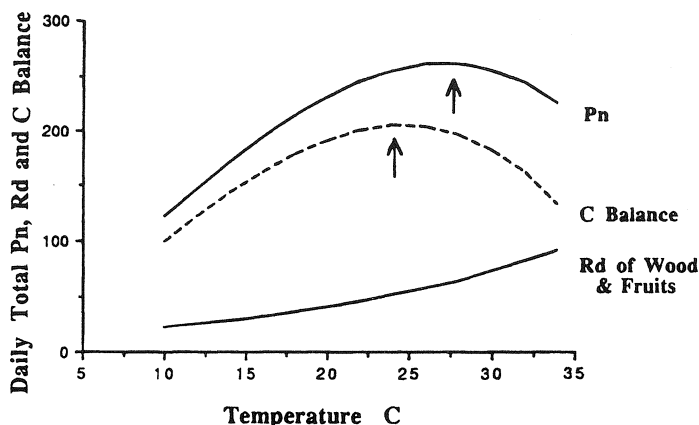
Estimates of total seasonal or yearly respiratory costs for whole trees are few. Hansen<sup>141</sup> estimated about 40–45% of fixed <sup>14</sup>C-carbon used for respiration, but it appears that this refers to the growing season when labeling experiments were done. Estimates for a 3-year-old tree for about one month in mid-summer by Proctor et al.<sup>64</sup> in England were only 6% of the fixed carbon, but that appears to be very low compared to most estimates for perennial plants. Likely this low value was due to cool temperatures, little vegetative growth, and very long days in that experiment, all conditions that would lower the respiratory costs. A very detailed study of apricot by Evenari et al.<sup>142</sup> may be relevant as they similarly estimated that about 45–50% of the total seasonal photosynthetic fixation was respired in irrigated or non-irrigated mature trees in the Negev desert.

Simulations of carbon balance of apple trees were run from budbreak to harvest with the simplified dry matter production model of Lakso and Johnson.<sup>143</sup> Assuming a semi-dwarf apple tree with a commercial crop (about 40 tons/ha) and average weather data for New York State and for Hawke's Bay in New Zealand, carbon fixation and respiration were estimated. The largest differences in carbon balance between locations were due to the cooler night temperature effects on lowering dark respiration in New Zealand. The accumulated total respiration estimates amounted to about 40–45% of fixed carbon for New Zealand to 45–50% for New York. Of the different plant organs, the dark respiration of leaves at night was estimated to account for about 60%, fruits about 30%, and structure about 10% of the total seasonal respiration for the semi-dwarf trees. Evenari et al.<sup>142</sup> estimated about 55% of seasonal respiration was by leaves in the apricot study.

Clearly, the respiratory activity of the apple tree appears to be both qualitatively and quantitatively important to carbon balance, yet we have inadequate information on whole-plant respiration in the apple. This is an obvious area of research that needs much attention. Establishment of sound relationships between respiration and growth rates of different organs is an approach that should be explored due to its potential to utilize the relatively abundant data on growth rates already available. Also, modeling will be another useful method to estimate respiratory sums as shown above.

### 4. Photosynthesis

Photosynthesis of apple leaves does not appear to have a strong response to temperature over a fairly wide range of temperatures from 15–35°C, with the temperature optimum generally near 30°C.<sup>13,134,144</sup> The decline at temperatures higher than 32–35°C may be partly due to temperature-induced increases in vapor pressure deficits (VPD) that can affect stomata. Excluding possible stomatal effects, declines in net photosynthesis of C<sub>3</sub> plants at high temperatures are due to the increases in photorespiration with temperature.<sup>17</sup> Lange et al.<sup>145</sup> found the seasonal adjustment of the temperature optimum of apricot leaf photosynthesis was almost 10°C higher in mid summer in the Negev desert. There is a need to determine if such temperature adaptations occur in apple. Measurements taken by the author in the field under many different temperatures suggest that apple leaf photosynthesis rates may be maintained up to about 37°C, but seasonal adjustments of temperature optima have not been documented yet for apple.



**Figure 9** Simulated apple tree net photosynthesis (includes leaf respiration), respiration of the wood and fruits, and the net balance ( $P_n - R_d$ ) responses to temperature in the light. (Simulations with model of Lakso and Johnson<sup>143</sup>)

Since the classic work of Heinicke and Childers,<sup>63,146</sup> the net  $\text{CO}_2$  exchange of whole apple canopies has been measured occasionally.<sup>65,147</sup> With the development of an inexpensive “balloon”-type chamber,<sup>62</sup> whole-canopy measurements will likely increase in the future. The photosynthetic temperature response peaks at about 28–30°C, but the respiratory response is a continuous logarithmic increase. The net effect is that a whole-canopy temperature response would be expected to be optimal at a lower temperature than that of the photosynthetic component (Figure 9). Results from the early studies of whole-tree gas exchange by Heinicke and Childers<sup>63,146</sup> indicated significant decreases in net  $\text{CO}_2$  uptake during the day if temperatures exceeded about 25–26°C. This may help explain why apples produce higher yields than might be expected in the cool climates of northern Europe or why productivity is particularly high in the long cool season in New Zealand.

## B. HIGH TEMPERATURE EFFECTS

High temperature or heat stress should be viewed in relative terms since the physiological responses we are generally concerned about are not as much related to any absolute temperature, as much as related to “supra-optimal” temperatures. A 35°C day in the early spring may induce physiological problems for a tree with tender foliage while in mid-summer these effects may be minimal. Consequently, the emphasis will be on response to supra-optimal temperatures, although for simplicity the term “heat stress” will be used.

### 1. Fruit Set

Temperatures above the optimum for photosynthesis lead to a strong decline in net gas exchange for the whole tree due to the simultaneous decline in the carbon fixation (supply) and increase in respiration (demand). The response of the tree to such a potential limitation should also depend on how critical the carbon balance is at the time of the heat stress. During the period before final fruit drop about a month after bloom, when it is proposed that the carbon balance may be critical,<sup>68</sup> high temperatures, especially at night, have been found to cause fruit abscission<sup>120,148–150</sup> or poor fruit growth.<sup>151,152</sup> Tukey<sup>151,152</sup> found greater fruit growth and development at 24°C versus 9 or 31°C, with the high temperature being particularly detrimental. Higher temperatures appeared to stimulate early fruit development for the first few weeks, but were detrimental at about 1 month after bloom. Similarly, Tamura et al.<sup>153</sup> found that raising night temperatures to 23°C was stimulatory for the first 3 weeks after bloom, then was detrimental, so that by 30–35 days the fruit were the same size. The fruit growth stimulation was due to increased early cell division that ended 7–10 days earlier than the controls, but gave the same final fruit size and cell numbers.

The mechanism responsible for the variable effects of temperature on fruit development is not clear. Changes in availability of carbohydrates at 3–4 weeks after bloom, but not earlier, has been suggested.<sup>68</sup> Fruit ethylene production is stimulated by high night temperatures has been suggested to be the mechanism by Kondo and Takahashi,<sup>154</sup> but Fukui et al.<sup>149</sup> presented evidence that the ethylene may be

a response to rather than a cause of abscission. The same high temperatures in mid-season, however, have essentially no significant effect on fruit ethylene production, indicating a differential sensitivity with stage of development.

Root temperatures may also be excessive in apple. Gur et al.<sup>155</sup> reported that temperatures above 30°C caused marked reductions in both root and shoot growth, with severe effects on leaves at root temperatures of 35°C and above. Respiration of the roots peaked at 35°C, apparently with damage at higher temperatures. Less resistant rootstocks accumulated larger quantities of ethanol in the roots, along with acetaldehyde. Root and leaf cytokinins were also reduced at the higher temperatures. Although these root temperatures would be unusual in most apple-growing regions, they are conceivable in potted plants used for experiments and perhaps in young trees in the field.

## 2. Water Relations with High Temperatures

Many of the effects of heat on plants are confounded by the effect of higher temperatures on the VPD. Assuming that the absolute water vapor pressure of the air remains constant (e.g., equal to 50% RH at 25°C) and leaf temperature increases with air temperature, the VPDs at 25, 30, 35, and 40°C would be about 1.6, 2.1, 2.8, and 3.7 kPa (1 kPa = 10 mbars), respectively. This increase in VPD can have dramatic effects on the evaporative demand,  $\Psi_l$  if  $E$  increases, stomatal conductance ( $g_s$ ), and photosynthesis. This author has found that reductions in apple  $g_s$  at higher temperatures began at 33–34°C if the RH was kept constant at 40% so that the VPD increased with increasing temperature; the decline began at about 37°C if the RH was also raised to maintain a constant 2-kPa VPD.<sup>113</sup>

With high temperatures, high VPD, and high  $E$ , stomates normally close partially, which may conserve water, but reduces evaporative cooling. Leaf temperatures will increase unless there is enough wind to cool the leaf via sensible heat transfer (see Jones<sup>17</sup> or Nobel<sup>196</sup> to review energy balance). Since the leaf temperature is very dependent on radiation load and boundary layer, particular care should be paid to measurement of leaf temperature. The use of infrared remote thermometry is the preferred method of measuring leaf temperature, since the boundary layers and heat capacities of instruments such as porometers or photosynthesis chambers may influence leaf temperatures markedly. Ideally, temperature response curves should be produced, then the natural leaf temperatures from IR thermometry be used to estimate leaf status at those temperatures. Due to the dependence on the evaporative demand, radiation load, and wind, the importance of water stresses in the response to heat stress will be variable and unique with each situation. Therefore, it is important to be aware of the interactions of temperature and water relations on leaf temperature and physiology.

Whole-plant responses due to high temperature-induced increases in  $E$  are also expected. Decreases in stem and shoot tip  $\Psi_l$  would also be expected to reduce vegetative growth rates as well, although little documentation is available. Specific heat-induced lesions such as sunburn on fruit or branches or sunscald on branches in the spring can have important effects on tree productivity. Sunburn of the fruit or branch surface occurs when the fruit is exposed to high direct sunlight and is usually more severe in more arid climates<sup>156</sup> or on trees with poor water status. This suggests that sunburn effects are due to excess water stress of the fruit or branch surface. Sunscald of branches or trunks in the winter or spring is actually more related to radiation-induced warming of the bark, followed by a precipitous drop in temperature in the evening, leading to cold damage of the tissue.

## C. LOW-TEMPERATURE EFFECTS

Extreme cold temperatures are an important limitation to long-term commercial success of apple growing in many marginal temperate regions. Spring frosts and severe winter cold have obvious detrimental effects on apple survival and production, but the emphasis in this section will be on less severe cold effects.

### 1. Cold During the Growing Season

The effects of cool or cold temperatures during the growing season depend heavily on the stage of development of the tree. In general, temperatures dropping below 15 or 20°C, but not below about 5°C, merely slow all aspects of metabolism and growth. During most of the growing season this range of temperatures does not tend to change any basic patterns of plant development, just slows the rate of development. However, late in the growing season as the temperatures decline, cool temperatures begin to induce basic changes in physiology. The complex processes of dormancy and leaf abscission are induced by decreasing temperatures. These allow the tree to develop the cold hardiness required for the winter.

## 2. Dormancy

The apple in general requires a chilling period during part of the year to allow the proper annual growth cycle to occur. Without adequate chilling budbreak is poor and/or very erratic, bloom is not synchronous, and yields are poor. The dormancy required to obtain the necessary chilling is a particularly complex physiological process that is difficult to study due to the lack of visible, macro-scale growth or gas exchange that can be easily measured. Many of the critical processes are at the cell or membrane level in complex, microscopic tissues and are influenced over long periods of fluctuating weather that make each situation unique. Therefore, much of the research has been directed toward controlled environment studies and the development of models to relate temperature patterns to observed phenomena.

The reader is referred to several reviews on the physiology and terminology of dormancy by Samish,<sup>157</sup> Lang,<sup>46</sup> Cannell,<sup>158</sup> and several papers in a dormancy symposium.<sup>159–162</sup> Apple appears to behave similarly to other fruit crops, thus research in the general mechanisms is likely applicable across species.

In the broadest sense, dormancy is the absence of active growth in an organ with a meristem. The terminology proposed by Lang<sup>159</sup> has gained general acceptance. During the normal yearly cycle of dormancy, there are three general periods of dormancy: (1) the initiation of dormancy in the late summer and autumn, “paradormancy”; (2) winter dormancy that is internally controlled in that growth will not occur even with higher temperatures, “endodormancy”; and (3) late-winter dormancy that is primarily controlled by an unfavorable environment for growth, “ecodormancy”. Prediction of rest completion is of importance to define the chilling requirement for a species or cultivar, an important limiting factor for cultivar choice in warmer climates that may have insufficient winter chilling temperatures.

Most commercial cultivars of apple require about  $1200 \pm 300$  chilling units (CU), defined as hours at optimum chilling temperature (considered to be between 3–8°C), although some cultivars have been selected for low chilling requirements. Apple requirements are similar to pear, but tend to be longer than most of the stone fruits.<sup>10,12</sup> Hauagge and Cummins<sup>163</sup> found that the range of chilling requirements of different cultivars and species over several years ranged from about 200 CU for the cultivar ‘Anna’ to about 1500 CU for ‘Wright #1’ under New York conditions. In one year ‘Anna’ only required 88 CU. It has also been reported that in Zimbabwe under tropical conditions ‘Anna’ may require no chilling and can produce two crops per year without dormancy-breaking sprays.<sup>164</sup> Therefore, great range exists in apple germplasm for the chilling requirements, and genetic studies on heritability patterns suggest that the low chilling requirement of Anna is due to a shallow dormancy.<sup>163,165–168</sup> This germplasm may provide excellent material for further physiological studies.

The cellular physiological transduction of the environmental signals has been studied in many species from many mechanistic approaches (hormonal, carbohydrate, protein, enzymes, lipid phase change, gene expression) and with exogenous treatments or manipulations of photoperiod, temperature regimes, dormancy-breaking chemicals, or pruning/defoliation. The reader is referred to the reviews of Lang<sup>46</sup> and Cannell<sup>158</sup> for a more complete review of this research. A particularly interesting new series of studies implicate changes in the free versus bound water in apple buds in relation to the stages of dormancy and perhaps cold hardiness.<sup>169</sup> Lipase activity has been found to be related to the water state changes and that membrane lipid composition may be important.<sup>170</sup> The availability of new technologies, such as magnetic resonance imaging, promise new opportunities for studying such subtle physiological changes.

Although most dormancy studies primarily have treated the buds, an interesting series of recent papers by Young and colleagues<sup>171–177</sup> have explored the root-shoot interactions in dormancy and spring development and have shown that chilling of the rootstock can have different effects on behavior of the top compared to scion chilling.

## 3. Cold Hardiness

The reviews by Burke and Gusta,<sup>178</sup> Ashworth and Wisniewski,<sup>179</sup> Ashworth,<sup>180</sup> and Flore on Stone Fruit in this volume are recommended for general review on woody plants and fruit crops. The resistance to extreme cold temperatures occurs during the dormant period. Although chilling and dormancy appear to be qualitatively required for adequate cold hardiness, they do not appear to be quantitatively related to cold hardiness. In general, death due to freezing is thought to be due to cellular disruption from ice crystal formation, while supercooled tissues remain alive. The migration of water from the supercooled cells to the intercellular spaces where ice crystals may form avoids the crystal formation within the cells. But if too much water migrates from the cells, dehydration effects may cause damage.

Apple is one of the hardiest fruit crops with maximum hardiness of close to  $-40^{\circ}\text{C}$ .<sup>181-183</sup> Studies of apple clones and heritability of cold hardiness indicate that there is genetic variation among rootstock and scion clones, but year-to-year variability is high.<sup>184-186</sup> This level of hardiness is greater than many other fruit crops and allows apples to be grown over a wide range of higher latitudes. Since economic pressures have forced the elimination of orchards in marginal sites or regions, the most obvious problems due to mid-winter cold have decreased. However, hardiness due to cold temperatures after early spring deacclimation (i.e., during ecodormancy) is still a problem in more continental regions that have periods of warm weather followed by sharp drops in temperature. Apple rootstocks have been found to differ greatly with Robusta 5, having great fall and winter hardiness, but it dehardens rapidly in the spring.<sup>186</sup> MallingMerton 106 also has good mid-winter hardiness and dehardens in the spring, but this rootstock has a much greater ability to reharden after a warm period.

Cold hardiness develops with increasingly cooler temperatures in the autumn. Cold acclimation in the autumn is concurrent with the cessation of growth, and deepens to maximum hardiness (during endodormancy) in mid-winter.<sup>183,187,188</sup> Hardiness is also dependent on other factors that affect the health and physiological status of the tree. Maximum hardiness develops when the trees are healthy, but not actively growing. Water deficits, flooding, poor nutrition, heavy cropping, and low light, especially in combination, are all detrimental to winter hardiness.<sup>189</sup> A well-known observation in the orchard is that trees pruned in early winter before the minimum temperatures have more winter damage than unpruned trees at the same location. The reasons for this are not clear, but it has guided the timing of pruning of commercial orchards.

Not all tissues of the apple tree attain equal hardiness as might be expected from the differences in tissue structure and location. Roots are typically less hardy than the tops of the trees, but the roots normally do not experience the severe cold temperatures due to the heat capacity of the soil. It appears that soil moisture content may play a buffering or insulation role, as root winter damage has been found to be related to sprinkler irrigation patterns.<sup>190</sup> Within the stem tissues it appears that bark and the xylem respond differently in the freezing process. The bark tissue appears to freeze extracellularly, while the cells in the xylem parenchyma and pith may supercool to almost  $-40^{\circ}\text{C}$ .<sup>191</sup>

The hardiness levels in apple shoots have been found to be correlated with sugar levels in the wood,<sup>192</sup> although hardiness does not apparently depend on the concentration of sugars in the tissues, since the sugar and hardiness levels can vary independently.<sup>193</sup> Recent work with cryopreservation of apple germplasm has indicated that during acclimation apple buds increase the amount of bound, unfreezable water; but once hardy, they need resistance to dehydration from the freezing that occurs in nearby free water or less hardy tissues.<sup>194-197</sup> Thus, intracellular water relations seem to be an important factor in cold acclimation of apple. Lipid metabolism was suspected to be involved in hardiness, but glyco- and phospholipid compositions were not found to be related to apple bark hardiness.<sup>198,199</sup> There do appear to be correlations with the peroxide-scavenging enzyme systems and some ultrastructural changes in the cell walls and membranes.<sup>200-202</sup>

While dormant, apple does have the ability, within limits, to reharden after a warm dehardening period.<sup>187,188</sup> The amount of rehardening ability declines as spring approaches. Once growth occurs in the spring, the tissue hardiness is lost rapidly, with developing spur leaves and flowers varying in temperature for 10% kill from about  $-9$  to  $-12^{\circ}\text{C}$  at budbreak to about  $-2$  to  $3^{\circ}\text{C}$  at bloom.<sup>203,204</sup>

#### IV. WATER DEFICITS

The normal functioning of the apple tree depends on appropriate water relations. Nonetheless, in the orchard water may not necessarily be a limiting factor for growth and productivity. The study of physiological responses to water deficits is probably more important in humid climates than in arid climates where irrigation is used routinely. In humid climates where irrigation is not normally used and economic feasibility is still questionable, apple trees in unirrigated orchards will experience more water stress during periodic droughts than irrigated trees in drier climates. Conversely, however, the opportunity to use water relations to control tree growth by irrigation management is greater in arid climates where water availability can be controlled.

##### A. TERMINOLOGY AND FUNDAMENTALS

This discussion will emphasize the water relations of apple, especially relative to other crops used to establish the textbook concepts of water relations. The basics of water relations [i.e., water potential

components, relative water content (RWC), hydraulic conductivity] can be reviewed in a variety of textbooks and reviews,<sup>205-209</sup> although the author recommends the excellent books by Nobel<sup>96</sup> for a biophysical approach and Jones<sup>17</sup> for a whole-plant/crop approach. Reviews of general fruit tree water relations by Jones et al.<sup>11</sup> and specifically for apple by Landsberg and Jones<sup>4</sup> are recommended. After a brief discussion of the fundamentals, the responses of apple trees to water deficits will be reviewed in a format to place the various responses in context.

A few terms and concepts used here need definition. *Drought* is a meteorological term that refers to the lack of significant rainfall for a period; it is not necessarily detrimental if there is no need for the water (e.g., in the winter or in irrigated orchards). *Stress* will be used in the common way to describe an imbalance between the supply of and the demand for water. In fact, the greatest concern is not drought or stress, but the response to stress. This describes the changes in physiology in relation to changes in the water status of the plant. It is quite common for plants to experience similar levels of stress, but the responses may differ greatly (e.g., apple functions normally at mid-day water potentials of  $-1.5$  MPa while many annual crops would be near death at the same potentials). Also, a change in soil moisture stress does not necessarily cause the same change in stress in the plant. Thus, it is important to recognize that there are environmental stresses that can lead to physiological stress responses; but it will be seen that the relationships among these are not always the same.

### 1. Total Water Potential ( $\Psi_w$ )

There is little evidence that  $\Psi_w$  itself has a direct effect on metabolism or enzyme activity within the range normally found in plants; normally turgor, osmotic, or other factors such as RWC or cell volume appear to be sensed more directly by plant cells.<sup>17,210</sup> The importance of total potential is primarily for determining the direction and gradient of the movement of water through the tree.<sup>205,207</sup>

### 2. Osmotic Potential ( $\Psi_\pi$ )

Osmotic potential is a colligative property, depending on the concentration of solutes in the cell and not on the mass of the solutes. This has some important implications. If a plant needs to accumulate solutes in the cells, 1 mol of a large molecule to reduce  $\Psi_\pi$  requires much more energy and carbon than 1 mol of a much smaller compound. Accumulations of ions may be more energy efficient than larger molecules such as sugars, but large concentrations of ions may be detrimental to metabolism. It appears that  $\Psi_\pi$  may also be adjusted by breaking large compounds into smaller compounds in response to water stress. For example, an invertase enzyme in a cell will convert 1 mol of sucrose into 1 mol of glucose and fructose; thus the  $\Psi_\pi$  decreases. In some systems invertase is stimulated by abscisic acid, which itself is stimulated by water stress.<sup>211</sup> This may be very important to the  $\Psi_w$  of apple fruits or other solute storage organs that accumulate small molecules, giving low  $\Psi_\pi$  to develop and maintain turgor for expansion growth.

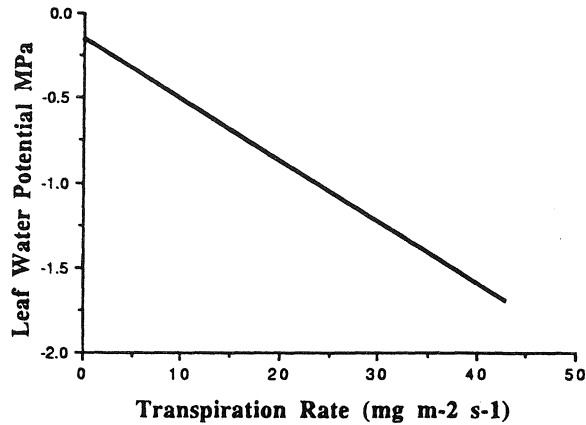
### 3. Turgor Potential ( $\Psi_p$ )

Turgor is likely the  $\Psi_p$  component most easily sensed by the plant cell. Thus, the regulation of turgor is very important. Hence, it is important to estimate osmotic and turgor components, and not just the total potential to understand the water status and the total plant response to stress.

Typical expected values for water potential components and RWC for exposed leaves on field apple trees under sunny conditions, moderate evaporative conditions, and adequate soil moisture are typically:  $\Psi_w = -1.5$  to  $-2.0$  MPa,  $\Psi_s = -2.5$  to  $-3.0$  MPa, and  $\Psi_p = 0.8$  to  $1.2$  MPa, with RWC = 85–90%. Of course, with soil moisture stress or differences in evaporative demand, radiation, or VPD the values will adjust. The discussion later will address these adjustments.

### 4. Significance of Plant Resistance to Control of Leaf Water Potential ( $\Psi_l$ )

Leaf water potential depends on three factors: (1) soil water potential ( $\Psi_{\text{soil}}$ ), which provides the upper limit for  $\Psi_l$ ; (2) the resistance of the plant-soil system to the flow of water; and (3) the rate of E from the leaves. In most grasses and annual plants, there is generally a low resistance to water movement through the plant. These plants have many roots in very good contact with the soil, the plant is small, and is efficient at moving water through its system. Apple trees, however, have a high total soil-leaf resistance due to (a) the size of the plant and distance the water has to flow, (b) the root systems are not dense,<sup>212</sup> do not explore the soil intensively to find moisture, hence more soil resistance; and (c)



**Figure 10** The reduction in leaf water potential of apple leaves in the field related to transpiration rate. (Adapted from Landsberg et al.<sup>213</sup>)

the root system itself has a high resistance.<sup>4,11,213</sup> A change in the rate of  $E$  induces lower  $\Psi_l$  in apple trees (Figure 10) while many annual plants show relatively little change in  $\Psi_l$  with changes in  $E$ .

A knowledge of the soil/plant resistance is important to understand which factors control leaf water potential. Unlike many annuals where control of leaf water potential is primarily a function of soil water potential, in apple there is a strong control of leaf water potential by transpiration. Consequently, any factor that affects transpiration (vapor pressure deficit, radiation, wind, stomatal opening) strongly affect leaf or stem water potential in the top of the apple tree. This places much greater relative emphasis on evaporative conditions and factors controlling stomatal opening than primarily on soil water status as in annuals. The experimental implications of this are that for apple trees:

1. soil moisture readings are not adequate to determine the stress level within the tree
2. atmospheric conditions must be monitored to understand the stress levels
3. water potentials can be highly variable since they depend heavily on the variable environmental conditions
4. atmospheric conditions must be much more constant to reduce variation when making comparative readings of water potentials between treatments.

## B. ORCHARD MICROCLIMATE AND MANAGEMENT CONSIDERATIONS

In the past decade much more appreciation has developed for the importance of structural characteristics of whole crops to water use and water relations.

### 1. Whole-Crop Water Use

The Penman-Monteith equation for crop  $E$  (see Jones<sup>17</sup> and Jarvis<sup>214</sup> for review) shows that  $E$  in the field depends primarily on three factors: net radiation, the humidity gradient from the crop to the bulk air, and the  $g_s$ . Whole-crop  $E$  for short, dense field crops or grasses is dependent on stomatal aperture when  $g_s$  is low. But as the stomata begin to open, whole-canopy  $E$  soon becomes relatively insensitive to changes in  $g_s$ . In orchards or forests, on the other hand, the  $E$  responds to the  $g_s$ . The reason for this is that low crops have a high crop boundary layer resistance so that the transfer of water vapor between the crop and the air above is slowed. If the stomates open further, the net result is primarily an increase in the humidity in the air within and above the crop, reducing the vapor pressure gradient and the boundary layer conductance ( $g_b$ ), thus countering the effect of increased stomatal opening. A dense, short crop essentially has its own microclimate. In that case crop  $E$  becomes primarily controlled by net radiation, not  $g_s$ . It is clear that crop water use results and methods from annual crops may not be directly applicable to apple orchards, since fruit or apple orchards, conversely, have small boundary layers due to their stature and roughness of the canopy. The water transpired from the leaves and the soil or cover crops can mix readily with the bulk air above so the humidity does not build up near the leaves. Therefore, whole-crop  $E$  is a strong function of the canopy conductance and vapor pressure gradient as well as of radiation.

**Table 2 Summary of responses to water deficits in apple trees following a format modified from Turner<sup>218</sup>**

| <b>Mechanism</b>   | <b>Response in Apple Tree</b>   |
|--|---|
| I. Drought avoidance/escape                                | Early development of spur canopy before drought development; perennial habit allows very rapid leaf development |
| II. Drought tolerance by maintaining high water potentials |   |
| (A) Reduction of water loss                                |   |
| (1) Stomatal/cuticle resistance                            | Coupling of stomatal opening to photosynthesis  |
| (2) Reduction of radiation absorbed                        | Folding of leaves   |
| (3) Reduction of leaf area                                 | Reduction of leaf area development initially, then leaf abscission  |
| (B) Maintenance of water uptake                            |   |
| (1) Increased root density and depth                       | (Responses not clear)   |
| (2) Increased root conductivity                            | Increase of root conductance  |
| III. Drought tolerance at low water potentials             |   |
| (A) Maintenance of turgor                                  |   |
| (1) Osmotic adjustment                                     | Osmotic adjustment of mature leaves, but no adjustment of shoot tips  |
| (2) Increase in elasticity                                 | Small if any  |
| (3) Decrease in cell size                                  | (Responses not clear)   |

Wind can alter crop water use by affecting the boundary layer. Thus, a field crop in wind will respond as an orchard does on a calm day. Also, as a crop canopy closes with development, there will be decreases in crop  $g_b$  and thus changes in crop E responses to crop conductance. Similarly, a densely planted dwarf orchard almost completely free of wind (as with surrounding windbreaks) may act more like a field crop. Jarvis<sup>214</sup> has pointed out that studies of fruit tree water use in closed glasshouses may not give results applicable to the orchard or forest. These effects need to be considered when planning and interpreting physiological studies of water use.

Apple tree water use is also related to total leaf area on the tree.<sup>215</sup> Mature orchards typically have leaf area indices on a whole-orchard basis (hectares of per hectare of land) of 1.5 to 4.5.<sup>3,6,50</sup> The relationship of leaf area to water use is not expected to be linear, as increases in leaf area per tree generally cause greater percentages of shaded leaves. Although interior shaded leaves do not transpire as much as exposed leaves, they do respond to the VPD so that the E in the shade may be 30–50% of that of exposed leaves, but at the lower light levels photosynthesis may be only 10% of maximum.<sup>216</sup> Consequently, the water use efficiency (WUE) of shaded leaves is poor. Overall WUE of a whole canopy may be better in more open canopies with fewer shaded leaves, but that has not been documented.

The relative influence of temperature, radiation, VPD, and wind speed will vary with the configuration and prevailing conditions in each orchard. Butler<sup>217</sup> evaluated the relative importance of radiation versus humidity components on water use in English apple hedgerows and concluded that the humidity component was the most important determinant of E, but that radiation was important as well. This would be expected for a crop well-coupled to the atmosphere as discussed above. For example, a comparison among mature training systems in New York has recently found that compared to a Slender Spindle, a Y-trellis system intercepted about 20–25% more light per hectare, but also developed twice the leaf area index<sup>58,60,119</sup> both would be expected to increase water use for the Y-trellis. In conclusion, there are many interactions of environmental factors and plant responses that must be considered concurrently when studying plant water relations in general, and especially under orchard conditions.

### **C. OVERVIEW OF APPLE WATER RELATIONS**

The study of the individual aspects of water relations does not provide the picture of the integrated responses of a species to water deficits. A useful method to place these components into context has been proposed by Turner<sup>218</sup> and is similar to that used by Jones.<sup>17</sup> This format breaks plant responses into broad categories that first deal with avoidance of drought stress, then avoiding stresses within the plant, then finally tolerating unavoidable stresses (Table 2). The discussion will follow this format.

## 1. Drought Avoidance/Escape

Drought avoidance/escape refers to mechanisms by which the plant avoids growing in drought conditions. The best examples are desert plants which lie dormant until rainfall comes, then complete their life cycle and produce seed before drought can develop. Apples have very rapid leaf area development during the spring due to the carbohydrate and nitrogen reserves that allow pre-formed leaves and shoots to develop very quickly and intercept radiation early in the spring. Flowering and initial fruit development also occur early in the season before possible summer drought can develop. Thus, the rapid development can be viewed as a drought-avoidance mechanism.

## 2. Drought Tolerance by Maintaining High Water Potentials

Under mild to moderate stress there are mechanisms that keep the water potentials in the top of the tree relatively high by reducing water loss and/or maintaining uptake from the soil. This involves developmental plasticity (i.e., the ability of the plant to change its development in response to its environment).

### a. Reduction of Water Loss

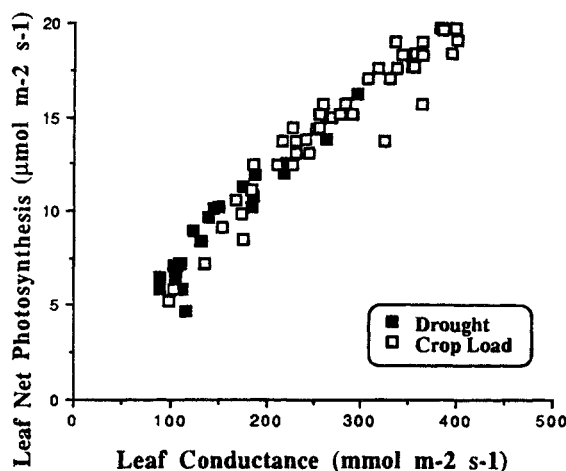
To reduce water loss through non-stomatal diffusion out of the plant, waxy cuticles develop. In general, apple leaves have quite thick waxy cuticles that have very low water vapor conductances, thus the vast majority of leaf E is via the stomata, which are found only on the abaxial surface on apple leaves.

### i. Stomatal and Cuticle Resistances

Stomatal regulation, thus, has been a major concern of water relations research in apples and other fruit crops.<sup>4,11</sup> Several factors affect stomatal behavior. Stomata respond directly to light, but the author has found that there is light saturation at about one tenth of full sunlight. Consequently, the light requirement for stomatal opening is lower than the light effect on photosynthesis even in shaded positions within the canopy. Thus, the direct light limit on stomata is normally not considered an important regulator of stomata. For many years it was thought that  $\Psi_1$  was the primary regulator of stomata, based on the obvious closure of stomata with increasing water deficits. The documentation of active osmotic adjustment in apple<sup>29,219,220</sup> led to the interpretation that  $\Psi_p$ , instead of  $\Psi_1$ , was regulating stomatal closure at variable  $\Psi_1$ .<sup>221</sup> Under non-extreme conditions in the orchard the typical diurnal pattern of  $g_s$  shows a peak in mid to late morning followed by a gradual decline for the rest of the day while the  $\Psi_w$  typically shows a symmetric pattern with minimum values in mid-day (mirroring the radiation pattern). This difference of patterns suggests that the water potential components were not controlling stomata under normal conditions.

Examination of the diurnal pattern of air VPD typically shows a mirror pattern to that of  $g_s$ , thus a high correlation is found between the  $g_s$  and VPD.<sup>134,222-224</sup> It appeared that humidity may be the controlling factor. However, based on the experience of the author there are times that contradict this conclusion.<sup>113,225</sup> The typical diurnal pattern of  $g_s$  can still be seen with trees placed in growth chambers with constant radiation and VPD. Also, trees with strongly growing sinks (vegetative, fruit, or both) may show only a mild afternoon decline in conductance, while under the same conditions non-cropping plants may show a strong decline. Over many experiments and observations, the stomatal behavior of apple leaves appears to be better correlated with the photosynthetic rate than with humidity or  $\Psi_1$ .

Response of stomata to changes in the photosynthesis has been found in many species.<sup>208</sup> Apple photosynthesis and  $g_s$  appear to be well coupled, especially under orchard conditions. An example is that the relationship of photosynthesis and  $g_s$  appears to be the same in data from a drought study as in a crop load study with high water status (Figure 11). Consequently, at any given time it is not at all clear whether photosynthesis is controlling stomatal behavior, or vice versa. An indirect method to estimate the relative stomatal versus non-stomatal changes with treatment was to calculate the internal  $\text{CO}_2$  concentration ( $C_i$ ) from the  $\text{CO}_2$  and water vapor fluxes<sup>14,17</sup> to determine if the effect was primarily stomatal closure ( $C_i$  decreasing) or non-stomatal reduction ( $C_i$  increasing). In most cases with apple in the field, the  $C_i$  remains essentially constant regardless of the type of stress. However, this type of analysis has been questioned recently with the finding that in some situations, especially during stress that induces high abscisic acid, stomata close in patches rather than uniformly.<sup>226,227</sup> Stomatal patchiness has not been documented yet in apple. This may give errors in the calculations of  $C_i$  from gas exchange data, so that calculated  $C_i$  values may be overestimated in stressed plants, and the stress effects may be essentially only stomatal. The simultaneous use of gas exchange and chlorophyll fluorescence



**Figure 11** The relationship between photosynthesis and leaf conductance in separate studies of drought stress and of varying crops loads with 'Empire'/M9 apple trees in the field. (Data from Lakso<sup>37</sup>)

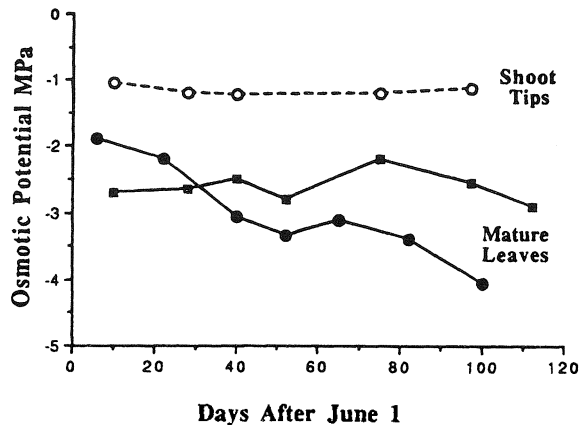
measurements are needed as recently reported by Massaci and Jones<sup>228</sup> on apple. Their results show that with rapid water stress development only the gas exchange was reduced (i.e., stomatal effect only); but with long-term stress both stomatal and the non-photochemical quenching photosynthetic component declined. Thus the relative roles of stomatal versus non-stomatal limitations in apple appear to depend on how rapidly the stress develops.

An important current area of research relates to regulation of  $g_s$  and photosynthesis by root-produced signals, generally thought to be abscisic acid. A variety of split root studies and other approaches have shown that leaf gas exchange tends to be more closely related to the soil water availability of the driest portions of the root system rather than to the  $\Psi_1$  components as previously thought.<sup>229</sup> This concept has been documented in apple recently by Gowing et al.,<sup>230</sup> who showed in a split root study that apple leaf E and leaf growth rates declined with the decline in soil water availability in the dry half while top water relations were maintained at normal levels with water from the wet half. Additionally, they showed that the apparent signal was from the dry half of the root system, since control growth and E rates were restored when the dry half was re-watered or excised. This mechanism of regulation appears to be widespread, as similar studies in grapes<sup>231,232</sup> have been reported.

There are several ramifications if stomata are regulated by photosynthesis. First, it has been shown that low crop load may lead to decreases in tree water use, due in part to less leaf area, but in greater part to lower E rates.<sup>233,234</sup> Second, since  $g_s$  is well coupled to photosynthesis, stomatal opening will only allow the E based on the photosynthetic rates, maintaining high WUE (photosynthesis per unit of E). Third, reductions in  $g_s$  can be caused by factors other than drought stress, so the crop water stress index (CWSI),<sup>235</sup> based on leaf-to-air temperature differentials caused by stomatal closure, can give erroneous readings of stress as recently demonstrated by Andrews et al.<sup>236</sup> For example, a non-cropping plant will transpire less, use less water, have higher  $\Psi_1$ , and maintain higher soil water reservoirs; yet the CWSI method would indicate that irrigation is necessary.

## ii. Reduction of Radiation Absorbed

Apple leaves respond to water stresses by a folding of mature leaves along the midrib and by the reduction in final leaf size in expanding leaves. The degree of folding of the mature leaves is positively related to the light exposure. For the whole canopy the radiation not intercepted by the folded exterior leaves may be intercepted by interior leaves so that the total light interception and water use may not change. The better distribution of light into the canopy should increase whole-canopy photosynthesis, thereby increasing whole-tree WUE, although this has not been experimentally verified in apple. Differences in orchard light interception can lead to different potentials for water use, but the light interception is only a component of water use, with humidity also playing an important role. Canopy form-induced differences in orchard light interception would tend to have its greatest effects on water use under clear skies and with low VPD values.



**Figure 12** Seasonal patterns of osmotic potentials of expanding shoot tips and mature leaves in 'McIntosh'/MM111 apple trees in the field in New York. The different patterns for mature leaves are two different seasons with different rainfall patterns. (Data from Lakso et al.<sup>29</sup>)

### iii. Reduction of Leaf Area

In apple trees, developing extension shoots grow more or less according to the amount of summer rainfall. Growing shoot tips do not osmotically adjust to increased water stress to the extent of mature leaves.<sup>29</sup> The result is that when stress develops, new leaf production slows or ceases while the existing canopy adapts to tolerate the stress. As stress reaches severe levels, leaf abscission occurs, which can reduce leaf area dramatically.

#### b. Maintenance of Water Uptake

With declining soil water availability, water stress in the top of the tree can be avoided by increased root exploration for water or by reducing the hydraulic resistance of the root system. Unfortunately, there has been little research on responses of apple root systems to water deficits.<sup>4</sup> It has been found, however, that the hydraulic conductivity of apple root systems can change in relation to the apparent evaporative demand on the top. Two-year-old container-grown apple trees growing outdoors for the first nine weeks of the second season had about three times the root conductivity of similar trees growing in a humid glasshouse for the same period.<sup>237,238</sup> This difference led to higher  $\Psi_i$  for the outdoor plants when both treatments were placed together in a high evaporative demand. Perhaps this adaptation may contribute to the wide adaptability of the apple to varying climates.

## 3. Drought Tolerance at Low Water Potentials

### a. Maintenance of Turgor

Maintaining cell turgor is the primary way of tolerating unavoidably low  $\Psi_w$ . Osmotic adjustment or changes in the physical properties of cells, such as elasticity or cell size, are the most common mechanisms to maintain turgor (see Jones<sup>17</sup> for general review).

Osmotic adjustment refers to the changes, in either direction, of  $\Psi\pi$  within a cell or tissue. Passive osmotic adjustment refers to the changes in  $\Psi\pi$  due solely to dehydration of cells leading to a concentration of existing solutes. Active osmotic adjustment refers to the changes that occur by active accumulations of produced or imported solutes in cells. Usually, active adjustment is measured at 100% RWC to eliminate the passive dehydration effect. Osmotic adjustment of mature leaves is a striking characteristic of the apple compared to many crops. The amount of active osmotic adjustment has been found to be up to 2.5 MPa over a season<sup>29,219,220</sup> (Figure 12). The adjustment is apparently reversible, since the seasonal pattern of  $\Psi\pi$  varies from year to year with different rainfall patterns (Figure 12). Osmotic adjustment maintains turgor to maintain leaf function such as  $g_s$  and photosynthesis with changes in water stress levels.<sup>29,221</sup> The advantage of this adaptation is that the apple is able to tolerate mild to moderate droughts while maintaining canopy photosynthesis. The disadvantage of osmotic adjustment is that if the drought is very prolonged, the apple may continue to deplete its soil water resources over too long a period. Species that are more conservative and sacrifice productivity by stomatal closure to

conserve water earlier would survive prolonged droughts better. Since under orchard conditions prolonged severe droughts are not allowed to develop in commercial orchards, osmotic adjustment may allow the apple to tolerate the occasional droughts that do occur in non-irrigated orchards.

Carbohydrates appear to be the primary osmotic solutes that change with increased water stress.<sup>220,239</sup> In an excellent detailed study of the biochemistry of osmotic adjustment in apple, Wang and Stutte<sup>239</sup> found that water stress induced the accumulation of sorbitol in apple leaves while starch levels declined. Sorbitol accounted for most of the osmotic adjustment, although glucose and fructose accumulated to some extent. It appears that water stress induces the preferential role of sorbitol as the osmoticum. Since sorbitol has been used as the osmoticum of choice for enzyme and organelle extractions for many years, it is suggested that it plays a role as a compatible solute (a solute that has minimal effect on metabolism as it accumulates). A fascinating report from research on desert plants indicates that sorbitol accumulation may also confer high-temperature resistance.<sup>240</sup> Clearly, more research is needed in this area to determine if there are interactions among multiple stresses.

#### 4. Cell Elasticity and Size

Changes in cellular physical properties, such as elasticity, have not been examined in great detail in apple. The studies that have been done indicate that there may be changes in bulk leaf elasticity, but that the changes are not enough to make a significant effect on the water relations of apple leaves.<sup>11,220,241,242</sup> The role of cell size in apple water relations has not apparently been determined.

### V. FLOODING

The detrimental effects of flooding are not due to excess water, but due to lack of oxygen (anoxia) and possibly the accumulation of soil CO<sub>2</sub>. The success of hydroponics with aeration demonstrates this point. In general, there has been relatively little work on flooding in apple, not because of the lack of effect on the tree, but because of improvements in site selection and affordable tile drainage. Also, economic pressures over the years have provided selection pressure on growers that undoubtedly has eliminated many orchards in poor sites with poor production due to frosts, flooding, or drought. Consequently, severe problems of flooding are uncommon in most apple industries, but short periods of flooding with less dramatic effects may still occur.

There have been several thorough reviews of flooding in plants, both for woody plants in general<sup>243</sup> and for fruit crops.<sup>9,244</sup> The reader is referred to these excellent reviews. This discussion will briefly summarize the general findings and what is known about flooding effects on apple tree physiology.

#### A. GROWTH AND PRODUCTIVITY

Apple has generally been characterized as having moderate tolerance to flooding compared to other fruit crops.<sup>9,244</sup> Childers and White<sup>245</sup> found that within several days of flooding E, photosynthesis, leaf growth, and root growth were reduced and leaf respiration was increased.

The timing and duration of flooding are important. Flooding for short periods of less than a month during the winter or early spring when the trees are dormant is common, yet appears to have little or no obvious effects on apple trees.<sup>246</sup> Once growth begins, the sensitivity to flooding increases dramatically, with one week of flooding reducing young leaf expansion and increasing wilting.<sup>246</sup> Olien<sup>248</sup> and Olien and Lakso<sup>247</sup> flooded cropping trees for six weeks in the spring, summer, and fall and found that spring and summer flooding were most detrimental to vegetative growth and yield, with spring flooding reducing yield most dramatically. The tree water relations reflected apparent reductions in the hydraulic conductance of the root system as the  $g_s$  and  $E$  decreased, but the  $\Psi_1$  remained the same or became more negative. Leaf N, P, K, and Cu levels on a dry weight basis in mid-season were reduced. Effects tended to accumulate over three years of flooding. The effects of flooding, low O<sub>2</sub>, or high CO<sub>2</sub> on nutrients are rather inconsistent, and are likely confounded by different amounts of growth reduction and possibly different dry matter accumulations in the leaves.<sup>247,248</sup> Overall, reduced growth and gas exchange, and changes in water relations appropriate to lower root hydraulic conductances, reductions in nutrient uptake, and poorer set and yield reflect reductions in root system growth and function. The sensitivity of the tree to flooding appears to correlate to the periods of most active growth in the spring and summer, as might be expected. In these responses, apple appears consistent with other fruit crops.<sup>9,244</sup> Even after the soil drains, there are carry-over effects of the damage to the root system on growth and physiology.

The detailed physiological effects of flooding on the regulation of growth and gas exchange processes have not apparently been examined in apple, but have been studied in many plants.<sup>9,243,244</sup>

## B. DIFFERENCES IN ROOTSTOCK RESPONSE

Due to the long use of clonal rootstocks in apple, there have been many observations and/or tests of rootstock differences to flooding. As with any complex response, the rankings show a great range of resistance, but have not been consistent. The rankings are summarized in the review by Schaffer et al.,<sup>244</sup> and more detailed discussion of rootstock responses can be found in Cummins and Aldwinckle.<sup>185</sup> The physiological bases of these variations by rootstock are not known, although the high-temperature effects shown by Gur et al.<sup>155</sup> earlier may provide some insights.

## C. SENSITIVITY AND RESPONSE TO PATHOGENS

A major concern with flooding, in addition to direct effects on the tree, is the increase in root pathogens, especially *Phytophthora* species, especially *Phytophthora cactorum*.<sup>185,244</sup> It is possible that some of the detrimental effects of short-term spring flooding may be due more to providing an infection period for pathogens than to the direct effects on the tree. In normal orchard conditions, it may be difficult to separate the effects of flooding and pathogens. Clearly, site selection and drainage that avoid flooding may help eliminate two related problems. Very little is known about the interactions of pathogen, environment, and host plant response in this case.

# VI. OTHER ENVIRONMENTAL FACTORS

## A. SALINITY

Apple trees are generally considered to be quite sensitive to salinity compared to other fruit crops. Yet, there is relatively little work on salinity effects on apple. This is likely due to the fact that apples have historically been grown in somewhat cooler, humid, or sub-humid areas or in arid regions that have used irrigation waters from mountainous areas. Salinity may become more of a problem in the future if apples are planted in more arid climates with limited quantities of high-quality irrigation water.

Long-term studies in Germany found that: (1) Na and Cl contents of apple leaves increased with treatment levels while K decreased,<sup>249</sup> (2) yields were reduced via early season effects of Na treatment on fruit size,<sup>250</sup> (3) leaf photosynthesis and E were reduced by Na treatment,<sup>251</sup> (4) in general, more damage was caused by early season treatment, and (5) the effects were more severe on trees grafted on M9 compared to M26 rootstock. Simultaneous treatments with K did not affect Na accumulation in the leaves or the water consumption by the tree.<sup>252,253</sup> The M9 and M26 rootstocks differed in the relative distribution of Na. The lack of many reports of long-term effects in the field leave the question of salinity effects open.

## B. POLLUTANTS

### 1. Air Pollutants

A significant effort has gone into examining air pollutant effects on horticultural crops, but mostly on herbaceous crops.<sup>254</sup> Apple is responsive to both ozone and sulfur dioxide, with high doses of each leading to severe foliar injury, leaf abscission, and reductions in  $g_s$  and growth in greenhouse-grown trees.<sup>255</sup> The injury when both pollutants were present was less than additive, since apparently each pollutant caused some stomatal closure that reduced the sensitivity to the other pollutant. Using lower ozone levels closer to ambient in outdoor chambers, Retzlaff et al.<sup>256</sup> found that apple leaf photosynthesis and  $g_s$  declined linearly with increasing ozone up to 0.12 ppm, but that no visual symptoms appeared and only slight reductions in trunk growth rates were found. Since no visual symptoms were apparent, yet photosynthesis was reduced, it is not safe to assume that apple does not suffer from ozone injury in the field. Compared to the other fruit crops, apple was moderate in response.

### 2. Acid Deposition

Since acid deposition has become a concern in many areas of the world where apples are grown, a few studies have examined its effects on apple. Fortunately, apple seedlings or trees in the field are relatively resistant to the effect of acid rain unless there are extended treatments with pHs of 3 or less.<sup>257-260</sup> When the lower pHs did cause lesions, the reductions in dry weight growth and photosynthetic rates were approximately proportional to the percent leaf area damaged. Yield or fruit quality in the field do not appear to suffer due to ambient acid rain episodes.<sup>257</sup>

### C. ATMOSPHERIC CO<sub>2</sub>

Predictions of global climate change are currently controversial because of the complexity of such climate models and the presence of natural global temperature cycles. The most agreed-upon change is the increase in atmospheric CO<sub>2</sub> that is much more under the control (or lack of control!) of humans. Unless there is an increase in political determination, the CO<sub>2</sub> concentration in the atmosphere is likely to continue to rise. At the current increase rates per year,<sup>261</sup> the atmospheric CO<sub>2</sub> would reach 425–475 ppm within about 40–50 years. Despite the extensive research being conducted on CO<sub>2</sub> effects on other crops, the author is aware of little being done on apples at this time. The reasons are several, but the major problems with experiments in the field are adequate replication due to tree size, cost, and the long-term enrichments needed to determine long-term effects.

An early study with seedlings found significant increases in shoot growth with elevated CO<sub>2</sub>.<sup>262</sup> A study of CO<sub>2</sub> enrichment (CDE) of cropping versus non-cropping young apple trees in chambers in a greenhouse in Denmark showed little effect of elevated CO<sub>2</sub> on non-cropping trees.<sup>263</sup> The effects on cropping trees were more striking, especially when supplemental lighting was provided. However, the CDE did not begin until after fruit numbers and potential sink demand, i.e., fruit cell numbers, were already established, thus the potential response was limited to increases in cell size only. Hansen<sup>264</sup> enriched container-grown trees in growth cabinets for several weeks at the start of the season and found that the tree began dependence on current photosynthates by about 3 weeks after budbreak. The effects were primarily on extension shoot growth, since the spurs apparently developed earlier with reserves. Tree gas exchange was not measured in these early studies. Corelli Grappadelli and Magnanini<sup>62</sup> show a light response curve of apple canopy gas exchange in ambient and 900 ppm CO<sub>2</sub>. The brief elevated CO<sub>2</sub> about doubled the net CO<sub>2</sub> uptake at full light, but the effect decreased at lower light levels even though enhancement still occurred at very low light and respiration was inhibited.

Will apple tree productivity respond very much to increased CO<sub>2</sub> levels? Not all crops respond equivalently to CO<sub>2</sub> enrichment.<sup>265,266</sup> The knowledge gained over the past decade indicates that some plants, especially in restrictive containers, demonstrate a compensatory decrease in gas exchange so that the net response to elevated CO<sub>2</sub> is small. It appears that much of the responsiveness to CO<sub>2</sub> enrichment is related to the source/sink balances and the ability of the plant to respond to the increased source with increased sink numbers or activity, as Kramer reviewed in 1981.<sup>267</sup> The few other longer term studies with fruit crops have evaluated citrus and have shown marked increases in growth and yields with little evidence of reductions in photosynthetic responses to CO<sub>2</sub>.<sup>268–272</sup> (see Chapter 4, Volume II). This suggests that fruit trees that have a supply of sinks may be very responsive to CO<sub>2</sub> enrichment. Clearly, such studies must be done with apple trees.

The potential of response of apple to elevated CO<sub>2</sub> may depend on how much additional vegetative growth may occur and how many additional fruits may be produced. Studies of the carbon balance of apple trees and potential limitations of carbon supply to fruit<sup>5,56</sup> suggest that apple fruit production may be quite responsive to increased CO<sub>2</sub>. If additional fruit are set due to increased carbon supply, then the increased sink demand may maintain the photosynthetic sensitivity to CO<sub>2</sub>. There may be many interactions that may not be obvious. Increased growth may lead to denser canopies, causing changes in canopy microclimate, fruit quality, or need for pruning. It will be extremely interesting to observe the progress in this area.

## VII. CONCLUSIONS

In conclusion, the apple is an adaptable, productive species that poses a major challenge to understand, especially if the goal is to improve agricultural productivity. Concerning environmental physiology, the apple is essentially a wild-type plant that has been changed little by breeding. It appears to draw its inherent productivity from long and adaptable leaf area duration, moderate photosynthetic rates, and stress tolerance mechanisms, such as good WUE, plasticity of canopy development, osmotic adjustment, and slow physiological aging. When considering the evolutionary pressures of occasional stress periods, it is difficult to imagine a better set of adaptations. Fortunately for humans, these adaptations have led to many mechanisms of good sustained productivity as long as we can understand how to keep the tree from switching from the fruit-producing mode to the fruit-abscising survival mode.

### A. NEEDS FOR FUTURE RESEARCH

To make progress in improving the productivity and efficiency of the apple in the orchard, it will be increasingly necessary to develop a sound understanding of the physiology of the plant. Progress was

made in the past by overcoming major limitations of nutrients by fertilization, water by irrigation, pest damage by chemical pest management, erratic production by thinning, and low yields by improved pruning, training, and orchard design. Progress in the future will require a much more subtle set of changes or improvements giving smaller increments of productivity. Physiology will need to change from the explanatory science that primarily follows practice to a science that understands principles and leads practice. This mandate within the areas covered in this review will require a crop physiology approach that evaluates the problem, determines the likely principles involved and the level of the problem (i.e., orchard, tree, organ, tissue, cell, or molecular), develops good testable hypotheses, and uses whatever techniques are necessary to conduct the research. Clearly, a broad view of the entire physiology and the environment is needed. Modeling will become more important as a means to integrate information more efficiently and to estimate some potential outcomes to evaluate.

Many more studies that evaluate interactions of multiple stresses and that integrate the different physiological process (especially in carbon, water, or nutrient balances) are needed. Good examples are the effects of increasing CO<sub>2</sub> and of foliar biotic stresses on productivity and fruit quality. In the latter case, effective chemical pest management for a generation has made biotic stress physiology almost irrelevant. But with the loss of available pesticides, modern pest management practices are founded on the concept that the tree can tolerate biotic stresses to some level called the "threshold" before reductions in yield or quality occur. This requires a detailed understanding of stress physiology to be able to utilize as few pesticides as possible while maintaining the risk for the grower at a reasonable level. Recent studies in our laboratory suggest that the effects of some foliar pests may be mediated via the carbon balance of the tree; thus, many other factors that affect the carbon balance (radiation, crop load, temperature, CO<sub>2</sub>, and other stresses) are expected to interact with pest thresholds.

The challenges outlined are not easy, but the high value of the apple and other fruit crops allows unique opportunities to put physiological understanding into practice to improve fruit production and quality for everyone.

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## Chapter 3

# Blueberries, Cranberries, and Red Raspberries

Frederick S. Davies and Rebecca L. Darnell

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## I. INTRODUCTION

Blueberries, cranberries, and raspberries are small fruits encompassing a range of species that are distributed worldwide. Blueberries and cranberries are in the family Ericaceae and the genus *Vaccinium* which contains about 400 species of shrubs, woody vines and small trees.<sup>1</sup> Two-thirds of the species are found in Malaysia, with the remaining ones distributed in southeast Asia, Japan, Africa, Europe, and North and South America. *Vaccinium* has been further subdivided into 10 sections.<sup>2</sup> The blueberries are in *Cyanococcus* which includes lowbush (*V. angustifolium* Ait.), highbush (*V. corymbosum* L.), and rabbiteye species (*V. ashei* Reade), although Vander Kloet<sup>1</sup> combines rabbiteye blueberries into *V. corymbosum*. Highbush blueberries are grown commercially in more than 30 states and provinces in North America; lowbush blueberries are grown primarily in Maine and five eastern Canadian provinces; and rabbiteye blueberries are produced primarily in Georgia, Florida, Mississippi, Texas, South Carolina, Louisiana, and Alabama. There are also several wild *Vaccinium* species that are not of commercial importance but have potential for use in breeding to improve existing cultivars, including *V. darrowi*, *V. tenellum*, *V. myrsinites*, and *V. ellioti* among others.<sup>3</sup> The cranberry (*V. macrocarpon* Ait.) belongs to the section *Oxycoccus*. Cranberries are grown primarily in Massachusetts, Wisconsin, New Jersey, British Columbia, Quebec, and Nova Scotia.

Raspberries are in the family Rosaceae and the genus *Rubus* which consists of shrubs, many of which are biennial bearing and woody.<sup>4</sup> *Rubus* is further subdivided into 12 sections including *Idaeobatus* (red raspberry), *Eubatus* (blackberry), *Cylactis* (related polar and alpine species), and *Anoplobatus* (related flowering species).<sup>5</sup> Red raspberry is of greatest worldwide importance with over 200 species.<sup>6</sup> Raspberry fruits readily separate from the receptacle, whereas blackberry fruit adhere to the receptacle.

Red raspberries are of two major genetic origins: *Rubus idaeus* subsp. *vulgatus* Arrhen. is native to northern Europe and Asia and *R. idaeus* subsp. *strigosus* Michx. to North America. The black raspberry, *R. occidentalis* L., is also native to North America.<sup>5,7</sup> The commercially important red raspberries are natural hybrids of the European and American types and thus have acquired advantageous traits of each group. The former have naturally superior fruit quality and the latter have superior drought tolerance and cold hardiness. Red raspberries are produced primarily in the United States (Oregon and Washington), Chile, eastern Europe, Scotland, in the western United States (Oregon and Washington), and British Columbia.

These two families of small fruits differ from most other fruit species discussed in this book because they represent multi-stemmed bushes and prostrate-growing shrubs rather than large trees. Most species remain relatively small at maturity compared to most tree crops, although some *V. ashei* plants may exceed 8 m in height if left unpruned.<sup>8</sup> In addition, some raspberry species are distinctly biennial bearing. Furthermore, *Vaccinium* species differ from other commercial fruit crops in their requirement for low pH soils. Consequently, the environmental physiology of these small fruits may differ in some aspects from that of large trees.

In this chapter we will discuss the effects of light, temperature, and water on the growth and development of commercially important *Vaccinium* and *Rubus* species. Some references will also be cited from related species from the wild, particularly for *Vaccinium*, where several heath and heather species have been studied in detail.

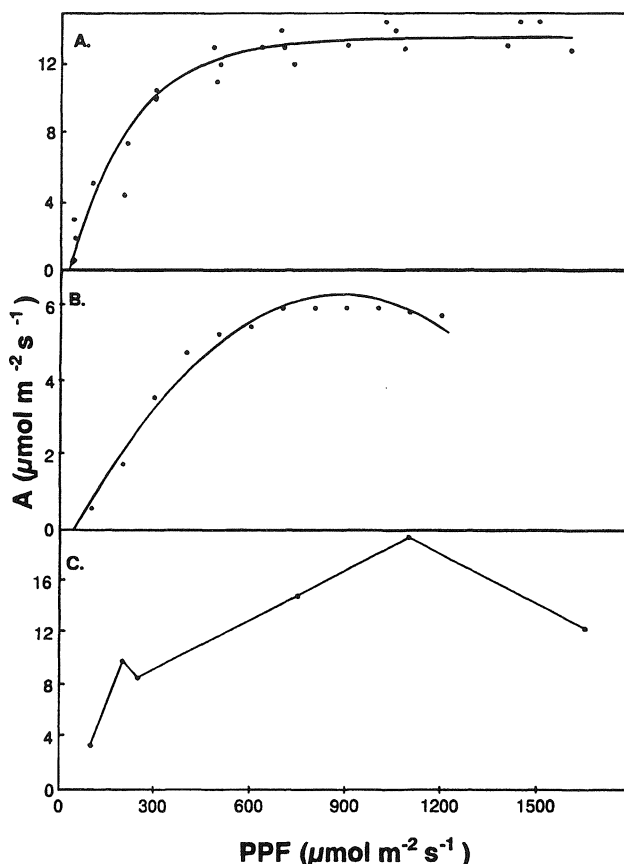
## II. IRRADIANCE

### A. VACCINIUM

#### 1. Irradiance Level

In nature, *Vaccinium* species are found in a wide range of light environments, ranging from full sun to partial or dense shade.<sup>9</sup> Many *Vaccinium* species grow in the wild as understory plants while others are found along river banks in full sunlight.<sup>8</sup> Optimum commercial growth and production, however, are greatest under full sun conditions.<sup>10</sup>

Leaf net CO<sub>2</sub> assimilation (*A*) and light saturation curves have been reported for leaves of lowbush, rabbiteye, and highbush blueberries. In general, *A* of lowbush and highbush blueberry averages 9–12  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,<sup>11–13</sup> substantially higher than rates in rabbiteye blueberry, which average 5–8  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .<sup>14–16</sup> Leaf *A* of cranberry averages 9–15  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,<sup>17</sup> although rates as high as 25  $\mu\text{mol m}^{-2} \text{s}^{-1}$  have been reported.<sup>11</sup> This range in cranberry leaf *A* rates may reflect temperature, seasonal, and/or cultivar differences. Leaf *A* increases with increasing photosynthetic photon flux (PPF),



**Figure 1** Effects of photosynthetic photon flux (PPF) on leaf net CO<sub>2</sub> assimilation (A) in 'Jersey' highbush blueberry (A), 'Woodard' rabbiteye blueberry (B), and 'Searle' cranberry (C). From Moon et al., *J. Amer. Soc. Hort. Sci.*, 112,134,1987 (A); Teramura et al., *HortScience*, 14, 723, 1979 (B); Stang et al., *Acta Hort.*, 165, 325, 1985 (C). With permission.

reaching light saturation at 600–800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for both blueberry<sup>13,14</sup> and cranberry<sup>17</sup> (Figure 1). Photosynthetic light saturation in lowbush blueberry occurs between 1000 and 1500 ft-c,<sup>11</sup> which although not readily convertible to SI units, is in the same range as light saturation for other *Vaccinium* species.

Photosynthetic photon flux of 250 to 300  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , sufficient for 50–60% of maximum photosynthesis, has been measured in the shaded canopy interior of 5-year-old rabbiteye blueberry bushes.<sup>14</sup> This, coupled with the low light compensation point of 25–35  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,<sup>18</sup> suggests that irradiance level effects on photosynthesis may not be a major yield limitation in blueberry. The relatively small size and multiple stemmed structure permits greater light penetration into the canopy than might occur for large, densely-foliated trees such as citrus or mango.

Stang et al.<sup>17</sup> reported that A of cranberry shoots grown for 30 or 60 days under 100, 80, 60, or 15% full sun were similar when measured under saturating PPF. The authors suggested that cranberry, unlike other species that exhibit reduced rates of photosynthesis in shade-developed leaves, has a "unique and rapid ecological adaptation to changing light levels" that is well-suited for the light competition that occurs in a dense cranberry planting. However, the proportion of the total photosynthetic area of the shoots that developed under the shaded conditions during the 30 or 60 day experiment was not indicated. If this proportion were small, then differences in leaf A due to the light environment during development may have been masked. Further work is needed to clarify this concept.

Recent research suggests that fruit photosynthesis may contribute a significant portion of the total fruit carbon requirement in blueberries, especially during early fruit development. Net CO<sub>2</sub> assimilation occurred in fruit from petal fall through color break, declining from about 19  $\mu\text{mol g}^{-1} \text{FW h}^{-1}$  to 0.2  $\mu\text{mol g}^{-1} \text{FW h}^{-1}$  during development.<sup>19</sup> During the first 10 days after anthesis, fruit photosynthesis

was estimated to contribute 50% of the total carbon required for dry weight gain and respiratory loss. From anthesis to fruit ripening, fruit photosynthesis contributed 15% of the total fruit carbon requirement. As with leaves,  $A$  of fruit is light dependent. However, light saturation for fruit photosynthesis in highbush blueberry occurred at a much lower PPF, approximately  $300\text{--}350\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ , with a light compensation point at  $100\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ .<sup>20</sup> This low light saturation level suggests that PPF may be saturating for fruit photosynthesis throughout much of development, even on the shaded side of the fruit.

Although PPF effects on photosynthesis may not be a major limitation to productivity under most conditions, evidence suggests that light is still a major factor regulating growth and development of *Vaccinium* species. Stang et al.<sup>17</sup> reported that increasing levels of shade decreased cranberry leaf thickness, due to a decrease in the number and size of mesophyll and palisade cells. Similarly, reproductive development is markedly influenced by light. Hall<sup>21</sup> found that flower bud number in lowbush blueberry decreased linearly with decreasing irradiance level from 100 to 11% full sun. In a subsequent study, Hall and Ludwig<sup>22</sup> reported that flower bud initiation of lowbush blueberry was significantly decreased when irradiance level was decreased below 60% full sun (a PPF of about  $1200\ \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ). These data indicate that PPF well above that required for light-saturated photosynthesis is required for optimum flower bud initiation in lowbush blueberry.

Fruit development period and fruit maturity are also influenced by light. Aalders et al.<sup>23</sup> found that the fruit development period was lengthened and fruit sugar content decreased in lowbush blueberry by decreasing irradiance level. Partial defoliation under high irradiance level also lengthened the fruit development period, but had no effect on fruit sugar content. Light also appears to be the primary factor in fruit development of rabbiteye blueberry.<sup>24</sup> Fruit from the top of the canopy, receiving full sun, ripened faster than fruit from other locations. The correlation between amount of light striking the canopy and fruit ripening rate in that area of the canopy was linear, as was the correlation between amount of light and fruit soluble solids. Overall, light exposure accounted for 64% of the variability in fruit maturity (as measured by fruit color) and 30% of the variability in soluble solids (Figure 2). Three hours of photosynthetic light saturation (25–30% full sun) were considered sufficient to ensure that light was not the overriding limitation in fruit development. However, the importance of light distribution over the course of the day was not addressed.

Ripening of highbush blueberry fruit (as measured by color development) was delayed when fruit clusters were bagged to exclude light.<sup>25</sup> This is evidence for light regulation of anthocyanin biosynthesis, and further indicates a distinct role of light in fruit development separate from its role in photosynthesis.

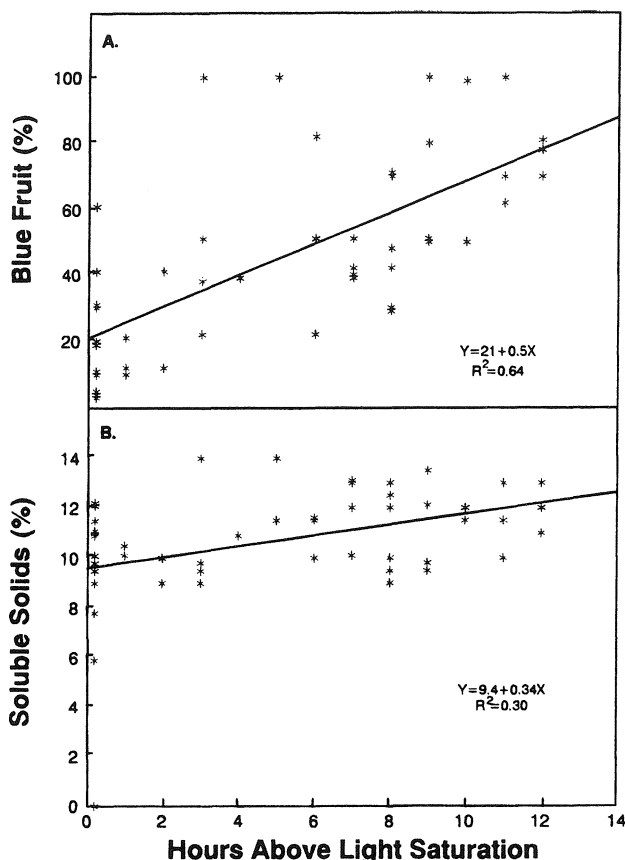
## 2. Photoperiod and Light Quality

A substantial amount of data indicates that growth and development in *Vaccinium* is dependent not only on irradiance level, but also on photoperiod. Flower bud initiation in lowbush blueberry is promoted under short days.<sup>26,27</sup> In general, at least 6 weeks of photoperiods less than 12 hours is needed for normal flower bud formation. The photoperiod response of highbush blueberries is similar to that of lowbush. Eight weeks of 8-, 10-, or 12-hour photoperiods resulted in flower bud initiation in highbush cultivars, whereas fewer flower buds were formed under 14- and 16-hour photoperiods.<sup>27</sup> Reproductive development in rabbiteye blueberry is also affected by photoperiod.<sup>28</sup> Six weeks of 8-hour photoperiods in the fall promoted flower bud initiation and decreased the length of the bloom period the following spring compared to 11–12 hour daylengths (Table 1). This suggests that short days not only increase the number of flower buds initiated, but may also result in more synchronized flower bud differentiation.

Concomitant with an increase in flower bud initiation under short days is a decrease in total shoot growth.<sup>22,27</sup> Conversely, long days promote an increase in shoot growth, shoot number, and leaf area in blueberry<sup>29,30</sup> and cranberry.<sup>31</sup>

Little information is available on light quality effects on growth and development of *Vaccinium* species. Since photoperiod effects appear to be phytochrome mediated,<sup>32</sup> it is possible that light quality would have a profound effect on development. Stushnoff and Hough<sup>33</sup> found that blueberry seeds exposed to red light had a much higher germination percentage than those exposed to white light. There is no information available on red:far red effects on other aspects of *Vaccinium* development.

High levels of UV-B radiation had no consistent effect on fruit number or berry weight in rabbiteye blueberries.<sup>34</sup> However, the waxy bloom on fruit decreased as UV-B radiation increased. Additionally, fruit exposed to high levels of UV-B developed a corky layer on the surface, having symptoms similar to sunscald.



**Figure 2** Relationship between the number of hours above light saturation and the development of blue fruit (A) and fruit soluble solids (B) for 'Tifblue' rabbiteye blueberry. From Patten and Neuendorff, *Proc. Texas Blueberry Growers Assoc.*, Beaumont, 1989, 109.

**Table 1** Daylength effect on flower bud initiation, bloom period, flower budbreak, and total flower number of 'Beckyblue' rabbiteye blueberry

| Daylength <sup>a</sup> | Flower buds/<br>plant |       | Bloom period<br>(days) |      | Flower buds<br>broken<br>(% flower<br>buds/plant) | Total florets<br>(no.) |      |
|------------------------|-----------------------|-------|------------------------|------|---|------------------------|------|
|                        | 1989                  | 1990  | 1989                   | 1990 | 1989 <sup>b</sup>                                 | 1989                   | 1990 |
| Natural                | 21.9                  | 183.7 | 12.7                   | 37.5 | 43.8  | 56                     | 1016 |
| SD                     | 48.0                  | 214.9 | 9.0                    | 32.9 | 61.7  | 177                    | 1194 |
| Significance           | **                    | *     | **                     | **   | **  | **                     | **   |

<sup>a</sup> Daylength during the 5 weeks just before defoliation and chilling. Natural = decreasing daylength from 12 to 11 hr; SD = decreasing daylength from 10 to 8 hr. <sup>b</sup> No data for 1990. \* $p = 0.10$ . \*\* $p = 0.05$ .

From Darnell, R. L., *J. Amer. Soc. Hort. Sci.*, 116, 856, 1991. With permission.

## B. RUBUS (RED RASPBERRY)

### 1. Irradiance Level

Information on irradiance level effects on A in raspberry is limited. Maximum A of 6–10  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at 25°C under saturating light conditions (24 klux) have been reported for mature, detached leaves of

field-grown red raspberry plants.<sup>35</sup> Goulart and Braun<sup>36</sup> measured PPF effects on *A* in five cultivars of greenhouse-grown, primocane fruiting red raspberry. They found little variation in light response curves among the cultivars. Leaf *A* measured at an average leaf temperature of 25.6°C increased with PPF up to 900 to 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , with maximum values averaging 5–7  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . However, average values of 9 to 12  $\mu\text{mol m}^{-2} \text{s}^{-1}$  have been found for raspberries in the field in New York.<sup>37</sup>

Light microclimate may have significant effects on vegetative and reproductive growth within the raspberry canopy. Individual raspberry canes are biennial; primocanes arising from adventitious buds in roots or basal buds on previous canes grow vegetatively throughout the season until flower bud initiation in the fall. The following year, the axillary buds on these canes produce lateral fruiting branches. Thus, a raspberry canopy is comprised of both vegetative primocanes and reproductive floricanes. Palmer et al.<sup>38</sup> compared light interception and intensity in vertical vs. horizontal raspberry training systems. Horizontal systems, planted at spacings of 5 m between rows, intercepted about 60% of the incident light in a pattern that was evenly distributed throughout the day. Vertical systems at the same spacing, however, intercepted about 40% of the incident light, with a mid-day decrease to about 20%. Although yield data were not taken, the authors concluded that horizontal training systems would increase productivity compared to vertical systems planted at the same spacing by promoting more even light distribution in the canopy throughout the season. In contrast, fruit became sunburned when light was maximized under Missouri growing conditions.<sup>39</sup> Braun et al.<sup>40</sup> estimated the light microclimate within the canopy of red raspberry and correlated irradiance level and distribution with growth and yield. Total floricanes canopy volume was similar throughout the season, but the extent of light exposure shifted during the season as primocanes grew. During the season, 60 to 70% of the total floricanes leaf area and 55 to 60% of the flowers and fruit were in the area of the canopy exposed to 0 to 25% of the PPF. Thus, on a whole plant basis, the area of the canopy exposed to 0 to 25% PPF was the most productive. However, on a leaf area basis, productivity increased with increasing light. Fruit set in canopy areas exposed to greater than 25% PPF averaged 90%, while fruit set in areas exposed to 25% or less averaged 35 to 50%.

Annual cropping systems, where both primocanes and floricanes are present each year, have been compared to biennial cropping systems, where primocane growth alternates yearly with floricanes growth. This biennial system is accomplished by removal of either floricanes or primocanes prior to the start of the growing season. Total light interception by the canopy was greater in the annual system than the biennial; however, light distribution was poorer.<sup>41</sup> There was a decrease in the number of primocanes produced, and an increase in primocane internode length in the annual system, consistent with the far-red enrichment that would occur as the fruiting canes filtered out the red light.<sup>42</sup> As primocane growth developed, the lower fruiting laterals in the annual system became heavily shaded, resulting in excess leaf loss and a decrease in fruit set and yield.<sup>41,43</sup> On the other hand, the biennial system resulted in increased primocane production and increased nodes per cane in the vegetative year, which translated into higher yields the following year.<sup>44</sup> However, even though productivity was decreased on the annual cropping system vs. the fruiting year of the biennial cropping system, yields averaged over a 2-year cycle were greater for the annual system.

Red raspberries, exposed to clear days and high temperatures, may develop symptoms of sunscald, where red coloration fails to develop on the sun-exposed portion of the fruit. Renquist et al.<sup>45</sup> found that 30 or 60% shade applied for the last 3 weeks or the last few days of fruit development prevented sunscald symptoms in the field. Use of fans to decrease fruit temperature did not significantly affect the development of sunscald. Therefore, they concluded that high light exposure just prior to fruit harvest was the major factor in the development of symptoms. In a subsequent study, Renquist et al.<sup>46</sup> observed that sunscald symptoms did not develop when fruit were exposed to high temperatures (37 to 44°C) in the absence of UV radiation. Significant injury occurred only when 4 to 7 hours of UV radiation was combined with high temperatures, indicating that methods of alleviating sunscald must include attenuation of UV radiation interception by the fruit.

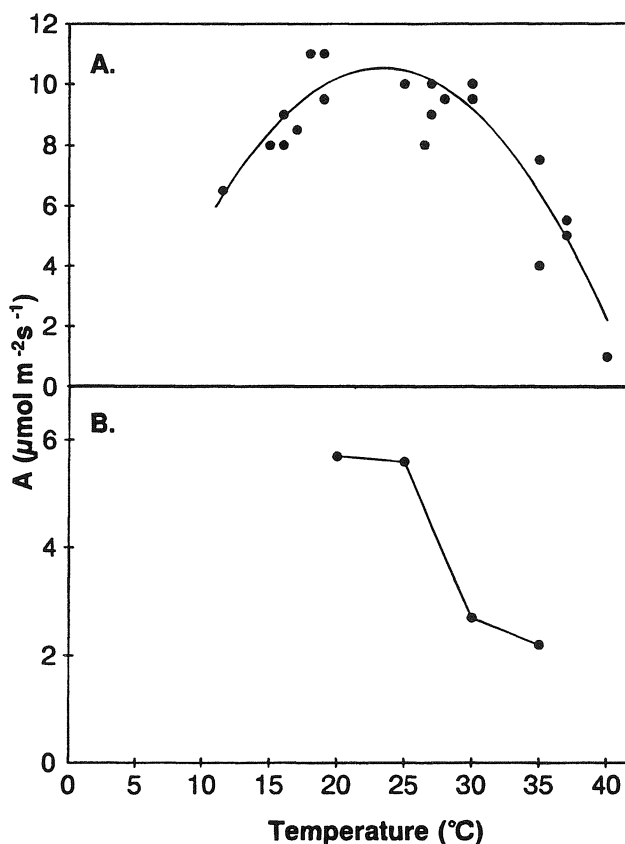
In general, there is a paucity of information on light effects on growth and development of raspberry compared to other fruit crops. Although correlations between light interception and yield have been drawn, there are limited data available on irradiance level, quality, or photoperiod effects. Further work on light effects on reproductive and vegetative growth of raspberry is warranted.

### III. TEMPERATURE

#### A. VACCINIUM

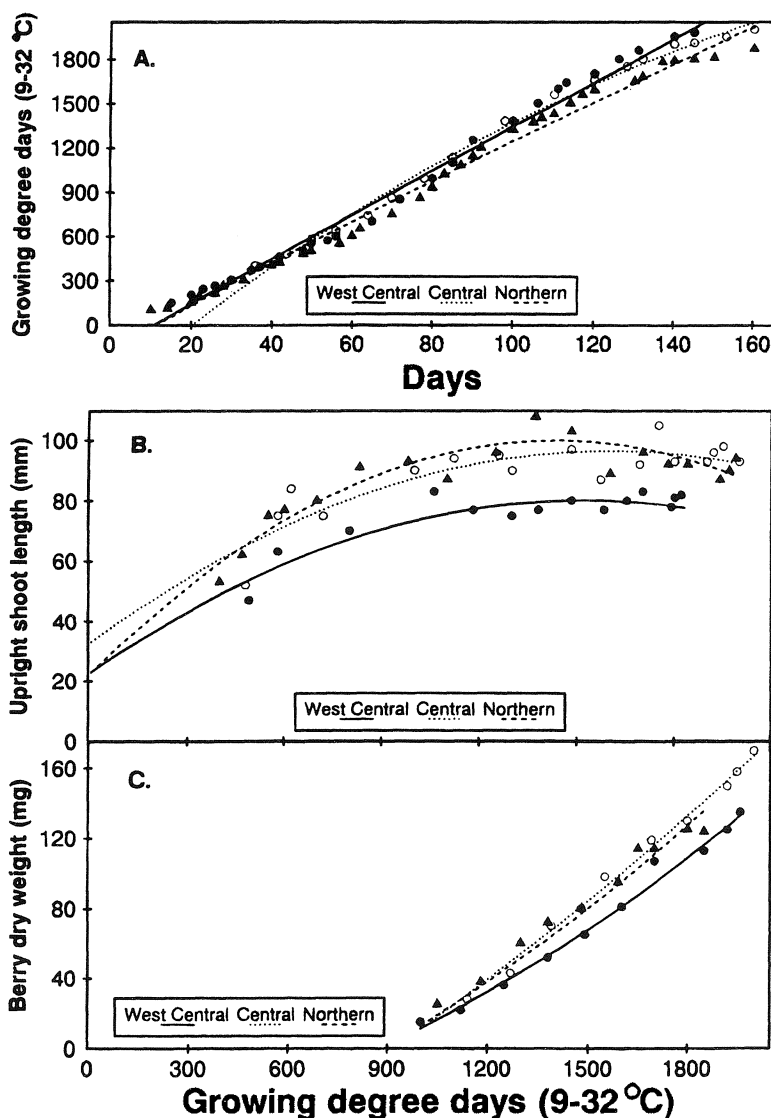
##### 1. Growing Season Temperatures

In general,  $A$  of lowbush, rabbiteye, and highbush blueberries increases as temperatures increase from 10 to 25–30°C, depending on species.<sup>12,13,47</sup> In cranberry, leaf photosynthetic rates, as measured by  $O_2$  evolution, increased linearly as temperature increased from 3.5 to 25.0°C.<sup>48</sup> Temperature optima for  $A$  in both highbush (Figure 3A) and rabbiteye (Figure 3B) blueberry are similar, ranging from 20–25°C.<sup>12,13</sup> As temperature increased to 30°C,  $A$  decreased significantly in both species, a somewhat unexpected result since rabbiteye blueberry plants are native to the southeastern United States and therefore might be expected to be better adapted to high temperatures than highbush blueberry plants. Crosses between *Vaccinium corymbosum* ('Bluecrop') and *V. darrowi* (Florida 4B), a wild diploid blueberry selection with a temperature optimum for  $A$  about 8–10°C higher than *V. corymbosum*,<sup>48</sup> resulted in an  $F_1$  hybrid and a progeny of the  $F_1$  hybrid with photosynthetic heat tolerance similar to that of Florida 4B.<sup>49</sup> In a later study, Hancock et al.<sup>50</sup> identified several benotypes from  $F_2$  and backcross populations derived from Florida 4B × 'Bluecrop' that also had increased heat tolerance. This suggests that the photosynthetic heat tolerance of *V. darrowi* can be transferred to commercial blueberry cultivars, which may be an important factor in potential yield increases, since high temperatures in the field may limit  $A$ . However, correlations between  $A$  and yield are often poor because other factors such as number of flower buds formed and amount of cross pollination also affect yields. Thus, field testing of progeny with increased photosynthetic heat tolerance is required.



**Figure 3** Effects of temperature on leaf net  $CO_2$  assimilation ( $A$ ) in 'Jersey' highbush blueberry (A) and 'Woodard' rabbiteye blueberry (B) From Moon et al., *J. Amer. Soc. Hort. Sci.*, 112, 134, 1987 (A); Davies and Flore, *J. Amer. Soc. Hort. Sci.*, 111, 565, 1986 (B). With permission.

There are limited data on temperature ranges for vegetative and reproductive growth of *Vaccinium*. Hall and Ludwig<sup>22</sup> found that shoot growth of lowbush blueberry increased as temperature increased from 10 to 21°C. Root growth of highbush blueberry was limited at soil temperatures below 8°C or above 18°C, with optimum growth occurring between 14 and 18°C.<sup>51</sup> However, total shoot growth of highbush blueberry increased as soil temperature increased from 13 to 32°C.<sup>52</sup> Several studies indicate that increases in blueberry growth due to mulching are due, in part, to the resultant decrease in soil and root temperatures.<sup>53-55</sup> Optimum temperatures for cranberry growth range from 16 to 27°C, and high temperature injury may occur at temperatures near 27°C if drying winds are present.<sup>56</sup> Hawker and Stang<sup>57</sup> in Wisconsin characterized vegetative and reproductive growth in cranberry by summation of growing degree days (GDD) within the range of 9 to 32°C. They found that accumulation of GDD in three locations within geographical and climatically distinct regions in Wisconsin were similar in their sigmoidal pattern (Figure 4A). Shoot length increased rapidly until the end of June (700 GDD),



**Figure 4** Seasonal growing degree days (GDD) accumulation at three Wisconsin cranberry producing locations (A), relationship between GDD and shoot growth of 'Searles' cranberry (B), and relationship between GDD and fruit dry weight for 'Searles' cranberry (C). From Hawker and Stang, *Acta Hort.*, 165, 311, 1985. With permission.

and terminal growth ceased by the end of July (1300 GDD) (Figure 4B). Shoot dry weight accumulation mirrored shoot length. Shoot length of plants growing in the most northerly location averaged 15 cm shorter than the other two locations; however, differences in shoot growth were not related to lower GDD accumulation since the rate of accumulation did not differ significantly among the three locations. Therefore, factors in addition to GDD, such as water relations or photoperiod, affect growth of cranberry plants. Cranberry floral buds bloomed about mid-June (510 GDD), and a rapid linear increase in berry dry weight occurred from mid-July (1000 GDD), when shoot growth had almost ceased, until the end of the growing season (2100 GDD) (Figure 4C). Berry anthocyanin accumulation began by the end of August (1600 GDD), with the fastest rate occurring at the more northerly location.

Reproductive development in *Vaccinium* may be limited by temperature. In cranberry, increased upright production, flower bud number, and fruit yield were correlated with minimum/maximum temperatures above 10 and 18°C, respectively, during the summer.<sup>58</sup> However, excessively high temperatures in spring, when coupled with moisture deficits, decreased fruit set.<sup>56</sup>

Within the temperature ranges studied (10 to 25°C), the rate of blueberry flower bud development increased as temperature increased, but there was little effect of temperature on flower bud initiation.<sup>22,26,59</sup> No differences in fruit set or berry weight were found when blueberry plants were grown under controlled, diurnal temperature conditions of 21/10 or 16/10°C,<sup>60</sup> although the fruit development period increased under the cooler conditions. However, Knight and Scott<sup>61</sup> reported that fruit set and berry size increased, and fruit development period decreased under warm (16–27°C) greenhouse conditions compared to cool (8–24°C) conditions. Increased fruit set was attributed to increased rate of pollen tube growth under the warmer conditions.

Empirical evidence suggests that temperature effects on the length of the fruit development period of blueberry occur primarily during growth stages I and III. Plants with late blooms followed by warm temperatures may exhibit shorter stage I periods than when early blooms are followed by cool temperatures.<sup>62</sup> Observation suggests a similar temperature effect on stage III, while the length of a stage II is thought to be genetically linked, as well as strongly influenced by the presence of viable seed. Carlson and Hancock<sup>63</sup> suggested that fruit development of highbush blueberry may be inhibited to some extent by temperatures ranging from 21 to 32°C, depending on cultivar. This may reflect the adverse effects of high temperatures on A.

Information on low temperature effects on *Vaccinium* fruit set is sparse. Rigby and Dana<sup>64</sup> reported that the time between pollination and fertilization of cranberry flowers under greenhouse temperature conditions of 18°C night and 24–32°C day was 24 to 72 hours. They suggested that the period for pollen tube growth and ovule fertilization in the field would be longer than this due to cooler night temperatures during bloom. In fact, night temperatures below freezing during cranberry bloom are not uncommon.<sup>65</sup> Low night temperatures may contribute to the low fruit set percentages observed in cranberry if pollen tube growth is delayed and the ovules deteriorate prior to fertilization.

Low temperatures after pollination also decrease fruit set and fruit development in blueberry. Hall et al.<sup>66</sup> found that 4 hours at –2°C or 2 hours at –3°C decreased fruit set in lowbush blueberry by 42 and 77%, respectively. Additionally, plants exposed to –1°C for 6 hours, or to –2°C for 4 hours produced small and late ripening berries. Injury was comparable on plants subjected to freezing temperatures immediately after pollination and plants subjected to freezing temperatures 6 days after pollination.

Fruit set in *Vaccinium* is also indirectly influenced by temperature effects on bee activity. Temperatures below 10°C inhibit bee flight.<sup>67</sup> In general, low temperatures, high winds, and/or rain during bloom will decrease bee activity and, therefore, pollination and fruit set.

Development of anthocyanins in *Vaccinium* leaves and fruit is highly temperature dependent. Hall and Stark<sup>68</sup> showed that anthocyanin content increased as temperature decreased from day/night temperatures of 23.9/18.3 to 12.8/7.2°C in detached cranberry fruit and intact cranberry plants. Anthocyanin content of lowbush blueberry leaves increased as temperature decreased from diurnal day/night temperatures of 25.6/15.6 to 15.6/4.4°C.<sup>59</sup> However, anthocyanin accumulation did not occur in harvested highbush blueberry fruit at temperatures below 10°C.<sup>25</sup> Between 10 and 15°C, only red pigmentation developed. At 16°C and above, blue pigmentation developed, with the rate dependent on temperature. The response difference in anthocyanin development between harvested cranberry and blueberry fruit may be due to a light interaction; the harvested blueberry fruit were held in the dark, while the cranberry fruit were exposed to a 12-hour photoperiod during their respective temperature treatments.

## 2. Cold Hardiness

The ability of plant tissue to withstand low winter temperatures is dependent on the degree of acclimation attained by that tissue prior to exposure to low temperatures. The timing and extent of acclimation depends on environmental and genetic factors. In the northeastern United States, highbush blueberry shoot tissue began acclimating in October and continued to acclimate through January, when maximum hardiness was attained.<sup>69</sup> Dehardening began soon after, and was gradual over the next 4 months. At maximum hardiness, shoot tissue tolerated  $-25^{\circ}\text{C}$  with little injury, but severe injury occurred in tissue subjected to  $-40^{\circ}\text{C}$ . Bittenbender and Howell<sup>70</sup> found that maximum hardiness of highbush blueberry cultivars occurred at the end of November in Michigan. Dehardening began between mid-January and early March. Under Wisconsin growing conditions, cranberry leaf and shoot hardiness increased very gradually, from  $0^{\circ}\text{C}$  early in the growing season, to  $-7^{\circ}\text{C}$  in mid-July, attaining maximum hardiness of  $-24^{\circ}\text{C}$  by mid-October.<sup>71</sup> Dehardening began in late April, and proceeded rapidly, reaching  $-7^{\circ}\text{C}$  by early May. The increase in leaf hardiness was associated with an increase in sugar concentration of the leaves. Similarly, Siekmann and Boe<sup>72</sup> found a 95% increase in total sugar concentration in cranberry leaves after plants were exposed to  $7^{\circ}\text{C}$  for 6 days. The increase in sugars during cold acclimation may be correlative rather than causal, however.

Although early research indicated that highbush blueberries in Minnesota were able to withstand winter temperatures only down to  $-20^{\circ}\text{C}$ ,<sup>73</sup> the short growing season in northern climates may prevent full acclimation, resulting in decreased hardiness and the reliance on snow cover as an insulator.<sup>74</sup> Additionally, variability in environmental factors during the season may affect the rate and extent of acclimation and the development of cold hardiness.<sup>75,76</sup> The degree of stem acclimation in highbush blueberry under Minnesota conditions varied from a maximum of  $-25$  to  $-40^{\circ}\text{C}$  in different years.<sup>75</sup> The decrease in the degree of hardening was attributed to drought conditions during the fall, which induced premature leaf senescence and prevented complete acclimation of the tissue. Bittenbender and Howell<sup>77</sup> used multiple regression analysis to determine which environmental factors affect cold hardiness of highbush blueberry. In the fall, bud hardiness was positively correlated with water content, supporting results from Quamme et al.<sup>75</sup> Both an increase in air temperature and photoperiod were correlated with decreased hardiness. Since air temperature would be expected to vary during fall, this suggests that tissue cold hardiness would also vary. In the winter and spring, hardiness was again negatively correlated with air temperature and duration of the photoperiod.<sup>77</sup> In contrast, water content was negatively correlated with bud hardiness,<sup>70,77</sup> and bud hardiness was found to increase linearly as bud water content decreased.<sup>78</sup>

Cold hardiness of blueberry plants is species dependent. Lowbush blueberry is inherently more cold hardy than highbush blueberry,<sup>75,79</sup> which is inherently more cold hardy than rabbiteye blueberry.<sup>80,81</sup> Recently, half-high blueberry genotypes (*V. corymbosum* L  $\times$  *V. angustifolium* Ait. hybrids) have been developed that are similar in growth and fruiting characteristics to highbush blueberry, yet exhibit greater cold hardiness.<sup>82,84</sup>

Within a species, flower bud hardiness is dependent on cultivar, bud developmental stage, and location on bush. In general, cranberry flower buds survive temperatures of  $-12$  to  $-18^{\circ}\text{C}$  without injury if fully acclimated.<sup>56,71</sup> Initial injury in dormant cranberry flower buds occurs at the abscission zone between the bud and the stem,<sup>56,71</sup> followed by injury to the ovary and filaments.<sup>71</sup> Open cranberry flowers cannot survive temperatures less than  $0^{\circ}\text{C}$ .<sup>71</sup> Flowers that were injured but not killed by low temperatures developed more slowly and had fewer primordia than uninjured flowers,<sup>85</sup> and may produce smaller fruit with fewer seed.<sup>86</sup> Cranberry flower buds that developed first on an inflorescence were more susceptible to cold than those developed later,<sup>56</sup> presumably reflecting differences in bud developmental stage. Abdallah and Palta<sup>71</sup> reported that young cranberry fruit were injured at temperatures of  $0^{\circ}\text{C}$ ; however, hardiness increased to between  $-3$  and  $-8^{\circ}\text{C}$  as fruit changed from green to red stage.

In rabbiteye blueberry, the temperature required to damage flower buds was inversely related to the stage of development.<sup>87</sup> Closed floral buds survived temperatures of  $-10$  to  $-15^{\circ}\text{C}$ , depending on cultivar, while open buds were killed at  $-1^{\circ}\text{C}$ . A similar inverse relationship was evident for southern highbush (*V. corymbosum* interspecific hybrids) flower buds and young fruit.<sup>81</sup> In general, flower buds of southern highbush and highbush cultivars exhibit less cold damage than buds of rabbiteye cultivars at similar stages of development<sup>81</sup> (Table 2).

Terminal flower buds of blueberry are less hardy than median or basal buds,<sup>78,88,89</sup> and within a floral bud, apical florets are less hardy than median or basal florets.<sup>78</sup> This probably reflects differences in bud development due to bud location on the stem and floret location within the bud.

**Table 2 Cold injury to blueberry flowers and young fruit as a function of germplasm and developmental stage**

| Type              | Cultivars  | Frost damage (% dead ovaries) <sup>a</sup><br>by flower developmental stage <sup>b</sup> |    |     |                |
|-------------------|------------|--|----|-----|----------------|
|                   |            | 4  | 5  | 6   | 7              |
| Rabbiteye         | Brightwell | 0  | 38 | 100 | — <sup>c</sup> |
|                   | Tifblue    | 10   | 74 | —   | 89             |
|                   | Climax     | 30   | 73 | 100 | 99             |
| Southern highbush | Blueridge  | 0  | 26 | 63  | 100            |
|                   | Cape Fear  | 0  | 22 | 79  | 95             |
|                   | Georgiagem | 0  | 13 | 53  | 94             |
| Highbush          | Croatan    | —  | —  | 0   | 76             |

<sup>a</sup> Damage assessed after freezes of  $-2$  to  $-4^{\circ}\text{C}$ . <sup>b</sup> Stages of flower bud development: 4 = bud scales abscised, florets visible; 5 = individual florets separated, corollas unexpanded and closed; 6 = corollas expanded and open, stigma receptive, and anthers dehiscent; 7 = corollas abscised. (Data are from Spiers, *J. Amer. Soc. Hort. Sci.*, 103, 452, 1978. With permission.) <sup>c</sup> No data taken.

From Patten et al., *HortScience*, 26, 18, 1991. With permission.

The data suggest there is little difference in the temperature responses of *Vaccinium* compared to other temperate fruit crops. Within the genus, species and cultivars express some diversity in terms of temperature effects on A and the ability to develop cold hardiness; however, temperature ranges for overall growth and development are similar.

### 3. Chilling

Most fruit crops require a period of low temperature or “chilling” following the onset of dormancy in order for normal growth and development to occur. Insufficient chilling results in delayed and erratic budbreak and a reduction in the number of buds that break.<sup>90-97</sup> Field observations have indicated that insufficient chilling also decreases fruit set in blueberry<sup>98</sup>; however, more recent data suggest the reduction in set is probably due to a decrease in the number of floral buds that break, rather than to a direct effect of chilling on the physiology of fruit set.<sup>97</sup> Chilling accumulation may be influenced by environmental and/or cultural factors both before and during the chilling process.

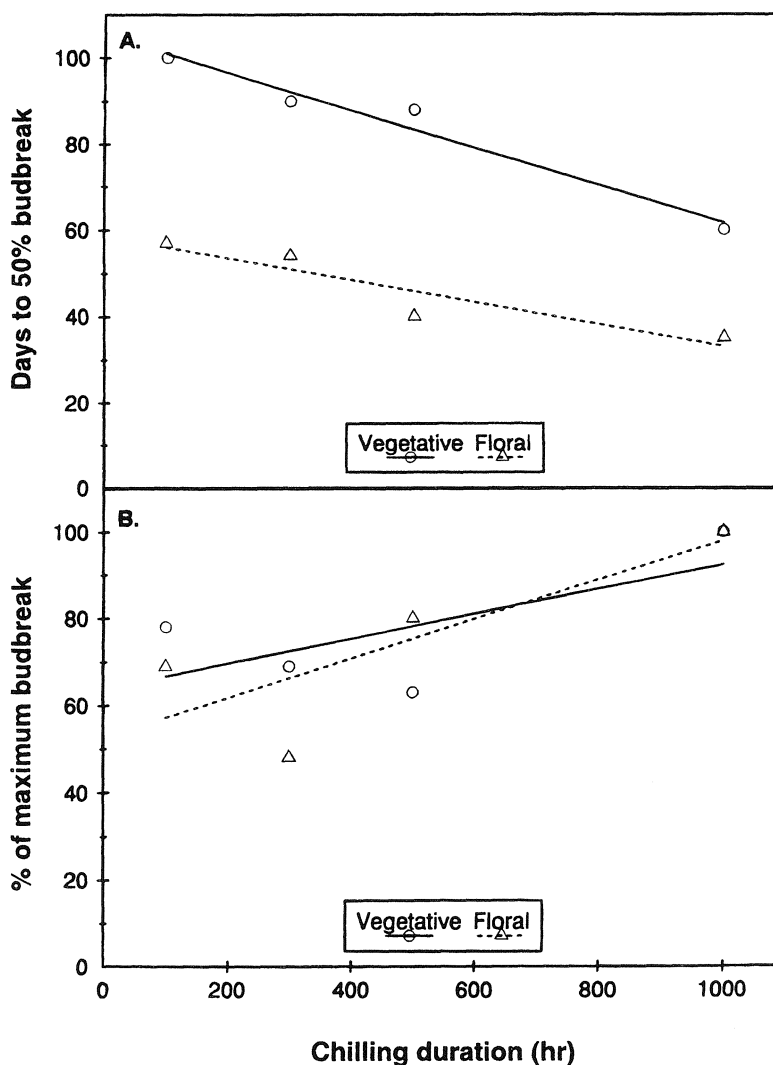
#### a. Factors Prior to Chilling Accumulation

There is no information on the effects of environmental or cultural factors prior to dormancy onset on chilling accumulation in *Vaccinium*. In general, young, vigorously growing blueberries are delayed in the onset of dormancy and grow into late fall and early winter. There is no evidence to suggest, however, that this directly affects the chilling requirement. Spiers and Draper<sup>92</sup> found that ‘Tifblue’ rabbiteye blueberries hand-defoliated prior to chilling temperatures broke vegetative buds faster the following spring than did non-defoliated plants. The presence of leaves on ‘Bonita’ rabbiteye blueberry plants during chilling inhibited both the rate and amount of vegetative and floral budbreak.<sup>99</sup> Interestingly, budbreak was also inhibited on defoliated canes when there were foliated canes present on the same plant. This suggests that the presence of foliated canes inhibits either chilling accumulation of buds on the defoliated canes or some process after chilling accumulation that leads to budbreak. Phloem girdling experiments on these plants indicated that the “inhibitor” was phloem mobile, and was apparently translocated from leaves to other parts of the plant. These findings are of particular relevance in areas such as the southeastern United States, where insufficient winter chilling of blueberry may occur.

Flower buds formed on spring growth flushes of rabbiteye blueberry usually bloom before flower buds formed on fall growth flushes.<sup>24</sup> In a study of several rabbiteye cultivars, Davies<sup>100</sup> reported that lateral flowers, which initiated later in the season than terminal flowers, also opened later in the spring. This suggests that flower buds formed later in the fall may begin chilling accumulation at a later date than do flower buds initiated earlier. Alternatively, buds initiated later in the season may be less developed upon entering dormancy and therefore require further development after the chilling requirement is met. There have been no studies in which precise bud developmental events have been correlated to chilling accumulation.

### b. Factors During Chilling Accumulation

A substantial amount of research has focused on the effects of different chilling regimes on vegetative and/or floral budbreak in *Vaccinium* species. Interpretation of temperature effects on chilling accumulation is complicated by the use of different models to estimate chill unit accumulation, as well as the use of constant vs. fluctuating temperatures, and growth chamber vs. outdoor experiments. In general, the rate and amount of floral and vegetative budbreak in blueberry and cranberry increases as constant chilling in the range of 0.6 to 15°C increases<sup>90-97,101,102</sup> (Figure 5). Blueberry floral buds generally break before or concomitant with vegetative buds (depending on chilling regime), implying that floral buds have a lower chilling requirement than vegetative buds.<sup>92,97</sup> Species vary with respect to temperature ranges and optima, as well as the number of chill units required. Chandler and Demoranville<sup>102</sup> reported that cranberries require 2500 hours below 7.2°C for completion of rest and normal budbreak. Although less chilling did result in some budbreak, the subsequent growth of those buds was abnormal. Eady and Eaton<sup>90</sup> found that the amount of budbreak in cranberry increased as chilling time increased from 650 to 2500 hours. Growth was normal at all chilling regimes, in contrast to findings by Chandler and Demoranville.<sup>102</sup> Rigby and Dana<sup>103</sup> concluded that 600 to 700 hours below 7.2°C was sufficient to



**Figure 5** Days to floral and vegetative budbreak (A) and percent floral and vegetative budbreak (B) in 'Woodard' rabbiteye blueberry after various chilling times at 7°C. From Darnell and Davies, *HortScience*, 25, 635, 1990. With permission.

**Table 3 Days to vegetative budbreak of rooted cuttings of 'Woodard' rabbiteye blueberry under continuous and interrupted chilling conditions**

| Chilling temp<br>(°C) | Days to budbreak          |      |      |        |        |                                  |        |        |      |        |
|-----------------------|---------------------------|------|------|--------|--------|----------------------------------|--------|--------|------|--------|
|                       | Hours continuous chilling |      |      |        |        | Hours chilling + 14 days at 30°C |        |        |      |        |
|                       | 250                       | 350  | 450  | 550    | 650    | 250                              | 350    | 450    | 550  | 650    |
| <b>Constant</b>       |                           |      |      |        |        |                                  |        |        |      |        |
| 0.6                   | 65.5ab <sup>a</sup>       | 46.0 | 54.5 | 48.0a  | 44.5a  | 39.0ab                           | 42.5a  | 30.3ab | 25.8 | 21.0ab |
| 3.3                   | 62.0ab                    | 56.3 | 50.0 | 42.0ab | 42.0a  | 52.0a                            | 30.3ab | 24.0ab | 23.5 | 17.8b  |
| 7.0                   | 61.3ab                    | 48.3 | 50.8 | 33.0c  | 31.0b  | 36.0                             | 20.0b  | 25.5ab | 21.8 | 14.0b  |
| 10.0                  | 63.0ab                    | 60.7 | 50.8 | 37.8bc | 38.6ab | 33.3ab                           | 14.8b  | 17.3b  | 21.0 | 18.8b  |
| 15.0                  | 64.7ab                    | 53.0 | 50.3 | 44.3ab | 40.3a  | 41.7ab                           | 22.5b  | 28.0ab | 22.5 | 19.5b  |
| <b>Diurnal</b>        |                           |      |      |        |        |                                  |        |        |      |        |
| 0/7                   | 69.5a                     | 56.0 | 52.8 | 39.3bc | 40.7a  | 48.7ab                           | 39.8a  | 34.7ab | 20.5 | 19.0b  |
| 7/15                  | 52.3b                     | 58.3 | 46.3 | 42.7ab | 41.5a  | 30.5b                            | 23.0b  | 24.5ab | 21.3 | 19.5b  |
| 7/30                  | 65.5ab                    | 58.0 | 54.4 | 34.5bc | 34.5bc | 41.7ab                           | 28.0ab | 35.0a  | 23.7 | 28.8a  |

<sup>a</sup> Mean separation within columns by Duncan's multiple range test,  $p = 0.05$  level.

From Gilreath and Buchanan, *J. Amer. Soc. Hort. Sci.*, 106, 625, 1981. With permission.

satisfy rest in cranberry when plants were given long days (i.e., 16 hours) subsequent to chilling. Increased chilling time was required if plants were subjected to short days (i.e., 8 hours) after chilling. They suggested that the failure of Chandler and Demoranville to demonstrate budbreak in cranberry at chilling times less than 2500 hours may have been due to inadequate day length duration subsequent to chilling.

Northern highbush blueberries have a greater chilling requirement (800–1000 hours below 7.2°C)<sup>96,101</sup> than do rabbiteye blueberries (300–600 hours below 7.2°C).<sup>92–94,97</sup> In general, the optimum chilling temperatures for rabbiteye blueberry floral and vegetative buds are higher than those for highbush buds.<sup>104</sup> Within cultivars, there is also variability in chilling requirement. Darrow<sup>101</sup> found that 'Rubel' highbush blueberry had the lowest chilling requirement (800 hours below 7.2°C) and 'Jersey' the highest chilling requirement (>1060 hours below 7.2°C) of those cultivars examined. Shine and Buchanan<sup>95</sup> reported that 'Woodard' and 'Aliceblue' rabbiteye blueberries had higher chilling temperature optima (7.2 and 11.0°C, respectively) and wider effective temperature ranges (–2.5 to 15.0°C and –2.5 to 13.8°C, respectively) than did 'Tifblue' (6.7°C optimum, –1.2 to 12.9°C range). Furthermore, 'Tifblue' had a longer chilling requirement than many other cultivars, even at optimum temperatures, requiring in excess of 500 hours below 7°C for any floral budbreak to occur.<sup>92,97</sup>

Temperature fluctuations during chilling influence the chilling response in fruit crops.<sup>105</sup> Eady and Eaton<sup>90,91</sup> found that alternating diurnal temperatures of 2/10°C were more effective than constant temperatures in promoting budbreak in cranberry. Norvell and Moore<sup>96</sup> chilled highbush blueberry cultivars at constant temperatures of 1, 6, or 12°C for 750 or 1000 hours, and found that only the 6°C/1000 hour chilling regime resulted in budbreak. However, budbreak was similar under chilling regimes of 1000 hours at constant 6°C or alternating temperatures of 6/1°C for 1000 hours, even though the latter treatment consisted of only 500 hours at the previously determined optimum chilling temperature of 6°C. Spiers<sup>93</sup> reported that 'Tifblue' rabbiteye blueberries exposed to day/night temperatures of 7/18°C or 7/23°C responded similarly in terms of vegetative budbreak to plants that received constant 7°C chilling treatments. Floral budbreak was delayed by the 7/23°C regime compared to the 7/18°C or the constant 7°C regime. This suggests that floral buds of blueberry may be more sensitive than vegetative buds to negation of chilling by high temperatures. Gilreath and Buchanan<sup>94</sup> found that budbreak in 'Woodard' rabbiteye blueberry under diurnal regimes of 0/7°C, 7/15°C, and 7/30°C was similar to that obtained under constant conditions (Table 3). Surprisingly, interruption of the chilling regimes midway through by 14 days at 30°C increased the rate of both floral and vegetative budbreak compared to non-interrupted constant or diurnal chilling. In this study, high temperatures (30°C) during chilling had either

no effect or a promoting effect on floral budbreak, in contrast to Spiers' findings, and may reflect cultivar and/or timing differences in response to warm temperatures.

### **c. Factors After Chilling Accumulation**

After chilling is completed, accumulation of heat units is required before floral and vegetative budbreak occurs in temperate fruit crops. The heat unit requirements for budbreak in *Vaccinium* have not been determined. Normal flower development in cranberry appears to depend on the accumulation of sufficient heat units after the completion of chilling. For 'Stevens', maximal normal flower development occurred when plants were exposed to 1000 to 1100 hours above 7.2°C after receiving between 1000 and 1500 chilling hours below 7.2°C.<sup>103</sup> Carlson and Hancock<sup>63</sup> reported low temperature thresholds for heat unit accumulation in several highbush blueberry cultivars ranging from -7 to 7°C, but the number of heat units required for budbreak was not determined. Mainland<sup>104</sup> observed that inadequate vegetative budbreak occurred in highbush and rabbiteye blueberry even when winter chilling was adequate. This was attributed to faster flower bud development compared to leaf bud development in response to warm temperatures after chilling. The more rapid flower bud development then inhibited vegetative budbreak. This suggests that flower buds may have a lower temperature threshold and/or a wider temperature range than vegetative buds for the accumulation of heat units needed for budbreak.

Species within *Vaccinium* encompass a wide array of chilling requirements, from the low chilling rabbiteye and southern highbush blueberry to the high chilling cranberry and northern highbush blueberry. Although much research has focused on the chilling responses of *Vaccinium*, the processes involved in chilling accumulation and budbreak remain unknown.

## **B. RUBUS (RED RASPBERRY)**

### **1. Growing Season Temperatures**

Temperature effects on shoot and root growth of red raspberry are similar to those of other temperate crops. Root growth has been correlated with soil temperature, with optimum growth occurring between 14 and 22°C.<sup>106</sup> Little root growth occurred at soil temperatures below 14°C, while no soil temperatures above 22°C were recorded during the experiment. Shoot elongation increased as air temperatures increased from 10 to 21°C.<sup>107</sup>

Temperature appears to have significant effects on flowering of both summer-bearing and fall-bearing (primocane-fruiting) red raspberries. In summer-bearing red raspberries, flower buds are initiated and differentiated starting in the fall, with development continuing until bloom the subsequent spring. In fall-bearing red raspberries, terminal flower buds are initiated and differentiated during the summer, giving rise to a crop in the fall. Axillary flower buds are initiated and differentiated similar to flower buds in summer-bearing cultivars. Flower bud initiation in 'Malling Promise', a summer-bearing cultivar, increased as temperatures decreased.<sup>107</sup> Initiation was inhibited by temperatures of 15.5°C under 9- or 16-hour photoperiods, and 12.8°C under 16-hour photoperiods. Under 9-hour photoperiods and 12.8°C, flower bud initiation occurred within 6 weeks. At 10°C, initiation occurred within 3 to 5 weeks under either photoperiod. Flower bud initiation occurred in the summer-bearing cultivar 'Latham' when grown at temperatures of 22 to 24°C, but development beyond initiation did not occur.<sup>108</sup> Similarly, initiation in axillary nodes of the fall-bearing cultivar 'Heritage' occurred at 22 to 24°C, but further differentiation required a cold treatment.<sup>108</sup> Thus, although flower bud initiation was temperature independent, differentiation was arrested at warm temperatures.

Low temperatures do not appear to be a requirement for initiation and differentiation of terminal flower buds in fall-bearing raspberries. 'Heritage' primocanes flowered terminally at 80 nodes of growth in plants grown at temperatures of 22°C or greater.<sup>109</sup> Exposure of developing primocanes to 25 days of 7°C at the 10–12 or 14–16 node stage shortened the vegetative growth stage and promoted earlier flowering, such that flowering occurred at 32 and 28 nodes, respectively. Thus, low temperatures were not a requirement for flower bud initiation and differentiation, but rather influenced the time or growth stage at which flowering occurred. Temperature had no influence on the number of nodes that formed flower buds. Lockshin and Elfving<sup>110</sup> exposed 'Heritage' plants to day/night temperatures of 29/24°C or 25.5/20°C under 16-hour photoperiods. Flowering occurred when plants reached the 24–25 node stage, regardless of temperature. The rate of cane elongation decreased under the lower temperatures, resulting in a 2-week delay in flowering compared to the higher temperature. Plants exposed to the lower temperatures also produced fewer flowering nodes per cane.

## 2. Cold Hardiness and Chilling

Dormancy induction in red raspberries, as in many other temperate woody plants, requires decreasing photoperiods and temperatures. More than 10 weeks of 10°C and 9-hour photoperiods were necessary for the development of full dormancy in the red raspberry, 'Malling Promise'.<sup>107</sup> The dormant condition was reversible if plants were returned to higher temperatures and longer photoperiods prior to 10 weeks. Induction also occurred at 10°C under 14-hour photoperiods, but full dormancy was much slower to develop.

With the induction of dormancy comes the ability to withstand low winter temperatures. As with blueberry and cranberry, the timing and extent of acclimation development in red raspberry varies from year-to-year. Under Minnesota conditions, the extent of cold acclimation in 'Latham' red raspberry was similar between two consecutive years, averaging -23°C.<sup>111</sup> However, in the first year, this degree of cold acclimation was reached by mid-November, while plants subjected to that temperature in the field the following year were severely injured, and did not attain full cold hardiness until mid-December. In both years, hardiness was attained rapidly, increasing from -10 to -23°C within 2 to 3 weeks. McCartney<sup>112</sup> found that canes of 'Latham' collected from a Minnesota field in January showed little damage when exposed to 8 hours at -29°C, and, in fact, withstood temperatures of -45°C, exhibiting some injury and bud death, but overall cane survival.

Cold acclimation in red raspberry may be rapidly lost. Brierley et al.<sup>113</sup> reported that if acclimated canes were exposed to 4°C for 4 hours on two consecutive days, severe injury resulted when canes were exposed to subsequent low temperatures. They concluded that daily exposure to temperatures less than 4°C was necessary to avoid cold injury in the field. In a subsequent study on dehardening, Brierley and Landon<sup>114</sup> found that dehardened red raspberry canes can reharden if the buds do not "become active". Canes that had been exposed to a low of -20°C in the field were collected, and subjected to different dehardening/rehardening regimes. Canes exposed to sub-freezing temperatures for 16 hours immediately after collection showed moderate injury at -34°C and severe injury at -40°C. Canes that had been dehardened for 5 days at 3°C showed severe injury when exposed to 1°C for 24 hours and were killed when exposed to -18°C for 24 hours. Canes rehardened by exposing them to 2°C for 8 hours, followed by -9°C for 3 to 10 days showed only slight injury when exposed to -18°C for 24 hours and severe injury when exposed to -23°C for 24 hours. Thus, canes were able to recover some cold acclimation after a short period of dehardening.

Dormancy release in red raspberry required a minimum of 670 hours at 3°C, and budbreak occurred more rapidly as chilling time was increased to 1300 hours.<sup>107</sup> In general, 800–1600 hours below 7°C is necessary to satisfy the rest requirement in raspberry.<sup>115</sup> There is no information on the heat unit requirement for budbreak in red raspberry.

In general, temperature responses in red raspberry appear to be better documented than light responses, particularly temperature effects on flower bud initiation and differentiation. However, there are few data available on dormancy and chilling requirements of raspberry, and no data available on heat unit requirements for growth and development.

## IV. WATER STRESS AND IRRIGATION

### A. VACCINIUM

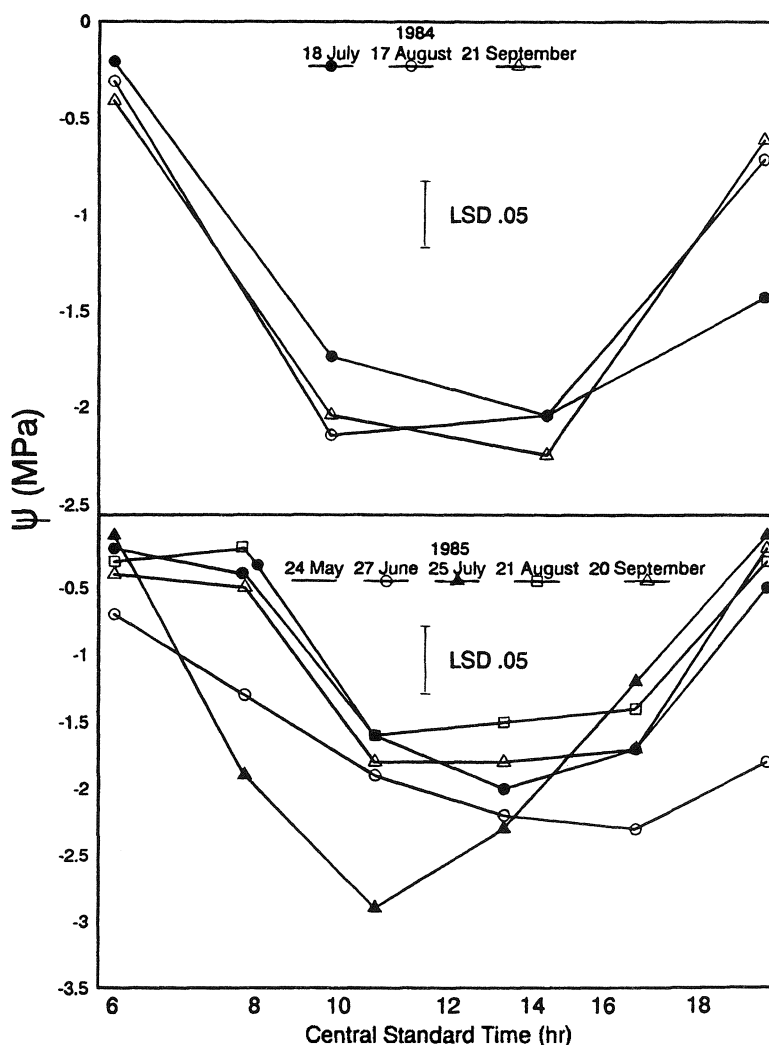
Water relations of *Vaccinium* species vary widely due to the wide range of ecological diversity found in the genus.<sup>8</sup> The cultivated species, *V. angustifolium*, *V. corymbosum*, *V. ashei*, and *V. macrocarpon* also differ significantly in their water relations, in particular their responses to drought and flooding stresses. In general, however, *Vaccinium* species are moderately drought<sup>8</sup> and flooding tolerant<sup>116</sup> based on physiological and anatomical factors. Diurnal and seasonal variations in leaf water potential ( $\Psi$ ),  $g_s$ , water use efficiency (WUE), relative water content (RWC), transpiration (E), and A will be discussed as they relate to drought and flooding tolerance.

### 1. Diurnal and Seasonal Water Relations

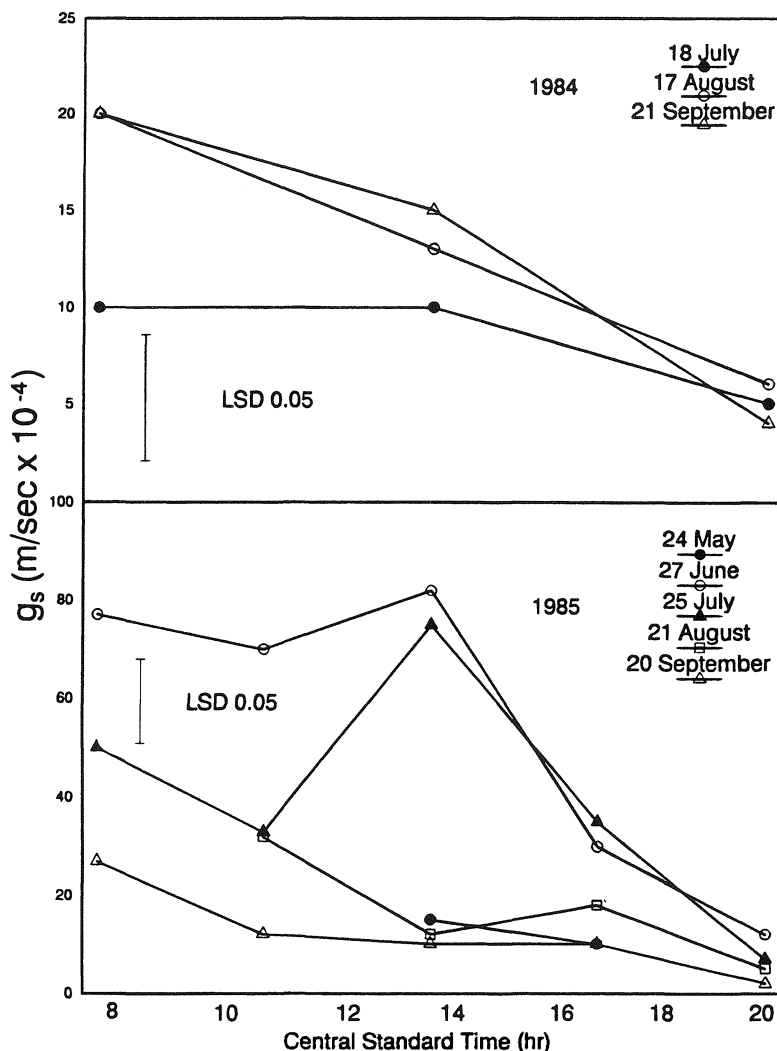
Diurnal changes in  $\Psi$ ,  $g_s$ , and E are closely related and thus it is difficult to isolate one factor from another. Nevertheless, diurnal changes in these factors follow a pattern fairly typical of many other plant species. Byers et al.<sup>117</sup> measured changes in  $\Psi$  (Figure 6) and  $g_s$  (Figure 7) in 2-year-old 'Bluecrop' highbush blueberries in the field. They found a typical late morning decrease in leaf  $\Psi$  with a minimum at 1000–1030 hour and a minimum value of -2.79 MPa. The  $\Psi$  remained low until about 1600 hours

and then became less negative, returning to predawn values of  $< -0.05$  MPa by 2000 hours. The pattern varied for different times of the year due to differing soil moisture and environmental conditions, viz., variations in vapor pressure deficit (VPD). The minimum  $\Psi$  attained was lower than that observed for mature rabbiteye blueberries in the field ( $-1.5$  MPa<sup>118</sup>) and young rabbiteye plants in the greenhouse ( $-2.30$  MPa<sup>119</sup>). The minimum is lower than that which causes damage to most herbaceous plants, but is less negative than found in many tree crops.

Diurnal patterns for  $g_s$  are associated with leaf  $\Psi$ , but as expected, are much more variable because factors other than  $\Psi$  also regulate  $g_s$ . Davies and Albrigo<sup>8</sup> observed a gradual decrease in  $g_s$  by mid-day for 'Bluegem' rabbiteye blueberry leaves, with a gradual increase by 1600 hours. Stomatal conductances ranged from about  $32\text{--}66\text{ mmol m}^{-2}\text{s}^{-1}$ , which are quite low; young, fully expanded leaves generally had lower  $g_s$  than old, mature ones. Diurnal patterns of  $g_s$  for rabbiteye leaves were similar to those observed by Byers et al.<sup>117</sup> for highbush leaves at some times of the year, but not at others (Figure 7). Moreover,  $g_s$  patterns were not necessarily correlated with  $\Psi$ <sup>117</sup> (compare Figures 6 and 7). During times of minimum  $\Psi$ ,  $g_s$  was often at a maximum. However, partial stomatal closure usually occurred in the afternoon after minimum  $\Psi$  had been reached, probably serving as a mechanism to reduce water loss and maintain cell turgor. This late afternoon reduction in  $g_s$  may also result from



**Figure 6** Diurnal patterns in young highbush blueberry leaf water potential ( $\Psi$ ) for various dates in 1984 and 1985. From Byers et al., *HortScience*, 23, 870, 1988. With permission.



**Figure 7** Diurnal patterns in young highbush blueberry leaf stomatal conductance ( $g_s$ ) for various dates in 1984 and 1985. From Byers et al., *HortScience*, 23, 870, 1988. With permission.

increases in internal  $\text{CO}_2$  as well as decreases in cell turgor. On some days (18 July),  $g_s$  remained consistently low with no characteristic diurnal pattern for the entire day, possibly due to high VPD. Similarly, Davies and Johnson<sup>119</sup> observed only a moderate correlation ( $r^2 = 0.42$ ) between  $\Psi$  and  $g_s$  for rabbiteye blueberry growing in the greenhouse, although they did determine that the critical  $\Psi$  for stomatal closure occurred at about  $-2.22$  MPa. In contrast, Byers et al.<sup>117</sup> did not observe complete stomatal closure even at  $-2.79$  MPa for 'Bluecrop' plants in the field. This observation probably reflects differences in growing conditions prior to imposition of water stress. The 'Bluecrop' plants had been growing in the field while the rabbiteye plants were grown in less stressful, lower VPD greenhouse conditions.

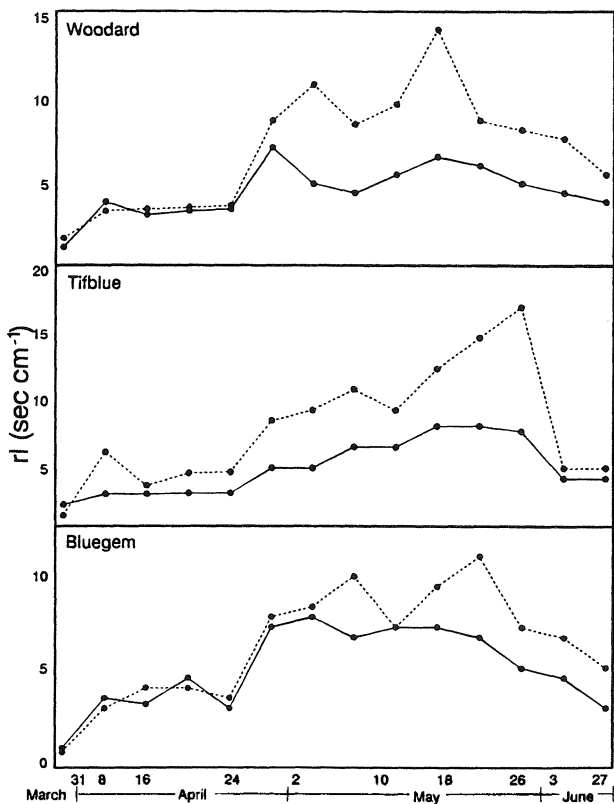
Andersen et al.<sup>118</sup> measured seasonal changes in  $\Psi$  for mature, 5-year-old rabbiteye blueberry bushes in the field. Mid-day stem  $\Psi$  varied from about  $-0.5$  to  $-1.5$  MPa. The smaller range of values observed here compared to previous studies probably resulted from the measurement of stem rather than leaf  $\Psi$ , which due to their greater mass would show less fluctuations than in leaves. Nevertheless, a distinct seasonal variation in  $\Psi$  occurred, again related to differences in VPD and soil moisture content.

Andersen et al.<sup>118</sup> also measured large seasonal variations in  $g_s$  (although they actually measured leaf resistance) (Figure 8). Estimated values for  $g_s$ , calculated from midday leaf resistance, ranged from 400

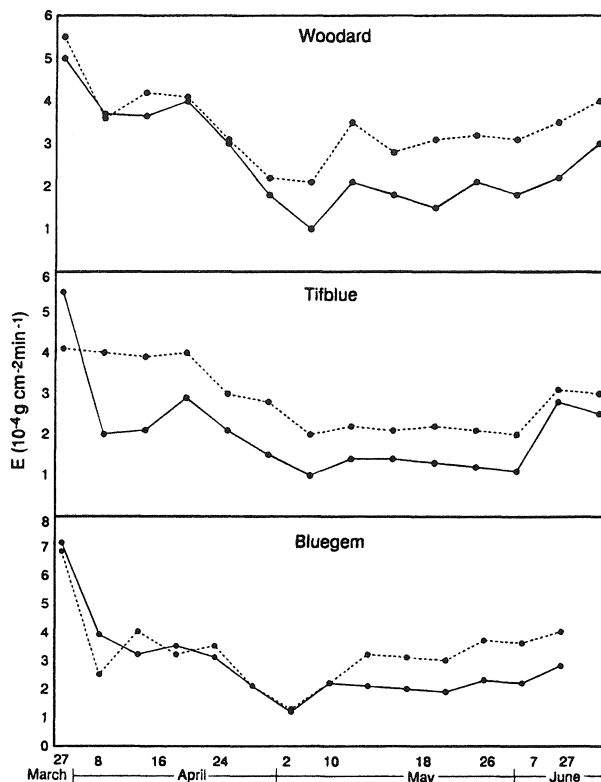
$\text{mmol m}^{-2}\text{s}^{-1}$  in expanded, young leaves in April (irrigated) to as low as  $20 \text{ mmol m}^{-2}\text{s}^{-1}$  in nonirrigated mature leaves later in the season (refer to next section on irrigation). There were also differences among cultivars, with 'Tifblue' generally having lower  $g_s$  than 'Woodard' and 'Bluegem'. In this study,  $g_s$  of young, expanded leaves was considerably greater than that of mature leaves, which differs from the previous findings of Davies and Albrigo.<sup>8</sup> However, Davies and Albrigo<sup>8</sup> compared  $g_s$  of fully expanded leaves during midseason, while Andersen et al.<sup>118</sup> compared young, expanded leaves which developed during the spring to mature leaves—a factor which may account for the discrepancies between the two studies.

Leaf E also varied seasonally as a function of  $g_s$  and most importantly VPD.<sup>118</sup> Midday E was greatest for rabbiteye blueberry leaves early in the season (April) (Figure 9) primarily due to high  $g_s$  in young leaves, even though VPD was lower in April than in June. Transpiration then remained relatively constant through the remainder of the season. This likely resulted from rodlet wax accumulation over the stomatal pore which stabilized water fluxes from the leaves. Transpiration was generally lower for all three cultivars for nonirrigated compared with irrigated bushes. Differences between the two irrigation treatments, however, did not occur until early May for 'Bluegem' and 'Woodard', but were apparent in April for 'Tifblue'. This difference in E under the same environmental conditions is related to differences in  $g_s$  among cultivars and reflects the greater water stress in 'Tifblue' compared to the other two cultivars.

In a controlled laboratory study, Moon et al.<sup>13</sup> compared E of 'Jersey' and 'Bluecrop' highbush blueberry to that of *V. darrowi*. *V. darrowi* was chosen because field observations suggest it is more drought tolerant than highbush cultivars. Transpiration of 'Jersey' ranged from 1.95–3.45, 'Bluecrop' from 2.25–3.75 and *V. darrowi* from 1.38–2.68  $\text{mmol m}^{-2}\text{s}^{-1}$  at varying controlled VPD levels, suggesting that *V. darrowi* has inherently lower E than the other cultivars. These values are similar to the range of E values for rabbiteye and highbush blueberries (0.6–4.2  $\text{mmol m}^{-2}\text{s}^{-1}$ ) under greenhouse conditions.<sup>12</sup>



**Figure 8** Midday leaf diffusive resistance ( $r_l$ ) for irrigated and nonirrigated plants of 3 rabbiteye blueberry cultivars, Gainesville, Florida, 1977. Dashed line = irrigated, solid line = not irrigated. Vertical bars = SD. From Andersen et al., *J. Amer. Soc. Hort. Sci.*, 104, 731, 1979. With permission.



**Figure 9** Midday maximum calculated leaf transpiration (E) for irrigated (---) and nonirrigated (—) plants of 3 rabbiteye blueberry cultivars, Gainesville, Florida, 1977. From Andersen et al., *J. Amer. Soc. Hort. Sci.*, 104, 731, 1979. With permission.

Andersen,<sup>120</sup> however, measured E as high as  $6.2 \text{ mmol m}^{-2} \text{ s}^{-1}$  for rabbiteye bushes in the field in Florida during the summer. Leaf temperature was  $36.9^\circ\text{C}$  and VPD reached as high as 5.5 kPa, which probably accounted for the high E observed in this study compared with laboratory or greenhouse studies.

Water use efficiency (WUE) is the ratio of  $\text{mmol CO}_2$  fixed: $\text{mmol}$  of water transpired. It is the reciprocal of E ratio ( $\text{g water transpired}:\text{g CO}_2$  fixed). Blueberry plants have moderate to high WUE depending on species or cultivar and environmental conditions during and before measurements. *V. darrowi* had a greater WUE and thus was more drought tolerant than the highbush cultivars, 'Jersey' and 'Bluecrop', averaging 6.5, 4.7, and 4.8, respectively, at 1 kPa VPD.<sup>13</sup> As VPD was increased to 3 kPa, however, WUE decreased by about 45% for 'Bluecrop' and 'Jersey' and 57% for *V. darrowi*. Teramura et al.<sup>14</sup> measured very low transpiration ratio (108) and high WUE (9.2) for detached cuttings of rabbiteye blueberry. Because detached shoots were used, however, these values are probably unrealistically high. Davies and Johnson<sup>119</sup> estimated whole plant WUE of 4.5 for 'Bluegem' rabbiteye blueberry in the greenhouse. This value is more consistent with WUE reported by Moon et al.<sup>13</sup> of 4.7 at a VPD of 1 kPa; WUE decreased significantly, however, to 2.6 at a VPD of 3 kPa. A decrease in WUE is typical under water stress conditions, as the photosynthetic capacity of the leaf decreases. Consequently, field calculated WUE was as low as 0.50 for 'Bluegem' bushes in Florida.<sup>120</sup> This very low value was due to the extremely high VPD (5.5 kPa) experienced in Florida during the summer. Conversely, Cameron et al.<sup>121</sup> found that WUE was relatively constant, ranging from 2.7–4.1 for water stressed and nonstressed 'Bluecrop' and 'Jersey' highbush blueberries growing in containers. These plants, however, were exposed to two short-term water stress cycles rather than long-term steady water stress, which could account for such differences.

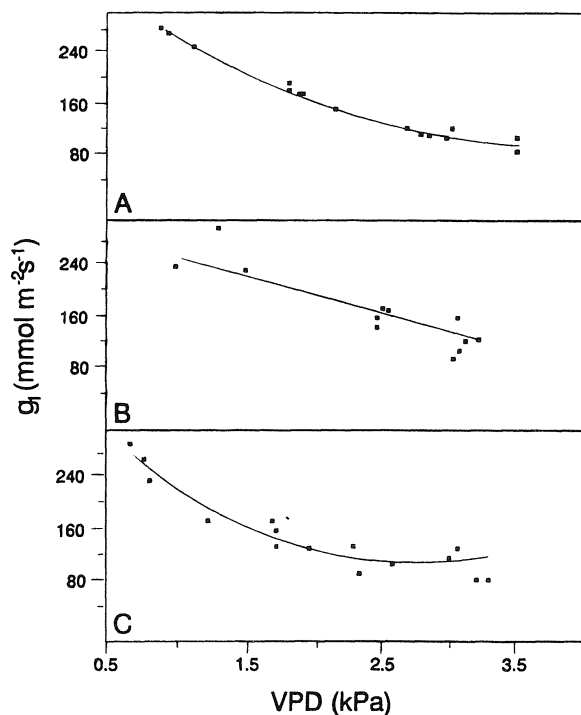
## 2. Factors Affecting Stomatal Conductance

Stomatal conductance is influenced by anatomical characteristics of stomata and possibly stomatal density. Limited information is available on stomatal density of *Vaccinium* species. 'Bluecrop' sun

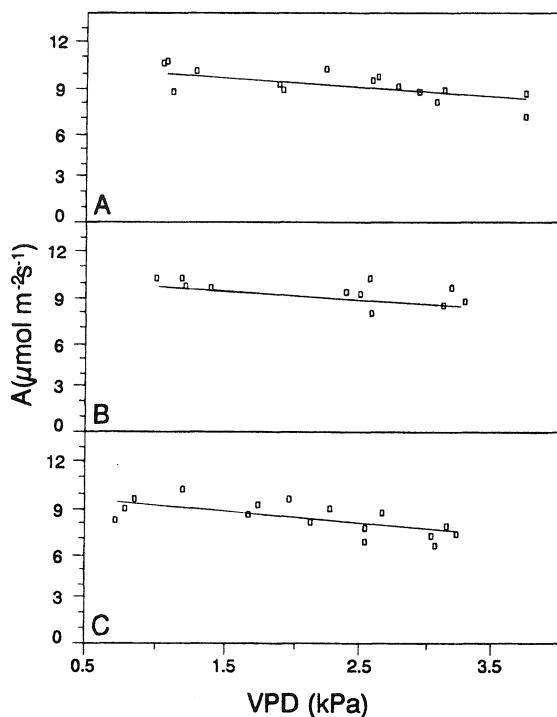
leaves averaged 553 stomata/mm<sup>2</sup>. In contrast, stomatal density of the whortleberry (*V. myrtillus*) averaged 990 stomata/mm<sup>2</sup> for shade leaves and 177/mm<sup>2</sup> for sun leaves,<sup>122</sup> clearly illustrating the effect of light on stomatal density. Janke<sup>122</sup> proposed that the increased stomatal density of sun leaves provided additional transpirational cooling compared to shade leaves. Stomata of rabbiteye blueberry have a large antechamber and are partially obscured by wax rodlets within and over the antechamber.<sup>118,123</sup> This anatomical adaptation decreases  $g_s$  and reduces  $E$  and may be an adaptive advantage during times of high evaporative demand for reducing plant water stress.

Environmental factors also affect  $g_s$ . Although light is necessary for stomatal opening, it is usually not a limiting factor since stomata open at relatively low light levels of about 50  $\mu\text{mol m}^{-2}\text{s}^{-1}$ .<sup>15</sup> Most important to stomatal response is VPD. Davies and Flore<sup>15</sup> exposed 'Bluecrop' highbush blueberry plants to VPD of 1 to 3 kPa under controlled laboratory conditions with light and temperature controlled at optimum levels. They observed a significant linear decrease in  $g_s$  with increasing VPD, but found  $A$  to be less affected by VPD than  $g_s$ . Similarly, Moon et al.<sup>13</sup> measured the effect of varying VPD on leaf conductance ( $g_l$ ) and  $A$  for 'Jersey' and 'Bluecrop' highbush blueberries and *V. darrowi*. They also observed a linear decrease in  $g_l$  with increasing VPD (Figure 10), again finding less of an effect of VPD on  $A$  (Figure 11). When VPD was increased from 1 to 3 kPa,  $g_l$  of highbush and *V. darrowi* decreased by about 50%, while  $A$  decreased only 10–20%. By comparison,  $E$ , which is strongly influenced by VPD, increased by 80–94% (1.5 to 3.4  $\text{mmol m}^{-2}\text{s}^{-1}$  for 'Jersey') over the same VPD range. Studies on *V. myrtillus* from the wild also suggest a strong dependency of  $g_s$  on VPD.<sup>123</sup>

A wide range of  $g_s$  values, probably reflecting both species and environmental differences, have been reported for *Vaccinium* species. Under laboratory conditions, maximum  $g_s$  were 323 for 'Bluecrop', 236 for 'Jersey', and 168  $\text{mmol m}^{-2}\text{s}^{-1}$  for *V. darrowi*.<sup>13</sup> Davies and Flore<sup>12</sup> reported maximum values of 291 for 'Bluecrop' highbush blueberry but only 219  $\text{mmol m}^{-2}\text{s}^{-1}$  for 'Woodard' rabbiteye blueberry, and in general,  $g_s$  for 'Woodard' was less than that of 'Bluecrop' under similar greenhouse conditions. However, Andersen et al.<sup>118</sup> measured  $g_s$  as low as 20–132  $\text{mmol m}^{-2}\text{s}^{-1}$  for rabbiteye cultivars in the field. In a subsequent study Andersen<sup>120</sup> measured  $g_s$  of 130  $\text{mmol m}^{-2}\text{s}^{-1}$  for 'Bluegem' leaves in the



**Figure 10** Effects of VPD on leaf conductance ( $g_l$ ) in 'Bluecrop' (A), 'Jersey' (B), and *Vaccinium darrowi* (C). Measurements were made at saturating PPF (1000  $\mu\text{mol s}^{-1}\text{m}^{-2}$ ) and at 26°C for 'Bluecrop' and 'Jersey' and at 30° for *V. darrowi*. Each value is the mean of 20 determinations. Different symbols represent different plants. From Moon et al., *J. Amer. Soc. Hort. Sci.*, 112, 134, 1987. With permission.



**Figure 11** Effects of vapor pressure deficit (VPD) on  $A$  in 'Bluecrop' (A), 'Jersey' (B), and *Vaccinium darrowi* (C). Measurements were made at saturating PPF ( $1000 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ ) and at  $26^\circ\text{C}$  for 'Bluecrop' and 'Jersey' and at  $30^\circ$  for *V. darrowi*. Each value is the mean of 20 determinations. Different symbols represent different plants. From Moon et al., *J. Amer. Soc. Hort. Sci.*, 112, 134, 1987. With permission.

field. The lower  $g_s$  values for rabbiteye vs. highbush cultivars again probably reflects the wax rodlet accumulation in and over the stomata and also the greater VPD usually encountered for rabbiteye plants growing in the southern rather than the northeastern United States.

### 3. Drought Tolerance

#### a. Physiological Factors

Physiological evidence strongly suggests that while *Vaccinium* species are clearly mesophytes, they are moderately drought tolerant, although some variability exists among species.<sup>8</sup> Water use efficiency<sup>125</sup> and  $g_s$ <sup>126</sup> values for *Vaccinium* are within normal ranges for mesophytes. The change in leaf RWC per change in  $\Psi$  is an indicator of relative drought tolerance.<sup>127</sup> For example, drought-sensitive plants such as tomato show a  $\Delta \text{RWC}/\Delta \psi$  of 25%, while xerophytic plants such as *Acacia harpophylla* show a change of only 2.7%. In comparison, *V. ashei* had a  $\Delta \text{RWC}/\Delta \psi$  of about 6.4%<sup>119</sup> and *V. myrtillus* about 10.5%,<sup>8,128</sup> again suggesting an intermediate position. Furthermore, critical leaf  $\Psi$  for stomatal closure of  $-2.2 \text{ MPa}$  is also intermediate to that observed for herbaceous and xerophytic species.<sup>119</sup>

#### b. Morphological and Anatomical Factors

Drought tolerance in *Vaccinium* species includes morphological and anatomical adaptations.<sup>8</sup> Morphological adaptations are found in the prostrate growth habit of *V. darrowi* and extensive root systems of *V. darrowi* and *V. arboreum* in the wild.<sup>8</sup> In contrast, highbush<sup>129</sup> and rabbiteye<sup>130</sup> blueberry plants are typically shallow-rooted with most feeder roots located in the upper 30 cm of the soil profile. However, maximum rooting depth of highbush plants reached 81 cm and lowbush blueberries produced taproots to 90-cm depths.<sup>131</sup> Some species such as *V. darrowi* also have leaves with a small surface area which reduces whole-plant  $E$ .<sup>8</sup> Development of a waxy cuticle on the leaf, which reduces cuticular  $E$ , is also an important anatomical adaptation to drought. Freeman et al.<sup>123</sup> studied seasonal changes in leaf epicuticular waxes for 'Bluegem' rabbiteye blueberries. They observed a rapid increase in  $\beta$ -diketones during early leaf expansion through mid-May, when levels decreased. Moderate levels of triterpenoids

and primary alcohols and low levels of fatty acids and paraffin were also present. By October,  $\beta$ -diketones had decreased with concomitant increases in triterpenoids and primary alcohols. Rodlet wax, which covers and occludes stomata, varied seasonally and the concentration was inversely correlated with leaf E. In contrast, *V. ellioti*, which is also moderately drought tolerant, does not have extensive rodlet wax covering of leaves, but instead produces trichomes. These may serve to decrease leaf boundary layer conductance and improve drought tolerance.<sup>132</sup> Certainly, drought tolerant *Vaccinium* species, such as *V. darrowi*, have several anatomical and physiological drought tolerance mechanisms.

### c. Species Variations in Drought Tolerance

Several studies have been conducted on wild *Vaccinium* species involving species-related differences in drought tolerance. Hygen<sup>133</sup> measured E of cowberry (*V. vitis-idaea*), a xerophyte, whortleberry (*V. myrtillus* L.), a mesophyte, and bog bilberry (*V. uliginosum* L.), a hydrophyte. *V. vitis-idaea* L. had lower E with open stomata than the other species and also more rapid stomatal closure. It also had much higher stomatal than cuticular E. These data imply that development of a less permeable cuticle and improved stomatal control of E are drought tolerance mechanisms found in some *Vaccinium* species. In a similar study, Bannister<sup>134</sup> measured diurnal fluctuations in E and RWC of heather (*Calluna vulgaris* [L.] Hull), bog heather (*Erica tetralix* L.), and Scotch heather (*E. cinerea* L.). The *Erica* species had lower E and more rapid stomatal closure than *Calluna*, factors which improve drought tolerance. However, the *Erica* species were also less ecologically competitive in dry climates because they accumulated less assimilates than *Calluna* due to rapid stomatal closure. Therefore, rapid stomatal closure, while improving drought tolerance within a region, may not be adaptive because it limits the ecological range of a species.

Most of the above-mentioned wild species have not been used to incorporate drought tolerance into cultivated *Vaccinium* species, however, several related species have been and are currently being used, in breeding programs, including *V. darrowi*, *V. tenellum*, *V. myrsinites*, and *V. ellioti*.<sup>3</sup> Erb et al.<sup>135</sup> screened several *Vaccinium* species for potential drought tolerance by evaluating shoot growth and biomass accumulation of seedlings under drought conditions. They found a wide range of inherent drought tolerance with *V. darrowi*, *V. ellioti*, and *V. ashei* being superior to *V. corymbosum* and *V. vacillans* (*pallidum*), all of which were superior to *V. myrtilloides* (Table 4). The percentage of biomass partitioned into roots did not appear to influence drought tolerance, as measured by shoot growth. The species having the greatest drought tolerance were native to the southern United States and evolved under high temperature and VPD conditions. The highbush blueberry, *V. corymbosum*, is native to the northern United States and southern Canada and *V. myrtilloides* is a lowbush species native to southern Canada.<sup>1</sup> Therefore, these species evolved under less extreme temperature and VPD conditions. The same researchers tested several *Vaccinium* hybrids also and found a range of potential drought tolerance with future possibilities as commercial cultivars.

## 4. Irrigation

Irrigation of blueberries and cranberries has not been a widely used practice in the past. Often growers believed there was sufficient rainfall to produce an adequate crop or the topography was too uneven

**Table 4 Mean shoot damage ratings and fraction of total biomass partitioned as roots for blueberry populations from open-pollinated species screened for drought resistance**

| Species                                    | n  | Shoot rating<br>mean <sup>a,b</sup> | Mean root biomass fraction <sup>a</sup> |
|--|----|-------------------------------------|---|
| <i>Vaccinium darrowi</i>                   | 54 | 7.3a                                | 0.13d                                   |
| <i>V. ellioti</i>                          | 54 | 7.2a                                | 0.22c                                   |
| <i>V. ashei</i>                            | 54 | 6.8a                                | 0.30b                                   |
| <i>V. corymbosum</i>                       | 54 | 4.3b                                | 0.39a                                   |
| <i>V. vacillans</i><br>( <i>pallidum</i> ) | 54 | 4.0b                                | 0.29b                                   |
| <i>V. myrtilloides</i>                     | 44 | 2.7c                                | 0.22c                                   |

<sup>a</sup> Mean separation by Duncan's multiple range test, 5% level. <sup>b</sup> Shoot damage ratings ranged from 1 = dead stems to 9 = a healthy, undamaged shoot.

From Erb et al., *J. Am. Soc. Hort. Sci.*, 113, 599, 1988. With permission.

to establish reliable irrigation systems, as is the case in some lowbush blueberry areas. Research studies suggest, however, that in many instances irrigation improves yields of blueberries and many new plantings are irrigated. Water table regulation has always been important in cranberry culture for irrigation, pest control, frost protection, and harvesting.

#### *a. Blueberries*

A limited amount of research data is available on irrigation of lowbush blueberries. Struchtemeyer<sup>136</sup> compared yields of irrigated and nonirrigated lowbush blueberries in Maine. Irrigation at 50–70% of available soil moisture produced a 2.6-fold yield increase by improving fruit size and number. Irrigation also produced more consistent cropping. Trevett<sup>137</sup> found that irrigation increased stem height after burning of lowbush blueberries; however, it had no influence on fruit bud number. Yield data were not presented. An elaborate greenhouse and field study was conducted by Benoit et al.<sup>138</sup> in Maine. Soil moisture tension was controlled at 2, 6, 10, or 50 kPa using tensiometers with 2 kPa being field capacity. More flowers/plant were produced in the greenhouse at 2 and 6 kPa than at the other irrigation levels. Similarly, irrigation at 2 kPa increased numbers of flowers and fruit even in the first year of the burn cycle. The improved yields resulted from increased fruit number, not weight. Moreover, irrigation also improved flower bud number in the following year.

Irrigation of highbush blueberry bushes has been used sporadically in most long-established plantings but is becoming more common in new plantings. Fry and Savage<sup>139</sup> conducted a study primarily to evaluate the effects of sawdust mulch on young blueberry plant growth. They also used irrigation as one of the treatments, finding no effect of irrigation on plant growth. No details were given on irrigation levels, however. Byers and Moore<sup>140</sup> conducted a 1-year study in Arkansas using 3-year-old ‘Bluecrop’ plants growing in barrels. They scheduled irrigation based on pan evaporation using crop coefficients of 1.0, 0.75, and 0.50 and also varying irrigation with developmental stage of the bush. They achieved a considerable reduction in water use with this method relative to recommended levels of 3.8 l/day; nevertheless, there were no differences in yields, fruit weight, quality, or vegetative growth related to irrigation levels. This lack of effect possibly resulted from the large plant-to-plant variability among bushes.

Similar irrigation studies were conducted in Missouri over a 3-year period using ‘Blueray’ bushes.<sup>141</sup> Irrigation was scheduled using tensiometers placed at 15- or 30-cm depths and included soil tensions of 10, 35, or 65 kPa vs. no irrigation. Results varied with location and season, sometimes with no effect of irrigation being observed due to high rainfall and the high water holding capacity of heavy, poorly drained soils. However, in general, irrigation at soil tensions less than 65 kPa increased bush height and cane diameter compared to nonirrigated plants. Leaf area,  $\Psi$ , and number of new canes, however, were not affected by irrigation levels. Dale et al.<sup>142</sup> working in Ontario, Canada varied irrigation levels from 18 to 4.5 l/day for 6 years after planting. They found that the highest irrigation level gave the greatest cumulative yield for both ‘Blueray’ and ‘Collins’ plants; bush height was also greatest for ‘Collins’ but irrigation levels did not affect growth of ‘Blueray’. Unfortunately, no adjustments in irrigation rates were made for bush size and soil moisture levels were not reported. It is apparent from these two studies that irrigation effectiveness is influenced by environmental and edaphic conditions and cultivar. Therefore, although irrigation is generally effective, local conditions also must be considered in deciding whether irrigation is economically warranted.

With the advent of low volume (trickle) irrigation there has been some concern that only a relatively small area of the blueberry root system would receive water. This prompted Abbott and Gough<sup>143</sup> to conduct a split-root experiment using 2-year-old ‘Bluecrop’ plants. One side of the root system received no water, while the other received 300 ml/day. There was little if any lateral movement of water within the plant as evidenced by significantly less dry weight production and no flower bud production of the dry side. These findings support the need for adequate coverage of the root zone during irrigation, although the percentage of the root area to be covered has not been established.

Irrigation is more widely used for rabbiteye compared with other blueberry species probably because many new plantings have been established recently in the south where daytime VPDs are extreme, sometimes reaching 5.5 kPa.<sup>144</sup> Therefore, the need for irrigation has been more apparent than in cooler, northern regions. Buchanan et al.<sup>145</sup> compared yields of 5-year-old ‘Tifblue’, ‘Bluegem’, and ‘Woodard’ rabbiteye blueberry bushes in Florida using 1, 2, or 3 drippers (emitters, 4 l/hour) per bush. Irrigation increased soil moisture levels from 12% in nonirrigated plants to 23% for irrigated treatments. All irrigation levels generally increased yields by increasing berry weight, not berry number/bush. Yield

increases of 20–25% occurred in seasons having a dry spring but no differences occurred during seasons with a wet spring, again illustrating the importance of environmental factors in success of irrigation. Similarly, Andersen et al.,<sup>146</sup> working in the same planting, found drip irrigation increased yields and berry weight, but decreased berry soluble solids by 24%. ‘Tifblue’ and ‘Bluegem’ yields were increased more than those of ‘Woodard’, possibly because ‘Woodard’ bushes were under less water stress than the other cultivars (see Figures 8 and 9).

Several studies have been conducted on irrigation of young (1 to 3-year-old) rabbiteye blueberry bushes. Spiers<sup>147</sup> found that irrigation increased survival and doubled dry weight for ‘Tifblue’ plants for the first 2 years after planting in Mississippi. He also observed that incorporating peat moss in the planting hole, which improved soil water holding capacity, increased bush survival and growth. In a subsequent study, Spiers<sup>148</sup> found that peat moss incorporation, plus irrigation and mulch increased root dry weight over nontreated bushes. Patten et al.<sup>149</sup> compared trickle with microsprinkler irrigation (40 or 360° patterns) on 3-year-old ‘Climax’ bushes in Texas, finding that the microsprinklers, particularly when combined with sawdust mulch, increased radial spread of roots from the main canes. Subsequently, Patten et al.<sup>150</sup> compared various trickle, microsprinkler, sod and mulch combinations on development of ‘Tifblue’ and ‘Delite’ rabbiteye blueberries for 3 years in the field (Table 5). In general, the 360° microsprinklers provided the greatest growth (canopy volume) and yields, with the 40° pattern intermediate but superior to the two drip irrigation treatments. Berry weight, however, was inversely correlated with yield, with the 360° treatment having the lowest weight, indicating that irrigation increased yield by increasing berry number. Fruit acidity was not affected by irrigation treatment. These data support previous studies by Abbott and Gough<sup>143</sup> on the importance of sufficient root coverage when irrigating blueberries, a factor that is even more important as bushes increase in size. Smajstrla et al.<sup>151</sup> and Haman et al.<sup>152</sup> studied effects of drip (trickle) irrigation on establishment of 2-year-old ‘Climax’, ‘Beckyblue’, and ‘Sharpblue’ bushes in Florida. They found that maintaining soil moisture tension at 10 kPa at 8- and 22-cm depths produced the greatest growth during the first year after planting.

In most blueberry growing regions, water quality, particularly total dissolved solids levels, is not a limiting factor in production. Occasionally, moderately high pH water (pH 7.5) is used to irrigate blueberries in Florida.<sup>153</sup> The water is quite high in calcium carbonates and plant vigor has been reduced, particularly on sandy soils, where this water has been used for irrigation. Water from some deep wells in Texas has a pH of 8.5 with electrical conductivities of 0.695 dsm<sup>-1</sup>. Under these conditions, Haby et al.<sup>154</sup> found that growth of ‘Tifblue’ bushes was considerably reduced when irrigated with high salinity water primarily due to sodium toxicity. In subsequent studies, Patten et al.<sup>155</sup> compared drip and microsprinkler application of low and high saltwater to 3-year-old ‘Tifblue’ bushes. Although bushes receiving the sodic water appeared chlorotic at the end of the season, growth was unaffected. However, leaves accumulated high levels of sodium. Mulching and use of microsprinklers vs. drippers decreased salinity levels in the soil. Consequently, Patten et al.<sup>156</sup> tested methods for reducing salinity damage to rabbiteye blueberry plants. Again, mulching and sprinkler irrigation were effective in reducing bush damage and soil amendments of gypsum also proved successful. Cultivars varied in sensitivity to high salinity levels with ‘Delite’ and ‘Brightwell’ being more tolerant than ‘Tifblue’, ‘Premier’, or ‘Climax’.

Therefore, irrigation of blueberries is generally effective in improving yields of mature bushes and growth of young bushes. The trend appears to be to provide as much root zone coverage as possible and to use irrigation in conjunction with peat moss and mulch to obtain maximum growth.

### **b. Cranberries**

Irrigation of cranberry plants has traditionally been done by adjusting the water table depth due to the unusual growth habit and plant configuration of a cranberry bog.<sup>56</sup> Plants are irrigated by adjusting water levels in adjacent canals and by allowing vertical water movement via capillary action. Most studies suggest that the water table should be maintained from 23 to 37 cm below the soil surface. Beckwith<sup>157</sup> found yields were numerically highest at water table depths of 23–30 cm, but yields were similar at 15–23 or 30–37 cm depths. Yields decreased only at the 7.5–15 cm depth. Similarly, Eck<sup>158</sup> studied effects of water table depth on ‘Early Black’ cranberry growth and yields over a 5-year period. Yields were greatest in most years at the 30–38 cm depths, although yields were also acceptable at the 38–46 cm depth. Length of uprights and runner growth were not affected by water table depth. Hall<sup>159</sup> compared three water levels using cuttings of ‘Beckwith’ and ‘Pilgrim’ cranberries growing in containers. Plants initially grew fastest at the highest water level (5.5 cm) with growth slowing later in the season. However, plants growing at the lowest (34.5 cm) water table depth grew most during the final 5 weeks

Table 5 Influence of cultivar, sod, mulch, and irrigation treatments on the growth, yield, frost damage, and bud development of rabbiteye blueberry plants

| Cultivar/treatment                      | Canopy volume (m <sup>3</sup> ) |       |       | Yield<br>(kg/ plant) |      | Frost<br>damage <sup>a</sup><br>1986 | Vegetative bud<br>development <sup>b</sup><br>1986 | Fruit wt (g) |      | Fruit from<br>first harvest |     | Titratable<br>acidity<br>(%)1985 |
|---|---------------------------------|-------|-------|----------------------|------|--------------------------------------|--|--------------|------|-----------------------------|-----|----------------------------------|
|   | 1984                            | 1985  | 1986  | 1985                 | 1986 |                                      |  | 1986         | 1985 | 1986                        |     |                                  |
|   |                                 |       |       |                      |      |                                      |  |              |      |                             |     |                                  |
| Tifblue                                 | 0.13                            | 0.31  | 0.75  | 3.02                 |      | 1.04                                 | 2.24   | 1.52         |      | 74                          | 58  | 1.45                             |
| Delite                                  | 0.07                            | 0.21  | 0.55  | 2.22                 |      | 2.20                                 | 2.20   | 2.15         |      | 81                          | 68  | 1.52                             |
|   | **                              | *     | *     | *                    |      | ***                                  | NS   | **           |      | *                           | *   | *                                |
| Sod                                     | 0.10                            | 0.27  | 0.69  | 2.54                 |      | 1.63                                 | 2.13   | 1.85         |      | 75                          | 62  | 1.53                             |
| No sod                                  | 0.09                            | 0.26  | 0.61  | 2.68                 |      | 1.61                                 | 2.30   | 1.82         |      | 79                          | 65  | 1.45                             |
|   | NS                              | NS    | NS    | NS                   |      | NS                                   | **   | NS           |      | NS                          | NS  | **                               |
| One drip emitter                        | 0.08c                           | 0.23c | 0.59b | 2.51c                |      | 1.49b                                | 2.29b  | 1.96a        |      | 82a                         | 68a | 1.47b                            |
| Two drip emitters                       | 0.07c                           | 0.21c | 0.59b | 1.90d                |      | 1.66ab                               | 2.48a  | 1.90a        |      | 83a                         | 68a | 1.59b                            |
| 360° low volume spray<br>emitter (LVSE) | 0.15a                           | 0.37a | 0.87a | 3.29a                |      | 1.83a                                | 2.05c  | 1.75b        |      | 76b                         | 64a | 1.44b                            |
| 40° LVSE                                | 0.10b                           | 0.26b | 0.53c | 2.76b                |      | 1.50b                                | 2.05c  | 1.73b        |      | 69c                         | 54b | 1.45b                            |
| Interaction significance                |                                 |       |       |                      |      |                                      |  |              |      |                             |     |                                  |
| Cultivar × mulch                        | NS                              | NS    | NS    | NS                   |      | NS                                   | NS   | *            |      | **                          | **  | ***                              |
| Cultivar × irrigation                   | **                              | ***   | *     | ***                  |      | NS                                   | NS   | NS           |      | NS                          | **  | **                               |
| Mulch × irrigation                      | **                              | ***   | **    | ***                  |      | NS                                   | ***  | NS           |      | ***                         | NS  | NS                               |
| Cultivar × mulch × irrigation           | **                              | NS    | ***   | ***                  |      | NS                                   | NS   | NS           |      | NS                          | NS  | NS                               |

Note: \* = Significant at  $p = 0.05$ ; \*\* = significant at  $p = 0.01$ ; \*\*\* = significant at  $p = 0.001$ ; NS = not significant.

<sup>a</sup> Rating of frost damage on 11 March 1986 (1 = no dead flowers, 5 = 100% dead flowers). <sup>b</sup> Rating of vegetative bud development on 11 March 1986 (1 = no vegetative bud break, 5 = majority of buds leafed out).

From Patten et al., *J. Amer. Soc. Hort. Sci.*, 114, 728, 1989. With permission.

of the season. Overall, the intermediate depth (19.5 cm) produced the greatest linear growth. Root distribution was also affected, with the high level producing a dense matted system, the intermediate level a deeper, spreading system, and the low level a root system with few, but long laterals. The superior root system at the intermediate depth was probably responsible for the improved vegetative growth and water relations.

Some growers have used sprinkling or perforated pipes for irrigation.<sup>56,160</sup> Chandler<sup>161</sup> found that sprinklers increased root growth near the surface and that root growth was improved compared to water table methods in dry soils.

The key to successful irrigation (water management) of cranberry plants is to maintain a well-distributed root zone that is not concentrated too near the soil surface. This practice provides a greater soil volume for water extraction during droughts and decreases water stress which may reduce growth and yields.

## **B. RUBUS (RED RASPBERRY)**

### **1. Irrigation**

Red raspberry plants, like blueberries, are usually rather shallow-rooted, and thus are susceptible to drought stress. Christensen<sup>162</sup> found 68–76% of the roots by weight in the top 25 cm of soil for 5-year-old plants. Therefore, irrigation would be expected to improve growth and yields of raspberry bushes. Goode and Hyrycz<sup>163</sup> varied irrigation levels using 20 or 50 kPa soil moisture tension at a 30-cm depth, or no irrigation, for ‘Malling Exploit’ and ‘Malling Jewel’ red raspberries. The irrigation treatments increased yields by 27% and produced a greater number of fruiting points/lateral than the nonirrigated treatment. Berry weight was increased by 20% and cane growth rate, height, and number also increased with irrigation. Goode<sup>164</sup> observed that irrigation reduced xylem tension and water stress in red raspberries, which is likely related to increased growth and yields. In contrast, Crandall and Chamberlain<sup>165</sup> withheld irrigation and increased the number of flower bud primordia formed in ‘Puyallup’ red raspberries. Late summer water stress, however, decreased carbohydrate reserves in the canes;<sup>166</sup> irrigation increased carbohydrate levels, but had no subsequent effect on cane diameter or fruit set in the following season. During a 10-year study in Scotland, MacKerran<sup>167</sup> compared growth and yields of ‘Malling Jewel’ red raspberry plants under 3 irrigation regimes. Irrigating at 40 kPa soil moisture tension improved growth and yields over nonirrigated plants in most regions, while irrigating at pink fruit stage alone did not increase yields. Irrigation improved berry size in only 4 of 10 years. Therefore, irrigation also increased berry number by increasing the number of fruiting canes/plant. DeBoer et al.<sup>168</sup> compared yields of ‘Boyne’ red raspberry using trickle compared with sprinkler irrigation over a 3-year period. Soil water content was monitored using tensiometers at various locations in the row, but irrigation was scheduled based on readings at a 20-cm depth. Soil water content was maintained between 30 and 35% from June to August for both irrigation systems. Net water requirements averaged 66.8 cm for the sprinkler and 32.8 cm for the trickle system. Therefore, trickle irrigation used considerably less water than the sprinkler, yet yields were comparable over the 3-year period.

## **V. FLOODING STRESS**

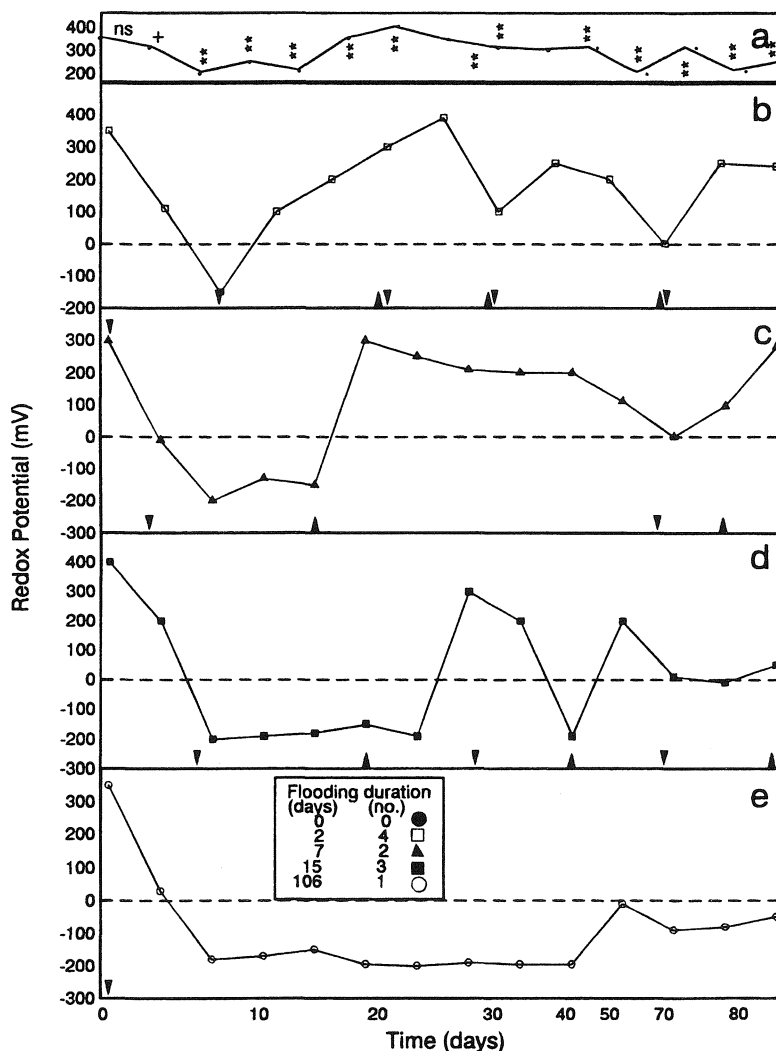
### **A. VACCINIUM**

#### **1. Blueberries**

Soil flooding, which may cause waterlogging, occurs periodically in many blueberry growing regions. In general, flooding is short-term, although some plantations have been inundated for 30 days or more under unusual conditions and have suffered considerable plant damage and yield reductions. During flooding, water displaces oxygen from the soil pore space. In addition, oxygen is respired by soil microbes and plant roots and oxygen levels decrease from 20% to less than 5% within 1–2 days of flooding.<sup>169</sup> Soils initially become hypoxic (low oxygen) and eventually anoxic (no oxygen), although this situation rarely occurs in the field. Redox potential of blueberry soils in Florida decreased from 300 mv (aerobic) (Figure 12a) to –100 mv within 1–2 days of flooding<sup>169</sup> (Figures 12b, c, d, e). As flood water subsided, redox potential returned to aerobic conditions in 5–10 days at a 15-cm depth (Figure 12b, c, d). In contrast, redox potentials remained at 0–200 mv during long-term flooding (Figure 12e). The time course and magnitude of changes in redox potentials, however, vary with soil type and temperature.

### a. Plant Survival

Survival time varies considerably for blueberries under flooded conditions due to environmental, edaphic and plant factors.<sup>116</sup> Survival durations range from 5 days for 'Tifblue' rabbiteye blueberries in Florida<sup>116</sup> to 30 months for 'Bluecrop' highbush blueberries growing in Rhode Island<sup>170</sup> (Table 6), with a range of durations between these extremes. Media or soil type and soil and air temperature are major factors influencing survival time. Survival duration is generally longer for plants growing in artificial media such as peat:perlite:sand (1:1:1 v/v) than in native soil because soil oxygen is depleted and redox potential changes more slowly in media. For example, redox potential of a peat:perlite:sand media remained  $>75$  mv for 30 months,<sup>170</sup> while it decreased to less than 0 mv in 1–2 days for Kanapaha sand as described previously.<sup>169</sup> Crane<sup>171</sup> flooded 'Woodard' rabbiteye blueberry plants under controlled conditions in the laboratory in either native soil (Kanapaha fine sand) or peat:perlite (1:1 v/v). The LD<sub>50</sub> for blueberry plants growing in native soil at 30°C ranged from 16–56 days but was consistently 61 days for plants growing in artificial media. However, redox potential for both media/soil types remained greater than 100 mv for the entire 70-day duration of the study. In contrast, Davies and



**Figure 12** Soil redox potentials for flooded and nonflooded plots of 'Tifblue' rabbiteye blueberry plants at the 15-cm depth during Spring 1985. Each point is the mean of three plots (10 replications per plot). Arrowheads indicate onset (▲) and release (▼) of flooding. From Crane and Davies, *J. Amer. Soc. Hort. Sci.*, 113, 488, 1988. With permission.

**Table 6 Survival percentage of *Vaccinium* species with soil flooding under various edaphic and environmental conditions**

| Species (cultivar)              | Age (yrs) | Season | Soil temp. (°C) | Media/soil              | Survival time (days)    | Ref.                                |
|---------------------------------|-----------|--------|-----------------|-------------------------|-------------------------|-------------------------------------|
| <i>V. corymbosum</i> (Bluecrop) | 2         | Spring | 16–32           | peat:perlite:sand 1:1:1 | 540                     | Abbott and Gough, 1987              |
| <i>V. corymbosum</i> (Bluecrop) | 2         | Winter | 10–16           | peat:perlite:sand 1:1:1 | 900                     | Abbott and Gough, 1987              |
| <i>V. ashei</i> (Woodard)       | 2         | Spring | 20–23           | peat:pinebark 1:1       | >58                     | Davies and Wilcox, 1984             |
| <i>V. ashei</i> (Woodard)       | 1.5       | Lab    | 20–30           | Kanapaha sand           | LD <sub>50</sub> 16–117 | Crane, 1987                         |
|                                 |           |        |                 | peat:perlite 1:1        | LD <sub>50</sub> 60–68  |                                     |
| <i>V. ashei</i> (Tifblue)       | 2–3       | Spring | —               | Kanapaha sand           | 106–117                 | Crane and Davies, 1988 (periodical) |
|                                 |           | Summer | —               | Kanapaha sand           | 78–90                   |                                     |
| <i>V. ashei</i> (Woodard)       | 3         | Spring | 22              | Kanapaha sand           | >35                     | Crane and Davies, 1988              |
|                                 |           | Summer | 33              | Kanapaha sand           | LD <sub>50</sub> <5     |                                     |
| <i>V. darrowi</i>               | 2–3       | Spring | —               | Kanapaha sand           | <55                     | Crane and Davies, 1989              |
|                                 |           | Summer | —               | Kanapaha sand           | <55                     |                                     |
| <i>V. stamineum</i>             | 2–3       | Spring | —               | Kanapaha sand           | <55                     |                                     |
|                                 |           | Summer | —               | Kanapaha sand           | <55                     |                                     |
| <i>V. ashei</i> (Delite)        | 2–3       | Spring | —               | Kanapaha sand           | <55                     |                                     |
|                                 |           | Summer | —               | Kanapaha sand           | <55                     |                                     |
| ( <i>V</i> × <i>V</i> )         |           | Spring | —               | Kanapaha sand           | <55                     |                                     |
| Sharpblue                       | 2–3       | Summer | —               | Kanapaha sand           | <55                     |                                     |
| Aliceblue                       | 2–3       | Spring | —               | Kanapaha sand           | <55                     |                                     |
|                                 |           | Summer | —               | Kanapaha sand           | LD <sub>50</sub> 55     |                                     |

Wilcox<sup>172</sup> observed no differences in survival duration for ‘Woodard’ and ‘Tifblue’ plants growing in native soil or peat:pine bark (1:1 v/v). However, redox potentials were not measured and the duration of the study (56 days) may not have been sufficient for differences in plant survival to occur.

Soil temperature during flooding also has a pronounced effect on plant survival in the field. ‘Bluecrop’ highbush plants survived 18 months when flooding was begun in April and 30 months when flooding was begun in December.<sup>170</sup> Rabbiteye blueberry plants growing in Florida survived more than 35 days of flooding in spring (March) at soil temperatures of 22°C, with no plants surviving 35 days during late summer (September) flooding at soil temperatures of 33°C.<sup>173</sup> In a related study, 83% of ‘Tifblue’ rabbiteye plants survived 106–117 days of flooding during spring, while 0 to 33% survived 78–90 days of summer flooding.<sup>169</sup> Both studies were done under field conditions in native soil, again illustrating the wide range of survival rates commonly observed among flooding experiments. This variability in survival time also occurred under controlled laboratory conditions. Crane<sup>171</sup> exposed flooded ‘Woodard’ rabbiteye blueberry roots to 20, 25, or 30°C soil temperatures and assessed LD<sub>50</sub> for survival. In all experiments LD<sub>50</sub> values were greatest at 20°C and least at 30°C, which is in agreement with generally observed trends in the field. However, in the first study, LD<sub>50</sub> ranged from 16–46 days, increasing to 33 to >64 days in the second experiment and to 56 to >117 days for the third study. These data suggest that plant age, size, or stage of maturity may also be factors in survival. Other studies, in contrast, suggested that neither stage of plant development nor soil temperature in the range from 20 to 31°C affected survival duration.<sup>172</sup> As stated previously, no soil redox potentials were measured; therefore it is difficult to assess the degree of anaerobiosis in this study.

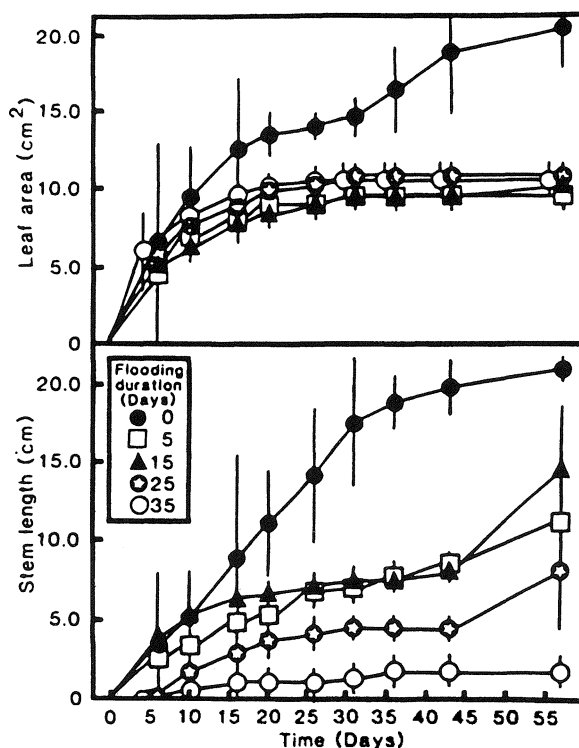
All of the studies listed in Table 6 evaluated plant survival from a horticultural viewpoint for plants that were not infected with *Phytophthora* root rot. Roots of highbush and some rabbiteye cultivars are very susceptible to *Phytophthora parasitica* damage. For example, ‘Tifblue’ plants died in only 3 to 7 days in the summer if *Phytophthora* was present in the soil compared with 25–35 days in the absence of *Phytophthora*.<sup>116</sup> Generally, flooded blueberry plants that are infected with *Phytophthora* exhibit rapid leaf desiccation and necrosis, almost as if they were burned. These symptoms develop basipetally, and are followed by leaf abscission. In contrast, when plants are flooded without *Phytophthora* present,

symptoms develop gradually. Leaves become chlorotic and reddened in an acropetal manner, and older, senescing leaves are usually affected before newer growth.<sup>116</sup>

Despite the many flooding studies conducted on blueberries, the reason for such variability in flooding survival is unknown. Even under carefully controlled conditions using clonal material, survival durations vary from plant-to-plant. One possible causal factor that has not been studied is the actual oxygen and physiological status of the roots themselves and not of the media/soil surrounding them. Physiological changes during flooding occur very rapidly in the shoot, usually within 24 hours of flooding (see Physiological Adaptations to Flooding, Section V.A.2.C). However, there is a paucity of information on changes in root physiology during initial flooding. Small variations in root responses among plants may cause rapid and cascading responses in the rest of the plant, ultimately producing differences in survival duration. This hypothesis is supported by the fact that blueberry plant survival duration is generally less at high vs. low soil temperatures. Root respiration is temperature dependent and it is logical to expect more rapid depletion of root oxygen at high vs. low temperatures, although there are no data correlating root oxygen levels with temperature making this hypothesis rather conjectural.

### b. Vegetative Growth

Although short-term flooding may result in plant death, it is more likely that the plant will survive, but vegetative growth will decrease. Flooding decreased shoot growth and number and leaf expansion of highbush<sup>170-173</sup> and rabbiteye blueberry bushes. Crane and Davies<sup>173</sup> measured leaf area and shoot growth for flooded and nonflooded rabbiteye blueberry plants in the field (Figure 13). Nonflooded shoots displayed a typical linear increase in length with growth rate slowing after 35–40 days. Leaf area increased rapidly, reached a plateau, and increased again in a double sigmoid pattern. In contrast, stems of continuously flooded plants grew very little and those of plants flooded for as little as 5 days grew at a much slower rate than shoots from nonflooded plants. Consequently, leaf area of flooded plants attained only 50% of that of nonflooded plants even after flooding was discontinued. Total and individual leaf areas decreased significantly after 35 days of continuous flooding. Similarly, Abbott and Gough<sup>170</sup>



**Figure 13** Effect of flooding duration on stem elongation and leaf expansion of 'Woodard' rabbiteye blueberry plants during Spring 1985. Each point is the mean of 3 leaves or stems of 6 plants per treatment  $\pm$  SD. From Crane and Davies, *J. Amer. Soc. Hort. Sci.*, 113, 180, 1988. With permission.

observed that average leaf area decreased from 4.4 to 2.2 cm<sup>2</sup> and shoot length decreased from 5.5 to 2.3 cm in nonflooded and flooded 'Bluecrop' highbush blueberry plants, respectively. Leaf area also decreased during periodic flooding, a situation that is more likely to occur under field conditions.<sup>169</sup> Flooding durations of 2 days reduced leaf area of 'Woodard' and 'Tifblue' rabbiteye blueberry plants if the flooding recurred on a regular basis. Flooding of two 7-day periods or three 15-day periods also reduced leaf area compared to controls. Herath and Eaton<sup>174</sup> also found leaf size of 'Bluecrop' highbush plants was reduced by periodic flooding.

It appears that overall flooding duration, whether accumulated in cycles or continuously, has a detrimental effect on growth. In general, the longer the total days of inundation, the greater the growth reduction. This fact is significant from a practical viewpoint, since most rabbiteye blueberry plantations are more likely to be exposed to several short-term flooding periods rather than to continuous long-term flooding.

### *c. Reproductive Growth*

Reproductive growth and development appears more sensitive to flooding than vegetative growth based on studies with 2- to 3-year-old bushes. Additionally, field observations on mature bushes also support this concept. Two-year-old 'Bluecrop' highbush plants were flooded for 4 or 30 months.<sup>175</sup> Flooded bushes had 60 or 74% fewer flower buds and 55 or 66% fewer flowers than nonflooded bushes after 4 or 30 months, respectively. In addition, anthesis of flooded bushes was delayed by 6 days. Similarly, Crane and Davies<sup>173</sup> observed even more dramatic short-term effects of flooding on reproductive growth of rabbiteye blueberry plants. Summer flooding of 2-year-old plants reduced flower bud formation in the fall by 31 to 67% after only 5 days of flooding. In a second study, summer flooding of 25 or 35 days totally inhibited flower bud formation in the fall. Percent fruit set was also decreased but only after 25 days of continuous flooding. Therefore, flower bud formation appears much more sensitive to flooding than fruit set, and most sensitive of all horticultural responses to flooding.

Since flooding reduced flower bud number and fruit set, yields should also be reduced. Yield of young rabbiteye plants in the field decreased after 25 or 35 days of flooding.<sup>173</sup> Abbott and Gough<sup>175</sup> also observed yield decreases for container-grown highbush plants. However, yield studies are not very meaningful on such young plants. Nevertheless, field observations also suggest that yields are reduced for mature bushes growing in poorly-drained areas. For example, yields were significantly reduced by 30 days of flooding for mature rabbiteye blueberry bushes in Georgia.<sup>176</sup> It has also been observed for many years that blueberry bushes growing in poorly drained areas are less vigorous and productive than those growing in well-drained locations.

### *d. Anatomical Adaptations to Flooding*

Flood-tolerant plants have evolved anatomical and morphological adaptations such as formation of aerenchyma cells, lenticels, or adventitious rooting to provide oxygen to flooded roots.<sup>177</sup> Similarly, highbush blueberry plants produced aerenchyma-like structures in the root epidermal layer and aerenchyma in the shoot cortex during prolonged flooding (4–30 months).<sup>178</sup> In contrast, Crane and Davies<sup>116</sup> did not observe the formation of similar structures in flooded rabbiteye plants. Most studies on rabbiteye plants, however, were conducted for less than 4 months, while the studies on highbush flooding were conducted for as long as 30 months. Possibly these adaptations would also occur for rabbiteye plants under such long-term flooding, although it is unlikely that rabbiteye bushes could survive this long.

### *e. Physiological Adaptations to Flooding*

Mesophytic plants have evolved several physiological and biochemical adaptations to flooding, including control and detoxification of glycolytic end products<sup>179</sup> and production of ethylene via 1-aminocyclopropane-1-carboxylic acid (ACC), which causes stomatal closure.<sup>180</sup> Flooding also decreases hydraulic conductivity of the root and may alter plant water relations.<sup>181,182</sup>

Blueberry plants also undergo physiological changes in gas exchange during flooding. Stomatal conductance decreased within 1 day of flooding in the laboratory<sup>15</sup> and within 1–5 days in the greenhouse.<sup>12</sup> Recovery of  $g_s$  to preflood levels did not occur for 18 days after plants were unflooded, despite the more rapid reoxygenation of the soil. With the decrease in  $g_s$ ,  $A$  also decreased within 1 day of flooding in the laboratory<sup>15</sup> and within 9 days in the greenhouse<sup>12</sup> (Table 7). By 11 days of flooding, 'Bluecrop' bushes had negative  $A$ , particularly at leaf temperatures above 28°C. Net CO<sub>2</sub> assimilation returned to control levels about 11 days after plants were unflooded. 'Bluecrop'  $A$  seemed to be more

Table 7 Effect of flooding duration on net gas exchange (A) of 'Bluecrop' and 'Woodard' blueberries (28 Aug. to 24 Sept. 1984)

| Duration<br>(days) | Leaf<br>temp.<br>(°C) | PPF<br>( $\mu\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$ ) | ‘Bluecrop’ <sup>a</sup> |         | ‘Woodard’ <sup>b</sup><br>A ( $\mu\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$ ) |         |    | Significance   |                          |
|--------------------|-----------------------|---|-------------------------|---------|--|---------|----|----------------|--------------------------|
|                    |                       |   | Non-<br>flooded         | Flooded | Non-<br>flooded  | Flooded | cv | Treat-<br>ment | cv $\times$<br>treatment |
| During flooding    |                       |   |                         |         |  |         |    |                |                          |
| 2                  | 29                    | 272   | 1.37                    | 1.10    | 3.83   | 2.61    | *  | NS             | NS                       |
| 9                  | 33                    | 904   | 3.23                    | 0.72    | 2.59   | 0.80    | NS | *              | NS                       |
| 11                 | 36                    | 920   | 4.41                    | −1.72   | 5.60   | 1.84    | *  | **             | NS                       |
| 19                 | 29                    | 388   | 4.83                    | −2.80   | 1.38   | −1.14   | NS | **             | **                       |
| 24                 | 34                    | 701   | 5.15                    | −2.43   | 4.71   | −0.56   | NS | **             | NS                       |
| Flooding released  |                       |   |                         |         |  |         |    |                |                          |
| 2                  | 28                    | 391   | 2.80                    | −0.49   | 3.28   | −0.82   | NS | **             | NS                       |
| 4                  | 26                    | 248   | 3.30                    | −1.32   | 3.60   | −0.20   | NS | **             | NS                       |
| 11                 | 24                    | 204   | 3.30                    | 1.10    | 2.70   | 2.90    | NS | NS             | NS                       |

Note: \* = Significant at  $p = 0.05$ ; \*\* = significant at  $p = 0.01$ ; NS = not significant.

<sup>a</sup>Mean of 10 plants per cultivar per duration. <sup>b</sup>From Davies and Flore, *J. Amer. Soc. Hort. Sci.*, 111, 565, 1986. With permission.

strongly reduced by flooding than that of 'Woodard' rabbiteye blueberry, which suggests a physiological difference between highbush and rabbiteye blueberries in their flooding, as observed in the field. The short-term effect of flooding on A appears to be stomatal, rather than nonstomatal, based on changes in the ratio of the external (Ca) to internal (Ci) CO<sub>2</sub> concentration.<sup>12</sup> The ratio of Ci:Ca averaged 0.77 to 0.80 for nonflooded plants compared to 0.65 to 0.70 for flooded plants. However, the validity of the Ci:Ca ratio depends on the homogeneity of stomatal response,<sup>183</sup> which was not tested in this study.

Flooding not only decreased  $g_s$  but also slowed the rate of stomatal opening.<sup>15</sup> Furthermore, stomata were less responsive to changes in VPD, O<sub>2</sub>, and CO<sub>2</sub> levels than those of nonflooded plants. Davies and Flore<sup>18</sup> exposed 'Bluecrop' highbush blueberry plants to varying levels of external CO<sub>2</sub> and O<sub>2</sub> in the laboratory and measured changes in A to determine if flooding affected gas exchange characteristics of blueberry plants (Figure 14). They found that nonflooded plants showed a typical C3 plant increase

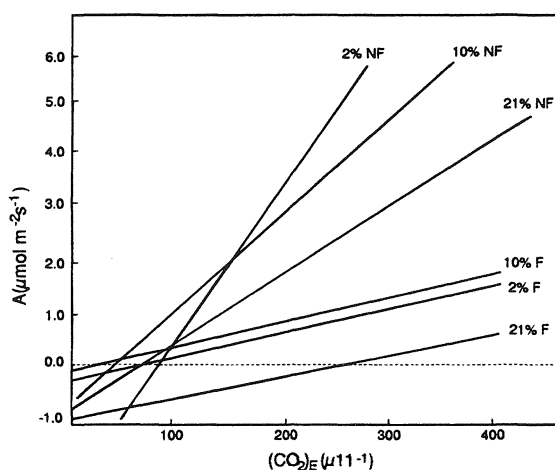


Figure 14 Effects of CO<sub>2</sub> concentration and O<sub>2</sub> percentage on net CO<sub>2</sub> assimilation (A) of nonflooded (NF) and flooded (F) 'Bluecrop' blueberry plants. O<sub>2</sub> percentages were 2, 10 or 21. From Davies and Flore, *Physiol. Plant*, 67, 545, 1986. With permission.

in  $A$  as  $O_2$  level was reduced from 21 to 2% and as external  $CO_2$  was increased from 100 to 400  $\mu\text{l l}^{-1}$ . Flooded plants, however, showed much less responsiveness both to a reduction in  $O_2$  and an increase in external  $CO_2$ . In addition, flooding decreased photosynthetic efficiency and apparent quantum yield of 'Woodard' rabbiteye blueberry leaves. Therefore, nonstomatal factors such as residual conductance also decreased with short-term flooding, but probably only after  $g_s$  decreased.<sup>116</sup> Nevertheless, with protracted flooding,  $g_s$  values approach those of residual conductance, and the latter has a significant controlling effect on  $A$ .

The biochemical changes in blueberry plants during flooding have not been widely studied, with the exception of ethylene's putative role. Crane<sup>171</sup> studied ethylene levels for flooded and nonflooded rabbiteye blueberry plants and soils and found only trace levels of ethylene in both treatments. Blueberry leaves showed no signs of epinasty, as found in tomato plants, further supporting the lack of involvement of ethylene in flooding responses of blueberry plants.

Water relations of flooded blueberry plants also changed, but more slowly than changes in  $g_s$  or  $A$ . Generally, leaf  $\Psi$  does not decrease for 3 to 5 weeks after flooding initiation.<sup>12,172</sup> This is probably a direct result of rapid stomatal closure that prevents the damaging effects of low leaf  $\Psi$  during flooding. With time, however, long-term flooding decreased  $\Psi$ .<sup>116</sup> In contrast, root hydraulic conductivity decreased within 4 to 6 days of flooding probably due to damage to root membranes as suggested by increases in electrolyte leakage at 6 to 10 days post-flooding.<sup>184</sup> Root hydraulic conductivity continued to decrease by as much as 81% of control values 2 to 3 weeks after flooding. Both hydraulic conductivity and  $g_s$  decreased within nearly equal timeframes in greenhouse and field studies and thus appear linked, possibly via substances synthesized in the roots of flooded plants and translocated to the shoots, causing stomatal closure.<sup>185</sup> This hypothesis, nevertheless, is speculative as no substances have been identified that cause stomatal closure during flooding of blueberry plants.

#### ***f. Time Course of Flooding Responses***

Several studies conducted with rabbiteye and highbush blueberry suggest a loosely structured time course for flooding responses, consisting of initial, intermediate, and late phases (Table 8).<sup>116</sup> This sequence occurs in the absence of *Phytophthora* or other root pathogens. During the initial phase,  $g_s$  to  $CO_2$  and water,  $A$  and quantum yield decrease within 1 to 2 days of flooding, followed by a decrease in root hydraulic conductivity. Because root water uptake is limited, stomatal closure protects the canopy from extensive and deleterious transpirational losses. A significant reduction in flower bud formation occurs within 5 days of flooding, and may be due to the decrease in  $A$  as well as a decrease in hormone translocation from roots. The plants recover rapidly when unflooded during the initial phases, with no lasting effects of flooding being apparent.

The second phase is characterized by a reduction or cessation of leaf and shoot expansion. Root hydraulic conductivity continues to decline, electrolyte leakage from the root occurs, and residual (nonstomatal) conductance decreases. At this stage,  $A$  becomes negative at temperatures greater than 28°C, causing the blueberry plant to use its stored carbohydrate reserves via temperature-linked increases in respiration. The plant recovers very slowly with unflooding and lasting reductions in growth and yields usually occur.

The blueberry plant continues further decline during the final phase. Leaves redden and abscission occurs acropetally; new growth flushes become chlorotic often showing iron deficiency symptoms. Fruit set is decreased and fruit may shrivel on the plant. Root hydraulic conductivity becomes extremely low and leaf  $\Psi$  becomes progressively more negative despite stomata closure. The plant is very slow to recover during unflooding and is usually permanently damaged. Plant death eventually occurs due to extreme desiccation, carbon starvation, loss of membrane integrity, and a reduction in ATP production. Highbush blueberry plants may produce aerenchyma or aerenchyma-like tissues during the final phase which extends the life of the plant.

High soil temperatures or VPD accelerate the time for each phase to occur, thus accounting for the observed differences in survival duration in summer compared with fall flooding. High temperatures cause rapid water losses (primarily cuticular) and increased respiration rates, thus using stored metabolites at a faster rate. High temperatures also cause rapid use of oxygen by microbes and roots, thus accelerating each stage of the process. The type of media (soil) affects the amount of oxygen available in pore spaces, and the types of microbes available to metabolize the oxygen. Therefore, the sequence of events in flooding, particularly survival duration, is generally longer in artificial media than in sands or clays

**Table 8 Time course of physiological and growth responses of rabbiteye blueberry plants to flooding duration**

| Time<br>(days of flooding) | Plant response  |
|----------------------------|---|
| <b>Phase 1</b>             |   |
| 0                          |   |
| 1                          |   |
| 2                          | $g_s(\downarrow)$ , $g'_s(\downarrow)$ , $A(\downarrow)$ , $\Phi(\downarrow)$             |
| 3                          | RLp ( $\downarrow$ ), $\Psi_w$ (no change)  |
| 4                          |   |
| 5                          | Flower bud number ( $\downarrow$ ) after summer flooding                                  |
| <b>Phase 2</b>             |   |
| 6                          | Leaf expansion and shoot elongation cease   |
| 7                          |   |
| 8                          | RLp ( $\downarrow\downarrow$ )  |
| 9                          | SLp ( $\downarrow$ ), EL ( $\uparrow$ ), $g'_r(\downarrow)$ , $\Phi(\downarrow)$          |
| 10                         | $A(\downarrow)$ may become zero or negative, $g_s$ less responsive to environment         |
| 11                         | New shoots and/or leaves may wilt   |
| 12                         |   |
| 13                         | Leaf senescence and abscission  |
| 14                         | $g_s(\downarrow\downarrow)$ , $A(\downarrow\downarrow)$ , $\Psi_w$ (no change)            |
| <b>Phase 3</b>             |   |
| 15                         |   |
| 16                         | RLp ( $\downarrow\downarrow$ ), SLp ( $\downarrow\downarrow$ ), EL ( $\uparrow\uparrow$ ) |
| 17                         | Fruit shriveling may begin  |
| 18                         |   |
| 19                         |   |
| 20–45                      | Continued decline in plant vigor and a reduction in yields                                |
| 46–120                     | $\Psi(\downarrow\downarrow)$ , eventual plant death                                       |

Note: *Phytophthora* root rot may rapidly accelerate flood-stress symptoms and decrease plant vigor, leading to more rapid plant death.  $g_s$  =  $G_s$  to water;  $g'_s$  =  $G_s$  to carbon dioxide;  $A$  = net  $CO_2$  assimilation;  $\Phi$  = quantum yield; RLp = root hydraulic conductivity;  $\Psi_w$  = leaf xylem  $\Psi$ ; SLp = stem hydraulic conductivity; EL = electrolyte leakage;  $g'_r$  = residual conductance to carbon dioxide;  $\downarrow$  decrease;  $\downarrow\downarrow$  greater decrease;  $\uparrow$  increase;  $\uparrow\uparrow$  greater increase. From Crane and Davies, *HortScience*, 24, 203, 1989. With permission.

especially those with high organic matter levels which provide carbon substrates for microbial respiration, thus rapidly reducing  $O_2$  levels in the soil. The above-mentioned sequence involves physiological and morphological responses to flooding which are not related to presence of *Phytophthora* root rot. In contrast, *Phytophthora* causes sudden and severe root damage and rapid plant death.

## 2. Cranberries

Flooding is an important part of cranberry production and effects of flooding on growth and yields have been widely studied. Short-term flooding has been used to control insects in the spring and summer and to prevent winter kill and frost damage in the spring.<sup>56</sup> It is also used for irrigation. Flooding of cranberry vines differs from that of blueberry bushes in that the entire plant is inundated, presenting a very different situation from blueberry root flooding. Flooding durations of more than 1 day may cause damage to vines. The critical floodwater oxygen level for cranberry plants is about  $5.7 \mu l l^{-1}$ ,<sup>186</sup> but varies with physiological status of vines. Alternative sources of oxygen may come from degradation of stored carbohydrates. Therefore, as with blueberry, plants with high carbohydrate levels tend to survive protracted flooding better than those with low levels.<sup>56</sup>

Table 9 Effects of oxygen deficiency on production of three cranberry cultivars

| Cultivar and degree of O <sub>2</sub> deficiency | Flowers         |               | Fruit         |               |
|--|-----------------|---------------|---------------|---------------|
|  | Per upright (%) | Dead buds (%) | Fruit set (%) | Yield (mt/ha) |
| Early Black                                      |                 |               |               |               |
| Severe   | 3.1             | 12.6          | 21.6          | 3.0           |
| Moderate   | 3.5             | 12.9          | 28.0          | 6.4           |
| Slight   | 4.0             | 5.2           | 28.3          | 8.6           |
| Howes  |                 |               |               |               |
| Severe   | 3.1             | 16.8          | 33.3          | 5.8           |
| Moderate   | 3.5             | 17.6          | 34.9          | 8.3           |
| Slight   | 3.7             | 4.8           | 49.4          | 11.5          |
| McFarlin   |                 |               |               |               |
| Severe   | 3.9             | 16.1          | 20.9          | 4.5           |
| Moderate   | 4.0             | 12.9          | 23.5          |               |
| Slight   | 4.0             | 10.0          | 30.0          | 9.3           |

Note: Degree of O<sub>2</sub> deficiency was obtained by artificially excluding light from the flooded plants. Severe deficiency resulted when O<sub>2</sub> content of water dropped below 2  $\mu\text{l/l}$ ; moderate deficiency at 2 to 4  $\mu\text{l/l}$  O<sub>2</sub>; and slight deficiency above 4  $\mu\text{l/l}$  O<sub>2</sub>.

From Franklin et al., *Mass. Agr. Expt. Sta. Bul.*, no. 402, 1943. With permission.

#### a. Plant Survival

Plant survival during flooding is generally not a factor with cranberry vines as it is with blueberry plants because flooding durations are controlled. Consequently, there is little information available on plant survival. However, plant damage thresholds have been extensively studied. The extent of injury is positively correlated with temperature during flooding, with less damage at low (near 0°C) than moderate temperatures.<sup>56</sup> Temperature affects the solubility of oxygen in water; oxygen is less soluble at high vs. low temperatures. Moreover, temperature is positively correlated with tissue respiration rate, with a Q<sub>10</sub> of about two.

#### b. Vegetative and Reproductive Growth and Development

Symptoms of oxygen deficiency in cranberry are manifested as terminal bud dieback, stem death, and leaf abscission.<sup>56</sup> Flowers, small fruits, and rapidly growing buds are most sensitive to oxygen deprivation probably due to their relatively greater respiration rates and thus oxygen usage rates.<sup>187</sup> Mature leaves are the least sensitive to low oxygen levels. Franklin et al.<sup>189</sup> compared the effect of three cultivars and three oxygen depletion levels on percent flowers/upright, fruit set, yields, fruit size, and bud damage (Table 9). For all cultivars, plants grown under slight O<sub>2</sub> deficiency (>4  $\mu\text{l l}^{-1}$ ) had the highest yields and percent fruit set and the lowest bud mortality due to flooding. As O<sub>2</sub> levels decreased to moderate (2–4  $\mu\text{l l}^{-1}$ ) or severe (<2  $\mu\text{l l}^{-1}$ ) depletion there was a progressive drop in yields and fruit set. 'Early Black' flowers were more susceptible to low O<sub>2</sub> levels than flowers of 'Howes' and 'McFarlin'.

#### c. Physiological Adaptations to Flooding

There are some important differences in physiological flooding responses between cranberries and blueberries. Since a large portion or all of the cranberry vine is inundated, the plant's sensitivity and response to flooding is more rapid than for blueberry plants where only the roots are flooded. Therefore, flooding of more than 48 hours may cause damage. When the soil only is flooded, some O<sub>2</sub> is trapped in soil pores and roots, whereas entire leaf and shoot inundation allows only limited O<sub>2</sub> storage in intercellular spaces. At high temperatures, the O<sub>2</sub> is rapidly respired. Differences in flooding tolerance of cranberries among tissue types and cultivars may be a function of the level of respiration.

## VI. CONCLUSIONS

Many aspects of the environmental physiology of blueberries, cranberries, and raspberries are similar to those of tree fruit crops. Light saturation (700–900  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ), light compensation points (25–35

$\mu\text{mol m}^{-2}\text{s}^{-1}$ ), and temperature optima for photosynthesis are typical of other C3 temperate fruit crops. Cardinal temperatures for seasonal growth and development are also characteristic of other temperate crops. *Vaccinium* species are moderately drought tolerant, as indicated by intermediate leaf  $\Psi$  for stomatal closure and a characteristic increase in  $A$  as external  $\text{CO}_2$  levels increase ( $100\text{--}400 \mu\text{l l}^{-1}$ ) and  $\text{O}_2$  levels decrease (21 to 2%). Flood-tolerance mechanisms are also similar to those of tree crops and include stomatal closure and reduced water uptake. The initial reduction in  $A$  however, appears due to stomatal, rather than nonstomatal, factors.

Nevertheless, there are some unusual features of *Vaccinium* species compared to other fruit crops. Blueberry bushes are the only fruit crop that exhibit net fruit photosynthesis throughout development. In fact, fruit photosynthesis in blueberry supplies a significant portion of the carbon requirement of young fruit, contributing as much as 50% of the carbon required for dry weight gain and respiratory loss during the first 10 days after anthesis. Blueberries are also unusual compared to most other fruit crops in that flower bud initiation is photoperiodically sensitive. Increased flower bud initiation under short photoperiods (less than 12 hours) suggests that blueberries are quantitative short-day plants.

Although light and temperature optima for photosynthesis are similar between *Vaccinium* and other fruit crops, leaf  $A$  in rabbiteye and highbush blueberry and red raspberry plants is low, ranging from 5 to  $12 \mu\text{mol m}^{-2}\text{s}^{-1}$ , compared with much higher values for many other fruit crops. For some *Vaccinium* species, this is due in part to the development of extensive rodlet wax on leaf surfaces that cover and occlude the stomata, thus reducing  $g_s$ . Although rodlet wax formation serves as a drought tolerance mechanism, it also decreases  $A$  and may contribute to the relatively low growth rates and yield of blueberries.

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# Grape

Larry E. Williams, Nick K. Dokoozlian, and Robert Wample

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## I. INTRODUCTION

### A. GRAPE PRODUCTION

Grapevines are the most widely planted fruit crop worldwide and are cultivated on all continents except Antarctica.<sup>1</sup> Grapevine acreage as of 1988 was greater than 10 million ha.<sup>2</sup> The widespread distribution of grapevines is due to a large genetic diversity of available species and cultivars and a low chilling requirement for the release of buds from dormancy. However, a single species, *Vitis vinifera* L., of which there are currently over 10,000 cultivars accounts for greater than 90% of the annual production worldwide. Sixty percent of the world production of grapes (>63 Tg) is produced in Europe with Spain, Italy, and France each having more than 1 million ha of land devoted to grapevines.

Grapes are primarily used for wine, juice, distilled liquors, dried fruit (raisins) and fresh consumption fruit (table grapes). Italy, France, and Spain produce more than 50% of the world's wine; European countries together with the Commonwealth of Nations (former Soviet Union) account for 80% of the world's production.<sup>1</sup> The production of raisins worldwide is approximately 800 Gg (dried fruit); the United States and Turkey are the top two producing countries. Annual world production of table grapes is approximately 7 Tg. Italy, the Commonwealth of Nations, and Turkey comprise the top table grape producing nations. Fruit juice is concentrated when production exceeds demand.

### B. CLIMATIC CONSTRAINTS TO GRAPE PRODUCTION

*V. vinifera* is a temperate climate species adapted to hot summers with mild winters. The suitability of a given grape cultivar to a local environment is based upon day length, heat summation, rainfall, length of the growing season, and minimum winter temperatures. On a broad scale the main grape production areas are found between 30 and 50°N and 30 and 40°S latitudes, corresponding to the 10 and 20°C yearly isotherms.<sup>1</sup> Grapes can be commercially grown in other areas where climate is moderated due to local geographical conditions (mountains, land masses, and ocean currents). Raisin production is limited to the latitudes of 30 and 39°N in the Northern Hemisphere and between 28 and 36°S in the Southern Hemisphere. This is due to the fact that the best suited raisin cultivars, 'Thompson Seedless' (syn. 'Sultinina') and 'Zante Currant', require warm temperatures for fruit bud differentiation and fruit maturation. In addition, the production of natural raisins (sun-dried grapes) requires high temperatures and lack of rainfall following harvest. Warm, dry weather also favors the production of table grapes as the incidence the fungal diseases is much reduced under these conditions.

### C. CYCLE OF VINE GROWTH

Vineyards are planted via vegetative means such as cuttings, rootings, or grafted vines. Vineyards commonly produce a harvestable crop in the third growing season, subsequent to establishment of a root system and training the vines to fit a specific trellis system.<sup>2</sup> Trellis choice depends upon intended use of the grapes (wine, raisin, or table grape production), methods of pruning and harvest (manual or mechanical),<sup>3</sup> and climate and soil conditions.

Current season's vegetative and reproductive growth occurs from compound buds (consisting of a primary, secondary, and tertiary bud) in the spring. The primary bud consists of eight to ten leaf primordia with zero or more cluster primordia. Budbreak is followed by rapid shoot growth. Flower differentiation on the cluster primordia begins prior to budbreak and continues up until anthesis. Anthesis occurs approximately eight weeks after budbreak, therefore, considerable leaf area has developed before pollination, fertilization, and berry set takes place. Berry growth of both seeded and "seedless" cultivars is of the double sigmoid type in which growth occurs in three stages. Vegetative growth commonly continues until veraison (the end of Stage II; characterized by softening of the fruit and change in color for red and black cultivars). Wine and raisin grapes are harvested when the soluble solids (°Brix) concentrations are between 16 and 25 °Brix. Table grapes are generally harvested when the soluble solids levels are 15 to 17 °Brix.

Leaves remain photosynthetically active and will remain such until the first killing freeze. Periderm will have formed on the main axis of the shoot throughout the growing season. Once the leaves abscise the vine goes dormant and the leafless shoots, now called canes, will be pruned during the winter to regulate next year's crop.

Cluster differentiation (for the next year's crop) within the compound buds of spur pruned cultivars (four basal nodes on a shoot) begins around anthesis and is complete prior to veraison for spur-pruned table grape cultivars in California (L.E. Williams, unpublished data). Cluster differentiation is complete at node 15 by late summer. Therefore, environmental conditions and stress during these periods can dramatically affect the next season's yield. Further details on the physiology, anatomy, and morphology of the grapevine can be found in Mullins et al.<sup>1</sup>

## II. IRRADIANCE

Solar radiation induces various biological responses through changes in light quality, quantity, direction, and periodicity.<sup>4</sup> Plant responses include thermal effects, photosynthesis, photomorphogenesis, and mutagenesis. Viticulturists have become increasingly aware of the positive effects of light on both the quantity and quality of the harvested fruit due in large part to the pioneering work of Dr. Nelson Shaulis and co-workers at the New York State Agricultural Experiment Station, Geneva, NY.

### A. INTERCEPTION BY GRAPEVINE CANOPIES

#### 1. Effect of Canopy Height and Row Direction

Light interception is dependent primarily upon canopy shape and orientation. Smart<sup>5</sup> predicted that sunlight interception by grapevine canopies declines rapidly as canopy height decreases and the distance between walls of foliage (i.e., distance between vine rows) is increased. While a smaller distance between rows increases solar radiation interception on an area basis, cross-row shading becomes a significant factor limiting sunlight interception of individual foliage walls as the distance between rows is reduced. A value of 1:1 for the ratio of canopy height to distance between canopies is recommended to avoid cross shading.<sup>5</sup>

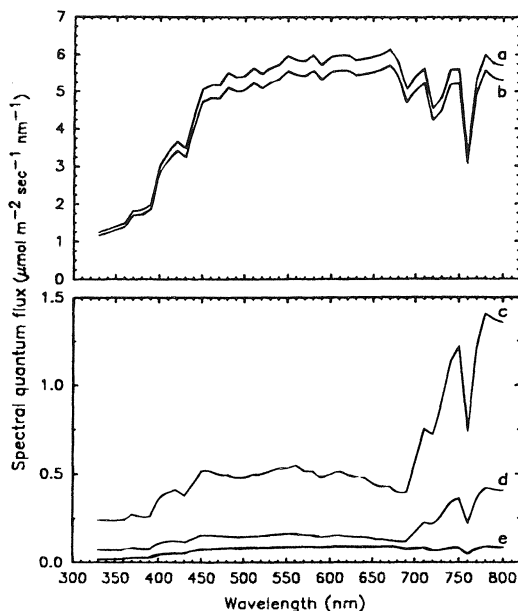
Row direction also has a pronounced effect on solar radiation interception. Greater amounts of direct light are absorbed by the canopy walls in the mid-morning and mid-afternoon in rows oriented north-south compared to east-west.<sup>5</sup> Canopies 1 and 3 m in height and spaced 4 m apart intercepted approximately 10 and 22% more sunlight, respectively, when rows were oriented north-south compared to the east-west row orientation.

#### 2. Effect of Trellis and Canopy Management

The amount of solar radiation intercepted by the grapevine canopy, as well as the light environment within the canopy interior, is largely determined by the training and trellis system employed and vine leaf area.<sup>6</sup> These factors, combined with such cultural practices as shoot positioning and basal leaf removal, determine shoot orientation, canopy surface area, and vine foliage density.<sup>7</sup> Shaulis and co-workers<sup>8</sup> were among the first to recognize the influence of vine training and trellis design on the light environment within grapevine canopies, and its effect on vine productivity and fruit composition. Vegetative growth normally increases as canopy width expands, thereby increasing the total amount of leaf surface available for solar radiation interception.<sup>9</sup> As a result of greater sunlight interception per unit row or canopy length, increasing both canopy height and width via vineyard layout and training/trellising generally increases vine yield.<sup>10-12</sup>

Solar radiation interception and penetration to the canopy's interior has been substantially increased by the separation of the canopy into two vertical curtains.<sup>8</sup> The Geneva double curtain training system has often resulted in greater bud fruitfulness and vine productivity, and improved fruit quality. Carbonneau and Huglin<sup>13</sup> reported that the surface of an open lyre or "U" shaped canopy with two distinct curtains of foliage intercepted 10% more solar radiation per day than a non-separated, single row canopy at wide row spacing. Light measured in the fruiting zone was 21% of ambient for the separated lyre canopy, compared to 6.4% of ambient for the single canopy. Kliewer et al.<sup>14</sup> reported that photosynthetic photon flux density (PPFD) within the fruiting zone of a non-divided canopy of 'Sauvignon blanc' was approximately 4% of ambient, while the fruit zone PPFD of this cultivar with a divided canopy was greater than 30% of ambient.

Additional canopy management practices may be employed to increase solar radiation interception and penetration into the canopy interior. Shoot positioning, either performed manually or mechanically, can be used to separate tangled foliage within the interior of divided canopies. Shoot positioning prevents shading and improves sunlight interception by maintaining canopy separation throughout the growing season.<sup>7</sup> Basal leaf removal, influences the light microclimate in the canopy interior. Bledsoe et al.<sup>15</sup>



**Figure 1** Spectral quantum flux of radiation between the wavelengths of 330 and 800 nm for: ambient sunlight (a), a sunfleck within the interior of a grapevine canopy (b), and for canopy light in the fruiting zone of 'Cabernet Sauvignon' grapevine canopies with 2.1 (c), 5.6 (d) and 12.2 (e)  $\text{m}^2$  leaf area  $\text{m}^{-1}$  canopy length. Each curve represents the mean of five separate scans. Determinations were made at 2-nm wavelength intervals using a scanning spectroradiometer with the sensor positioned horizontally near solar noon under clear skies in Oakville, CA. (N.K. Dokoozlian, unpublished data.)

reported that basal leaf removal following berry set increased PFD within the fruiting region of 'Sauvignon blanc' grapevines by approximately 20% when compared to the untreated control.

## B. LIGHT ENVIRONMENT WITHIN GRAPEVINE CANOPIES

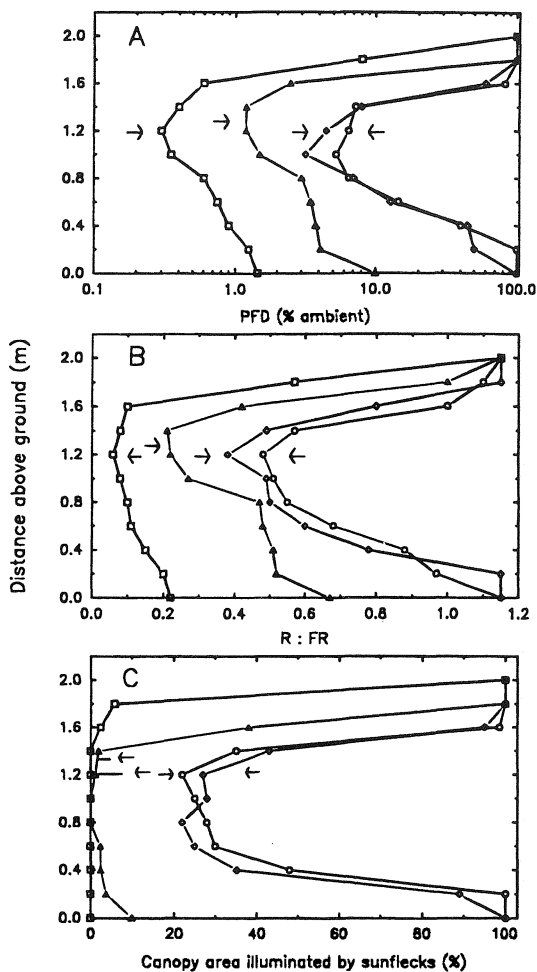
Of the PFD arriving perpendicular to the surface of a grape leaf, 80 to 90% is absorbed and the remainder is either transmitted or reflected.<sup>16</sup> The low levels of PFD (5% of ambient or less) commonly measured within the interior of dense grapevine canopies is a result of this high degree of absorption.<sup>17</sup> The spectral quality also is altered when compared to ambient solar radiation in that the blue (400 to 500 nm) and red (650 to 700 nm) wavelengths are absorbed by the vine's canopy to a greater extent than the far-red (710 to 800 nm) wavelengths (Figure 1). This results in a decrease in the amount of blue light in the canopy interior relative to other wavelengths, as well as a decrease in the red (R) to far-red (FR) ratio (R:FR). The spectral composition of sunflecks, which occur when direct solar radiation penetrates through gaps in the canopy, closely resembles that of incident radiation (Figure 1).<sup>18</sup>

The relationship between canopy leaf area and PFD, R:FR, and sunflecks within the canopy of wine grapes grown under the standard (non-separated) training/trellis system used in California is presented in Figure 2. PFD decreased to 10% or less of its ambient value approximately 0.5 m below the canopy surface. PFD was lowest near the fruiting zone, with values of 7.0 and 0.3% of ambient, for vineyards with 2.2 and 12.2  $\text{m}^2$  of leaf area per meter canopy length, respectively. PFD increased below the fruit zone, and ambient values of PFD were found at ground level of canopies with low leaf area densities. Patterns of the R:FR ratio and sunfleck attenuation within low and high leaf area density canopies were similar to those observed for PFD (Figures 2B and 2C, respectively). The R:FR ratio decreased immediately below the canopy surface, and reached its lowest level at or near the fruit zone. The R:FR also increased gradually moving downward along the vertical transect from the fruit zone to the ground. Sunflecks illuminated about 20% of the fruit zone at harvest within the low density canopy, but were nearly absent along the vertical transect in a high density canopy. This study also revealed that the patterns of PFD, R:FR, and sunfleck attenuation changed little during the course of fruit development, despite an approximate doubling of canopy leaf area in various vineyards during this same time period.<sup>19</sup> A close, positive relationship exists between PFD and the R:FR ratio (Figure 3). In very dense canopies PFD may approach 0.1% of ambient sunlight and the R:FR ratio may drop as low as 0.05.

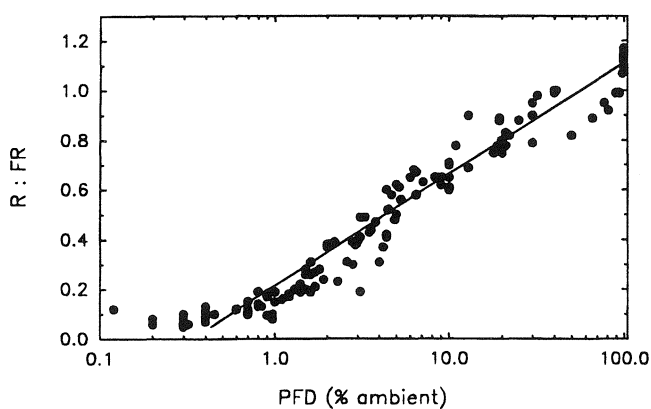
## C. EFFECTS ON VINE GROWTH AND METABOLISM

### 1. Cluster Differentiation

The differentiation of anlagen into either cluster or tendril primordia is dependent upon the irradiance level reaching the compound bud during development as demonstrated by experiments conducted under



**Figure 2** Relationship between photosynthetic photon flux density (PFD) (A), the red:far red (R:FR) ratio (B), and the percent canopy area illuminated by sunflecks (C) as a function of canopy depth for 'Cabernet Sauvignon' canopies at harvest. Symbols correspond to the following canopy leaf areas: ( $\circ$ ) 2.2, ( $\diamond$ ) 3.3, ( $\triangle$ ) 8.7, and ( $\square$ ) 12.1 m<sup>2</sup> leaf area m<sup>-1</sup> canopy length. Readings were taken with sensors positioned vertically upward, at solar noon under clear skies. Arrows indicate the locations of the fruit zone in each canopy. (N.K. Dokoozlian, unpublished data.)



**Figure 3** Relationship between the red:far red (R:FR) ratio and photosynthetic photon flux density (PFD) (% ambient, log scale) within grapevine canopies. Values represent a wide range of vineyard sites and canopy densities and depths. Measurements were made with light sensors positioned horizontally at solar noon under clear skies. Data were fitted to a linear function:  $y = -0.431 + 2.147x$ ,  $r^2 = 0.96$ . (N.K. Dokoozlian, unpublished data.)

controlled environmental conditions<sup>20,21</sup> and in the field.<sup>22,23</sup> Low irradiance favors the differentiation of tendril primordia. The number and size of cluster primordia generally increase with an increase in irradiance level.<sup>20</sup> Bud fruitfulness and subsequent yield are increased by improving the light environment of developing buds by the use of divided canopies<sup>8</sup> or retention of spurs or canes developing at the top of the canopy.<sup>1</sup>

The specific mechanisms responsible for the regulation of bud fruitfulness by light are unknown. However, increased cluster initiation under well-exposed conditions appears to be primarily due to increased light quantity; the R:FR ratio was shown to have no effect on bud fruitfulness.<sup>24,25</sup> Although shading individual buds decreases cluster initiation, some controversy remains regarding the influence of irradiance on the leaves immediately subtending the bud on fruit bud differentiation.

The irradiance required to maximize bud fruitfulness varies among *Vitis vinifera* cultivars.<sup>26</sup> 'Sultana' (syn. 'Thompson Seedless') and 'Ohanez' require relatively high irradiance (approximately one third full sunlight) for notable cluster initiation. In comparison, significant cluster differentiation of 'Rhine Riesling' buds was obtained with only 10% of full sunlight.

It is generally accepted that photoperiod has little effect on cluster differentiation of *V. vinifera*.<sup>1</sup> However, American *Vitis* species will respond to increased day length. For example, the *Vitis* × *labruscana* cultivar 'Delaware' had three times more clusters when grown under long days compared to those grown under short days.<sup>27,28</sup>

## 2. Leaf Gas Exchange

As for other C<sub>3</sub> species, the relationship between leaf net CO<sub>2</sub> assimilation rate (A) and PFD for grapevine leaves can best be described as a rectangular hyperbole. Light saturation for individual leaves of grapevines may change due to conditions under which the vines are grown.<sup>29,30</sup> However, recent studies using field-grown grapevines indicate that light saturation occurs at approximately 1500 μmol quanta m<sup>-2</sup> s<sup>-1</sup>.<sup>1,31,32</sup> The light compensation point for A of grapevines is between 10 and 20 μmol quanta m<sup>-2</sup> s<sup>-1</sup>.<sup>32,33</sup>

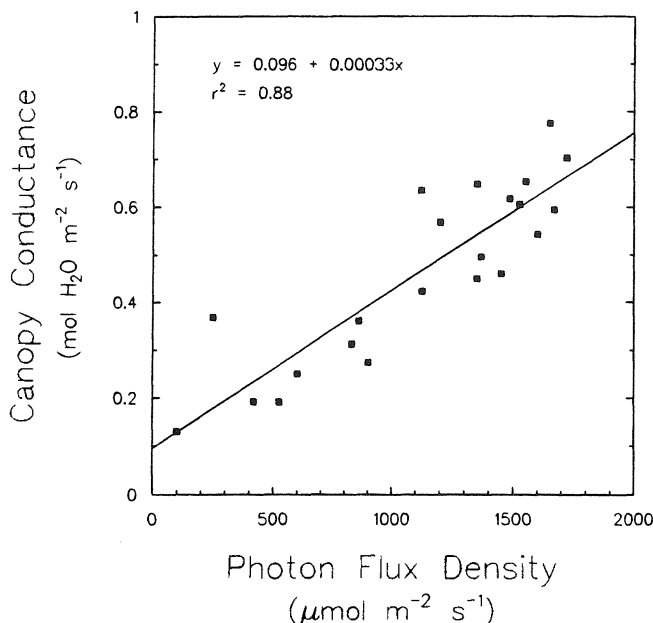
Stomatal conductance to water vapor (g<sub>s</sub>) of well-watered vines showed a hyperbolic response to PFD.<sup>34,35</sup> Maximum stomatal opening of an individual leaf has been recorded at a PFD of 130 to 300 μmol quanta m<sup>-2</sup> s<sup>-1</sup>.<sup>30,34,35</sup> Canopy conductance of a grapevine at full canopy, unlike single leaf g<sub>s</sub>, is linearly related to PFD (Figure 4). This is expected as individual leaves located throughout the canopy are simultaneously exposed to different PFDs due to shading, leaf angle, zenith angle of the sun, and row and shoot direction. Therefore, maximum canopy conductance is associated with maximum PFD and occurs when the greatest proportion of the leaf canopy is exposed to direct solar radiation.<sup>37</sup>

It has been suggested that there is a high PFD-stress effect on *V. vinifera* leaves that causes an afternoon depression of A independent of leaf temperature.<sup>38,39</sup> This contradicts studies on well-watered field-grown grapevines in which there was no midday depression of A at high irradiance levels.<sup>31,40,41</sup> Data demonstrating the midday depression of A, though, were collected on potted vines either without a measure of vine water status<sup>38</sup> or grown in a glasshouse with measurements taken in the lab.<sup>39</sup> Düring<sup>33</sup> has shown that A of potted glasshouse-grown but not field-grown Riesling vines was slightly depressed at high PFD.

The most extensive research investigating photoinhibition of A in grapevines has been conducted on the native California species *V. californica* Benth. At high PFD both the light and dark reactions of A were more severely inhibited at high (41.5°C) and low (22.7°C) temperatures than at intermediate temperatures.<sup>42</sup> The inhibition of A at high PFD was greater for growth chamber grown vines relative to vines grown outside. Exposure to either high light or high temperature caused reductions in PSII photochemical activity with a subsequent recovery the following day.<sup>43</sup> However, exposure of *V. californica* leaves to both high light and high temperature caused PSII inhibition that was severe and persistent. Finally, field studies using unrestrained and horizontally held leaves of this species confirmed that high PFD (>1800 μmol quanta m<sup>-2</sup> s<sup>-1</sup>) had no adverse impact on A.<sup>44</sup>

## 3. Berry Growth and Composition

Much of the recent information regarding the influence of light on grape berry growth and composition has been obtained from studies investigating the influences of training-trellis systems and other canopy management practices on grapevine yield and fruit composition.<sup>13,14,45,46</sup> In cool climates canopy management practices which improve the exposure of vine foliage and fruit to solar radiation have generally improved grape and wine composition. Fruit of vines in which the canopy interiors are well exposed

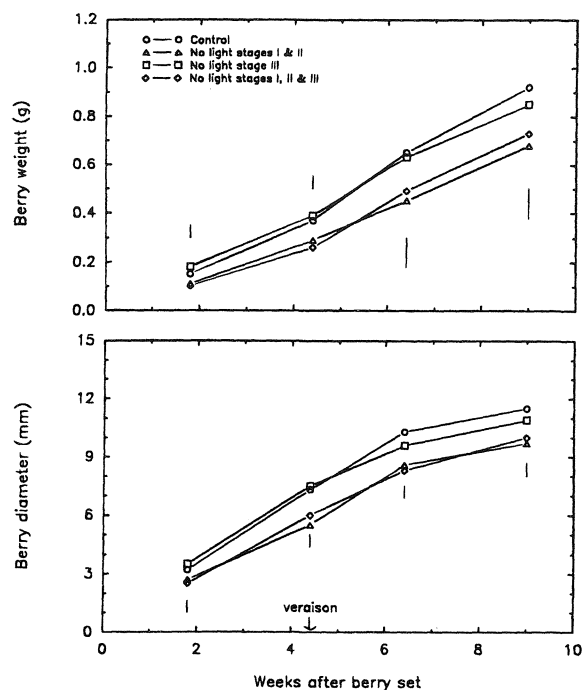


**Figure 4** The relationship between canopy conductance and photosynthetic photon flux density. Total vine conductance was calculated according to the method of Grantz and Meinzer.<sup>36</sup> Canopy conductance was calculated as the difference between total vine conductance and aerodynamic conductance.<sup>37</sup> The data were collected on two separate days during the month of August, 1992. (L.E. Williams, unpublished data.)

to sunlight have normally exhibited increased rates of sugar accumulation, greater concentrations of anthocyanins, and total phenols, yet decreased levels of malic acid, potassium, and pH compared to fruits produced from vines with little interior canopy exposure. The above-mentioned practices are used to alter the fruiting zone light environment and have likely influenced other aspects of vine microclimate. For example, training-trellis systems, shoot positioning, and other canopy management practices, alter the light environment of both shoots (leaves) and clusters thus creating uncertainty as to whether improvements in berry composition are attributable to increased fruit exposure, leaf exposure, or both. In addition, increased levels of solar radiation exposure can result in substantial increases in both berry<sup>47</sup> and leaf<sup>8</sup> temperatures.

Recent investigations have shown that a photoreceptor localized in the grape berry is responsible for the detection of the light environment and thus the photoregulation of grape berry growth and composition.<sup>19</sup> The exclusion of light to fruit of field-grown 'Sultana' (syn. 'Thompson Seedless') for a period 2 weeks prior to softening until harvest increased berry weight and soluble solids compared to fruit exposed to natural light in the canopy.<sup>48</sup> Fruit of 'Thompson Seedless' vines exposed to direct solar radiation had similar soluble solids (°Brix), but were lower in weight and acidity and had a higher pH than fruit that ripened in the canopy interior.<sup>49</sup> Anthocyanin concentrations and soluble solids of 'Emperor' berries were decreased when they received 15% compared to berries receiving 54 or 100% of ambient solar radiation.<sup>50</sup> Field-grown 'Cabernet Sauvignon' berries exposed to sunlight had lower berry weights but higher concentrations of tartrate, malate, glucose, fructose, and anthocyanins compared to berries ripened in the canopy interior.<sup>51,52</sup> Morrison<sup>53</sup> reported on the independent effects of cluster shading and leaf shading on the growth and composition of fruit from field-grown vines of 'Cabernet Sauvignon'; cluster shading reduced fruit anthocyanin and total soluble phenolic concentrations, while leaf shading reduced berry weight and decreased the rate of sugar accumulation.

During Stage I of the double sigmoid curve of grape berry growth,<sup>54</sup> berry pericarp growth is rapid due to both cell division and cell expansion while growth during Stage III is due to cell enlargement. Light affects grape berry growth and composition differently during the three stages of fruit development. It was found that when sunlight was excluded from clusters during Stages I and II, berry growth was significantly less compared to those which received 20% of ambient sunlight during these two stages (Figure 5). It is unknown whether the reduction in berry growth was due to a reduction in cell division,



**Figure 5** The influence of solar radiation exclusion during various stages of fruit development on the fresh weight (upper) and diameter (lower) of 'Cabernet Sauvignon' grape berries. Sunlight was excluded from the clusters by enclosing the fruit in aluminum lined, paper bags at the appropriate stage of growth. Data represent the mean of four, single-cluster replicates grown on potted vines in a phytotron. Bars represent LSDs ( $p < 0.05$ ) on each sample date. (N.K. Dokoozlian, unpublished data.)

cell enlargement, or both. Berries of these clusters also exhibited reduced rates of solute and color accumulation during Stage III compared to berries exposed to sunlight during Stages I and II. Exclusion of sunlight during Stage III had little effect on berry weight, berry diameter, or solute accumulation. However, berries from these clusters exhibited lower rates of anthocyanin and phenol accumulation indicating that light has the greatest effect on both berry growth and fruit composition during Stages I and II.

The importance of phytochrome in the control of grape berry growth and composition is a topic of interest. Smart et al.<sup>55</sup> reported that 'Cabernet Sauvignon' vines shaded with neutral shade cloth and receiving supplemental red light in the fruiting zone (i.e., exposed to 10% of ambient PFD, and a R:FR ratio of 3.0) produced fruit with greater concentrations of glucose, fructose, and anthocyanins than shaded vines which received no supplemental red light. In a similar study, 'Cabernet Franc' vines grown under artificial (neutral shade cloth) and natural (foliage) shade received similar levels of PFD, but the R:FR ratios of the two treatments were 0.7 and 0.07, respectively.<sup>56</sup> Compared to the controls, both shading treatments reduced berry weight, soluble solids, and anthocyanin concentrations. The effects of natural shade on fruit growth and composition were partially reversed by supplemental red light (R:FR ratio of 3.0) in the fruiting zone indicating the involvement of phytochrome.

By contrast, a study of 'Cabernet Sauvignon' and 'Pinot Noir' fruit exposed to various combinations of light quantity (20 and 1% of ambient PFD) and light quality (R:FR = 1, 0.6, 0.3, or 0.1) indicated that light quantity rather than light quality was of primary importance. A reduction in light quantity from 20 to 1% of ambient PFD, regardless of the R:FR ratio, decreased berry weight and diameter, and delayed the accumulation of sugars, anthocyanins, and phenolics. Also, varying the R:FR ratio under continuous illumination had no influence on anthocyanin accumulation and did not reverse the R to FR mediated anthocyanin synthesis. These results indicate that a photoreceptor which is dependent upon light quantity is most likely involved in the regulation of anthocyanin accumulation in grape berries.

#### 4. Nitrogen Metabolism

The nitrate concentration of grapevine petioles and leaf blades has been shown to be inversely related to the PFD environment.<sup>57</sup> The petiole  $\text{NO}_3$  concentrations of 'Chardonnay', 'Zinfandel', and 'Malbec' vines were five-fold higher and nitrate reductase activity was lower in vines grown at 8% of ambient PFD compared to vines grown in full sunlight. Smart et al.<sup>55</sup> reported that shading increased the concentration of  $\text{NO}_3^-$  in petioles and leaf blades, and the concentration of  $\text{NH}_4^+$  in the leaf blades, peduncles and juice of 'Cabernet Sauvignon'. In addition, supplemental red light partially restored leaf nitrate reductase activity of heavily shaded vines, suggesting a phytochrome mediated regulation of nitrate reductase. However, red light has not stimulated leaf nitrate reductase activity of field-grown *V. vinifera* cultivars (Dokoozlian, unpublished data).

### III. TEMPERATURE

Temperature is the environmental factor primarily responsible for the distribution of *V. vinifera* throughout the world. Grapes are produced in some of the hottest cultivated areas of the earth. Air temperatures in the Jordan Valley of Israel and the interior valleys of California during the summer often exceed 35°C with maximum temperatures approaching 43°C. Over 40% of the grapes produced in China are grown in the Turpan depression of Xinjiang Province, Northwest China, the mean temperature during July is 33°C, daily temperatures exceed 35°C and the maximum is 48°C.<sup>58,59</sup> While the loss of a grape crop due to high temperatures is rare, partial yield loss in individual vineyards can occur. When the daily high temperature increased from an average of 30 to 47°C over a 3-day period in the Coachella Valley of California, clusters of 'Thompson Seedless' grapevines, which had just been girdled (the removal of a strip of phloem from around the trunk), in several vineyards became desiccated and resulted in crop loss (L.E. Williams, personal observation). It is unknown whether this crop loss was due solely to the high temperatures or a combination of high temperature and improper irrigation applications.

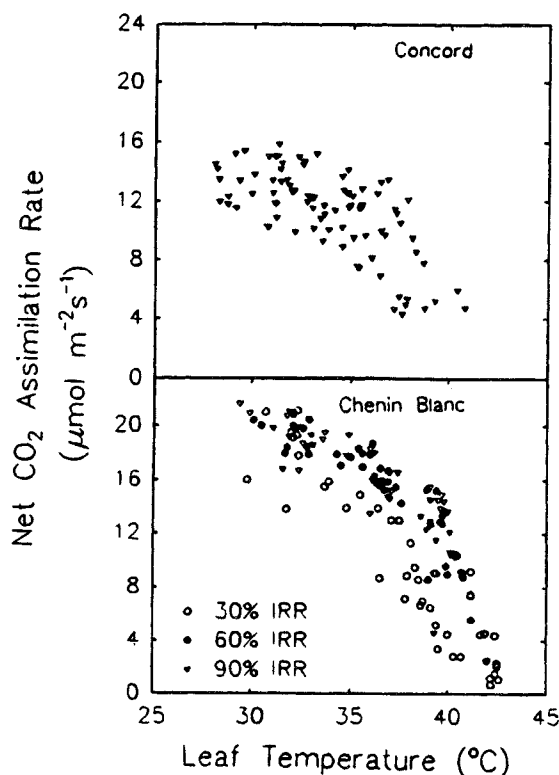
Potential crop loss of grapes due to low temperatures is far greater than that for high temperatures. "Potential crop loss" is used because in many cases, the result of a winter freeze is reported as the percent primary bud loss.<sup>60-62</sup> The interpretation of crop loss is often complicated by the adjustment in pruning practices made by the vineyard managers to compensate for bud injury or compensation by the vine producing fruitful shoots from secondary or tertiary buds, or by increasing total fruit set and berry size.<sup>62,63</sup> Losses due to late spring and especially early fall freezes are less likely to be compensated for by either the vineyard manager or the grapevine. For instance a spring freeze in 1985 caused a reduction in 'Concord' grape yield in the state of Washington from 151,000 tons in 1984 to only 90,000 tons in 1985.<sup>64</sup>

The growth and productivity of many crops are temperature dependent in the range of 5 to 20°C assuming all other factors are non-limiting.<sup>65</sup> One of the first attempts to use this concept was the development of a relationship between air temperatures and the dates of grape harvest.<sup>65</sup> In viticulture, temperature summations (i.e., termed in the literature as degree-days, growing degree days, day degrees, or heat summations) have been used as dependent variables in describing the timing of various grapevine phenological events and growth.<sup>1</sup> Amerine and Winkler<sup>66</sup> used accumulated degree-days above 10°C to formulate recommendations for the growing of wine grape cultivars in California.

While their method has gained wide acceptance, recent studies have indicated that degree-days may not be the most accurate basis for viticultural recommendations.<sup>67,68</sup> A major limitation in calculating degree-days, by taking the mean of the daily maximum and minimum temperatures and subtracting a base temperature, is that periods of fog, cloud cover, or wind, factors which may not affect the daily maximum and minimum temperatures but undoubtedly will affect vine growth. Degree minutes calculated with dataloggers may improve the accuracy of degree-days.<sup>69</sup>

#### A. EFFECTS ON GAS EXCHANGE

Every aspect of plant growth, such as physical processes, enzyme reactions, ion and carbohydrate transport, and membrane permeability, is controlled by temperature. Vine growth and productivity are dependent upon the assimilation of carbon via photosynthesis and subsequent carbon translocation and allocation. The production of biomass is the result of a balance between carbon gains and losses due to respiration, organ death, and other means where biomass may be lost (i.e., pruning, herbivory).

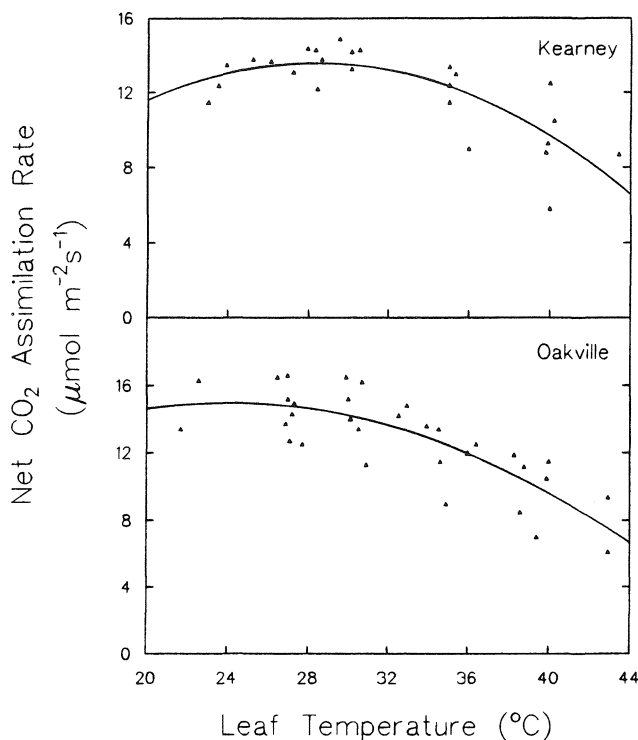


**Figure 6** The effect of leaf temperature on net CO<sub>2</sub> assimilation of 'Concord' and 'Chenin blanc' grapevines grown in Washington, USA. The 'Chenin blanc' vines were irrigated with 30, 60, or 90% of daily evapotranspiration. (R. Wample, unpublished data.)

The optimum leaf temperature for photosynthesis of field-grown grapevines is quite broad; generally between 25 and 35°C<sup>1,29</sup> while other studies have demonstrated a more narrow temperature optimum (25–30°C).<sup>29,30</sup> This variation may be due to cultivar, growth conditions or seasonal variation.<sup>70</sup> This could perhaps also explain some of the variation in the data presented in Figure 6 since it is a compilation of data from several seasons and dates of measurement. Photosynthesis generally declines at temperatures above 35°C, for both American and European species of grapevines, yet a positive A occurs even up to 40°C (Figure 6).<sup>1,30,43,44</sup> It is also noteworthy that the leaf temperature of 'Chenin blanc' vines receiving 90% evapotranspiration replacement barely exceeded ambient temperature, i.e., 40°C, as a result of evaporative cooling. The temperature dependency of A of 'Concord' leaves appeared to be similar to 'Chenin blanc' and reports of other *V. vinifera* cultivars.<sup>1</sup> Thus, air temperatures up to 40°C, unless experienced for an extended period of time would not appear to be a major limiting factor in grape production.

Plants grown in thermally contrasting habitats exhibit photosynthetic temperature responses that reflect an adaptation to the temperature regimes of their respective habitat.<sup>71</sup> The photosynthetic temperature response curves of 'Chenin blanc' grapevines grown in two thermally contrasting climates in California are presented in Figure 7. Although fitted curves for the two data sets were similar at temperatures greater than 32°C, the decrease in A occurred more rapidly for vines grown in the San Joaquin Valley as leaf temperature decreased.

Preconditioning temperatures may also influence photosynthetic processes. Baló et al.<sup>72</sup> found that 3 to 6 h of chilling (6 ± 2°C) had little effect on gas exchange, fluorescence kinetics, and water relations of rooted cuttings of 'Merlot' grapevines. However, durations of over 24 h of chilling caused significant reductions in these variables. Chilling stress (6°C) for 4 h under low light reduced A by 10% for leaves of 'Leanyka' and 20 to 70% in 'Zold veltelini'.<sup>73</sup> The effect was reversible and longer exposure resulted in acclimation and improved A rates. Stomata of 'Leanyka' closed in response to chilling while the

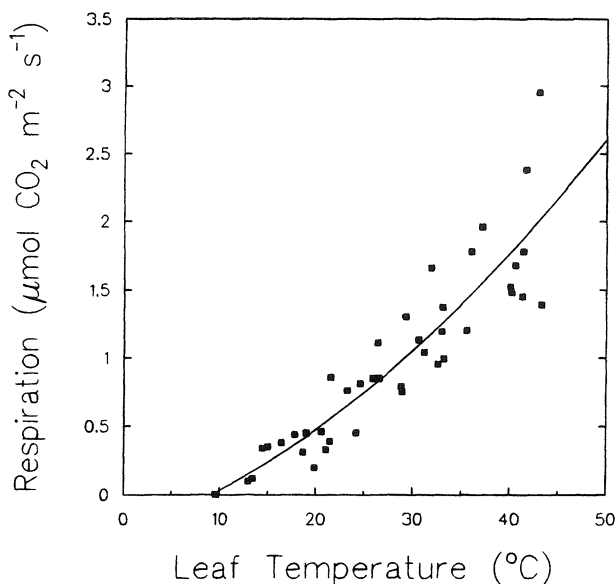


**Figure 7** The effect of leaf temperature on net CO<sub>2</sub> assimilation of 'Chenin blanc' grapevines grown either in the Napa Valley (UC-Davis Oakville Field Station) or in the San Joaquin Valley (UC Kearney Ag Center) of California. Leaves were placed inside temperature controlled cuvettes and net CO<sub>2</sub> assimilation was measured after CO<sub>2</sub> exchange reached steady state (approximately 30 to 45 minutes after the temperature was changed). Data were fit to nonlinear functions: Kearney  $y = -9.4 + 1.62x - 0.029x^2$ ,  $r^2 = 0.62$ ; Oakville  $y = 2.9 + 1.0x - 0.021x^2$ ,  $r^2 = 0.65$ . (L.E. Williams, unpublished data.)

more chilling-sensitive 'Zold veltelini' showed a loss of stomatal control. Both cultivars developed more negative water potentials in response to chilling stress. Sherer<sup>74</sup> found the time for the induction curve of light induced chlorophyll fluorescence to return to a stationary level at 5°C was longer in cold-susceptible cultivars of grapevines than in cold-tolerant cultivars; an indication of a greater effect of chilling on the photosynthetic mechanism of chill-sensitive cultivars.

It is probable that respiration by an entire grapevine commands a large portion of the daily photosynthate as the percentage of photosynthate utilized in respiration by other woody perennial species ranges from 38 to 65%.<sup>75</sup> Respiration can be divided into two components: respiration required for growth and respiration needed for organ maintenance. Carbon requirements for growth and maintenance respiration during the 3 weeks prior to anthesis of an individual grape flower was 0.23 mg CO<sub>2</sub> (3 J) and 0.83 mg CO<sub>2</sub> (10.8 J), respectively.<sup>76</sup> Maintenance respiration costs of mature organs may vary from 0.015 to 0.6 kg CO<sub>2</sub> kg<sup>-1</sup> dry mass d<sup>-1</sup>. Even when little growth is occurring, grapevines still demand large amounts of carbon for maintenance respiration and the larger the plant the greater the carbon requirement.

Temperature is the most important abiotic factor affecting respiration under most conditions.<sup>72</sup> The  $Q_{10}$  of respiration is approximately 2 in the range of physiological relevant temperatures.<sup>77</sup> For example, respiration rate of mature leaves of Perlette grapevines growing in southern California was close to zero at a leaf temperature of 10°C and doubled with each 10°C increase in temperature (Figure 8). Several factors may affect the  $Q_{10}$  and actual rate of respiration such as organ type and age, tissue N content, availability of carbon substrates and growth temperature. For example, leaves of 'Chardonnay' grapevines grown in a cool climate continued to respire down to a leaf temperature of 7°C, at which time respiration rates were too small to quantify (L. E. Williams, unpublished data). It also has been found that the  $Q_{10}$  of grapevine leaf respiration may change during leaf ontogeny (H. Schultz, personal communication).



**Figure 8** The effect of leaf temperature on respiration rate ( $\text{CO}_2$  evolution) of mature leaves of 'Perlette' grapevines grown in the Coachella Valley of California. Measurements were made in temperature controlled cuvettes. (L.E. Williams, unpublished data.)

## B. EFFECTS ON ROOT GROWTH

There is generally little information regarding the effects of high root temperatures on grapevine growth and development or physiology due largely to the depth of rooting and the smaller variations in root, compared to shoot, temperatures. In addition, in many of the hottest viticultural areas, irrigation is a normal practice minimizing root zone temperature fluctuations. Furthermore, the shade provided by the grapevine canopy would reduce the heat load on the soil as will the presence of a cover crop. Thus, high temperature effects on roots of grapevine have received relatively little attention.

By contrast, low temperatures may result in root injury or death. Several reports have shown differences in cold hardiness between rootstock selections<sup>78</sup> and for own rooted commercial cultivars.<sup>79,80</sup> In the colder regions of grape production, temperatures as low as  $-13^\circ\text{C}$  at 20-cm depth have been recorded.<sup>78</sup> Low soil moisture results in lower soil temperatures and increased chance of root injury. Thus, late season irrigation is recommended in viticultural areas that routinely experience low winter temperatures accompanied by low fall and winter precipitation.

## C. HIGH TEMPERATURES

### 1. Species and Cultivar Differences

There has been no comprehensive survey of the high temperature tolerance of *Vitis* species or cultivars, although several species or cultivars have been classified into different groups requiring varying levels of heat units to mature.<sup>81</sup> It was shown that the temperature at which heat injury occurred in leaf discs of 'Venus' was  $48^\circ\text{C}$  while that for 'Veeblanc' was only  $44^\circ\text{C}$ . The same two hybrids in tissue culture were both injured at  $42^\circ\text{C}$ . Damage resulted from irreversible changes in the plasma membrane for both. The loss of membrane function leads to symptoms of water stress.

Fanizza and Ricciardi<sup>83</sup> noted a decline in shoot growth of *in vitro* propagated grape cultivars when subjected to sequential subculture at 35 or  $38^\circ\text{C}$ . Four of the seven cultivars examined showed no apex growth or died at  $35^\circ\text{C}$ ; all cultivars died at  $38^\circ\text{C}$ .<sup>83</sup> Growth rates recovered when temperatures were lowered to  $25^\circ\text{C}$ . The authors were not certain if the reduction in growth was due to a loss in an unknown heat tolerance mechanism of the apices or ageing of the cultures. Pre-rooted cuttings of 'Muscat of Alexandria' grown in growth chambers showed maximum growth and dry weight at 25/20°C day/night temperatures followed by 30/25°C.<sup>20</sup> During the 13 weeks of this study, leaves represented

an increasing percentage of total dry weight; the apparent level of apical dominance with increasing temperature within the temperature range of this study (20 to 30°C).

Buttrose<sup>21</sup> demonstrated that high temperatures increased the number of clusters per shoot. Cluster initiation in 'Muscat of Alexandria' was almost nonexistent at 20°C but increased between 25 and 35°C.<sup>84</sup> Stem dry weight at 20°C increased indicating a change in the sink strength or allocation pattern at this temperature that was not conducive to fruit bud initiation.

The effect of the previous season's temperatures, particularly during the initiation period, on current seasons vine fruitfulness has not been thoroughly researched. Smit<sup>85</sup> studied this in the production of 'Sultana' vines and recognized the potential effect on a commercial level. Unfavorable conditions during the period of bud initiation and early development of the inflorescence primordia lead to a reduction in the crop potential the following year. This reduction in flower initiation and development may be misinterpreted as a reduction in fruit set. Very little is known about the effect of high temperatures on flower buds following initiation, although there appears to be no major detrimental effects on crop production in regions of the world where temperatures often reach 35 to 40°C after flower bud initiation has occurred.

Bud fruitfulness may be affected even during the period just prior to and following budbreak. For example, the number of clusters per shoot was greater at higher temperatures and the number of flowers per cluster was reduced.<sup>86</sup> Hence there is an extended period of time, prior to anthesis, over which the potential productivity of a grapevine can be influenced by temperature.

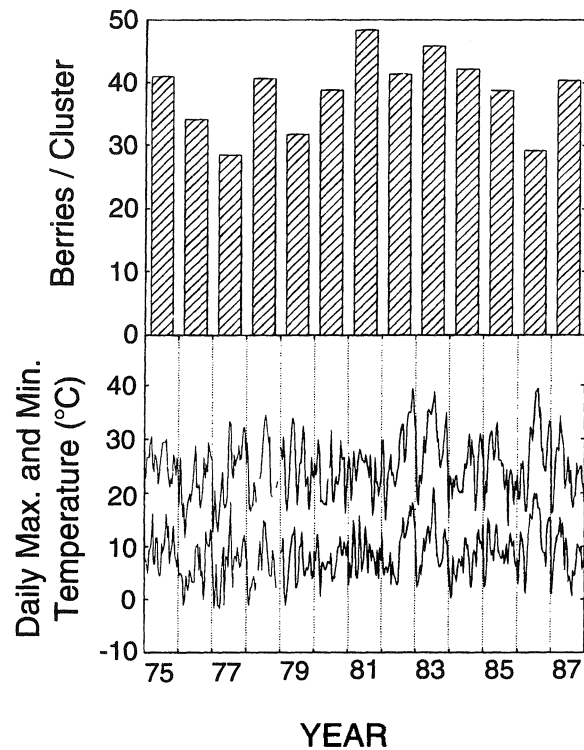
Cluster development following budbreak of container-grown 'Cabernet Sauvignon', 'Shiraz', 'White Riesling', and 'Clare Riesling' potted vines was increased at 32/27 and 38/33 compared to 14/9, 20/15, and 26/21°C, day/night temperatures.<sup>87</sup> The number of days to flowering was reduced from 70 to 18 over this temperature range. There was a difference of only 2 days between the 26/21 and the 38/33 treatments suggesting a reduction in flowering at the higher temperature. In this same paper, maximum fruit set occurred at 20/15°C with no fruit set occurring at either 14/9 or 38/33°C for the cultivar 'Cabernet Sauvignon'. While the above information may not be directly transferable to field-grown vines, the authors note that in most areas where grapes are grown, the temperature rarely reaches these higher levels during the period from budbreak to bloom.

Numerous reports indicate that fruit set in grapes is inhibited by high temperatures.<sup>88-92</sup> Potential causes of reduced set include a reduction in ovule or pollen viability and/or in pollen tube growth, changes in hormonal status and, indirectly, water stress. Kliewer<sup>88</sup> demonstrated a loss of ovule viability for 'Pinot Noir' and 'Carignane' grapes at 35 and 40°C compared to 25°C. Reduced ovule viability, which results in fewer seeds per berry, could contribute to smaller berries and yield based on the known relationship of seed number, hormones, and berry size.<sup>93</sup> Pollen germination and pollen tube growth in Petri dishes was unaffected in 'Muscat of Alexandria' at 35°C compared to 22 or 25°C<sup>94</sup> while that for 'Delaware' (*V. labruscana*) was reduced to about 30% at 30°C compared to 24°C.<sup>89</sup>

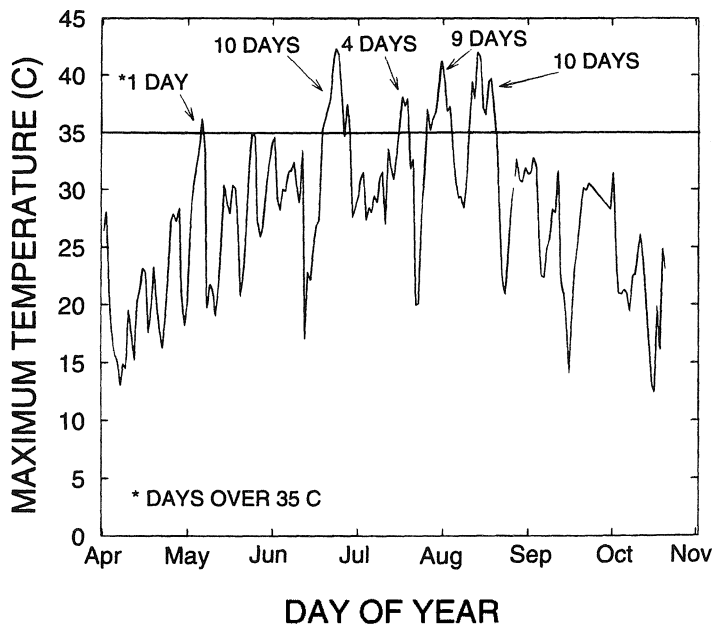
Thirteen years of data collected at over 100 vineyard sites in the Yakima Valley of Washington, showed that high temperatures during bloom did not generally reduce the number of berries per cluster for 'Concord' vines (Figure 9). In fact temperatures above 25°C often gave higher berry set than lower temperatures. This data clearly shows that low temperatures are more detrimental to berry set than high temperatures in this cultivar.

Matsui et al.<sup>95</sup> investigated the effect of plant hormones and high temperature effects on fruit growth of 'Thompson Seedless' and 'Napa Gamay' grapevines. Four-year-old potted vines, with the root temperature being controlled, were subjected to 40/22°C (day/night) for 4 days and fruit development compared to plants held in a greenhouse (temperature range 22 to 32°C). Pre-stress treatment with gibberellic acid (GA<sub>3</sub>) or GA<sub>3</sub> plus a cytokinin (benzyladenine) partially overcame the negative effect of high temperature on berry size and total soluble solids accumulation. Only GA<sub>3</sub> overcame the effect on berry weight. Estimates of total endogenous GA<sub>3</sub> levels from 'Thompson Seedless' berries indicated a reduction in the level and a change in the qualitative nature due to heat stress and suggests the reason for recovery with GA<sub>3</sub> applications.

High root temperatures (20 vs. 11°C) have also reduced the number of berries per cluster in 'Cabernet Sauvignon'.<sup>96</sup> High air temperatures do not always have a deleterious effect on fruit development. For example during 1992, the U.S. Pacific Northwest experienced two periods of 10 days or greater when the temperature was 35°C or higher (Figure 10). However, fruit maturation occurred from 2 to 4 weeks earlier than average with normal crop loads for this grape production area.



**Figure 9** Number of berries per cluster and daily maximum and minimum temperatures for 2 weeks before and 2 weeks after full bloom of ‘Concord’ grapevines grown in the Yakima Valley of Washington, US, from 1975 to 1987. Data represent the mean of approximately 100 different vineyard sites. (R. Wample, unpublished data.)



**Figure 10** Daily maximum, ambient temperatures during the 1992 growing season at Paterson, Washington, US. The number of days in which the maximum temperature exceeded 35°C are at the top of the graph. (R. Wample, unpublished data.)

## 2. Effects on Water Relations

Differences have been found in the stomatal response of grape cultivars to temperatures ranging from 34 to 43°C.<sup>97</sup> 'Cardinal' showed the least response to heat stress although the control treatment (25 to 29°C) had a relatively low  $g_s$  compared to the other cultivars studied. The response of 'Chardonnay' and 'Chenin blanc' to heat stress was similar whether measured on a diurnal basis or over 4 to 12 days. This work underscores the influence of vapor pressure deficit when evaluating  $g_s$  in heat-stressed vines (see Humidity Section).

## 3. Other Physiological Processes

Growth of grapevines, as well as other plants, at constant high temperatures (>35°C) for extended times (>30 days) is also important as an essential procedure in the elimination of viruses, viroids, mycoplasmas, and perhaps some bacteria. The effect of such treatment appears to have more effect on the microorganism than the grapevine. The response of grapevines to high temperatures and elevated CO<sub>2</sub> concentrations has been examined.<sup>98</sup> Rooted cuttings of 'Cabernet Sauvignon' subjected to heat treatment and elevated (1200–1300 ppm) CO<sub>2</sub> levels manifested a reduced transpiration (E), elevated A and growth rates and a change in the allocation of photosynthates that promoted more root growth. Increased A was apparently due to reduced nonstomatal limitations of carboxylation and a lower level of photorespiration since  $g_s$  was lower.

Excessively high temperatures for extended periods of time generally result in a delay of fruit maturation, and a reduction in fruit quality.<sup>99–103</sup> Both of the above characteristics have been associated with a decline in total titratable acidity and increased pH<sup>104</sup> caused primarily by a reduction in the synthesis and the increased catabolism of malic acid;<sup>105</sup> increased mono- and di-basic salts of tartaric acid and di-basic salt of malic acid have also been noted.<sup>101</sup> High temperatures also reduce color development of grape berries.<sup>88,102</sup> For example, at 35°C pigment development was completely inhibited in 'Tokay' and reduced in 'Cardinal' and 'Pinot Noir' compared to 20 or 25°C.<sup>106</sup> In general, cool nights or days improve coloration and a beneficial effect of night cooling by sprinkling has been found<sup>103,107,108</sup> and has become a commercial practice in other fruit crops such as apple. Such a practice in grapes should be carefully managed to prevent disease problems from developing in the fruit and canopy.

High temperatures can also affect the partitioning of photosynthates within the leaf. As temperature increased the concentration of starch within the leaves of 'Cabernet Sauvignon' vines decreased.<sup>109</sup> For example, leaf starch concentrations of vines grown in growth cabinets and exposed to day temperatures of 18, 25, and 35°C were 23.3, 10.9, and 1.3% of dry weight, respectively. Increasing leaf temperature resulted in a shift in lipids from 5.8 to 16% of dry weight over this same temperature range. Interestingly, total chlorophyll content increased from 0.6% of dry weight at 18°C to 1.2% (equivalent to 5.6 mg dm<sup>-2</sup>) at 35°C. Roper and Williams<sup>40</sup> reported that the starch levels in field-grown grapevine leaves from a warm climate also remained very low. However, it is not clear if changes in lipids and chlorophyll will occur under field conditions.

Translocation of photosynthates, a major factor in fruit development and maturation, may be influenced by high temperatures. Sepulveda et al.<sup>110</sup> exposed a mature leaf of non-bearing 'Chenin blanc' and bearing 'Chardonnay' grapevines to <sup>14</sup>CO<sub>2</sub> for 30 minutes after 4, 8, or 12 days in a greenhouse (29/15°C) or a phytotron (40/20°C). Twenty-four h after <sup>14</sup>CO<sub>2</sub> exposure, heat stress enhanced the transport of <sup>14</sup>C photosynthates to the shoot tip at the expense of the roots, trunk, and clusters. High temperatures did not reduce A. Sucrose concentrations increased in all vine organs due to heat stress in both cultivars. Heat-stressed 'Chardonnay' vines had lower concentrations of glucose and fructose in the fruit.

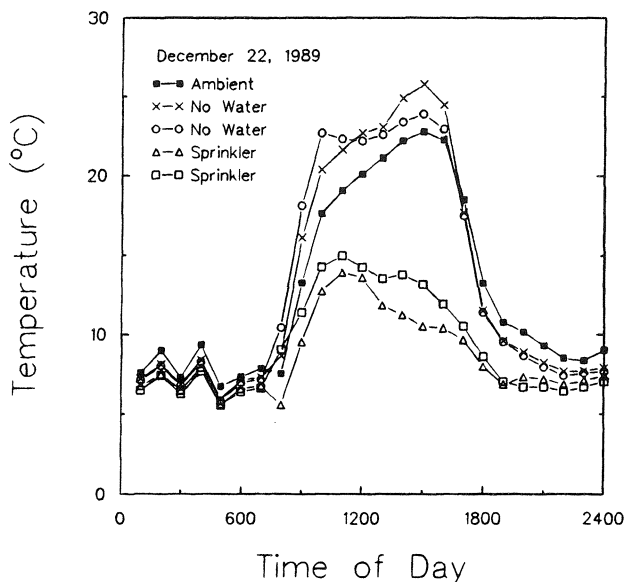
## 4. Vine Adaptations

Like many other living organisms, the genus *Vitis* is presumed to produce heat-shock proteins (HSP) which apparently play a role in the metabolism of other proteins and in their protection against thermal degradation.<sup>111</sup> Despite the apparent heat tolerance of *Vitis* spp. the authors are not aware of any reports that demonstrate the importance of HSP in grapevines.

## D. LOW TEMPERATURES

### 1. Chilling

Grapevines vary greatly in chilling tolerance. A brief period of chilling (4 h) caused only a 10% reduction in A in the cultivar 'Leanyka' but as much as a 70% reduction in 'Zold veltelini' but in both



**Figure 11** The effect of evaporative cooling on bud temperature of 'Perlette' grapevines grown in the Coachella Valley of California. Vines were either cooled with overhead sprinklers while the controls were not sprinkled with water. Bud temperatures were measured with hypodermic thermocouples connected to a data logger. Individual data points are the hourly means of bud or ambient temperatures measured every minute. (L.E. Williams, R. A. Neja, and E. A. Walker, unpublished data.)

cases this was reversible within 24 h.<sup>76</sup> Some recovery in photosynthetic capacity occurred following chilling periods longer than 12 h. McIntyre et al.<sup>67</sup> working with 100 cultivars of grapes in Davis, CA reported that differences in susceptibility to either spring or fall frosts were dependent upon phenology (i.e., date of budbreak or fruit maturation). This demonstrates the possibility of two levels of tolerance to chilling temperatures. First is the inherent genetic tolerance to low temperatures and the second the effect of environmental and management factors on vine phenology which may confer more or less risk to a low temperature event.

## 2. Effects on Growth

Although there is some controversy regarding the absolute chilling requirement of grapevines,<sup>112</sup> evaporative cooling and other practices are used to achieve more rapid and uniform budbreak in many warm grape growing areas.<sup>113,114</sup> Evaporative cooling reduced bud temperatures by 10 to 15°C (Figure 11), and resulted in increased yield, and advanced, more uniform berry maturity.<sup>113,114</sup> Chilling has also been linked to decreased catalase enzyme activity in grapevine buds and this has been associated with release from dormancy.<sup>115</sup> Weaver and Iwasaki<sup>116</sup> reported that 4 to 8 weeks of chilling (0°C) were required for rapid and uniform budbreak of 'Zinfandel' grape. They were unable to establish any meaningful relationship between either free or bound ABA and bud response to chilling or calcium cyanamide treatment. Takeno et al.<sup>117</sup> showed that chilling somatic embryos of hybrid grape (*V. vinifera* × *V. rupestris*) for 1 week at 4°C caused an increase in GA-like activity which declined during the second and third week of chilling.

Roubelakis and Kliever<sup>91</sup> reported cultivar differences in fruit set at day/night temperatures of 15/10°C. Higher light intensities enhanced fruit set at those temperatures. Fruit set in 'Concord' appeared more sensitive to high (32–35°C) than to low (15–18°C) temperatures.<sup>90,118</sup> The temperature range associated with maximum fruit set for most species/cultivars has been between 20 and 30°C.

Several studies have reported an improvement in vine microclimate with evaporative cooling during the growing season.<sup>103,108,109</sup> Evaporative cooling during this stage of vine growth results in changes in vine temperature and vapor pressure deficit (VPD) and may improve vine water relations, photosynthesis, and fruit quality. In Montpellier, France, it was observed that maximum shoot growth occurred at 28°C and that growth ceased at 10°C and below.<sup>120</sup>

### 3. Effects on Water Relations

Chilling of container-grown *V. vinifera* cvs. in controlled environment chambers for more than a few hours decreased plant water potential ( $\Psi$ ) despite a significant reduction in  $g_s$  indicating that water uptake and/or transport might have been affected.<sup>75,76</sup> However, it is possible that increased water stress was the result of much lower root temperatures (or a greater rate of temperature reduction) in the growth chamber than would have been experienced under field conditions. Cold nights ( $<10^\circ\text{C}$ ) have also induced higher leaf resistances the following day in 'Concord' vines grown in New York. This inhibition of stomatal opening appeared to be independent of  $\Psi$ , and it was speculated that this might be due to a chilling-induced reduction in starch hydrolysis and an inhibition of A.

Thus it seems that chilling may have both direct and indirect effects on plant water relations. Unfortunately, there are few field studies on the effects of chilling on grapevines to help clarify our understanding. This research could be valuable in viticultural areas where low ( $0\text{--}10^\circ\text{C}$ ) temperatures are common during the growing season.

### 4. Other Physiological Processes

Ahmedullah<sup>121</sup> found that exposing 1-year-old 'Cardinal' grapevines to  $15^\circ\text{C}$ , as compared to  $25^\circ\text{C}$ , led to increased basipetal transport of photosynthates. He also found a higher rate of total recovery of  $^{14}\text{C}$ -labelled photosynthates at  $15^\circ\text{C}$  indicating a lower respiration rate (see Figure 8). In some viticultural areas, the night time temperatures often, even in mid summer, drop to  $15^\circ\text{C}$  or lower. Increased basipetal transport of photosynthates coupled with lower rates of respiration at night may contribute to more rapid fruit maturation and may account for the ability to mature some cultivars of grapes in areas that would not appear to have enough heat units.

To our knowledge there has been very little research designed specifically to evaluate grapevine adaptations to chilling. However, the above-mentioned reports indicate that grapevines can acclimate and adjust to changing temperatures.

## E. FREEZING TEMPERATURES

### 1. Cultivar Tolerance

A wide range of cold hardiness exists in the genus *Vitis* and this genetic variation has been utilized in breeding and cultivar evaluation programs.<sup>122</sup> In a report covering 88 European, 34 American, and 14 French Hybrid cultivars, Clore et al.<sup>123</sup> ranked grapevine cold hardiness and demonstrated the wide range in genetic cold hardiness potential.

Cold hardiness may encompass mid-winter hardiness as well as spring and fall frost hardiness. Mechanisms of cold hardiness may involve tolerance and/or avoidance. For instance, avoidance of spring frost damage due to late budbreak is an important distinction from the ability to survive (i.e., tolerate) frost. Species as well as cultivar differences in timing of budbreak, flowering, and fruit maturation are important in the selection of grapes for a given vineyard. McIntyre et al.<sup>67</sup> found up to 25 days difference in budbreak and more than 100 days difference in the maturity date among 100 cultivars. Often, cultivars with early budbreak are susceptible to spring frost but are also early maturing thereby avoiding crop losses due to fall frost. It appears that vines whose origins are further from the equator are more sensitive to changes in photoperiod and thus less susceptible to fall frost.<sup>124</sup>

An example documenting the need to understand this relationship was reported by Wolf and Cook<sup>125</sup> who found that 'Cabernet Franc' was 1 to  $2^\circ\text{C}$  more hardy throughout the winter than 'Cabernet Sauvignon'. However, 'Cabernet Franc' deacclimated more rapidly in the spring and was more susceptible to spring frost or late winter freeze. Comparable results also were found examining the deacclimation of 'Concord', 'White Riesling', and 'Cabernet Sauvignon'.<sup>125</sup> Similarly, Proebsting et al.<sup>126</sup> reported that although cold hardiness of 'Concord' buds was much greater than either 'White Riesling' or 'Cabernet Sauvignon', they deacclimated 1 to 2 weeks earlier thereby explaining the greater crop loss for 'Concords' compared to wine grapes in Washington during a major spring frost on April 28, 1985.

Differences in cold hardiness within a *Vitis* species may be influenced by changes in temperature and water content. Damborska<sup>127</sup> found that warm temperatures induced a cultivar and/or season-specific reduction in cold hardiness. 'Riesling' maintained its hardiness better than 'Muller-Thurgau' in mid-winter after exposure to 10, 12, or  $15^\circ\text{C}$ , although 'Riesling' was less cold hardy in the spring. Such cultivar- and species-specific changes were also evident during a winter freeze in the U.S. Pacific Northwest during December 1990. Bud injury following a brief (36 h) period of high temperatures

Table 1 Percent of primary and secondary bud injury of seven cultivars of *Vitis vinifera* and *V. labruscana* cv. Concord as affected by irrigation

| Cultivar           | Bud injury (%) |           |          |           |
|--------------------|----------------|-----------|----------|-----------|
|                    | Irrigated      |           | Stressed |           |
|                    | Primary        | Secondary | Primary  | Secondary |
| Chenin Blanc       | 98.8           | 64.3      | 97.5     | 60.5      |
| Chardonnay         | 96.0           | 64.3      | 87.0     | 67.0      |
| Cabernet Sauvignon | 96.3           | 73.5      | 81.3     | 52.5      |
| Gamay Beaujolais   | 59.0           | 16.0      | 56.0     | 26.0      |
| Meunier            | 58.0           | 27.0      | 39.0     | 13.0      |
| Pinot Noir         | 71.0           | 39.0      | 53.0     | 33.0      |
| Semillon           | 100.0          | 97.0      | 100.0    | 96.0      |
| Concord            | <19.9          | <5.0      | <10.0    | <5.0      |

*Note:* Data were collected following a severe winter freeze in December, 1990. Percentages represent the mean of 10 or more vines and 100 or more dissected buds per vine. Stressed vines had received only one irrigation compared to 4 or more for irrigated vines.

From Wample, R., unpublished data.

(10°C) was followed by temperatures as low as  $-28^{\circ}\text{C}$  is presented in Table 1. A consistent reduction in primary bud injury was associated with less irrigation the previous season for all but 'Concord' grapevines. Mild water stress during bud development appears to improve winter survival and is associated with smaller cane diameter and shorter internodes. Wolpert and Howell<sup>128</sup> noted the importance of low water content on cold hardiness development during early acclimation. Our understanding of temperature and water interactions on grapevine bud, cane, and trunk cold hardiness is incomplete and in need of additional research.

## 2. Effects on Vine Growth

Growth following freezing injury may be separated into events that occur pre- and post-budbreak. In a pre-budbreak state, low temperature injury may influence one or more of the following: the primary, secondary, or tertiary bud; the phloem of the trunk and canes or roots; the xylem parenchyma of the trunk and canes or roots; and/or the vascular and cork cambia of the permanent structures. The simplest and perhaps the most frequent case, low temperature injury of the primary bud, results in very few changes in overall growth of the vine, but frequently results in a significant loss of yield for that season. Some cultivars such as 'Tokay' and 'Folle blanche' have fruitful secondary buds and may still produce nearly a full crop.<sup>129,130</sup> Loss of more than the primary bud is often accompanied by damage to other vine organs, frequently resulting in the loss of permanent structures and requires retraining of the vine if it survives. This is a major problem in grafted vines and either regrafting or replanting may be required if the scion is completely killed.

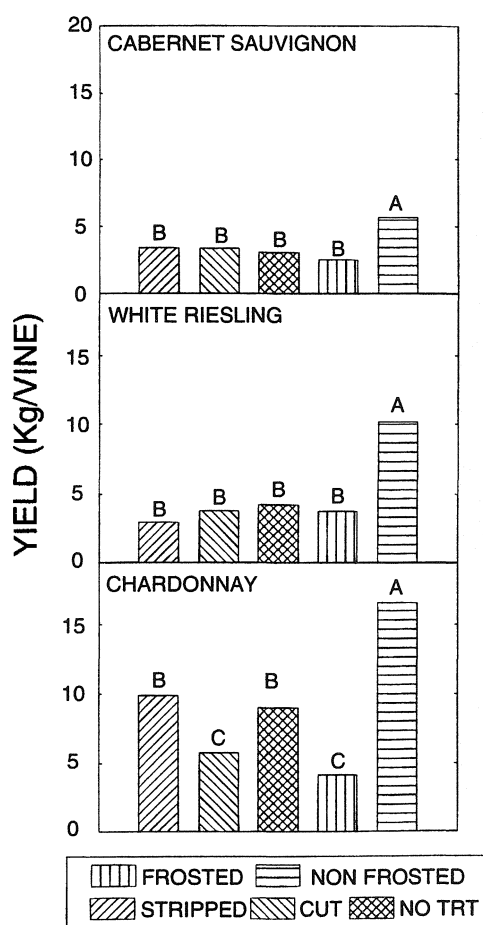
Situations have been recorded where the root system has been injured by low temperature while the majority of the shoot system has been undamaged. This occurred during the winter of 1978–79 in the Pacific Northwest of the United States when a shortage of irrigation water was combined with very little rainfall after harvest. This led to dry soils and resulted in freezing to a depth of 30 to 40 cm. Air temperature varied between 0 and  $-20^{\circ}\text{C}$  which resulted in a minimum of bud damage but significant root damage. In the spring, budbreak occurred and shoot growth began normally. After a few weeks of shoot growth, and during a very warm period, the injured root system was unable to meet the water requirements of the shoot system and resulted in the collapse of the green shoots and in many cases vine death. Although not confirmed, there appeared to have been effects of this root damage as much as 3 to 5 years later, as the root system became infected by soil born pathogens.

Low temperature injury may facilitate the development of crown gall [*Agrobacterium tumefaciens* (E.F. Smith and Townsend) Conn, biovar 3] in grapevines which may be more deleterious than low temperature injury itself. Therefore, propagation wood should be from crown gall free vines when possible. Methods of eliminating this bacteria from grapevine cuttings are proceeding.<sup>131–134</sup>

The extent of injury when freezing occurs after budbreak depends upon the severity of the freeze and the subsequent management of the vines. Winkler<sup>129</sup> studied frost injury to 'Thompson Seedless',

'Malaga', and 'Tokay' grapes during the spring of 1932 and 1933. He concluded that if the injury did not extend basipetally beyond the clusters there was little need to adjust the vine. However, if the injury extended below the clusters in cultivars with fruitful secondary and tertiary buds, removal of the shoots to stimulate the growth could result in increased yields. In cultivars with non-fruitful secondary and tertiary buds it made little difference to the present year's crop whether or not the frosted shoots were removed. However, the development of the next years fruiting wood was improved by shoot removal if the injury were such that an excessive number of axillary buds began to grow. Lider<sup>135</sup> in a similar study in the spring of 1964 on 'Folle blanche', 'Cabernet Sauvignon', and 'White Riesling', found that doing nothing was the most economical practice following frost injury. He was unable to confirm the benefit of shoot removal in 'Folle blanche' which reportedly has fruitful secondary buds. A study of 'Chardonnay', 'White Riesling', and 'Cabernet Sauvignon' in Washington (Stimson Lane Wine and Spirits, personal communication) confirmed the results of Lider in that "no treatment" was the most economical practice following frost injury. Despite some significant differences in the number of clusters per vine and cluster weight due to post-frost treatments, there was no difference in yield for 'Cabernet Sauvignon' or 'White Riesling' (Figure 12). For 'Chardonnay', however, shoot removal following frost injury significantly reduced yield.

Pratt and Pool<sup>136</sup> have provided an anatomical description of the recovery of canes of *V. vinifera* from simulated freezing. They found that recovery was dependent upon a sufficient quantity of viable undifferentiated tissues (cork and vascular cambia, and xylem and phloem parenchyma) capable of undergoing cell division. In the case of bud injury, a surviving lower-order bud was required to replace those injured since adventitious buds in grapes have not been reported. The apparent required characteristics for recovery included an apical meristem and at least two vascular traces.



**Figure 12** Yield response of 'Cabernet Sauvignon,' 'White Riesling' and 'Chardonnay' vines following spring frost injury during May 1992 in Washington, US. Treatments included removal of the partially frosted shoots by hand (stripped), removal of the frosted portion of the shoot with hand shears (cut), no treatment of partially frosted shoots (no trt), vines that were severely frosted with no additional treatment (frosted), and control (non-frosted) vines. Columns with different letters are significantly different at the  $p = .05$  level or better. (R. Wample, unpublished data.)

### 3. Effects on Water Relations

Continuous periods of below freezing, non-lethal temperatures often result in the formation of extracellular ice which has the consequence of establishing a strong vapor pressure gradient between the extracellular water and the liquid water in the cells. The slow, continuous diffusion of water out of the cells to the extracellular ice results in an increase in grapevine cold hardiness.<sup>126,127,138-140</sup> This occurs through a combination of reduced cellular water content, a concentration effect of the cellular solutes and additional physiological changes in membrane and protein structure.<sup>158</sup> This “water transfer” process appears to occur in buds but may not take place in cane and trunk tissues.<sup>141</sup> Results similar to these for *V. riparia* have been noted for several cultivars of *V. vinifera* including ‘Cabernet Sauvignon’, ‘White Riesling’, and ‘Chenin blanc’.

As a part of the acclimation process, the formation of tyloses and other vascular blockages play a role in the reduction of vine water content.<sup>142,143</sup> Vascular blockages also have the effect of inhibiting the rehydration process during the winter and may be important in the maintenance of low water content throughout most of the dormant period. One of the hazards near the end of dormancy is the rehydration of cane and bud tissues which if followed by subfreezing temperatures results in significant vine injury.

### 4. Other Physiological Processes

Nitrogen nutrition is related to grapevine performance, and may influence cold hardiness.<sup>144</sup> A review of the literature found little evidence to support the contention that high nitrogen nutrition resulted in direct loss of grapevine cold hardiness.<sup>145</sup> Nitrogen metabolism in grapevines during the acclimation and dormant periods is known to be dynamic.<sup>146-148</sup> Total and protein nitrogen levels rise at the onset of acclimation and continues into the second phase of hardening.<sup>147</sup> Higher levels of total nitrogenous substances were found in the more cold hardy cultivars.<sup>147</sup> Higher nitrogen concentration may have resulted from the slower growth rate of these cultivars, and are thus indirectly related to cold hardiness. Similarly, it has been shown that grafting European grapevines onto winter-hardy American rootstocks led to higher mid-winter nitrogen levels and improved cold hardiness.<sup>149</sup> High protein to total nitrogen ratios have also been linked with more winter-hardy cultivars.<sup>148</sup> Despite these reports, two recent publications indicate little or no effect of different nitrogen nutrition levels on the cold hardiness and survival of ‘Chardonnay’<sup>150</sup> or ‘White Riesling’<sup>151</sup> grapevines.

Cold acclimation and near freezing temperatures have been associated with increases in the soluble carbohydrate levels found in bud and cane samples of grapevines.<sup>151-156</sup> Low temperatures influence the magnitude of the apparent conversion of starch reserves into soluble carbohydrates, but the absolute nature of this relationship is not fully understood. The concentrations of soluble carbohydrates are slightly lower in cane tissues than in buds, but relative seasonal changes were similar.<sup>151,156</sup> Sucrose is the primary soluble carbohydrate with glucose and fructose making up the majority of the balance. Sucrose levels appeared to peak during late winter and early spring while glucose and fructose declined during this time.<sup>155,156</sup> Starch levels showed an inverse relationship to soluble carbohydrates.<sup>151,156</sup>

Increased solute concentrations have been correlated with cold hardiness and deep supercooling (the presence of water in a liquid state below the normal ice nucleation point) of grapevine tissues.<sup>157</sup> Although some reports have associated the rise in soluble carbohydrates with a cause and effect relationship with grapevine cold hardiness, the increase in soluble carbohydrates is probably responsible for only a few degrees freezing point depression and therefore cannot account for the changes in hardiness observed.<sup>151,156,158</sup> Deep supercooling, the primary cold hardiness mechanism in grape,<sup>157,159</sup> is not known to be directly related to the level of soluble carbohydrates.<sup>151,156</sup>

### 5. Vine Adaptations

Supercooling has been associated with the geographic distribution of some plants.<sup>158</sup> However, because the temperature at which the low temperature exotherms occur varies with different species and cultivars, precise distribution limits have not been established for all *Vitis* species. It may be possible to estimate the limits of distribution for a given cultivar if its minimum exotherm temperature were known and were compared with low temperature isotherms for a geographical area. Other adaptations that exist in some *Vitis* species are the deposition of callose and suberin in the phloem and phellem, which reduces the uptake of water during dormancy and limits mechanical injury due to intracellular ice formation.<sup>142</sup>

The ability of different cultivars of grape to respond to photoperiod is important to survival in cold climates. A synergistic effect of photoperiod and temperature enhanced the development of cold hardiness in ‘White Riesling’ grapes.<sup>160</sup> Fennell and Hoover<sup>161</sup> reported similar responses for *V. labruscana* and

*V. riparia* but with distinctions between these species. Interruption of the dark period did not significantly affect the cold hardiness of 'Concord' buds out to the 12th node or in the extent of cane maturation.<sup>162</sup> They did record more actively growing shoots on the night interrupted vines.

## IV. WATER STRESS

Grapevines are often cultivated in regions of low rainfall and high evaporative demand and if irrigation is limited vines may experience some water stress during the growing season. Reviews of the effects of water stress on various aspects of grapevine growth and physiology have recently been published.<sup>1,2,163,164</sup> Therefore, in this section we will review much of the basic aspects of vine water stress and whatever new information has been published since 1989. In addition, preliminary data from an irrigation experiment with treatments varying from 0 to 140% of vine water use, determined with a weighing lysimeter, will be included to demonstrate trends between available water and vine response.

### A. HUMIDITY

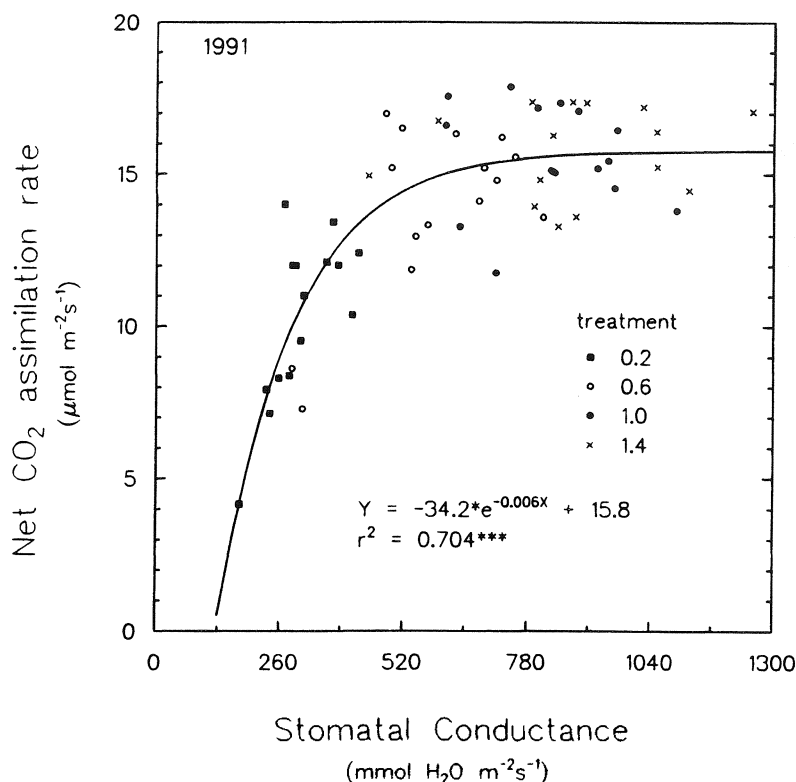
Experimental evidence indicates that the reduction in  $g_s$  induced by abscisic acid causes heterogeneous stomatal closure in many plant species<sup>165</sup> including *V. vinifera*.<sup>166</sup> Heterogeneous stomatal closure in response to ABA may be associated with the species' mesophyll anatomy.<sup>165</sup> It appears that plant species having their leaf mesophyll separated into intercellular chambers hermetically sealed from other areas (heterobaric type as compared to homobaric type mesophyll anatomy) will respond to ABA applications or stress with non-uniform stomatal closure<sup>167</sup> although there are exceptions.<sup>168</sup> Heterogeneous stomatal behavior will provide erroneous infrared gas analyzer-calculated values of intercellular  $CO_2$  concentrations ( $C_i$ ) as a result of the nonlinear relationship of  $g_s$  and  $A$ .<sup>166</sup>

Stomata are controlled by numerous environmental factors (in addition to internal factors). Generally an increase in VPD above a certain threshold, causes a reduction in  $g_s$  in most plant species<sup>169</sup> including *Vitis* spp.<sup>170</sup> The effect of VPD on  $g_s$  of grapevines is cultivar dependent.<sup>35,170</sup> Düring<sup>167</sup> recently has shown that high VPD in addition to ABA causes non-uniform stomatal closure in *Vitis* species as determined by the water infiltration technique.

The response of  $A$  to VPD may differ from that of  $g_s$  in *V. vinifera* depending on where on the curve of the relationship between  $A$  and  $g_s$  the measurements were taken. The relationship between  $A$  and  $g_s$  of field-grown 'Thompson Seedless' grapevines is curvilinear with maximum  $A$  leveling off at a conductance to water vapor of approximately  $500 \text{ mmol m}^{-2} \text{ s}^{-1}$  (Figure 13). Thus, there may be a reduction in  $g_s$  due to an increase in VPD without a concomitant decrease in  $A$  when measurements are taken beyond the linear portion of the curve. Düring<sup>170</sup> found a linear decrease in both  $A$  and  $g_s$  with increasing VPD, however, he also found that  $A$  and  $g_s$  were linearly related up to a  $g_s$  of  $160 \text{ mmol m}^{-2} \text{ s}^{-1}$ , the maximum  $g_s$  measured in that study. This would be equivalent to the linear portion of the curve in Figure 13.

Decreases in  $g_s$  due to increases in VPD may also be more pronounced for vines grown under drought conditions.<sup>171,172</sup> Stomatal conductance decreased significantly when 'Müller-Thurgau' and 'Riesling' vines were grown with an aerial environment kept at 50% relative humidity (RH) and soil water content maintained at 60% of field capacity compared to vines grown at 50% RH and a soil water content held at 95% of field capacity.<sup>172</sup> This response can also be measured on field-grown vines. Stomatal conductance decreased as VPD increased throughout the day for vines receiving less than full vineyard evapotranspiration ( $ET_c$ ) (Figure 14). An increase in VPD from 1 to 3 kPa reduced  $g_s$  50 and 75% for vines irrigated at 60 and 20%, respectively, of vine water use determined with a weighing lysimeter. In semi-arid environments, such as found in the San Joaquin Valley of California, VPD and ambient temperature are highly correlated.<sup>174</sup> Therefore, the relationship between  $g_s$  and ambient temperature are similar to the relationship found in Figure 14 for this particular data set.

Investigations into the response of grapevine growth and development to VPD are limited. If carbon assimilation is decreased due to VPD effects on  $g_s$  then one would expect a reduction in vine growth. In addition, high evaporative demand may also induce water stress again limiting the uptake of  $CO_2$ . A study conducted in growth cabinets demonstrated that vines grown under low RH (50 compared to 95% RH) produced more leaf but less stem (main axis of shoot) biomass than vines grown under the higher humidity.<sup>172</sup> There was no effect on dry matter partitioning to the root. It also was shown that budbreak occurred earlier and more buds broke at 95% RH than at 50% RH in that study for both



**Figure 13** The relationship between net CO<sub>2</sub> assimilation rate and stomatal conductance of 'Thompson Seedless' grapevines measured at solar noon approximately every 2 weeks throughout the 1991 growing season. Vines were irrigated daily at various fractions (treatments 0.2, 0.6, 1.0, and 1.4) of vine water use determined with a weighing lysimeter. A complete description of the weighing lysimeter is found in Phene et al.<sup>173</sup> (L.E. Williams, unpublished data.)

'Müller-Thurgau' and 'Riesling'. The effect of VPD on reproductive development of the current season's crop in grape is unknown.

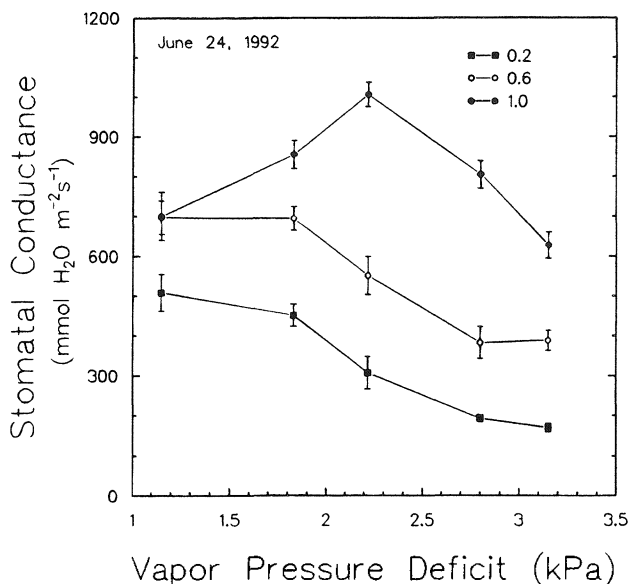
## B. DROUGHT

As mentioned earlier in this chapter the majority of the grape production areas of the world are characterized by Mediterranean type climates having warm to hot temperatures and little rainfall during the summer. Supplemental irrigation, therefore, is necessary if one is to produce a harvestable crop of high quality. However, irrigation generally is not permitted in European Community (EC) vineyards where grapes are destined for "quality wine" while in many other viticultural areas throughout the world the availability of supplemental water is limited. Therefore, vines may undergo a considerable amount of water stress sometime during the growing season in these viticultural production areas.

### 1. Species and Cultivar Tolerance

It is thought that the cultivation of the grapevine began during the Neolithic era (6000–5000 BC) in the region known as Transcaucasia.<sup>1</sup> By 4000 BC grape growing extended from Transcaucasia to Asia Minor and into the Nile Delta. Many of these regions today are characterized by low summer rainfall and periods of drought. It is probable that many of today's grape cultivars evolved in warm climates with little rainfall during the growing season and therefore may have indirectly been selected early for drought tolerance.

There have been attempts to classify both *V. vinifera*<sup>175</sup> and rootstock cultivars<sup>176</sup> with regards to drought tolerance although the basis for the rankings are not necessarily given. It is thought that *V. vinifera* is very drought-tolerant, and the American species *V. berlandieri* and *V. cordifolia* also are



**Figure 14** The relationship between stomatal conductance of 'Thompson Seedless' grapevines and vapor pressure deficit (VPD). Measurements were taken at 2-h intervals during the day. Thus, the measurements obtained at the highest VPDs were collected subsequent solar noon (at 1500 and 1700 h) at which time solar radiation may have become a limiting factor. Each value is the mean of nine individual leaf replicates. The numbers in the upper right corner of the figure represent the fraction of full vine-water use the treatments received. (L.E. Williams, unpublished data.)

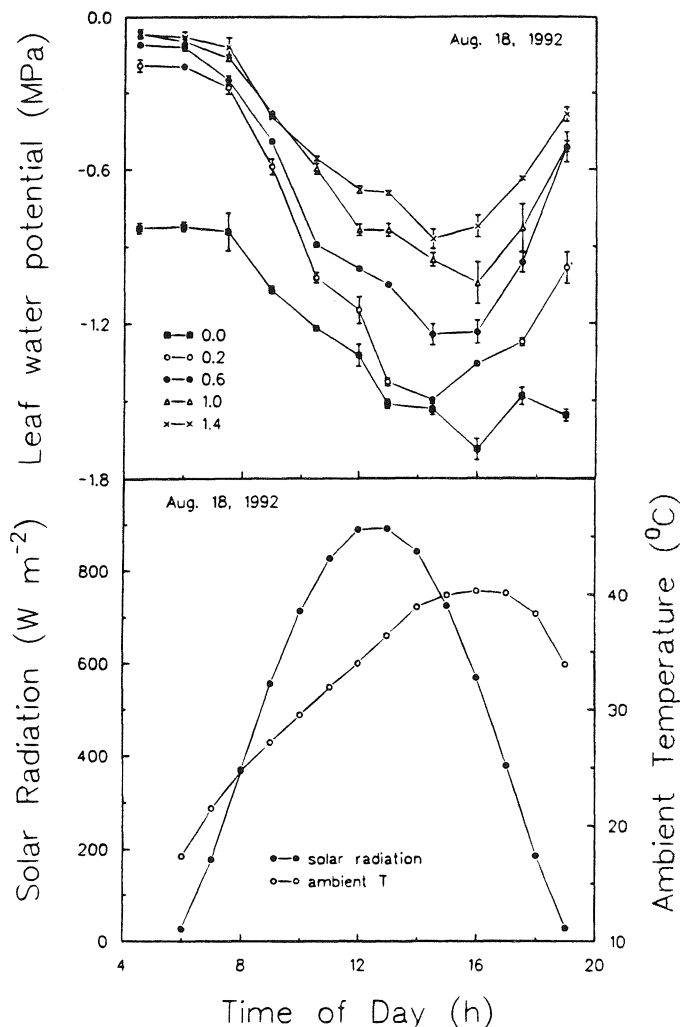
known for their drought tolerance.<sup>177</sup> Galet<sup>178</sup> has classified the performance of the hybrids of *berlandieri-rupestris* as the most satisfactory in very dry soils. *V. riparia* and *V. rupestris* are thought to be sensitive to soil-water deficits.<sup>177</sup>

## 2. Effects on Vine Water Relations

Grapevine  $\Psi_i$  will undergo diurnal fluctuations<sup>1,2</sup> regardless of the amount of water available to the vine.<sup>179</sup> Vines with adequate soil moisture will have a pre-dawn  $\Psi_i$  between  $-0.01$  and  $-0.1$  MPa while those with less available water will have a more negative  $\Psi_i$  (Figure 15). The daily minimum  $\Psi_i$  potential typically occurs after midday (solar noon) and then increases as solar radiation and evaporative demand decrease in the late afternoon. Pre-dawn  $\Psi_i$  of well-watered vines will remain relatively constant throughout the growing season while that of deficit irrigated vines will become less.<sup>179,180</sup> For the data set in Figure 15, vines which had not been irrigated throughout the season had a pre-dawn  $\Psi_i$  close to  $-0.9$  MPa on August 18. While midday  $\Psi_i$  is dependent upon evaporative demand, this value should not become much less than  $-1.0$  MPa if the vines are irrigated at full vineyard ET even under semi-arid conditions.<sup>181</sup> Midday  $\Psi_i$  of deficit irrigated vines will continue to decrease as soil-water content decreases.<sup>179,181</sup>

Stem and cluster water potentials also will fluctuate on a diurnal basis.<sup>34,179</sup> Pre-dawn cluster water potential ( $\Psi_{\text{cluster}}$ ) is more negative than  $\Psi_i$  and remains such until evaporative demand increases after sunrise with  $\Psi_i$  decreasing more rapidly as the day proceeds.<sup>34,179</sup> Clusters will reach their minimum water potential values later in the afternoon than leaves and may ameliorate changes in  $\Psi_i$  by supplying water to leaves especially during midday. As with  $\Psi_i$ ,  $\Psi_{\text{cluster}}$  is more negative for deficit irrigated vines compared to those receiving adequate water on both a diurnal and seasonal basis.<sup>179,182</sup>

It has been suggested that drought avoidance rather than tolerance is the mechanism by which grapevines respond to soil water deficits.<sup>164</sup> However, there are a few studies that indicate *V. vinifera* cultivars are able to osmoregulate.<sup>181,183,184</sup> Experiments conducted in the lab and field indicate that a decline in the osmotic potential ( $\Psi_{\pi}$ ) of between  $0.4$  and  $0.7$  MPa can occur in drought stressed vines.<sup>181,184</sup> The ability to adjust the vine's  $\Psi_{\pi}$  appears to be cultivar/species dependent.<sup>185</sup>

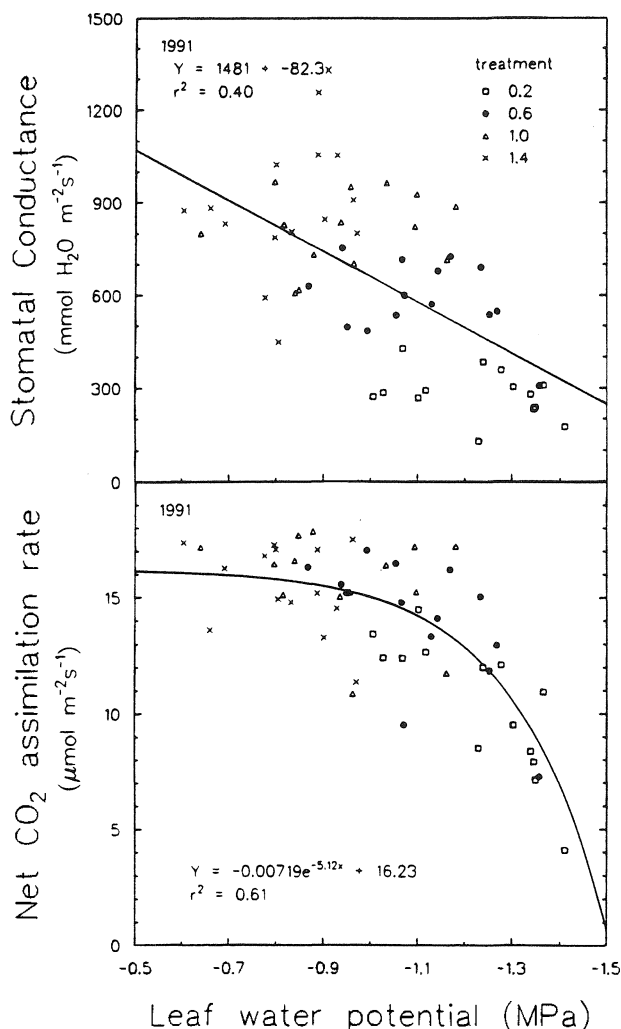


**Figure 15** The diurnal time course of leaf water potential for 'Thompson Seedless' grapevines receiving various fractions of full vine water use (top). The diurnal time course of ambient temperature and solar radiation for this day also is included (bottom). Leaf water potential values represent the means of six individual leaf replicates per treatment. Treatments represent irrigation amounts at various fractions of full vine-water use (1.0 treatment). (L.E. Williams, unpublished data.)

### 3. Effects on Leaf Gas Exchange

Water stress will cause a reduction in  $g_s$  of grapevines. The  $\Psi_1$  at which stomatal closure begins varies between  $-0.9$  and  $-1.6$  MPa<sup>30,34,179,180,182</sup> depending upon environmental conditions and the rate of water stress imposition (i.e., rapid for potted vines; slow for field-grown vines). The relationship between midday  $\Psi_1$  and  $g_s$  throughout the 1991 growing season for 'Thompson Seedless' vines irrigated at various fractions of vine water use (ET), however, results in a linear reduction in  $g_s$  with a decrease in  $\Psi_1$  (Figure 16). The low coefficient of determination indicates that other factors (either internal or environmental) must contribute to the reduction in  $g_s$ . It was demonstrated in Figure 14 that vines experiencing soil water deficits are more sensitive to changes in VPD than well-watered vines. A similar  $r^2$  value for the relationship between midday  $\Psi_1$  and  $g_s$  of 'Colombard' grapevines has been reported by van Zyl.<sup>179</sup>

Studies during the past decade on numerous plant species indicate that the reduction in stomatal conductance and growth of plants due to soil water deficits may be a response to some sort of "root signal".<sup>186</sup> This signal probably arises due to the roots sensing a reduction in soil water content or an

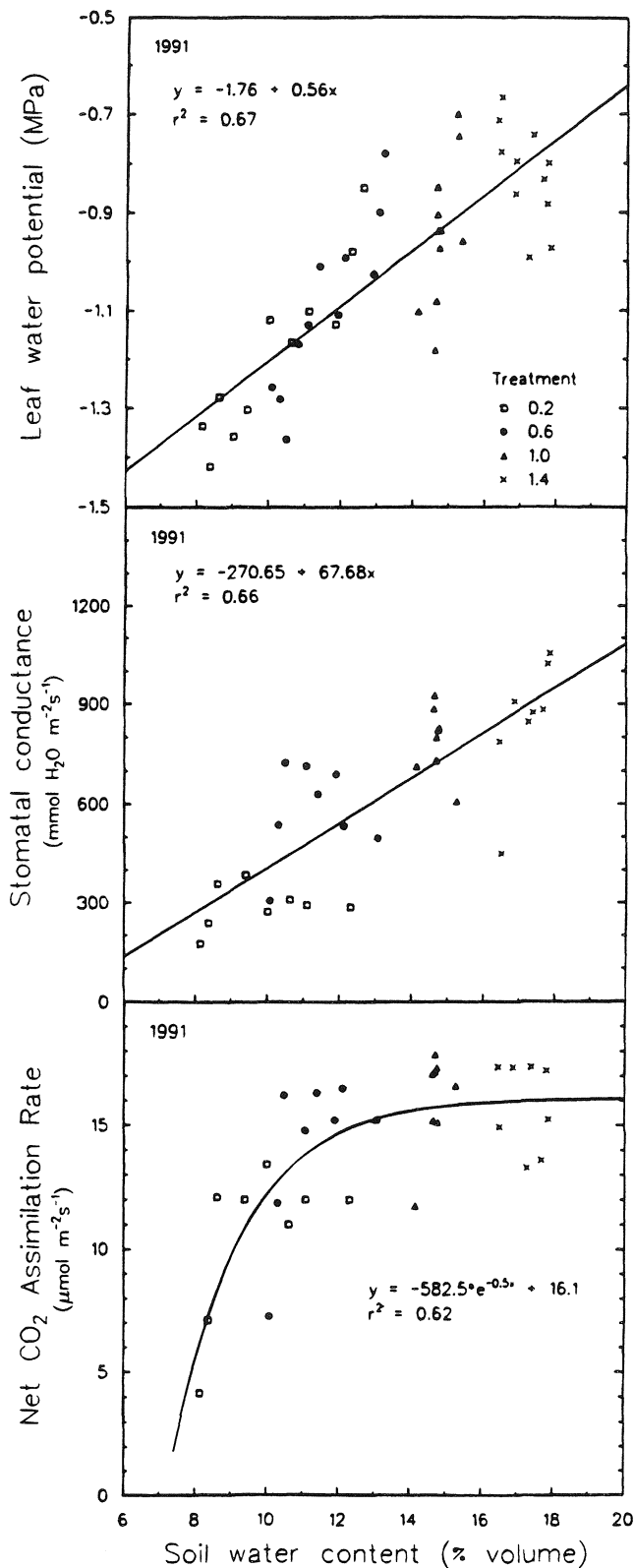


**Figure 16** The relationship between midday measurements of net CO<sub>2</sub> assimilation rate and stomatal conductance and leaf water potential of 'Thompson Seedless' grapevines grown in the San Joaquin Valley of California. Data were collected throughout the 1991 growing season. Each data point is the mean of nine individual measurements of  $A$  and  $g_s$  and six individual  $\Psi_l$  measurements. Treatments are as outlined in Figure 13. (L. E. Williams, unpublished data.)

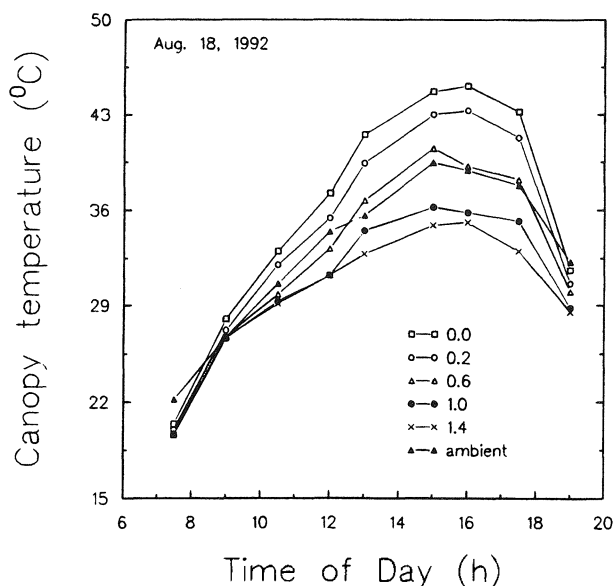
increase in the mechanical impedance as the soil dries out. The most likely candidate for this signal is ABA produced in the roots or an as-yet unidentified regulator.<sup>186,187</sup>

It has been found in grapevines under well-irrigated conditions and exposed to a minimum level of stress that the ABA content of leaves increases after sunrise and peaks at approximately twice the pre-dawn level at midday.<sup>188,189</sup> Decreases in  $g_s$  during the day were correlated with ABA accumulation in the leaves. Loveys<sup>190</sup> suggested that ABA is exported from leaves to roots, and then transported back to the leaves via the xylem which ultimately controls  $g_s$  optimizing water use efficiency.<sup>189</sup> ABA also will increase in the leaves of water-stressed grapevines.<sup>191-193</sup> The involvement of ABA in stomatal regulation of grapevines is further supported by the fact that water stress causes heterogeneous stomatal closure in grapevine<sup>193</sup> which also has been shown to occur in grapevine leaves supplied with ABA.<sup>166</sup>

van Zyl<sup>179</sup> found that pre-dawn and midday  $\Psi_l$  were highly correlated with both soil water content and soil water potential ( $\Psi_{soil}$ ). Coefficient of determinations were highest between  $\Psi_{soil}$  and both pre-dawn and midday  $\Psi_l$ . Studies on other plant species indicate that soil water content is the factor responsible for eliciting root sensed responses in the shoot.<sup>194,195</sup> Data in Figure 17 demonstrates that



**Figure 17** The relationship between midday measurements of net CO<sub>2</sub> assimilation rate, stomatal conductance, and leaf water potential of 'Thompson Seedless' grapevines and soil water content. Treatments are the same as those outlined previously (Figure 13). Soil water content was measured as described in Grimes and Williams.<sup>181</sup> The nine access tubes per individual vine were replicated three times in each irrigation treatment. Soil water content is the mean of those three replicates (nine access tubes measured to a depth of 3 m per individual vine replicate). (L.E. Williams, unpublished data.)



**Figure 18** The diurnal time course of 'Thompson Seedless' canopy temperature as a function of irrigation treatment on August 18, 1992. Canopy temperature was measured with an infrared thermometer. Each value is the mean of nine individual measurements per irrigation treatment. Ambient temperature was measured 0.5 m above the canopy. Other information as given in Figure 13. (L.E. Williams, unpublished data.)

during the growing season midday  $\Psi_1$  and  $g_s$  were highly correlated with soil water content (SWC). Soil water content accounted for up to two thirds of the variation of both plant-based measures of vine water status. It should be pointed out that measurements were taken on vines irrigated at various fractions of full vine ET throughout the season and that only the 0.2 and 0.6 ET<sub>c</sub> treatments experienced decreasing soil water content as the season progressed. In a study where water was withheld for 13 days for drip irrigated vines, there also was a linear relationship between SWC and midday  $\Psi_1$  ( $\Psi_1$  decreased as SWC decreased), and the coefficient of determination was 0.91.<sup>196</sup> The results found in Figure 17 and those of Araujo,<sup>196</sup> would indicate that the rapidity in which the soil dries out affects the degree of coupling between root sensed responses and the aerial portion of the vine.

Water stress is associated with a reduction in A and E of grapevine leaves.<sup>164</sup> The exponential relationships found in Figures 16 and 17 do indicate that A will decrease once the plant or soil water status reaches a particular level. A relationship similar to that shown between  $\Psi_1$  and A in Figure 16 previously has been demonstrated on leaves from excised shoots of grapevines.<sup>30</sup> It appears that stomatal control of A occurs during the early stages of drought, perhaps due to ABA's (irrespective of site of origin) effect on stomatal closure. The previously reported non-stomatal limitation to A when  $\Psi_1$  exceeds  $-1.3$  MPa may actually be due to non-homogeneous stomatal closure.<sup>193</sup> For example, PSII photochemical efficiency was not a primary target of water stress in *V. californica*.<sup>43</sup>

Canopy temperature (measured via portable infrared thermometers) has often been used to rapidly evaluate plant water status.<sup>181,197,199,200</sup> If plants are well supplied with water and stomata are open, transpiration will proceed at the maximum rate determined by soil and plant hydraulic conductance and by climatic evaporative demand. As VPD increases, transpiration of nonstressed plants will increase with greater evaporative cooling resulting in foliage that is cooler than the surrounding air. As water becomes limiting, transpiration will decrease and the canopy temperature will increase, becoming greater than that of the nonstressed plants. Canopy temperatures of vines irrigated at full vineyard ET or greater always were lower than ambient temperature throughout a hot, summer day in the San Joaquin Valley of California (Figure 18). Vines irrigated at less than full ET had canopy temperatures greater than ambient at least during some portion of the day. Canopy temperature is an average of all of the leaves in the field of view of the infrared thermometer, therefore, individual, sunlit leaf temperature will be warmer than that of the canopy.<sup>197</sup> Canopy-to-ambient temperature differentials of up to 10°C have been

measured on grapevines.<sup>198</sup> The concept of a Crop Water Stress Index (CWSI) based upon the difference between canopy and air temperature eventually may be used as a means to schedule irrigations.<sup>201</sup>

Diurnal measurements of  $A$  indicate that vines with less soil water availability can be as great as that of well-irrigated vines early in the morning.<sup>202</sup> However, as the day progresses  $A$  of stressed vines will decrease as opposed to a near constant rate of  $A$  of the nonstressed vines.<sup>202</sup>

#### 4. Effects on Vegetative Growth

Few studies have determined the effects of soil moisture deficits on the growth of the permanent structures (i.e., roots, trunk, and cordons) of field-grown grapevines.<sup>164</sup> A recent study using field-grown 'Chenin blanc' vines demonstrated that dry biomass of the roots was reduced approximately 30% for vines irrigated at 52% of vineyard ET when compared to vines irrigated at full ET, after the completion of a 4-year experiment. Root growth of container-grown vines was affected less than shoot growth.<sup>203</sup> It has been shown that the number of actively growing root tips diminish due to soil water deficits.<sup>204</sup>

Soil water deficits, due to irrigation at 52% of calculated ET, decreased trunk and cordons biomass by 17 and 30%, respectively. van Zyl<sup>204</sup> concluded that trunk circumference measured annually was a reliable indicator of vine water stress. While there were reductions in biomass of the roots, trunk, and cordons due to deficit irrigation, there was no significant difference in the concentration of non-structural carbohydrates (glucose, fructose, sucrose, and starch).<sup>1</sup>

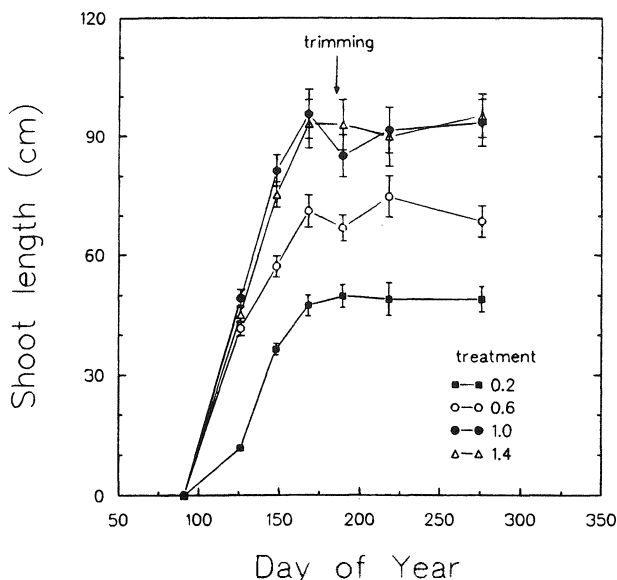
The effects of soil water deficits on budbreak and subsequent phenological events have been assessed in a few studies. Water stressed vines generally have earlier budbreak than those receiving greater amounts of irrigation water<sup>205,206</sup> whether vines are deficit irrigated throughout the season<sup>205</sup> or subsequent to fruit harvest on vines grown in the desert.<sup>206</sup> In the first year of a timing-of-irrigation study it was shown that differences in vine water status had no significant effect on the duration of vine developmental periods (i.e., between anthesis and veraison) expressed either on calendar days or degree days.<sup>207</sup>

Growth inhibition and final growth cessation due to water stress was shown to be similar among internodes, leaves, and tendrils of container-grown White Riesling.<sup>208</sup> The relative partitioning of growth among these three organs was unaltered when growth was inhibited due to water stress. The pre-dawn tissue  $\Psi$  of leaves, internodes, and tendrils which completely inhibited growth of each was  $-1.0$ ,  $-1.2$ , and  $<-1.2$  MPa, respectively. The growth of each organ was inhibited initially at a  $\Psi_{\text{soil}}$  of  $-0.065$  MPa and ceased completely at a  $\Psi_{\text{soil}}$  of  $-0.54$  MPa. It was concluded that the sensitivity of growth to water stress increased with ontogeny as some growth was maintained in younger tissues when inhibition was complete in older tissues.

These data contrast with those of field-grown vines. Soil matric potentials ( $\Psi_m$ ) of  $-0.05$  MPa were insufficient to decrease midseason shoot growth in a cool environment,<sup>209</sup> while the same soil  $\Psi_m$  decreased shoot growth in a hot environment with shoot growth ceasing at a  $\Psi_m = -0.065$  MPa measured at a depth of 0.3 m.<sup>210</sup> Kliewer et al.<sup>180</sup> found that the rate of shoot elongation of 'Carignane' was reduced by water stress before any differences were detected in pre-dawn  $\Psi_1$  and that water stress reduced shoot growth but had no effect on the growth rate of leaves. The differences in results between field- and container-grown vines could possibly be because soil water status in the field was measured only in a limited portion of the root zone and therefore may not reflect the soil  $\Psi_m$  of the entire rooting profile. In addition, the study on container-grown vines was conducted on vegetative vines while those in the field had a crop.<sup>208</sup>

A reduction in shoot growth is the first visible symptom of vine water status in the field<sup>211</sup> and may be more sensitive to  $\Psi_{\text{soil}}$  than physiological processes occurring within the leaf (Figure 17), and recent studies on annual crops indicate that non-hydraulic signals from the roots in drying soil may inhibit leaf elongation without influencing  $g_s$ .<sup>212</sup> Such a response may act to conserve water as the soil dries but before the onset of water stress in the aerial portion of the plant. The reduction in shoot elongation is clearly demonstrated on vines irrigated daily at various fractions of vine ET (Figure 19). The soil  $\Psi_m$ , for the 1.0, 0.6, and 0.2 irrigation treatments on day-of-year 150 were  $-0.025$ ,  $-0.05$ , and  $-0.06$  MPa, respectively.

Weights of canes pruned from the vine during the dormant portion of the growing season is often used as a measure of shoot growth the previous season. Pruning weights may increase up to 137% with irrigation;<sup>164</sup> the relative increase in pruning weight being largely dependent on the volume and timing of irrigation throughout the season.<sup>213</sup> When vines were irrigated daily at various fractions of full vineyard ET (from 0 to 140%) pruning weights increased linearly with irrigation quantity (L. E. Williams,



**Figure 19** Average shoot length of 'Thompson Seedless' grapevines throughout the 1991 growing season as a function of irrigation treatments. Each value is the mean ( $\pm$  SE) of all shoots on three individual vine replicates per irrigation treatment measured repeatedly during the season. (L.E. Williams, unpublished data.)

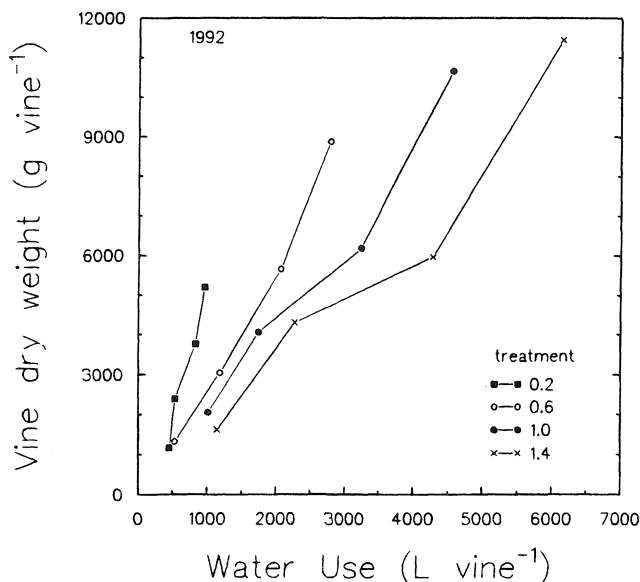
unpublished data). Irrigation at full ET, under the conditions of this study, increased pruning weights to almost three times that of the non-irrigated control.

Water use efficiency (WUE) is the amount of plant biomass produced per amount of water transpired and is a useful parameter in assessing the effects of water stress on productivity and drought tolerance.<sup>214</sup> WUE can be constant despite differences in crop water use due to different irrigation regimes.<sup>215</sup> However, the WUE (g dry wt produced per kg water transpired) of container-grown vines ranged from 1.5 to greater than 5 for different cultivars of *V. vinifera*.<sup>216</sup> The authors concluded that WUE increased with increased vegetative growth (vigor) of the vine. The WUE decreased as vine ET increased for 'Thompson Seedless' vines grown in a semi-arid environment over the period from budbreak to veraison (Figure 20) despite increased vine vigor with greater irrigation amounts. WUE decreased from 5.85 for the 0.2 irrigation treatment to 1.84 for the 1.4 treatment. These values are similar to those calculated by Smart and Coombe<sup>164</sup> with data from a study by van Zyl and van Huyssteen.<sup>217</sup> One may expect differences in WUE due to differing amount of applied water with 'Thompson Seedless' grapevines as the relationship between A and  $g_s$  is curvilinear (Figure 13). The greatest efficiency between A and transpiration in this study occurred at a  $g_s$  of approximately  $500 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ . Most of the midday values of  $g_s$  for vines irrigated at 100 and 140% of vine water use are greater than  $500 \text{ mmol m}^{-2} \text{ s}^{-1}$ .

## 5. Effects on Reproductive Growth

Reproductive growth of grapevines is less sensitive to water stress than vegetative growth.<sup>2,163,164,204,218</sup> Information on the effects of water stress on bud fruitfulness of grapevines is limited due to the inability of separating specific effects of water stress from those of temperature and light intensity in the field.<sup>1</sup> Water stress has decreased bud fruitfulness of container-grown vines under controlled environmental conditions.<sup>219</sup> However, it was suggested that bud fruitfulness is not adversely affected by the levels of water stress experienced in the field,<sup>220</sup> and may even increase bud fruitfulness.<sup>213</sup> Increased fruitfulness may be due to the reduction in vegetative growth which improves the exposure of the buds to light (see Section II.C). However, severe reductions in shoot growth due to water stress will result in fewer buds available for next year's fruiting canes for cane pruned cultivars if there is not sufficient shoot growth.

Using 3-year-old, container-grown vines, it was demonstrated that severe water stress (predawn  $\Psi_1 < 0.6 \text{ MPa}$ ) for the 3-week period after anthesis, induced cluster abscission and reduced berry set.<sup>221</sup> While severe water stress at anthesis in the field is uncommon, cluster abscission did occur early in the season (shoot length 30 cm) for vines irrigated at 0 and 20% of full vineyard ET the previous



**Figure 20** The relationship between the accumulation of dry biomass (leaves, main axis of shoots, and clusters) of 'Thompson Seedless' grapevines and water use throughout the 1992 growing season. Water use of each irrigation treatment was determined by adding the amount of water applied via drip irrigation to each vine and the amount of water depleted in the soil. Each value is the mean of three individual vine replicates. (L.E. Williams, unpublished data.)

growing season (L. E. Williams, unpublished data). Vines in these two treatments lost 70 to 90% of the clusters present on the vines during the period of delayed shoot growth noted in Figure 19.

Water stress will reduce the growth of berries, but does not influence the characteristic double-sigmoid growth curve.<sup>204</sup> A given water deficit during Stage I (when cell division is occurring) will generally reduce final berry size more than water deficits during Stages II and III (growth by cell expansion).<sup>2,54,204,207,221,222</sup> Also, the reduction in berry size due to soil moisture deficits during Stage I cannot be reversed by supplemental irrigation during Stages II and III.<sup>213,223,224</sup>

The sink potential of the fruit, determined during Stage I, appears to dictate the amount of carbon allocated to the cluster regardless of water stress. GA<sub>3</sub> applied at berry set will increase final berry size in seedless cultivars due to increased cell division.<sup>225</sup> An application of GA<sub>3</sub> to non-irrigated 'Thompson Seedless' vines at berry set resulted in comparable berry size and yield to the irrigated control vines (Table 2) underscoring the importance of events occurring during Stage I in determining final berry size. Final yields were similar between the irrigated control vines and the non-irrigated vines that were sprayed with GA<sub>3</sub> at berry set despite large differences in leaf area per vine at harvest. In addition, the ability of the water stressed vines (with reduced leaf area) to mature a crop, similar to that of irrigated vines indicates that alterations in source/sink relationships may be able to overcome the detrimental effects of water stress. Berry growth rate of irrigated and non-irrigated vines is similar subsequent to

**Table 2** The interaction of irrigation amount and gibberellic acid (GA<sub>3</sub>) applied at berry set on berry size and yield of 'Thompson Seedless' grapevines

| Irrigation treatment | Berry weight (g) |                 | Yield (kg vine <sup>-1</sup> ) |                 |
|----------------------|------------------|-----------------|--------------------------------|-----------------|
|                      | Control          | GA <sub>3</sub> | Control                        | GA <sub>3</sub> |
| Irrigated            | 2.0              | 2.8             | 16.5                           | 23.4            |
| Nonirrigated         | 1.2              | 1.8             | 9.0                            | 16.1            |

*Note:* Mean leaf area per vine at harvest for the irrigated treatment was 20.3 m<sup>2</sup> while that for the nonirrigated treatment was 6.2 m<sup>2</sup>. There were no significant differences in berry weight and yield between the irrigated control vines and the nonirrigated vines sprayed with GA<sub>3</sub>.

From Williams, L.E., unpublished data.

Stage I despite differences in vine water status.<sup>205</sup> These results indicate that the involvement of plant hormones, other than ABA, should also be studied in plants under water stress.

The effects of water stress on berry growth are reflected in final yield.<sup>164,205</sup> Post-veraison water deficits had less of a detrimental effect on final yield than pre-veraison water deficits when compared to a continuous weekly irrigation treatment.<sup>207,222</sup> Hepner et al.<sup>226</sup> reported no significant differences in yield due to different irrigation amounts for 'Cabernet Sauvignon' vines between May and July 15th or subsequent to July 15th until harvest. There was a linear increase in yield for 'Thompson Seedless' grapevines irrigated daily at fractions of full ET<sub>c</sub>, 40 to 100%.<sup>181</sup> Thus, both the timing and degree of water stress will have an important effect on the yield of field-grown grapevines.

## 6. Effects on Fruit Quality

Vine water status affects fruit solute composition throughout berry development. However, the literature contains conflicting data as to the exact effects of water stress on the berry composition. The accumulation of sugars is less affected by water deficits than is berry growth<sup>2</sup> although severe water stress may decrease sugar accumulation.<sup>205,221</sup> Sugar accumulation may also be delayed by increased water applications or by increased vegetative growth resulting in a less favorable light environment in the fruit zone (see Section II.C).

Organic acids contribute to the quality of the harvested fruit. A decrease in titratable acidity may occur with vine water stress.<sup>204,223,227</sup> Malic acid is the primary acid affected by water deficits; its concentration is dependent upon the specific time the deficit is imposed in relation to veraison.<sup>204,227</sup> The reduction in malate may be due to increased fruit temperature, and therefore increased respiration, as clusters become more exposed because of lack of leaf shading. The losses of malate may be balanced by similar decreases in counter-balancing cations or by accumulation of other acidic moieties such as amino acids.<sup>2</sup> The effects of water deficits on pH of the juice is less clear as some studies report that pH is increased by irrigation while others found no effect of supplemental irrigation.<sup>2</sup>

Water deficits will improve fruit color of red- and black-fruited cultivars.<sup>2</sup> The increase in color is the result of an increase in the production of anthocyanins. It is unknown whether this is a direct effect of water stress or an indirect one due to increased fruit exposure as a result of a reduction in vegetative growth.

Both early and late season water deficits increased juice and skin phenolics in berries of 'Cabernet franc' vines.<sup>228</sup> Wine sensory characteristics also can be manipulated by vineyard irrigation amounts and timings.<sup>229</sup> Wine made from continually irrigated vines differed from those irrigated only before or after veraison while the early season water deficit differed from the late season water deficit in appearance, flavor, taste, and aroma.<sup>229</sup> The wine effects may be associated with reduced berry size and increased skin content.

## C. FLOODING

Waterlogging is a serious problem of grapevines.<sup>230</sup> Some species used for rootstocks may have tolerance to excessive soil water. *V. rupestris* is the most sensitive species to low soil O<sub>2</sub>.<sup>177</sup> Less sensitive species are *V. solonis*, *cinerea*, *candicans*, and the *riparia* × *rupestris* hybrids. For example, the rootstock (Couderc) 3306 (a *V. riparia* × *rupestris* hybrid) has been shown to tolerate poor soil drainage in Australia.<sup>231</sup>

Sensitivity of grapevines to waterlogging depends upon the time of year. Subsequent to leaf fall, grapevines are little affected by waterlogging conditions. In fact, flooding a vineyard in midwinter for a period of up to 6 weeks has been used as a means to control grape phylloxera (*Daktulosphaira vitifoliae* Fitch).<sup>232</sup> Waterlogging after budbreak will cause reduced shoot growth, leaf chlorosis, and death.<sup>233</sup> Excessive irrigation, resulting in saturated soils reduces new root initiation<sup>234</sup> and inhibits the growth of roots into water saturated soil layers.<sup>204</sup>

Webber and Jones<sup>235</sup> have recently summarized the indirect effects of waterlogged conditions on vine growth. Many of the American *Vitis* species used for rootstocks are intolerant of lime and they will suffer from chlorosis,<sup>231</sup> which is aggravated by waterlogging. In addition, waterlogging can change soil pH and affect the availability of nutrients.

While waterlogged soils may have deleterious effects on vine performance, over-irrigation (water applications slightly greater than vineyard ET) has more subtle effects on growth, productivity and fruit quality. Such vines have reduced bud fruitfulness and yields but increased pruning weights (L. E. Williams, unpublished data). Excessive irrigation generally will reduce fruit sugar concentration, titratable

acidity and delay color development.<sup>204</sup> This is thought to be due to competition for photosynthates between the fruit and post-veraison vegetative growth.<sup>164</sup> However, much of the negative effects of over-irrigation may actually be due to shading effects due to excessive vegetative growth (see Section II.C).

## V. MISCELLANEOUS ENVIRONMENTAL FACTORS

### A. SALINITY

Grapes are grown in areas where salinity is a problem, most notably in areas of Australia, Israel, and portions of southwestern United States. Grape has been classified as moderately sensitive to salinity (chloride) based upon vegetative growth measurements.<sup>239</sup> Most annual crops are affected by the reduction in  $\Psi_{\pi}$  of the soil solution due to salinity while woody perennial crops are primarily affected by specific ion toxicities.<sup>236</sup> Grapevines accumulate chloride readily either via the root system<sup>237</sup> or through the leaf.<sup>238</sup>

The visible symptoms of salt stress on grapevines first appear as marginal chlorosis on the leaves followed by necrosis progressing towards the center of the leaf blade. These toxicity symptoms are probably due to the uptake of the chloride ion as grapevines grown on sodic soils rarely exhibit these symptoms.<sup>240</sup> The maximum permissible chloride in soil water without leaf injury was shown to range from 60 to 80 mol m<sup>-3</sup> for three container-grown, commercial rootstocks.<sup>236</sup> However, Prior et al.<sup>241</sup> found that symptoms of leaf damage (marginal necrosis) in the field were more closely related to the onset of hot dry weather than with reaching a particular Cl or Na concentration in the lamina. Under severe salt stress the entire vine may defoliate.

There is variability in the uptake of salt among *Vitis* species, cultivars, and rootstocks.<sup>1</sup> Downton<sup>242</sup> categorized *V. rupestris* as the most salt tolerant species followed in order of descending tolerance by *berlandieri*, *riparia*, *candicans*, *champinii*, *longii*, *cinerea*, *cordifolia*, and *vinifera*. Antcliff et al.<sup>243</sup> found the order of *V. berlandieri*, *champinii*, and *cinerea* similar to that of Downton<sup>242</sup> but that the only clone of *V. rupestris* used by Downton, 'Rupestris du Lot' (syn. 'Rupestris St. George'), was atypical of that species. Their data indicated *V. rupestris* salt tolerance as comparable to that of *V. cinerea*. The variation in Cl exclusion both among and within species indicates there may be a genetic basis for this characteristic.<sup>244</sup> The ability to exclude Cl by the *V. champinii* species (the 'Ramsey' rootstock, syn 'Salt Creek') is probably due to the action of many genes.<sup>245</sup> The genetic basis for Cl exclusion in *V. berlandieri* may be due to a single dominant gene.<sup>246</sup> In that study, Cl exclusion was independent of both yield and berry weight.

*V. champinii* rootstocks 'Dogridge' and 'Ramsey'<sup>242,243,247,248</sup> and the *berlandieri* × *rupestris* hybrids '110 Richter', '140 Ruggeri', and '1103 Paulsen'<sup>243,247</sup> are effective Cl excluders.<sup>243,247</sup> Salt tolerant *V. vinifera* cultivars include 'French Colombard' (most tolerant) > 'Grenache', 'Chenin blanc', 'Thompson Seedless' > 'Barbera', 'Muscat of Alexandria', or 'Ribier' (susceptible).<sup>1,240</sup>

Reductions in growth and A have been observed to occur in response to soil salinity before any toxic symptoms appear in grapevines.<sup>249</sup> Prior et al.<sup>241</sup> found that the response of A to salinity of field-grown grapevines was almost identical to that found by Downton<sup>249</sup> on container-grown vines and was more strongly correlated with leaf Cl than leaf Na. The reduction in A is due to a uniform decrease in  $g_s$  up to a tissue concentration of 165 mM Cl.<sup>250</sup> It also was found that at tissue concentrations above 165 mM Cl non-stomatal inhibition of A was actually due to non-uniform stomatal closure (determined visually using <sup>14</sup>CO<sub>2</sub> uptake and autoradiograms). It has been observed that ABA levels in the leaves of salt-stressed grapevines increase rapidly and remain such for several weeks.<sup>251</sup> Therefore, in grapevines the salt-induced reductions in A (mediated by the increase in ABA levels) are a result of heterogeneous stomatal closure.

Container-grown grapevines exposed to saline water are able to osmotically adjust shortly after exposure.<sup>252</sup> Osmotic adjustment is due to the accumulation of Na, K, and Cl ions and an increase in reducing sugars.<sup>251</sup> It was concluded that the maintenance of turgor pressure and osmotic adjustment during salt stress prevents immediate damage to PSII activity. However, the continued accumulation of chloride eventually causes membrane permeability changes, cell damage, and the loss of turgor.

As mentioned above, grapevine tissue ion content will change with the use of saline water. Prior et al.<sup>253</sup> found that the accumulation of Na and Cl in leaves and petioles of field-grown vines was not linear but tapered off at high irrigation water electrical conductivity (EC) values, indicating that the tissue was becoming saturated with salt. K concentrations in petioles and leaf blades generally are reduced due to elevated levels of NaCl in the rooting medium.<sup>240,241</sup> However, it was shown that leaves of container-grown grapevines began to accumulate K<sup>+</sup> and Cl within 6 h of exposure to high levels

of NaCl while the uptake of Na was not evident until the next day.<sup>251</sup> The accumulation of  $K^+$  and Na generally balanced the accumulating Cl ion. The effect of saline water on the accumulation of other mineral nutrients in vine tissues is less clear and differs depending whether the study is conducted on container-grown vines over a short period or on field-grown vines over a long-term period.

Vegetative growth (shoot length, pruning weights, and leaf weight) of 'Sultana' (syn. 'Thompson Seedless') was reduced by salinity to a much greater extent than yield.<sup>241</sup> In that study, all vegetative growth parameters measured were reduced by salinity with the effects of salinity were more severe on heavier soils. Growth reductions occurred despite the fact that there were no differences in  $\Psi_i$  among salinity treatments. Root density was reduced to a greater extent than the reduction in total leaf area.<sup>253</sup> Root growth was severely restricted on container-grown 'Cabernet Sauvignon' even in concentrations of NaCl as low as 20 mM in the rooting medium.<sup>254</sup> Soil salinity has also reduced starch levels in the canes and increased the concentrations of reducing sugars.<sup>241,250</sup> It was concluded that the reduction in vegetative growth and photosynthetic area was the primary reason for a reduction in yield in the study of Prior et al.<sup>241,253,255</sup>

A 6-year study on own-rooted 'Sultana' vines conducted in the River Murray flood basin of Australia<sup>241,253,255</sup> showed that vine performance declined with the duration of exposure to salinity and was strongly influenced by soil texture.<sup>255</sup> Yield response to salinity levels in the lightest textured soil resembled the model developed by Maas and Hoffman,<sup>239</sup> although more severe losses than predicted occurred in the heavier soils. Yield was correlated with EC<sup>253</sup> of the soil extract, but that relationship was not as good as that derived between yield and plant-based measures (lamina content) of salinity.<sup>241</sup> For own-rooted 'Sultana': (1) there was no evidence of a yield threshold in response to soil salinity when averaged across all soil texture types; (2) there was a 10% yield loss when EC at the end of the winter exceeded 1.0 dS m<sup>-1</sup>; (3) vine-based measurements of salinity effects were better than soil-based measurements as they were able to integrate the rootzone salinity over space and time; (4) the best relationship between yield and vine tissue concentrations was obtained using petiole Cl and Na values; and (5) petiole Cl and Na values should be kept below 420 and 191 mmol kg<sup>-1</sup> dry weight, respectively, to avoid the detrimental effects of salinity on vine productivity.

There are instances when salt in the irrigation water may be present only for a short period of time. A study investigating transient (two-month period), soil salinization of a Colombard vineyard on 'Ramsey' rootstock found that the treatments increased EC values and petiole Na and Cl concentrations and decreased  $\Psi_i$ <sup>256</sup>, however, vegetative growth or yield were not affected.<sup>256</sup> The authors concluded that the lack of growth or yield response in this vineyard was not due the use of the 'Ramsey' rootstock as other studies have found that growth of various scion/rootstock combinations will decline over a range of saline water.<sup>257</sup> Thus, it appears that transient exposure to high EC levels (3 to 6 dS m<sup>-1</sup>) for 2-month periods may not necessarily reduce vine productivity. Of significant importance in minimizing the effects of salinity is to ensure that adequate leaching of salts take place sometime during the growing season.<sup>253</sup>

Fruit composition may be affected by salinity. The accumulation of sugars in the fruit was not affected for the first 3 years of soil salinization,<sup>255,258</sup> but declined subsequently. Juice titratable acidity increases with salt treatments as does the concentrations of Na, K, and Cl ions; wines made from the fruit were similarly affected.<sup>242</sup> The use of rootstocks, known to exclude Cl, reduced the levels of Cl in the wine.<sup>242</sup>

## B. WIND

Wind can affect the physiology and growth of plants in numerous ways.<sup>259</sup> Wind speed is of significant importance as it affects heat and mass transfer of individual leaves and the vine canopy as a whole. High wind velocities can lead to structural damage of plant tissue while constant winds at low to medium velocities can lead to deformation and disruption of physiological processes. Vineyards in many regions may be exposed to chronic low- to medium-wind velocities; the effects of chronic wind exposure on vine physiology and productivity have not been quantified.

Vineyards are considered aerodynamically rough as their surfaces are covered by discontinuous canopies. Wind will determine the depth of the boundary layer which ultimately affects the exchange of CO<sub>2</sub> and water vapor between the plant and the atmosphere. Weiss and Allen<sup>260</sup> did not find a constant flux zone over the vineyard in which their measurements were made as has been found for other crops. They concluded that the vineyard boundary layer actually consisted of an inner and outer zone. Wind direction also influences the degree of roughness of a vineyard. The drag coefficient, which is a

nondimensional measure of the roughness of a surface, is higher for cross-row flow than for down-row flow of air in a vineyard.<sup>260,261</sup> Wind speed also has been shown to be more important than wind direction in maintaining between-row circulations.<sup>262</sup>

An increase in wind speed will increase the boundary layer conductance which generally increases the rate of transpiration from leaves and plant canopies.<sup>215</sup> Hicks<sup>261</sup> found that vineyard ET increased 10 to 20% with cross-row flow as compared with down-row flow of air. This indicated that ET increased due to an increase in the drag coefficient (see above). However, studies conducted both in the lab and the field on individual leaves of grapevines have shown that  $g_s$  and transpiration is decreased when wind speed exceeds a given threshold;<sup>263–265</sup> wind velocities greater than  $3 \text{ m s}^{-1}$  were required to significantly decrease  $g_s$  and transpiration. Preliminary results from Australia indicate that ABA increases in leaves of grapevines exposed to chronic, low- to medium-wind velocities (B.R. Loveys, personal communication). The reduction in  $g_s$  of grapevines exposed to wind may be due to the accumulation of ABA as others have found that ABA increases in plant tissues that are exposed to wind.<sup>266</sup>

Wind has been reported to have little effect on the water relations of various plant species<sup>215,259</sup> including *V. vinifera*.<sup>264</sup> However, in studies examining the differences in water relations between sheltered and non-sheltered, field-grown grapevines in windy locations,  $\Psi_1$  of the sheltered vines always was more negative than that of the controls.<sup>263,265</sup> This may be expected as  $g_s$  was always greater for the sheltered vines.

The only report documenting a wind-induced reduction of A of grapevines did not include  $g_s$  measurements.<sup>267</sup> Many of the authors who have studied the effects of wind on grapevines suggest that the reduction in  $g_s$  due to increased wind speeds also will reduce A. The degree in which A is reduced due to increased wind speeds is largely dependent (although not linearly dependent) upon the extent that  $g_s$  is reduced. However, preliminary assessment of wind-breaks on vine physiology and growth indicates that there may not always be a large reduction in A when  $g_s$  is reduced due to chronic wind exposure (Figure 21).

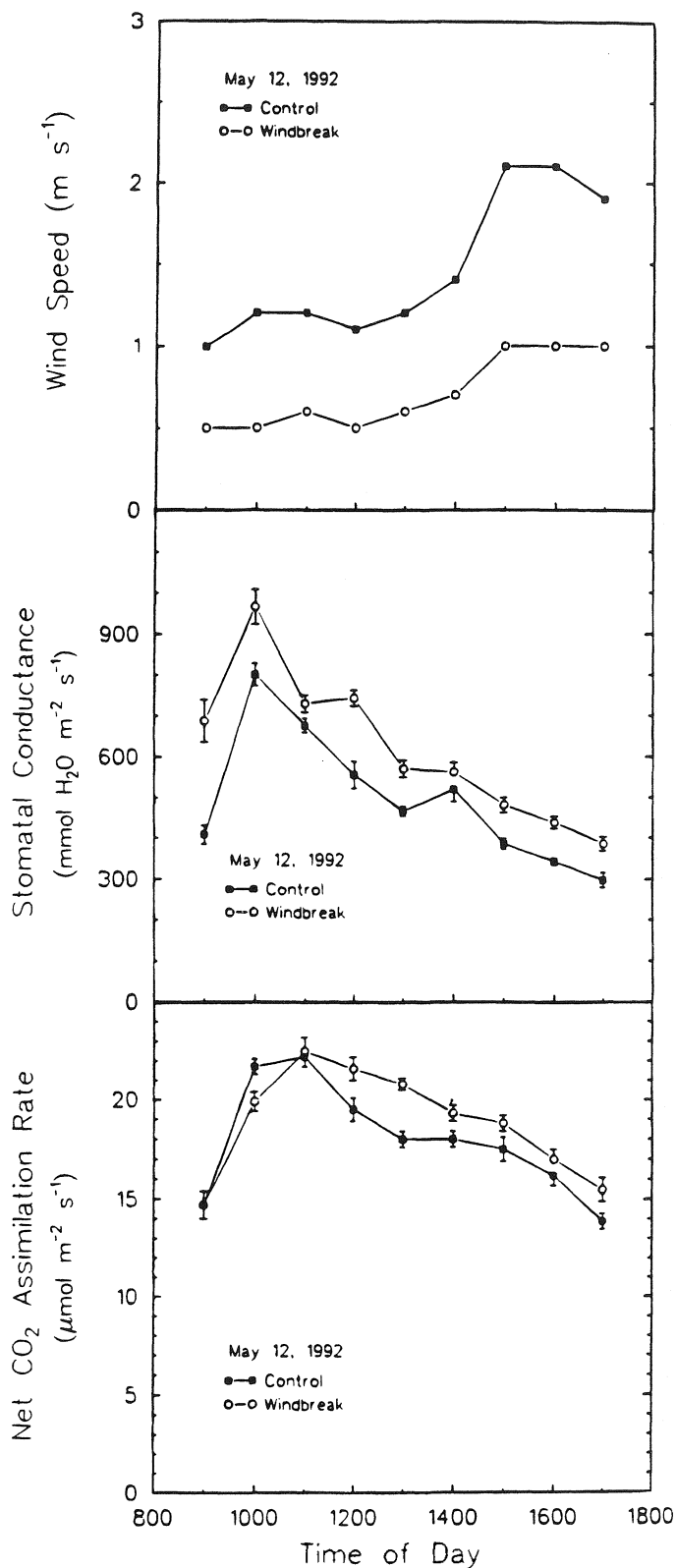
Kobringer et al.<sup>264</sup> reported a carryover effect on  $g_s$  by wind velocities greater than  $10 \text{ m s}^{-1}$  but not at  $3.6 \text{ m s}^{-1}$ . Stomatal conductance remained depressed for up to 4 days after the treatment stopped, however, there were cultivar differences. A similar type of response has been observed in the field using windbreaks in a 'Chardonnay' vineyard (L. E. Williams, unpublished data). Wind has been shown to both increase and decrease the density of stomata on leaves of other plant species.<sup>259</sup> The carryover effect on  $g_s$  reported by Kobringer et al.<sup>264</sup> was not due to a reduction in stomatal densities as measurements were made only on mature leaves over a short period. It is uncertain whether this was true for the field study as the leaves had been exposed to chronic wind stress throughout the growing season.

While extremely high winds can cause physical damage in vineyards,<sup>268</sup> constant exposure to medium velocity winds (i.e.,  $1$  to  $2 \text{ m s}^{-1}$ ) also may affect vine growth and productivity.<sup>269</sup> At vineyard sites planted perpendicular to prevailing winds the vines will have an asymmetric growth habit (i.e., growth is much reduced on the windward side). The reduction in shoot growth is primarily due to a reduction in internode length (Table 3). There also is a reduction in individual leaf size and it is this parameter which is principally responsible for the reduction in total vine leaf area. The reduction in total vine leaf area is probably a more important determinant of reduced vine growth due to wind than the small decreases in leaf A. The reduction in growth may be the result of physiological and/or mechanical effects.<sup>215</sup> The production of ethylene in response to mechanical perturbation may be responsible for thigmomorphogenic responses of plants.<sup>270</sup>

Yields are greater for vines grown within windbreaks (Table 3) or close to windbreaks in vineyards when compared to vines grown further away or upwind from the break.<sup>268,269</sup> Simon<sup>271</sup> found that growth and productivity of vines increased when grown within a distance of five times the height of the windbreak. The reduction in yield was due both to reduced berry weight and cluster numbers per vine. Fruit soluble solids were lower for exposed vines when compared to the sheltered vines.<sup>269</sup> Other differences in fruit composition measured between sheltered and non-sheltered vines may be the result of differences in maturity between the treatments.

### C. AIR POLLUTION

Extensive reviews of the effects of airborne pollutants on the grapevine were published in the early 1980s.<sup>272–274</sup> Therefore, this section will briefly review the effects of air pollutants on vines and present some more recent data on this subject.



**Figure 21** The effect of a windbreak on the diurnal time course of net  $\text{CO}_2$  assimilation rate, stomatal conductance, and wind speed of 'Chardonnay' grapevines grown in the Salinas Valley of California. Control vines were exposed to ambient wind velocities. For an explanation of the windbreak see Table 3. Each value of  $A$  and  $g_s$  are the means of eight individual leaf measurements. Wind speed values are the hourly means of measurements taken every minute by a datalogger. (L.E. Williams, N.K. Dokoozlian, and L. Bettiga, unpublished data.)

**Table 3 The influence of windbreaks on the growth and yield of 'Chardonnay' grapevines grown in the Salinas Valley**

| Treatment | Internode length (cm) | Shoot length (cm) | Individual leaf area <sup>a</sup> (cm <sup>2</sup> ) | Total vine leaf area (m <sup>2</sup> ) | Vine yield (kg) |
|-----------|-----------------------|-------------------|--|--|-----------------|
| Control   | 3.3                   | 62                | 77   | 8.5                                    | 6.8             |
| Windbreak | 4.6                   | 99                | 112  | 11.7                                   | 7.6             |

*Note:* The windbreak consisted of 50% density shade cloth surrounding seven vines. The shade cloth extended from the soil surface up to 3.05 m into the air. Each plot was replicated eight times.

<sup>a</sup>These values represent the area of individual leaves from the primary shoot. Leaves from lateral shoots are not included.

From Dokoozlian, N. K., Bettiga, L., and Williams, L. E., unpublished data.

Airborne pollutant injury to grapevines was first reported in France early in the Twentieth Century.<sup>272</sup> Pollution injury in the Western Hemisphere was first reported to occur in the 1950s in Southern California.<sup>275</sup> Since those times there have been numerous reports of air pollution affecting grapevines in vineyards throughout the industrialized world. Exposure of grapevines to air pollutants results in foliar symptoms as these molecules are taken up through the stomata.<sup>276</sup> Symptoms of pollution injury may vary among cultivars and might be confused with mineral nutrient deficiencies or toxicities. Exposure of grapevine leaves to ozone results in small patches of necrotic tissue surrounded by healthy green tissue and is termed 'Oxidant stipple'.<sup>275</sup> These lesions are localized in the palisade tissue of the leaf. Severe injury will result in chlorosis, bronzing, and premature leaf senescence and abscission. Older leaves are more susceptible to O<sub>3</sub> than younger leaves.

There is evidence of tolerance to airborne pollutants by native *Vitis* species, various cultivars of *V. vinifera*, and some French and American hybrids.<sup>272</sup> Tolerance is based upon foliar symptoms. For example, it was found that grape oxidant stipple (symptom of ozone exposure) was more prevalent on 'Carignane' and 'Grenache' than on 'Zinfandel' and 'Thompson Seedless'.<sup>275</sup> Similar categories have been established for susceptibility to hydrogen fluoride and sulfur dioxide.<sup>272</sup> Unfortunately, foliar symptoms of grapevines in response to air pollutants are dependent upon concentration and dose of the particular pollutant, stage of shoot development, leaf age, and cultural practices. Thus, there is some disagreement among studies with regard to the tolerance classification of individual cultivars.

Ambient partial pressures of O<sub>3</sub> (12-h mean 50 to 60  $\mu\text{Pa Pa}^{-1}$ ) will reduce grapevine A anywhere from 5 to 13%.<sup>41</sup> The authors concluded that reductions in A were due to an O<sub>3</sub>-induced decline in g<sub>s</sub> which resulted in decreased C<sub>i</sub>. This differs from the findings of Shertz et al.<sup>277</sup> who found that stomata of grapevine were opened by exposure to O<sub>3</sub>. Studies on other plant species have shown ambient partial pressures of O<sub>3</sub> will reduce g<sub>s</sub> to a greater extent than mesophyll conductance.<sup>278,279</sup> Even O<sub>3</sub> partial pressures greater than ambient levels significantly reduced g<sub>s</sub> while having no significant effect on grapevine A over a 5-h fumigation period.<sup>41</sup> The exact mode of action of O<sub>3</sub> on grapevine g<sub>s</sub> is unknown. ABA may be produced in response to pollutant exposure.<sup>280,281</sup> As discussed previously, the reduction in grape A when ABA is taken up is due solely to its effect on g<sub>s</sub> and results in heterogeneous stomatal closure.<sup>166</sup> Heterogeneous stomatal closure in response to ozone fumigation has been shown on other plant species.<sup>282</sup> The symptoms of O<sub>3</sub> damage in grape leaves, oxidant stipple, would be consistent with heterogeneous stomatal closure upon exposure to this air pollutant. Stomata which remain open allow ozone to diffuse into the mesophyll and may result in acute damage to cells; stomata which remained closed would ostensibly protect the tissue from damage.

Most studies characterizing the effects of air pollutants on growth and productivity of grapevines have been conducted on container-grown plants.<sup>272</sup> However, there have been three studies conducted in the field assessing the effects of ambient oxidants (O<sub>3</sub>) using open-top chambers. The chambers are constructed around mature vines and then either charcoal-filtered air or ambient air is forced through the chambers and out the top. Studies conducted on 'Zinfandel',<sup>283,284</sup> and 'Thompson Seedless',<sup>285</sup> grapevines in California, indicate that ambient pollution reduced pruning weights ca. 25 and 12%, respectively, compared to the charcoal-filtered controls. A study conducted on 'Concord' vines in New York found no significant effects of ambient oxidants on vegetative growth although there was a trend for less growth in the ambient air chambers.<sup>286,287</sup>

Thompson and co-workers<sup>283,284</sup> found that yields of 'Zinfandel' vines exposed to ambient air were reduced 12 and 61% when compared to vines in the charcoal-filtered chambers in the first and second years of the study, respectively. Yields of 'Thompson Seedless' were reduced 28 and 17% after the second and third years of exposure to ambient oxidants, respectively.<sup>285</sup> The number of clusters per vine was the yield component affected most for 'Thompson Seedless'.<sup>285</sup> It appears that O<sub>3</sub> exposure affects the differentiation of clusters within the compound bud; however, it is unknown whether O<sub>3</sub> directly affects the differentiation of cluster primordia or indirectly affects the process via a reduction in available vine carbohydrates due to a reduction in A.

Berry weight and the accumulation of soluble solids within the fruit of 'Zinfandel' were reduced due to exposure of vines to ambient oxidants.<sup>283,284</sup> Apparently, the reduction in A on both a single leaf basis<sup>41</sup> and whole vine basis (foliage levels estimated) reduced the amount of photosynthate available for growth of the fruit. In addition to a reduction in A, premature leaf abscission and loss of effective leaf area due to toxic levels of O<sub>3</sub> can cause a reduction in plant biomass.<sup>288</sup>

Sulfur dioxide injury results in grayish-brown lesions along the margins or tip of the leaf with middle-aged leaves most susceptible.<sup>272</sup> The first symptom of fluoride injury is a gray-green color at the margins of young leaves which then becomes brown or reddish-brown in color.<sup>272</sup>

The effects of sulfur dioxide and hydrogen fluoride on grapevine productivity is less clear.<sup>272</sup> Sulfur dioxide and ozone may exert a synergistic effect on vine physiology.<sup>289</sup> Reduced yields due to exposure to hydrogen fluoride may depend less on the degree of foliar injury than on characteristics of exposure over one or more growing seasons and stage of vine development.<sup>272</sup>

There have been no studies assessing the effects of air pollutants on the post-harvest storage of fruit used for table grapes (fresh market). This is crucial as appearance and storeability are important quality characteristics of table grapes. Crisosto et al.,<sup>290</sup> found that elevated partial pressures of O<sub>3</sub> decreased wax deposition and cuticle thickness of plum fruit (*P. salicina*, cv. Casselman) and the highest O<sub>3</sub> partial pressures resulted in a greater weight loss. Unfortunately, no data are available for grapevines.

## VI. SUMMARY

The world-wide distribution of grapes (*Vitis* sp.) attests to the large genetic diversity both across the genus and within a species. The diverse climates, under which grapevines are grown, has resulted in a remarkable selection of cultivars that meet a variety of uses. Fortunately, there has been a minimum of "gene pool" reduction within the *Vitis* genus which will provide opportunities for grape breeding programs in the future.

Although there are several commercially-grown species, *V. vinifera* constitutes the majority of the acreage in the United States and around the world. The major limitations in the distribution of *Vitis* are low temperatures, seasonal heat accumulation, and water availability. Despite the fact that low temperature stress is the predominant limitation to the distribution of grapevines, little is known about the acclimation and deacclimation processes that are important for continued production in geographically and climatically extreme areas. For *V. vinifera*, high temperatures are clearly not a limiting factor and this species may have some unique characteristics as a crop plant in this regard. This species is also very tolerant to drought stress although irrigation may improve vine productivity.

A major theme present throughout this chapter is the mechanism by which grapevine leaves respond to various environmental stresses. It has been documented that heterogeneous stomatal closure in the leaves of grapevines occurs due to applied ABA, increases in VPD, soil water deficits, and salinity. A similar response may occur when grapevines are exposed to air pollutants and wind. It is tempting to suggest a causal relationship between the accumulation of ABA in grape leaves and the vine's response to environmental stresses as ABA causes heterogeneous stomatal closure.<sup>166</sup> Interestingly, a recent study has shown that ABA accumulates in the leaves of grapevines and grape callus tissue in response to high temperatures.<sup>291</sup> The authors suggested that ABA may be a factor in high-temperature acclimation and heat-tolerance induction in grape.

While the involvement of ABA in mediating environmental stresses at the leaf level in grapevines is apparent, other phytohormones may also play a role.<sup>292</sup> This is exemplified in the data from Table 2. It was demonstrated that the application of GA<sub>3</sub> at berry set of the seedless cultivar, 'Thompson Seedless', was able to overcome the negative effects of soil water deficits on berry growth. Further studies are needed to clarify how stress affects phytohormones in grape and other horticultural fruit crops.

Temperature extremes and fluctuations and availability of water will determine in large part the global distribution of species and cultivars of grapevines used for commercial purposes. However, it is possible to manipulate a vine's microclimate with the use of various training and trellising systems. While temperature, VPD and wind are ameliorated to some degree by the use of these cultural practices, it is the light microclimate within and at the surface of the canopy that is most impacted by training and trellising systems. Beginning with the pioneering work of Shaulis and co-workers, great advances have been made regarding our understanding of the effects of irradiance on vine growth, productivity, and fruit composition. Much attention has also been given to canopy management practices such as basal leaf removal and shoot positioning, for the improvement of the canopy's light environment.

Although some uncertainty remains regarding the location of the photoreceptor responsible for the regulation of bud fruitfulness, it is generally believed that irradiance received directly by the bud governs cluster initiation. Existing evidence suggests that light quantity rather than quality regulates fruit bud differentiation. Recent work also has revealed that many aspects of grape berry growth and composition are regulated by light and that the photoreceptors are located in the fruit. Much speculation has centered around the involvement of phytochrome for the photoregulation of berry metabolism. Again, it has been shown that light quantity rather than light quality is responsible, suggesting that chlorophyll or the putative blue light photoreceptor cryptochrome, may be involved in the regulation of grape berry growth. The elucidation of the exact location and nature of the photoreceptor(s) regulating vine growth and metabolism should be of high priority for future research.

Further improvements in vine productivity and fruit quality may only be possible by increasing our basic understanding of the interactions of solar radiation interception by the vine and other environmental factors. Therefore, future studies in viticultural research must be conducted under a wide variety of vine training and trellising systems in contrasting mesoclimates. With this knowledge and a subsequent expanded database, modelling vine performance will be enhanced, and the use of expert systems in viticulture will become common place.

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## Kiwifruit

Garth S. Smith and James G. Buwalda

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### I. INTRODUCTION

The kiwifruit of commerce [*Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa*] is a warm-temperate deciduous vine that has been subjected to little genetic selection and is essentially indistinguishable from the plant which grows wild in its natural habitat in China.<sup>1</sup> Only a small part of the gene pool of this species has been exploited. The majority of commercial plantings throughout the world are of the one cultivar, 'Hayward'.<sup>2</sup> This cultivar was selected in New Zealand just over 50 years ago from an extraordinarily small group of about 40 seedlings, which themselves can be traced back to a small quantity of seed introduced from China in 1904.<sup>3</sup> The first commercial planting of 'Hayward' was in New Zealand in the late 1930s. However, commercial success of the fruit did not

**Table 1 World production of kiwifruit from 1985 to 1991**

| Country          | Proportion of total production (%) |       |
|------------------|------------------------------------|-------|
|                  | 1985                               | 1991  |
| New Zealand      | 57.5                               | 40.4  |
| Italy            | 16.7                               | 31.5  |
| USA              | 8.7                                | 3.6   |
| Japan            | 7.4                                | 6.0   |
| France           | 7.1                                | 6.8   |
| Greece           | 1.2                                | 1.4   |
| Australia        | 0.9                                | 1.0   |
| Chile            | 0.5                                | 6.0   |
| Spain            | 0.0                                | 0.6   |
| Portugal         | 0.0                                | 0.3   |
| Others           | 0.0                                | 2.4   |
| Total production | 194.6                              | 665.7 |

Note: Data given in thousands of tonnes.

From New Zealand Kiwifruit Marketing Board, 1992.

take place internationally until much later in the late 1960s. Although kiwifruit vines were introduced from New Zealand into many countries in the 1970s, it was not until after 1980 that the area planted in any single country other than New Zealand exceeded 1000 ha.<sup>4</sup> The dramatic increase in the quantity of kiwifruit being produced worldwide has seen the total annual trade in fruit increase from approximately 195,000 t in 1985 to the current level of production of 666,000 t (Table 1). New Zealand and Italy are now the main kiwifruit producing countries.

The rapid increase in plantings of kiwifruit in many parts of the world has resulted in vines being grown under a diverse range of soils and climatic conditions. In their natural habitat in southern and central China, kiwifruit vines are confined to the sides of forest-covered hills and mountains where they grow in well-illuminated environments at forest margins.<sup>1</sup> Annual rainfall in these areas is evenly distributed and ranges from 1045 to 1950 mm, maintaining a relatively high humidity of 75–85%.<sup>5</sup> The local soils are very acidic (pH < 5) with high contents of organic matter (6–18%) and moderate reserves of nitrogen and potassium.<sup>5</sup> The climate is continental in nature with winter temperatures often falling well below 0°C. There are long frost-free periods during the growing season of 210–280 d, while summer temperatures occasionally reach 40°C.<sup>6</sup> By contrast, conditions under which kiwifruit vines are now grown commercially range from the cool humid environment of New Zealand where rainfall during the growing season often exceeds 800 mm and the average temperature rarely exceeds 17°C,<sup>7</sup> to the hot dry environment of the Central Valley of California where the average rainfall is often less than 300 mm and the average temperature usually exceeds 23°C.<sup>8</sup> Associated with the increased diversity of these growing areas has been a range of physiological disorders, of which many can be linked to environmental stresses.<sup>9</sup>

As the history of research into the physiology of the kiwifruit vine is very recent compared to that for most other fruit crops, little attempt has been made to develop an integrated understanding of the functioning of the entire vine. Hence, solutions to many disorders affecting the vine have been considered in isolation. In this chapter, growth and development of the kiwifruit vine are described to provide a basis for examining the physiological responses of the vine to environmental stress and opportunities for minimizing the effects of these stresses on fruit production and quality. Unless stated otherwise, the growth patterns described in this chapter are typical of vines grown under New Zealand conditions. While much of the research reviewed in this chapter was carried out in New Zealand, reflecting the influence this country has had on the culture of the kiwifruit vine, the conclusions drawn have direct relevance for kiwifruit culture elsewhere.

**Table 2 Typical distribution of leaf area and fruit number in “replacement cane” and “fruiting” zones of the canopy of kiwifruit vines (planted at 400 vines ha<sup>-1</sup>) in New Zealand**

|                       | Leaf area<br>(m <sup>2</sup> vine <sup>-1</sup> ) | Fruit number<br>(vine <sup>-1</sup> ) |
|-----------------------|---|---------------------------------------|
| Replacement cane zone | 64.5  | 338                                   |
| Fruiting zone         | 25.7  | 789                                   |
| Total                 | 90.2  | 1127                                  |

From Buwalda, J. G. and Smith, G. S., *Sci. Hortic.*, 42, 29, 1990.

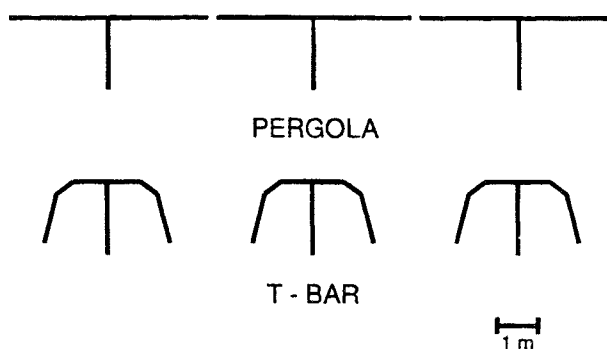
## II. VINE GROWTH AND DEVELOPMENT

### A. VINE ARCHITECTURE

Kiwifruit vines are dioecious and up to 25% of the vines in an orchard may be staminate.<sup>10</sup> In New Zealand, the planting density is typically 400 vines ha<sup>-1</sup> (25 m<sup>2</sup> vine<sup>-1</sup>). The components of the pistillate vine have been classified as perennial (trunk, cordon or leader, and structural roots), transient (laterals and shoots), and deciduous (fruit, leaves, and fibrous roots).<sup>11</sup> This classification reflects both the natural growth pattern and conventional management practices. Usually the trunk is about 1.8 m high. A single cordon is retained and laterals (fruiting canes) trained at right angles from the cordon. Laterals are usually retained for only 1 year, and are replaced using shoots (replacement canes) emerging from or near the cordon during the growing season. Such management of the canopy enables a further division of the canopy into “replacement cane zone” and “fruiting zone”<sup>12</sup> to reflect the predominant locations of the vegetative and reproductive components of the canopy (Table 2).

Vines, either wild or cultivated, can live for more than 50 years and develop trunks of more than 0.2 m in diameter.<sup>13</sup> However, the vines do not become self-supporting and require a strong framework on which to grow. Almost all commercial kiwifruit vines are supported on one of two trellis types (Figure 1); (1) a horizontal and continuous trellis known as a “Pergola” in New Zealand and a “Tendone” in Italy (which will be subsequently referred as Pergola in this chapter), and (2) a discontinuous trellis with a central horizontal plane and inclined planes on either side usually facing east and west known as a “T-bar” in New Zealand<sup>10</sup> and a “Pergola” in Italy (subsequently referred to as T-bar in this chapter). The ratio of canopy surface area to apportioned orchard area is 1.0 for the horizontal pergola, and typically 1.0–1.2 for the T-bar trellis.<sup>9</sup> Leaves typically comprise 92% of the total surface area of the canopy components, with wood comprising 5% and fruit 3%.<sup>14</sup>

Two main types of shoot can be identified. “Terminating” shoots are variable in length but have no terminal buds and the shoot tips usually wither and die within 40 d of emergence, leaving shoots with three to six full-sized leaves.<sup>15</sup> Short-terminated shoots are sometimes called spurs. “Non-terminating” shoots continue growing, and can reach 3–5 m in length during a single growing season. A large proportion of non-terminating shoots develops within the replacement cane zone of the canopy, although both types of shoot arise from apparently identical buds. The cause of the differences in the pattern of



**Figure 1** Schematic representation of the major trellis types used to support kiwifruit vines. The “Pergola” comprises a continuous horizontal trellis so that the ratio of the canopy surface area to appointed ground area (surface area ratio) is 1.0. The “T-Bar” comprises a discontinuous trellis including in each row a central horizontal portion and two inclined portions usually facing east and west, respectively.

shoot growth is not known, although the level of carbohydrate reserve laid down the previous growing season may be involved.<sup>9,16</sup>

The term "water shoots" has been used to describe a sub-group of non-terminating shoots that are especially vigorous.<sup>1</sup> These shoots generally arise close to the cordon, and are relatively unfruitful in the season following their development. Morphologically, water shoots are similar to shoots on juvenile vines. In commercial culture, these shoots are often pruned during the growing season, or removed during dormant pruning.<sup>10</sup> However, in their natural habitat water shoots represent a means of moving kiwifruit vines to new areas of the forest canopy, where subsequent generations of shoots would again become fruitful with the better light conditions. Such cycling between juvenile and mature forms appears to be very similar to that reported for another vine, *Syngonium* spp., in response to increases and decreases in soluble carbohydrate levels in the plant.<sup>17</sup>

Root development and distribution are much more variable than the growth characteristics of the above-ground components of the vine<sup>13</sup> due to the influences of the soil conditions.<sup>18-21</sup> The distribution of roots of noncultivated kiwifruit vines growing in the wild in China indicate that the roots are largely found in the top 1.0 m of soil, with the greatest densities ( $\text{m m}^{-3}$ ) about 0.4 m below the surface.<sup>5,13</sup> In New Zealand, roots of mature cultivated kiwifruit vines, grafted to seedling rootstocks<sup>10</sup> have been found to depths of at least 4.0 m in deep porous soils and extend well beyond the area occupied by the leaf canopy.<sup>22</sup> However, it is more typical to find over 50% of the total root within 0.5 m of the soil surface<sup>23-25</sup> and more than 90% of the roots within the top 1.0 m.

The expansion of the root system as a vine matures determines the soil volume for water and nutrient supply, and occurs by a combination of root extension and branching. The root system of immature vines occupies a bowl-shaped soil volume and the root density ( $\text{m m}^{-3}$ ) decreases with both depth and radial distance from the crown.<sup>26</sup> Roots from adjacent vines usually meet within 4–6 years of planting. For mature vines, the root density decreases with depth but at any soil depth is unaffected by distance from the crown.

## B. VINE DIMENSIONS

Annual fruit yields for mature vines (>6 years) are 10–25  $\text{t ha}^{-1}$  but can exceed 30  $\text{t ha}^{-1}$ , with a fruit water content at harvest of 81–85%.<sup>11</sup> The biomass (dry weight) of mature vines with a fruit yield (fresh weight) equivalent to 30  $\text{t ha}^{-1}$  is about 21.5  $\text{t ha}^{-1}$ .<sup>9</sup> For maturing vines (aged 3–6 years), the distribution of dry matter among the component organs, especially for the deciduous and transient organs, remains almost constant.<sup>25,27</sup> The root system accounts for about 40% of the total plant biomass. This contrasts with apple, where the root system usually comprises 20% or less of the total tree biomass.<sup>28,29</sup> The biomass of the current season's growth (leaves, shoots, fruit, and fibrous roots) may constitute more than 50% of the total vine biomass (Table 3). For mature vines, the proportion of total biomass in perennial organs may be greater than in developing vines, but the relative dry weights of deciduous and transient organs appear to be very similar to those for younger vines.<sup>30</sup>

The mean root density in the surface 0.5 m of soil is usually about 5–10  $\text{km m}^{-3}$ .<sup>22,23,31</sup> This density is comparable to (or greater) than that of other perennial fruiting crops including apple,<sup>32</sup> cherry<sup>32</sup> and grape.<sup>33</sup> The fibrous roots (<2 mm diameter) comprise more than 98% of the total root length, but less than 20% of the total root biomass.<sup>25,27</sup> Over a wide range of soil types, the distribution of roots of mature vines has been shown to be extremely clumped.<sup>26</sup>

**Table 3 Typical distribution of biomass for mature kiwifruit vines with fruit yield (fresh weight) of 30  $\text{t ha}^{-1}$**

|                  | Biomass<br>( $\text{t ha}^{-1}$ ) | Total (%) |
|------------------|-----------------------------------|-----------|
| Leaves           | 2.52                              | 10.8      |
| Fruit            | 4.97                              | 21.2      |
| Shoots           | 2.66                              | 11.4      |
| Laterals         | 1.94                              | 8.3       |
| Cordon           | 0.73                              | 3.1       |
| Stem             | 0.94                              | 4.0       |
| Structural roots | 7.60                              | 32.9      |
| Fibrous roots    | 1.92                              | 8.2       |

From Buwalda, J. G. and Smith, G. S., *Tree Physiol.*, 3, 295, 1987.

For cultivated vines, the leaf area depends on dormant and summer pruning practices, but a total leaf area index ( $\text{m}^2$  leaf area  $\text{m}^{-2}$  apportioned orchard area) of about 3.0 is common.<sup>12</sup> Location of the leaves in space depends on the growth and management of the shoots. While individual shoots may extend more than 2 m from the trellis on which the vine is supported, more than 80% of the leaf area is located within 0.6 m of the trellis.<sup>14</sup> Leaf area distribution within the canopy is highly heterogeneous (Figure 2). More than 70% of the total leaf area for a vine is located within the replacement cane zone.<sup>12</sup> The leaf area index can vary greatly (i.e., more than four-fold) within distances of less than 0.2 m, anywhere within the canopy (Figure 2). Leaf orientation within the canopy usually shows no significant azimuthal preference.<sup>14,34</sup> The distribution of leaf inclination angles is non-spherical and is consistent with an ellipsoidal model, and mean inclination angles ranging from  $29^\circ$  to  $33^\circ$  have been reported.<sup>14,34</sup>

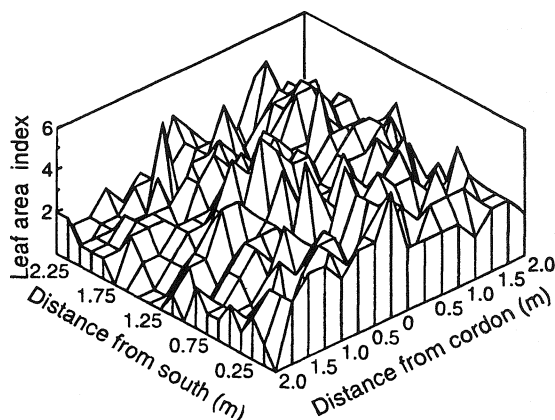
Flowers are borne on current season's terminate and non-terminate shoots arising from axillary buds on lateral canes that developed the previous growing season.<sup>35</sup> The inflorescence is potentially a compound dichasium containing a terminal flower and primary and secondary lateral flowers.<sup>35</sup> Many of the lateral flowers of 'Hayward' abort, but in some years they complete their development resulting in inflorescences with two or three flowers. The number of fruit on commercially managed vines often ranges from 25–40  $\text{m}^{-2}$  of apportioned ground area.<sup>10</sup> Fruit location within the canopy also depends strongly on vine management, although more than 65% are usually located within the fruiting zone. The disparate arrangement of leaves and fruit within the canopy results in leaf:fruit ratios varying greatly between the two canopy zones, ranging from 2:1 in the fruiting zone to 10:1 in the replacement cane zone.<sup>12</sup>

## C. ANNUAL GROWTH

### 1. Shoots and Leaves

Shoots of the current season's growth develop from axillary buds on laterals (canes) of the previous season's growth, although some growth can occur from the buds on older wood. Vines are pruned during winter to retain about 25–40 axillary buds  $\text{m}^{-2}$  of apportioned orchard area. Under New Zealand conditions, fewer than 50% of these axillary buds develop into shoots.<sup>15</sup> However, the proportion of buds that break can be greater in other countries such as Italy.<sup>36</sup> Many of the buds on the long vigorous laterals or on the undersides of the laterals remain dormant. The proportion of buds that break can be modified through the use of the dormancy-breaking chemical, hydrogen cyanamide,<sup>37–39</sup> which increases the uniformity of shoot development, advances the date of bud break, and compresses the bud break period. A large increase in the concentration of proline in the buds of vines treated with hydrogen cyanamide has been associated with the onset of flowering and increased fruitfulness.<sup>40</sup> Bud break usually occurs over a period of about 20 d.<sup>41</sup> Shoots that develop early tend to be more fruitful and they also appear to suppress growth from other buds.<sup>41,42</sup>

Shoot extension proceeds rapidly after bud break, with the relative growth rate peaking at 0.25–0.30  $\text{m m}^{-1} \text{d}^{-1}$  during the first 20 d.<sup>31</sup> The relative growth rate of the shoots then declines rapidly between 20–60 d after bud break, followed by a much lower growth rate of  $<0.01 \text{ m m}^{-1} \text{d}^{-1}$  for the remaining 150–170 d of the growing season.



**Figure 2** Spatial distribution of leaf area index for a kiwifruit vine. Leaf area index was measured at 320 canopy positions by counting the number of interceptions with leaves as a long needle passes through the canopy at an angle normal to that of the trellis surface. The total leaf area index for the whole vine was 2.74.

Leaf numbers increase rapidly during the first 60 d after bud-break to more than 200 leaves  $\text{m}^{-2}$  of apportioned orchard area, with only a slight increase thereafter.<sup>12</sup> The leaves are arranged in a spiral phyllotaxis of 2/5 or 2 + 3; the spiral may be either clockwise or anticlockwise.<sup>43</sup> The total leaf area on an individual shoot can be linearly related to shoot length.<sup>44</sup> Increase in leaf area follows a sigmoid pattern with time. Maximum rate of expansion occurs about 20 d after appearance, with final leaf size occurring about 60 d later.<sup>16</sup> As the leaves enlarge they change shape, with more growth in width than in length.<sup>13</sup> The average final area of individual leaves can range from 0.013  $\text{m}^2$  for leaves in the fruiting zone to 0.020  $\text{m}^2$  for leaves in the replacement cane zone.<sup>12</sup>

The specific leaf weight changes with leaf age, increasing from 0.09  $\text{kg m}^{-2}$  about 30 d after leaf emergence to 0.20  $\text{kg m}^{-2}$  after the leaves have fully expanded.<sup>45</sup> Leaves on non-terminating shoots accumulate dry weight for an extended period compared to those on terminating shoots.<sup>46</sup> A transitory decline in dry weight of the leaves occurs during the period of rapid fruit growth. This decline coincides with a marked reduction in the starch content of the leaves.<sup>47</sup> The weight of leaves in shaded positions within the canopy is usually much lower than that of leaves in exposed positions.<sup>48</sup> Leaf chlorophyll (chlorophyll *a* + *b*) increases during the initial 100–150 d after leaf emergence, reaching maximum values of 1.2 to 1.4  $\text{g m}^{-2}$ .<sup>45</sup> The lower surface of the leaf is covered by a dense layer of stellate trichomes which are found largely along the veins.<sup>13</sup> Trichomes on the upper surface are also found along the primary and secondary veins, but they do not persist for any length of time. Stomata are found only on the lower leaf surface.<sup>49</sup> Large raphide cells are found in the palisade and spongy mesophyll, alongside the veins, and in the trichomes.<sup>1,50</sup> Styloids are also found in the palisade tissue and in the spongy mesophyll.

Leaves abscise in autumn, usually after the first frost.

## 2. Flowers and Fruit

Flower primordia are not present in the buds during dormancy, but begin to differentiate at bud swell, approximately 10–15 d prior to bud break.<sup>15</sup> Flowering occurs about 50–70 d after bud break. The fruit develops from a multicarpellate ovary borne on a pedicel.<sup>1</sup> The pattern of fruit enlargement can be related to three distinct growth phases within the fruit.<sup>51</sup> During the first 70 d after anthesis cell division in the central core, inner and outer pericarp, followed by cell enlargement in all tissues, results in rapid growth and weight gain. During the next 20–30 d, cell enlargement slows in both the inner pericarp and central core so that growth and weight gain are reduced. Cell enlargement in the inner pericarp and central core results in a second period of growth and weight gain in the final 70–85 d until harvest. The dry weight of the fruit increases linearly with time.<sup>16,51–53</sup> The double sigmoid curve for gains in fruit volume and fresh weight therefore implies that assimilates are incorporated into the fruit with variable quantities of water.<sup>9</sup>

The relative growth rate of fruit volume is greatest ( $>0.1 \text{ mm}^3 \text{ mm}^{-3} \text{ d}^{-1}$ ) during the first 20–30 d after anthesis, then declines rapidly during the following 40 d to a rate less than  $0.005 \text{ mm}^3 \text{ mm}^{-3} \text{ d}^{-1}$  for the remaining 90–100 d until harvest.<sup>9</sup> Fruit are harvested in autumn, about 160–180 d after anthesis.

## 3. Roots

The root system is highly dynamic, with continual growth and senescence (turnover) of the roots. Seasonal turnover appears to be limited mainly to the fibrous roots.<sup>9</sup> The seasonal pattern of root growth, described as incidence of non-suberised (white) root expressed as a fraction of the total root length, shows an increase in early spring to a peak in late summer, before declining during late autumn and winter.<sup>31</sup> The presence of white root throughout the year indicates that there is at least some root growth occurring at all times. The relative growth rate of new roots ranges from  $0.5 \times 10^{-3} \text{ m m}^{-1} \text{ d}^{-1}$  in spring to  $3.5 \times 10^{-3} \text{ m m}^{-1} \text{ d}^{-1}$  in late summer. Root growth was especially low during the period of flowering and early fruit growth,<sup>54</sup> and appears to be very sensitive to changes in assimilate supply within the whole vine.<sup>12,47,54</sup>

In mature vines, the total root length declines during spring, and increases during late summer and autumn, so that the initial root length is restored by the following winter.<sup>54</sup> These changes imply that considerable turnover of the roots occurs during the season. An assumption that new roots remain white for 4 weeks led to an estimate that more than 30% of the total root length of mature vines was replaced annually.<sup>31</sup> However, more rapid suberization of roots during summer<sup>32</sup> would imply that root turnover rates are greater, perhaps 100%  $\text{year}^{-1}$ .<sup>9</sup> If turnover is limited to the fine root fraction ( $<2 \text{ mm}$  diameter), this would involve 6–8% of the total biomass annually. It is further possible that rapid death of a large

proportion of new roots may mask considerable root growth. For apple, pear, and sour cherry seedlings, 2–4.8% of the root tips are often found dead at sampling time.<sup>55</sup> Assuming that dead roots are sloughed off quickly (i.e., less than 1 week), this incidence suggests a rate of replacement of root tips greater than 100% per year.

### III. IRRADIANCE

The radiation environment of the orchard, the interception of available radiation by leaves within the canopy, and the irradiance response of photosynthesis (net CO<sub>2</sub> assimilation, *A*) and hence carbon acquisition, for individual leaves are the main factors determining the effects of irradiance on the whole vine.

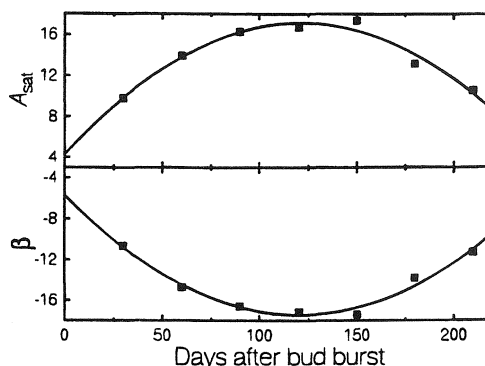
#### A. RESPONSE OF SINGLE LEAVES

An early report, based on spot measurements of *A* with variable photosynthetically active radiation (PAR), suggested that *A* was radiation saturated at 500–700 μmol PAR m<sup>-2</sup> s<sup>-1</sup>.<sup>56</sup> Later measurements of *A* at variable ambient PAR,<sup>48</sup> fitted to a rectangular hyperbola, indicated that an irradiance greater than 1400 μmol PAR m<sup>-2</sup> s<sup>-1</sup> was required to saturate *A*.<sup>9</sup> However, interactions between the influences of irradiance and other environmental variables (e.g., temperature, leaf-to-air vapor pressure gradient) limit the value of such descriptions of the irradiance response of *A*.<sup>57</sup> More recently, an examination of the irradiance response of *A* for single leaves, made using a climate controlled mini-cuvette system, led to the description of this response with an asymptotic exponential equation<sup>45</sup>

$$A = A_{sat} - \beta \rho^{\text{PAR}} \quad (1)$$

where *A<sub>sat</sub>* is the radiation saturated rate of photosynthesis (μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>), and β and ρ are empirical parameters (ρ < 1). Other leaf gas exchange characteristics such as the dark respiration rate (*R<sub>d</sub>*) and the quantum yield of photosynthesis (φ<sub>*i*</sub>), can be estimated from the fitted parameters. For kiwifruit, the asymptotic exponential curve (Equation 1) describes the irradiance response of *A* for single leaves more accurately than rectangular hyperbola or non-rectangular hyperbola curves.<sup>58</sup>

Measurements made throughout the season have shown that kiwifruit leaves exhibit considerable temporal variation in the irradiance response of *A*.<sup>45</sup> The stage of growing season was found to be less important than the age of the leaves at the time of measurement (Figure 3). *A<sub>sat</sub>* increased from about 10 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> at 30 d after leaf emergence to a peak of about 17 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> at 120–180 d after leaf emergence, and declined with leaf senescence (Figure 3). The *A<sub>sat</sub>* levels so far defined are within the range reported for other fruit crop species, such as grape,<sup>59</sup> apple,<sup>60</sup> and peach.<sup>61</sup> Factors that enhance leaf senescence may accelerate the rate of decline of *A<sub>sat</sub>* at the end of the growing season. An early study indicated that *A<sub>sat</sub>* declined from mid-summer to the end of the growing season.<sup>48</sup> The radiation level required to saturate *A*, PAR<sub>sat</sub>, increased from about 600 μmol m<sup>-2</sup> s<sup>-1</sup> at 30 d after leaf emergence to peak at about 800–900 μmol m<sup>-2</sup> s<sup>-1</sup> at about 90 d after leaf emergence, before declining again at the end of the season. These estimates of PAR<sub>sat</sub> are consistent with those reported for a wide range of agricultural and horticultural crops.<sup>57,62</sup> Photosynthesis for the leaves of kiwifruit vines is



**Figure 3** Variation with leaf age in parameter values for the asymptotic exponential curves used to describe irradiance response of single leaf photosynthesis.

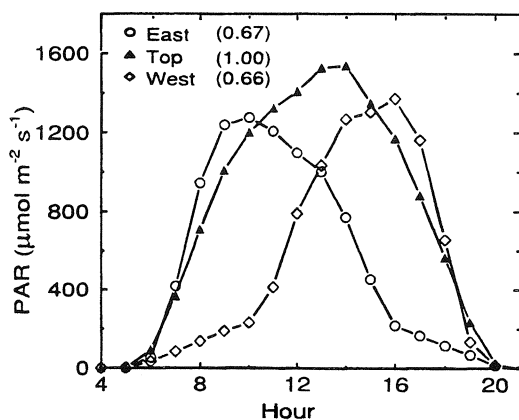
therefore likely to be radiation limited for much of the growing season. Relatively low  $PAR_{sat}$  and  $A_{sat}$  levels have been reported for kiwifruit vines grown in controlled environments.<sup>63–65</sup> However, the irradiance levels used in these studies were usually less than the equivalent of one-third of full sun, so the results probably reflect acclimation to low light.  $R_d$  showed no significant temporal variation, averaging  $0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . However, expressed on a leaf dry weight basis,  $R_d$  decreased with increasing leaf age. This decline coincided with a decline in the concentration of leaf nitrogen expressed on a dry weight basis.  $\phi_i$  increased slightly with leaf age from about  $0.05 \text{ mol CO}_2 \text{ mol}^{-1} \text{ PAR}$  30 d after leaf emergence to about  $0.07 \text{ mol CO}_2 \text{ mol}^{-1} \text{ PAR}$  by 120–180 d after leaf emergence (Figure 3). As  $R_d$  and  $\phi_i$  were affected little by leaf age, the compensation point was also little affected, averaging  $22 \mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ .

Leaves within the canopy show spatial variation in photosynthetic capacity at any time. The radiation environment within which leaves grow can affect photosynthetic capacity. Leaves growing in shaded parts of the canopy have been shown to be acclimated to lower irradiance conditions with lower  $A_{sat}$  and  $PAR_{sat}$ , and changes in chlorophyll a/b ratios, although  $\phi_i$  is little affected.<sup>34,48</sup> These responses are typical of those reported for a wide range of C-3 species.<sup>66</sup> Exposure of previously shaded leaves to high levels of irradiance can lead to photoinhibition of photosynthesis, especially at low temperatures.<sup>67</sup> The low  $A_{sat}$  rates for leaves growing in shaded positions in the canopy are unlikely to limit canopy photosynthesis. Radiation levels in the shaded positions of the canopy are usually very low, and photosynthesis will be affected more by  $\phi_i$  than by  $A_{sat}$ .

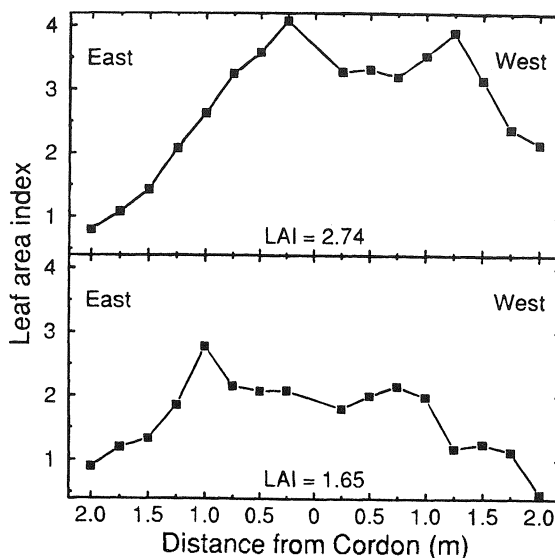
The slow development of  $A_{sat}$  after leaf emergence limits whole-plant photosynthesis during canopy expansion. For many species, maximum photosynthetic capacity for any leaf is attained at or prior to full leaf expansion; e.g., within 15–17 d for strawberry,<sup>68</sup> and 11 d for bean.<sup>69</sup> While  $A_{sat}$  generally develops more slowly for leaves of perennial plants compared to leaves of annual plants,<sup>70</sup> the development of  $A_{sat}$  for leaves of kiwifruit vines is still slower than that reported for other perennial species such as cherry.<sup>71</sup> Stepwise multiple regression analysis indicated that the slow development of  $A_{sat}$  for kiwifruit vines was related more closely to leaf nitrogen (per unit of leaf area) than to other leaf attributes such as leaf chlorophyll and stomatal conductance.<sup>45</sup> In fact, the limited photosynthetic capacity in young leaves is physiologically similar to that usually associated with nitrogen deficiency.<sup>72</sup> It is possible that the ontogenetic trend in leaf nitrogen content regulates photosynthetic capacity for kiwifruit leaves. Nitrogen deficiency has been shown to affect directly the radiation saturated rate of  $A$ .<sup>63</sup>

## B. INTERCEPTION OF RADIATION

Canopy shape strongly affects the radiation environment for leaves at different positions. The irradiance on the surface of canopies trained on a horizontal Pergola shows no spatial variability, so temporal variability depends mainly on incoming radiation.<sup>73</sup> For T-bar vines, however, irradiance at the surface also varies according to the variable angle of incidence of the surface and the solar beam. The east-facing surface typically experiences relatively high irradiance during the morning, while the west-facing surface experiences relatively high irradiance for a period during the afternoon (Figure 4). However, the east- and west-facing surfaces of the T-bar vines are shaded by other parts of the canopy for long periods of the day, so diurnal integrals of incident radiation decrease with distance down the inclined surfaces, and can be only 66% of those for the central horizontal surface (Figure 4).



**Figure 4** Average diurnal trend of surface irradiance for eastern, central (top), and western faces of a kiwifruit vine supported on a T-bar trellis. Data represent mean hourly irradiance over a 5-week period during mid-summer. Diurnal integrals for the east and west facing surfaces were 67 and 66%, respectively of the integral for the central (top) horizontal surface.



**Figure 5** Mean leaf area index at different distances from the central cordon for vines with total leaf area index (LAI) of (a) 2.74 and (b) 1.61. The LAI was measured as described in Figure 2.

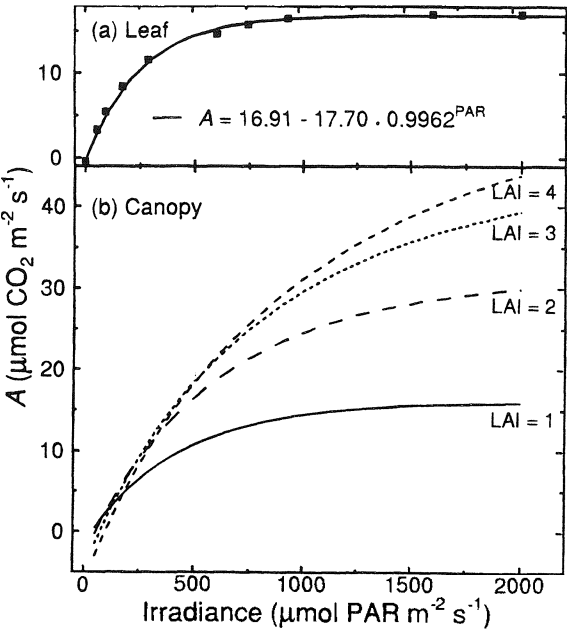
Spatial variation in leaf area for canopies of kiwifruit vines also affects radiation interception. Typical distributions of leaf area index across a surface of vines trained on a T-bar trellis are shown in Figure 5. Such vines are characterized by continuity of canopy within a row, but discontinuity between adjacent rows (Figure 1). The leaf area index is generally highest in the inner region of the vine near the cordon, and may be up to 50% greater in that position than the average for the whole vine. Conversely, the leaf area index tends to be lowest near the ends of the laterals, at the edges of the canopy. Within any part of the canopy, the leaf area index can show substantial spatial variability, often ranging from 1.0 to 6.0 within distances of 0.3 m. This variability results in localized areas of heavy shade or light transmission within the canopy.

### C. CANOPY PHOTOSYNTHESIS

Together, spatial variation in leaf arrangement and temporal variation in irradiance conditions lead to highly dynamic irradiance of individual leaves within the canopy. Furthermore, at any time the canopy includes leaves of widely varying photosynthetic capacity, due to varying leaf age within the canopy and age-related changes in the photosynthetic capacity of individual leaves. Consequently the photosynthetic integral for all leaves within the canopy is highly dynamic. The complex plant-environment interactions and the seasonal dynamics of canopy photosynthesis for a kiwifruit vine have been described using a mathematical model of carbon acquisition and utilization.<sup>44</sup> This model considers radiation attenuation through the leaf canopy (assuming Beer's Law for exponential attenuation),<sup>74</sup> and computes integrated canopy photosynthesis according to the irradiance of leaves at different layers. Leaf arrangement within the canopy influences radiation attenuation. An ellipsoidal distribution of leaf inclination angles, with a mean inclination angle of 29° is assumed.<sup>34</sup> The asymptotic exponential curve describing the irradiance response of  $A$  for single leaves must be integrated numerically, but "Gaussian 3-point" integration<sup>75</sup> enables rapid and convenient computation of canopy  $A$ .<sup>58</sup>

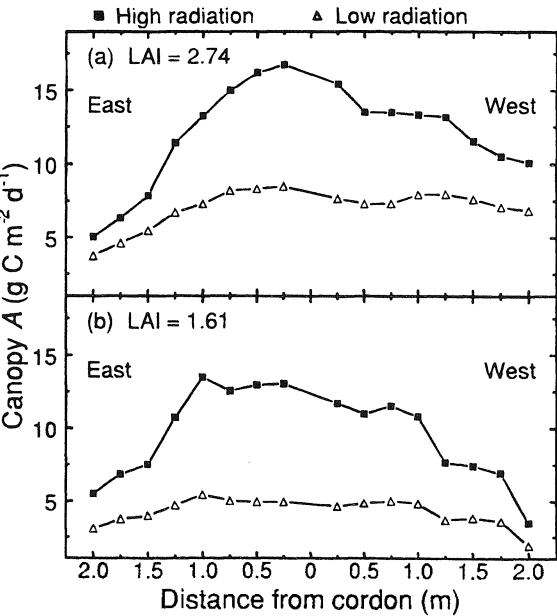
Canopy  $A$  for vines trained on a horizontal trellis can be simulated by assuming uniform incident radiation at all points on the canopy surface. The simulated irradiance response of canopy photosynthesis depends on the irradiance response of single leaf photosynthesis (Figure 6a) and the leaf area index (Figure 6b). Typically,  $A_{sat}$  and  $PAR_{sat}$  for the canopy increase with increasing leaf area.

A modified canopy photosynthesis model enabling estimation of the incident radiation at any point on surfaces with complex shapes, and distribution of photosynthesis within canopies with non-homogeneous distribution of leaf area, has recently been developed.<sup>73</sup> For vines on a T-bar trellis with the leaf area shown in Figure 5,  $A$  near the cordon is usually greater than that near the ends of the laterals (Figure 7). On a clear day (e.g.,  $PAR > 1800 \mu\text{mol m}^{-2} \text{s}^{-1}$  at midday), this difference was about 60% for vines with a high leaf area and 85% for vines with low leaf area. On cloudy days  $A$  at different parts of the canopy was more uniform, but still 10–20% greater near the center of the vine than near the ends of the laterals.



**Figure 6** Irradiance response of photosynthesis ( $A$ ) for (a) single leaves, and (b) entire canopies. The single leaf response was described with an asymptotic exponential equation which was then used to estimate canopy photosynthesis for vines with different total leaf area index using a mathematical model.<sup>44</sup>

Canopy  $A$  has been measured directly for kiwifruit vines using whole-canopy gas exchange cuvettes.<sup>76,77</sup> The irradiance response of a canopy on a T-bar trellis was described with an asymptotic exponential curve similar to that used for single leaves. For measurements made during late summer, diel trends of canopy  $A$  indicated that  $R_d$  averaged  $-8.24 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ,  $\phi_i$  averaged  $0.091 \text{ mol CO}_2 \text{ mol}^{-1} \text{ PAR}$ , the compensation point averaged  $105 \mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ ,  $\text{PAR}_{\text{sat}}$  averaged  $1312 \mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ , and  $A_{\text{sat}}$  averaged  $28.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .<sup>76</sup> The  $R_d$  rate reflects respiration of non-photosynthetic components (fruit and wood) of the canopy as well as respiration of the leaves. The higher  $\text{PAR}_{\text{sat}}$  and  $A_{\text{sat}}$  for the canopy compared to that for single leaves illustrate the capacity for increased photosynthesis where radiation is attenuated through a canopy with overlapping leaf layers. The higher apparent  $\phi_i$  for the canopy compared to that for single leaves is difficult to explain. The



**Figure 7** Diurnal integrals of simulated photosynthesis ( $A$ ) at different distances from the cordon of kiwifruit vines with (a) high and (b) low total leaf area index. These simulations used a modified canopy photosynthesis model,<sup>73</sup> and radiation data for a sunny and cloudy day in late summer.

irradiance response for the canopies was described according to diurnal measurements of canopy *A* as irradiance varied. It is possible that the diffusing effect of the film used to clad the gas-exchange cuvette and the canopy shape affected the diurnal trend for radiation interception. Expressing  $\phi_i$  in terms of intercepted radiation, rather than incident PAR would enable better comparisons to be made between canopies and single leaves. A more recent study of whole-canopy gas exchange illustrated clearly increased canopy *A* for vines with a leaf area index of 2.7 compared to vines with leaf area index of 1.6.<sup>78</sup> Direct measurement of canopy *A* also illustrated mid-day declines in *A*, typically after 09:00–10:00 h on days with high radiation levels.<sup>78</sup> Such declines led to canopy *A* rates in the afternoon of only 70–80% of those recorded at similar radiation levels in the morning. Increased respiration with increasing temperature was insufficient to account for the decline in canopy *A*. Feedback inhibition of *A* has been suggested as a possible contributor to this phenomenon.<sup>78</sup>

The cyclic behavior of the stomata of kiwifruit leaves may also be an expression of feedback inhibition.<sup>79</sup> Typically the period of stomatal cycling for most plants studied has been about 10–60 min.<sup>80</sup> However, an average cycle found for kiwifruit vines was of 4–6 d duration and corresponded closely to the fluctuations in PAR.<sup>79</sup> The strongly negative relationship between stomatal conductance and PAR is consistent with the suggestion that accumulation of photosynthate in the leaves may be responsible for the partial closure of the stomata.<sup>81</sup>

#### D. EFFECTS OF REDUCED IRRADIANCE ON VINE GROWTH AND DEVELOPMENT

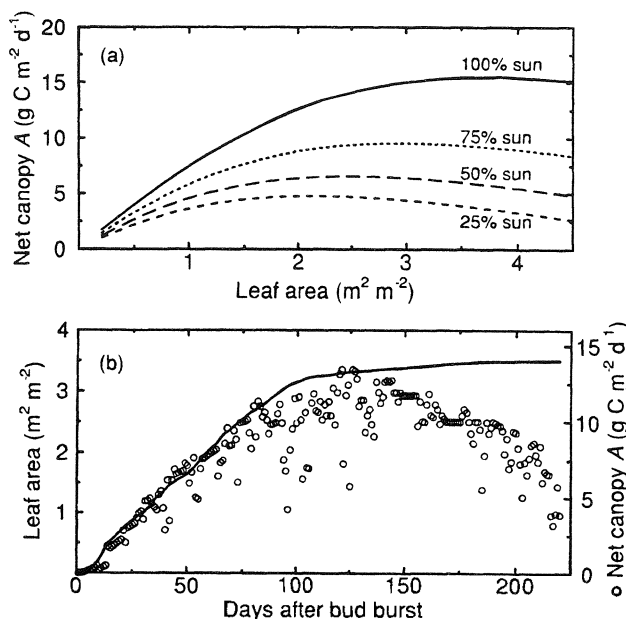
A feature of kiwifruit cultivation in New Zealand is the use of dense networks of windbreaks (shelter trees or shelter cloth) to protect the vines from wind damage.<sup>82</sup> Radiation interception by vines growing adjacent to shelter belts has been shown to be reduced by up to 40% where the shelter trees were 20 m in height.<sup>83</sup> For vines growing in a controlled environment where the radiation was reduced from 600 to 220  $\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ , there was a marked reduction in shoot growth and leaf weight, while bud break and flowering in the following year were also reduced.<sup>84</sup> Overhead shading of vines to 45% of ambient radiation for three consecutive seasons reduced the average fruit weight by 14 g and the return bloom by 56%.<sup>85</sup> During cold storage, fruit from shaded vines had lower soluble solids concentrations, and were only slightly less firm, than fruit from unshaded vines.<sup>85</sup> By contrast, shading had no effect on the starch content or the internal color of the fruit. Shading vines for short periods during the growing season can also affect fruit growth. Shading the canopy during the most rapid phase of growth of the fruit immediately after anthesis, had a greater effect on final fruit size than shading later in the growing season.<sup>85</sup>

Low irradiance within the canopy can limit carbon acquisition by the leaves and may lead to premature leaf senescence, particularly those leaves in the denser parts of the canopy. Low irradiance within the canopy may result from low irradiance at the periphery of the vine and/or high leaf area. However, the effects of these two factors can be difficult to discern. Simulation modelling of canopy photosynthesis<sup>44</sup> has been applied to examine the interaction between incoming radiation and leaf area index on net carbon acquisition of the canopy. While light interception and hence total photosynthesis continue to increase with increasing leaf area (Figure 6b), marginal gains in photosynthesis at high leaf area are small relative to marginal costs of tissues synthesis and maintenance. Accordingly, there is an optimum leaf area beyond which the carbon cost of tissue synthesis and maintenance exceeds the carbon acquired by photosynthesis. The optimum leaf area reduces with decreasing radiation (e.g., cloudy weather or shading from shelter). Net carbon acquisition by the canopy is reduced slightly at excessive leaf area, but is reduced strongly by low radiation (Figure 8a). For kiwifruit in New Zealand conditions, the optimum leaf area index appears to be about 3.0–3.5  $\text{m}^2 \text{ m}^{-2}$ .<sup>34</sup> This leaf area is typically attained about 100 days after bud break (Figure 8b). During canopy expansion, canopy photosynthesis is limited more by low leaf area (i.e., low radiation interception) than by irradiance.

### IV. TEMPERATURE

#### A. PHENOLOGY AND GROWTH

Estimations of the chilling requirements of kiwifruit vines to “break” dormancy have been based on both laboratory and field observations. A significant delay in bud break was found for vines that received less than 950–1000 h of chilling at 4°C.<sup>86,87</sup> These authors also showed an increase in flower numbers per shoot with an increase in the duration of chilling during the early to mid stages but not in the later stages of dormancy. Constant temperature conditions were less effective in breaking dormancy than where there was a change in the temperature between day and night.<sup>87,88</sup>



**Figure 8** (a) Interaction between radiation and leaf area (LAI) for diurnal integral of simulated net canopy photosynthesis (A); simulations assumed fractions of radiation recorded for a clear day in mid-summer. (b) Seasonal trend of canopy leaf area and simulated canopy photosynthesis (A).

Field observations initially indicated that kiwifruit vines required approximately 700–800 Richardson Chill Units (RCUs) to break dormancy.<sup>89</sup> However, a later report claimed that only 500 RCUs were needed to produce a crop.<sup>90</sup> In New Zealand, RCUs calculated for the winter period typically range from 1033 in the warmest kiwifruit growing district to 1892 in the coolest district.<sup>91</sup> Bud break was reported to be approximately 10% greater in the cooler regions than in the warmer regions.<sup>91</sup> However, recent research has shown that RCUs cannot be used to reliably predict bud break and flowering in kiwifruit vines as the response of vines to winter chilling occurs over a wide range of accumulated RCUs.<sup>92</sup> The main effects of increased winter chilling are to improve the proportion of dormant buds that break in spring and to reduce the number of developing flowers that abort.

The rate of leaf appearance (leaves per shoot per day) in spring increases approximately linearly with temperatures above 10°C to a maximum rate at 20°C, above which the rate declines.<sup>93</sup> The time from bud break to flowering also appears to be temperature dependent. Full bloom was shown to occur approximately 360 growing degree days (calculated from a threshold temperature of 7.5°C) after bud break.<sup>94</sup> Controlled environment studies using container-grown vines have shown that bud break was 16 d later when the temperature was maintained at 10°C than it was at 19°C.<sup>41</sup> The duration from bud break to flowering increased approximately 10 d for every 1°C reduction in temperature. In the same experiment, flowering was found to be spread over 34 d with a mean temperature of 12°C, but only over 13 d where the temperature was 19°C.

Temperature is also thought to have an important influence on fruit maturity. Harvest maturity is determined in kiwifruit by the concentration of soluble solids (Brix) of expressed juice.<sup>95</sup> In New Zealand, the required minimum Brix for harvest is 6.2°.<sup>96</sup> Cool temperatures during autumn enhance the rate of increase in the Brix level of the fruit.<sup>97</sup> At a mean temperature of 11°C, starch in the fruit degrades very quickly with a coincidental increase in total sugar.<sup>98</sup> In contrast, at a mean temperature of 17°C there is little degradation of starch and a proportionally smaller increase in total sugar. Changes in total sugar are similar to those recorded for Brix values.<sup>98</sup>

The seasonal pattern of new root growth has been shown to be broadly related to the annual changes in soil temperature.<sup>31</sup> Experiments where the temperature of the root and shoot environments were controlled independently have shown that vine growth ceased when the temperature of the root zone was maintained at 10°C, whereas maximum root growth occurred at 20°C.<sup>99</sup> Root growth of kiwifruit vines therefore appears to have a temperature optimum lower than that for other deciduous fruiting plants. Root growth of apple, for example, has an optimum root temperature of 25°C.<sup>100</sup> Soil temperatures could have a major influence on the commencement of root growth in spring, as soil temperatures in New Zealand, for example, do not exceed 10°C until late spring or early summer.<sup>99</sup> By this stage of

the season the vine has undergone several major growth phases, including bud break, leaf growth, anthesis, and early fruit growth.<sup>9</sup>

## B. LOW-TEMPERATURE STRESS

The minimum temperature tolerated by kiwifruit vines depends on the stage of growth. In spring, flower buds, flowers, and young actively growing shoots are seriously damaged by temperatures of  $-1.5^{\circ}\text{C}$  or less for durations as short as 30 min.<sup>101</sup> In autumn, following leaf fall, temperatures as low as  $-5.0^{\circ}\text{C}$  have been found to cause no obvious shoot damage or reduction in the number of buds that developed the following spring, but temperatures of  $-7.0^{\circ}\text{C}$  were damaging.<sup>102</sup> By mid-winter, vines can tolerate temperatures of  $-7.0^{\circ}\text{C}$ , but exposure to  $-10.0^{\circ}\text{C}$  for 1 h has been shown to damage dormant shoots.<sup>101</sup>

Studies in controlled environments have shown that leaves of kiwifruit vines suffer severe damage when exposed to moderate light ( $650\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ ) at  $10^{\circ}\text{C}$ , including photobleaching, yellowing of the leaf margins, reduced expansion rates of the leaf, and death of the stem apices.<sup>93</sup> However, these symptoms were not apparent when vines were grown at lower light ( $280\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ ) at  $10^{\circ}\text{C}$ , suggesting that the vines were affected more from high-light stress at low temperatures than directly from low temperature stress. Photoinhibition of photosynthesis has been cited as the cause of this leaf damage.<sup>67,103</sup> A reduction in the photon yield of photosynthesis and changes in the chlorophyll fluorescence emission at 77K occurred when shade-grown leaves were exposed to high light ( $1500\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ ). Photoinhibition occurred at all temperatures examined ( $5\text{--}35^{\circ}\text{C}$ ), but was greatest at low temperatures. Recovery from the effects of photoinhibition was also found to be temperature dependent with little or no recovery occurring below  $20^{\circ}\text{C}$ , but rapid recovery at  $30\text{--}35^{\circ}\text{C}$ .<sup>67,104</sup> Visual leaf symptoms typical of high-light low-temperature stress have been observed during early spring in New Zealand. Gas exchange and fluorescence analysis have also shown that exposed leaves can exhibit symptoms of partially impaired photosystem II activity, particularly in spring and autumn, which are consistent with high-light low-temperature stress.<sup>105</sup> Photoinhibition in the field appears to be at a much lower level than would be expected from studies on plants grown in controlled climate facilities.

## C. EFFECTS OF HIGH TEMPERATURE

While optimal temperatures for the growth of various components of the kiwifruit vine have not been defined, temperatures greater than  $35^{\circ}\text{C}$  have been shown to cause significant reductions in photosynthesis and excessive rates of transpiration.<sup>106</sup> For vines growing in the field, increasing the average air temperature during late winter and early spring from  $12.2$  to  $17.1^{\circ}\text{C}$  increased the rate of growth of the apical shoots, which in turn reduced the number of subtending shoots that produced flowers.<sup>107</sup> Elevated temperatures during spring, however, advanced the date of flowering. At harvest fruit from the vines grown at the higher temperature were significantly larger and had higher soluble solids concentrations than fruit from the vines grown at the ambient temperature.<sup>107</sup>

Root temperatures in excess of  $25^{\circ}\text{C}$  reduced both shoot and root growth.<sup>99</sup> The effects on the shoots however, were less severe so that the shoot/root ratio increased from 4.6 at  $20^{\circ}\text{C}$  to 6.4 at  $30^{\circ}\text{C}$ . Increased root respiration with increasing temperature,<sup>108</sup> and hence increased carbon losses from the root system, may partly explain this reduction in root growth.

# V. WATER

## A. WATER RELATIONS

Stomatal conductance to water vapor ( $g_s$ ) at saturating irradiance ( $2000\ \mu\text{mol PAR m}^{-2}\ \text{s}^{-1}$ ) varies with leaf age, increasing from  $0.2\text{--}0.3\ \text{mol H}_2\text{O m}^{-2}\ \text{s}^{-1}$  at about 30 d after leaf emergence to  $0.6\text{--}0.9\ \text{mol H}_2\text{O m}^{-2}\ \text{s}^{-1}$  at 90–120 d after leaf emergence.<sup>45</sup> The temporal changes in  $g_s$  and  $A$  influence the water-use efficiency. The slow increase in  $A_{sat}$  with leaf age results in the transpiration ratio at saturating irradiance increasing from about  $3\text{--}5\ \text{mmol CO}_2\ \text{mol}^{-1}\ \text{H}_2\text{O}$  at 30–60 d after leaf emergence to  $9\text{--}10\ \text{mmol CO}_2\ \text{mol}^{-1}\ \text{H}_2\text{O}$  at 120–150 d after leaf emergence.

The typical diurnal pattern of  $g_s$  for leaves of unstressed vines shows a rapid rise in the early morning with little change during the day until radiation levels decline again during the evening.<sup>48,77,109,110</sup> However, partial stomatal closure about midday has recently been reported, which resulted in a reduction in  $g_s$  by 20–30% and was associated with a reduction in leaf and canopy  $A$ .<sup>77</sup> Relatively high values for  $g_s$  have been recorded at night, especially for vines growing in advective conditions,<sup>110</sup> and are consistent with nocturnal water use measured for whole canopies.<sup>78</sup> As a consequence, up to 20% of the water use by the vine may occur at night.<sup>111</sup>

Because  $g_s$  is high for kiwifruit leaves, water use is influenced strongly by the boundary layer conductance. Any additional limitations due to trapping of a boundary layer by the stellate hairs could therefore be significant.

## B. DROUGHT STRESS

Like most other plants, drought stress reduces  $g_s$  of the leaves of kiwifruit vines, with a  $g_s$  of  $0.016 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$  being recorded for severely droughted vines in the field.<sup>48</sup> Effects of water stress appear to be closely related to the leaf water potential ( $\Psi_l$ ). Typically  $\Psi_l$  for vines without water stress is lowest at about midday, but generally no lower than  $-0.6 \text{ MPa}$ .<sup>48,109,110,112</sup> Stomatal conductance has been shown to be insensitive to  $\Psi_l$  greater than  $-0.6 \text{ MPa}$ , but declines once  $\Psi_l$  falls below  $-0.6 \text{ MPa}$ . Leaves may become severely wilted when  $\Psi_l$  falls below  $-0.9 \text{ MPa}$ , but the stomata do not close fully even where  $\Psi_l$  as low as  $-2.9 \text{ MPa}$  has been measured.<sup>48</sup>

Measurements of  $\Psi_l$  at dawn have been found to be useful for predicting drought stress of kiwifruit vines. The degree of wilting during peak evaporative demand at midday has been related to dawn measurements of  $\Psi_l$ .<sup>109</sup> Vines with  $\Psi_l$  of less than  $-0.12 \text{ MPa}$  at dawn readily wilt during peak periods of evaporative demand during sunny days, but were shown to regain turgor at night. Wilting was also shown to be irreversible where the  $\Psi_l$  at dawn was less than  $-0.65 \text{ MPa}$ .<sup>109</sup>

The effects of drought stress on  $A$  are larger than those on  $g_s$ , so that the transpiration ratio increases as the stomata close.<sup>48</sup> In fact, an early report suggesting that the water-use efficiency increased with leaf age<sup>48</sup> probably reflected restricted stomatal conductance due to water stress.

### 1. Effects on Growth

Studies of kiwifruit vines grown in a polyethylene lined trench have shown that drought stress reduces dry matter accumulation of all vine components of kiwifruit.<sup>27</sup> In an experiment where the supply of irrigation water was restricted for 3 years, root length increased from  $19.8 \text{ KM vine}^{-1}$  for the irrigated kiwifruit vines to  $27.5 \text{ KM vine}^{-1}$  for the non-irrigated vine.<sup>118</sup> The corresponding volume of soil explored by the roots increased from  $6.9 \text{ m}^3 \text{ vine}^{-1}$  to  $11.8 \text{ m}^3 \text{ vine}^{-1}$  respectively. This result is consistent with an increased root:shoot ratio, typical of responses of many plant species to drought stress.<sup>113</sup>

Drought stress has immediate and significant effects on fruit growth, with a severe stress level halting growth. While reducing water supply per se may affect fruit growth directly, it is also possible that an indirect effect, through reduced assimilate supply as a result of partial closure of the stomata and altered allocation to the root system, may also contribute to reduced fruit growth during periods of drought stress. Relieving the vine of drought stress restores the growth rate of the fruit to that of fruit on non-stressed vines but growth lost during the period of drought stress is never recovered.<sup>114,115</sup> Although fruit size can be restricted by drought stress, beneficial effects on the post-harvest storage characteristics of the fruit can result. Fruit from non-irrigated vines were found to be firmer and have greater concentrations of soluble solids at harvest and during storage than fruit from irrigated vines.<sup>116</sup> Storage life of fruit has also been found to be enhanced when vines were drought stressed in early summer, during the cell division phase of fruit growth.<sup>117</sup>

### 2. Effects on Root Activity

Measurements using a neutron probe indicated that kiwifruit roots extract water from deeper soil horizons as the water deficit increases in the soil.<sup>109</sup> For vines with large and extensive root systems, the increased soil volume explored and the capacity to extract water from soils at lower water potentials reduces the dependence of the vine on irrigation.<sup>118</sup> Results from a recent study of vines growing on deep volcanic loam soils in the Bay of Plenty in New Zealand, where root systems are usually large and extensive,<sup>22,23</sup> indicate no significant response to irrigation over a 6-year period.<sup>119</sup>

## C. ROOT ANOXIA

Kiwifruit vines are not well adapted to tolerate low concentrations of oxygen in their root zone. The reported death of over 30,000 vines in New Zealand as a result of excessive rainfall (six times the seasonal average) during early summer, graphically demonstrates the sensitivity of kiwifruit vines to root anoxia.<sup>120</sup> The death of large numbers of vines in Italy has been associated with high winter water tables of  $0-0.5 \text{ m}$ .<sup>21</sup> Fruit yields were significantly reduced on the surviving vines growing on these soils as a result of a reduction in the number of fruit per vine.

There are a number of physiological and morphological features of kiwifruit vines which make them especially vulnerable to root anoxia. The rate of consumption of oxygen ( $9.1 \times 10^{-10} \text{ mol m}^{-1}\text{s}^{-1}$  at  $20^\circ\text{C}$ ) by the roots is relatively high, and it has been estimated that the time taken to deplete the oxygen supply in a well aerated soil to an anaerobic condition would be approximately 5 h assuming no replenishment of oxygen.<sup>99</sup> Generally, plant species with root porosities of less than 5% are highly sensitive to anaerobic conditions in the soil.<sup>121,122</sup> The average air space between the cells of kiwifruit roots accounts for 2% or less of the total root volume of aerated as well as oxygen stressed vines.<sup>99</sup> Unlike plant species more tolerant of root anoxia, kiwifruit roots do not develop aerenchyma tissue in response to decreasing oxygen concentrations in the root zone.<sup>79,99</sup> Aerenchyma formation has been shown to be triggered by enhanced internal concentrations of ethylene.<sup>123</sup> Anoxia is known to cause a stimulation of the ethylene precursor, 1-amino-cyclopropane-1-carboxylic acid (ACC) in the roots of many plants.<sup>121,124</sup> A key co-factor in the production of ACC is methionine<sup>125</sup> and it is interesting to speculate that the absence of free methionine in the tissues of kiwifruit vines<sup>126</sup> may be responsible in part for the lack of formation of aerenchyma in the roots.

## 1. Effects on the Roots

Within 3 d of the roots being exposed to anaerobic conditions the fibrous roots change from an opaque cream color to a translucent grey color.<sup>79</sup> Substantial losses of up to 50% of dry weight of the fibrous roots have been recorded for vines growing under anaerobic conditions in the field and under controlled conditions.<sup>18,19,79</sup> The loss of tissue has been shown to be caused by the detachment of the cortex from the central stele.<sup>79</sup> The point of separation occurs at the endodermis where a layer of cortical cells, usually packed with starch, collapses.

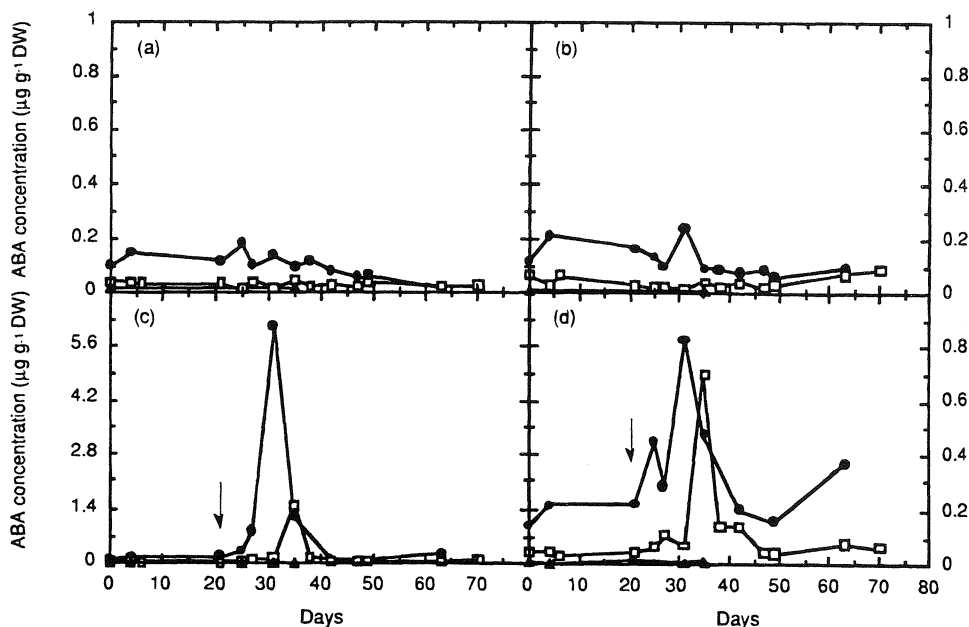
The speed with which the roots of kiwifruit vines die under anoxic conditions greatly limits their ability to resume growth once the supply of oxygen to the roots has been restored. However, in situations where partial recovery has occurred, growth of new fibrous roots from the base of the trunk is one of the first signs of compensation for the loss of the original root system.<sup>20,79</sup> The extent of the growth of new roots was found to be inversely related to the exposure time to anoxia.

## 2. Effects on the Leaves and Fruit

A rapid reduction in  $g_s$  of the leaves occurs in response to a decrease in the concentration of oxygen in the root zone.<sup>79,99,122,127</sup> Exposing as little as 25% of the total root system to anaerobic conditions has been found to result in substantial reductions in  $g_s$  after only 2 d.<sup>128</sup> While leaf turgor of the oxygen-stressed vines has been shown to be maintained in the short term, the stomata eventually close completely after the roots have been exposed to anoxic conditions for as little as 4 d.<sup>79</sup> Characteristic leaf symptoms and reduction in gas exchange by the leaves develop once the oxygen concentration in the root zone falls below 3%. One of the first symptoms to appear is the temporary wilting of the older leaves. These symptoms are quickly followed by the sudden appearance of interveinal necrotic patches, which on some leaves coalesce to form large areas of affected tissue.<sup>99,127</sup> In some cases an interveinal chlorosis precedes the necrosis. The rapid desiccation of the leaves associated with the closure of the stomata may be partly explained in terms of temperature stress. A marked increase in the maximum daily temperature (from 28 to  $42^\circ\text{C}$ ) has been found for leaves attached to oxygen stressed vines.<sup>99</sup>

Marked increases in the concentration of abscisic acid (ABA) in the leaves, but not the roots, of oxygen stressed kiwifruit vines growing under controlled conditions have been found to accompany the closure of the stomata.<sup>129</sup> While elevated concentrations of ABA have more recently been found in the leaves of waterlogged kiwifruit vines growing in the field, the greatest accumulation of ABA was found in the fruit (Figure 9). Elevated concentrations of ABA were detected in the fruit almost immediately after the roots were flooded with water, whereas ABA did not begin to accumulate in the leaves until 12 d after the vines were flooded and the stomata began to close.

Field studies have also shown that the damaging effects of root anoxia on the leaves of kiwifruit vines were greater in early summer when the ambient temperature was higher and the evaporative demand was greater than in late summer or early autumn.<sup>128</sup> Naturally low concentrations of oxygen in the soil during mid-summer following increased consumption of oxygen by soil micro-organisms as a result of the higher temperatures in the soil<sup>130</sup> are also likely to have contributed to the susceptibility of the vine to root anoxia during this period. By contrast with the effects on the leaves, a greater percentage of fruit was found to be soft at harvest on those vines that had been stressed during late summer or early autumn than on non-stressed vines or those that had been stressed for a similar length



**Figure 9** ABA concentrations in the root (▲—▲), leaves (□—□), and fruit (●—●) of (a) low nitrogen control vines, (b) high nitrogen control vines, (c) low nitrogen vines subjected to root anoxia, and (d) high nitrogen vines subjected to root anoxia. The arrow indicates when leaf symptoms were first observed. The anoxic vines were flooded on day 1. The treatments were applied in early summer. Note the different scale for ABA concentrations in (c).

of time in early summer (Table 4). The nitrogen status of the vines was also shown to influence the extent to which root anoxia damaged the vine and the speed with which the vine recovered from the stress. Vines that were nitrogen deficient were much more susceptible to root anoxia than vines that had received adequate quantities of nitrogen fertilizer.<sup>128</sup> Although nitrogen fertilizer was applied well before the imposition of oxygen stress, there was a much greater production of new roots, and hence recovery, by those vines that received nitrogen fertilizer than those which received no nitrogen fertilizer (Table 4).

## VI. MINERAL NUTRITION

### A. NUTRIENT UPTAKE

For young kiwifruit vines growing in soils with non-limiting nutrient supply the annual uptake of nutrients is determined by the combined requirements for deciduous growth and the expansion of the perennial components.<sup>11</sup> At maturity, the annual uptake by the vine is proportional to productivity and reflects the nutrient composition of the deciduous and transient components rather than that of the perennial components, which by this stage of development show little net increase in size. Differences

**Table 4** Effect of waterlogging on root growth and fruit quality

| Time when vines waterlogged | Proportion of new root (%) |               | Soft fruit at harvest (%) |
|-----------------------------|----------------------------|---------------|---------------------------|
|                             | Low nitrogen               | High nitrogen |                           |
| Control                     | 24                         | 21            | 3                         |
| December                    | 36                         | 68            | 2                         |
| January                     | 2                          | 14            | 14                        |
| March                       | 6                          | 23            | 28                        |

From Smith, G. S. and Miller, S. A., *Acta Hortic.*, 297, 401, 1991.

have been found, however, among the vine components in their ability to accumulate nutrients. For example, 49% of the total quantity of nitrogen in the vine accumulates in the deciduous components, 16% in the transient components, and 35% in the perennial components; whereas 63% of the total quantity of potassium is in the deciduous components, 11% in the transient components, and only 25% in the perennial components.<sup>25</sup> The relatively high concentrations of nitrogen in the perennial tissues results in a disproportionate accumulation during vine development, such that developing vines may take up 50% more nitrogen over a year than mature vines with the same fruit yield.<sup>11</sup> Likewise developing vines may take up 22% more potassium than mature vines with similar yields.

At maturity, annual uptakes are greatest for nitrogen, potassium, and calcium (between 125 and 180 kg ha<sup>-1</sup>), while smaller quantities of chlorine (60 kg ha<sup>-1</sup>) phosphorus, magnesium, and sulfur (<25 kg ha<sup>-1</sup>) are taken up.<sup>25,131-133</sup> The quantity of nutrient recovered from fertilizer by mature kiwifruit vines is usually less than 50% for most elements.<sup>11,133</sup> A recent study using <sup>15</sup>N-labelled nitrogen fertilizer applied in a single dose at 100 or 200 kg ha<sup>-1</sup> in early spring showed that 48 to 53% of the applied nitrogen had been recovered by the vines.<sup>134</sup> The proportion of added <sup>15</sup>N utilized by the vines tended to be slightly greater at the lower application rate. Removal of <sup>15</sup>N in harvested fruit was small, at 5 to 6% of the total applied in the first year and 8% over three years. After 2-3 years, over 60% of the <sup>15</sup>N in the vine resided in the roots. Estimates of <sup>15</sup>N removal in harvested produce of other perennial crops have also been relatively low, ranging from 3-4% for asparagus,<sup>135</sup> 11% for citrus,<sup>136</sup> and up to 10-25% for almonds.<sup>137</sup>

For most nutrients, over 65% of the annual accumulation by the leaves occurs during the first 10 weeks of growth after budbreak,<sup>46</sup> although accumulation by the whole vine continues until harvest.<sup>133</sup> Uptake studies using <sup>15</sup>N confirm that the accumulation of nitrogen by kiwifruit vines is rapid and almost complete within 10 weeks of application in either late spring or early summer.<sup>138</sup> Initially most of the <sup>15</sup>N was present in the leaves and the roots, but this declined due to the translocation to other components of the vine. Analysis of xylem sap approximately 4 weeks after bud break showed that more than 50% of the nitrogen absorbed by the roots and transferred in the xylem, remained as nitrate.<sup>138</sup> The other half of the nitrogen in the sap which had been derived from soil and fertilizer nitrogen was first reduced in the roots and translocated predominantly as glutamine.<sup>126,139</sup> During summer and autumn, the nitrogen required for developing fruit and shoots was met to a large extent by the redistribution of the recently absorbed nitrogen from the leaves and roots. Hence, the decline in leaf <sup>15</sup>N coincided with an equivalent accumulation of <sup>15</sup>N in the fruit.<sup>138</sup>

While a large fraction of the annual uptake of nutrients occurs during the first 10 weeks after bud break, mobilization of nutrients stored in the vine from the previous season also makes a contribution during this period of growth. Sufficient quantities of nitrogen, potassium, phosphorus, and magnesium can be mobilized from the laterals of the vine to support the growth of 20-40% of the leaves during the first 30 d after bud break.<sup>46</sup> An analysis of the xylem sap has indicated that remobilization of nitrogen stored in the roots contributes about 60% of the total nitrogen for new growth at 4 weeks after bud break and about 30% approximately 4 weeks later.<sup>138</sup>

In addition to the buffering effects of the nutrient reserves in the vine, the rate of uptake is also influenced by environmental variables. For example, a strong association has been found between soil temperature and the concentration of potassium in the leaves in spring, suggesting that the uptake of potassium by kiwifruit vines is temperature dependent.<sup>46</sup> While there are no published results on direct measurements of the uptake of nutrients per unit length of root of vines growing in the field, estimated rates for macronutrients range from  $13.7 \times 10^{-12}$  mol m<sup>-1</sup> s<sup>-1</sup> for nitrogen to  $0.82 \times 10^{-12}$  mol m<sup>-1</sup> s<sup>-1</sup> for phosphorus.<sup>11</sup> These values are similar to the uptake rates measured in the field for annual *Graminaceous* sp.,<sup>140,141</sup> and estimated for apple.<sup>11</sup>

An unusual feature of kiwifruit vines is their relatively high requirement for chlorine. Kiwifruit vines require at least 2-6 g kg<sup>-1</sup> dry weight of chlorine in their leaves to maintain healthy growth.<sup>142,143</sup> These levels are at least 10 times those required by other non-halophytic plants.<sup>144,145</sup> Typically the concentration of chloride in the leaves of high-producing kiwifruit vines in New Zealand ranges from 8-20 g kg<sup>-1</sup> dry weight.<sup>132</sup> Chlorine toxicity is not usually observed in kiwifruit until the concentrations in the leaf exceed 25 g kg<sup>-1</sup>.<sup>132</sup> A close association between the availability of nitrate and the absorption of chloride ions by kiwifruit vines has been established.<sup>143</sup> The high requirement for chlorine was considered to be an adaptation which minimizes the expenditure of energy on the generation of osmotic pressure, and probably reflects the high availability of chloride and ammonium ions in the habitat in which this species has evolved.<sup>143</sup>

Recently the effects of potassium fertilizer applied with chloride or sulfate as the accompanying anion on the potassium nutrition of kiwifruit vines have been assessed in the field. The concentrations of potassium in the leaves during the first 6 weeks after bud break were significantly greater for those vines receiving potassium chloride compared to those receiving potassium sulfate.<sup>146</sup> Subsequently there was no significant difference in the concentration of potassium in the leaves for the vines receiving potassium in the chloride or sulfate form. This transient effect of the accompanying anion on the potassium status of the leaf was associated with large effects on flowering with the resulting fruit yields being about 28% greater for the vines receiving potassium chloride rather than potassium sulfate. Applying potassium in the chloride form increased the concentration of chloride in the leaf, especially in spring, while applying potassium in the sulfate form had no significant effect on the concentration of sulfur in the leaf at that time. Kiwifruit vines are well adapted to using chloride ions rather than organic-acid anions such as malate for charge balance.<sup>142,143</sup> Hence, it is likely that the requirement for organic-acid anions for charge balance and maintenance of potassium uptake was greater where potassium sulfate rather than potassium chloride was the source of potassium. The lower concentrations of potassium in the leaves of kiwifruit vines in spring following the application of potassium sulfate, suggests that organic-acid anion availability at this time limited potassium uptake, as has been reported for other plant species.<sup>147,148</sup> For kiwifruit vines this effect may be associated with the slow canopy development in spring,<sup>9,34</sup> which in turn limits the availability of carbon skeletons for synthesis of organic-acid anions.

The developing fruit are undoubtedly responsible for many of the seasonal changes in the distribution of mineral nutrients within the vine during the growing season. Generally it has been found that leaves close to the fruit are the main suppliers of nutrients accumulated during early fruit growth.<sup>46</sup> The losses of potassium and nitrogen from the leaves, especially those close to the fruit, reflect the large demand of the developing fruit for these two elements; whereas the much smaller losses of phosphorus, sulfur, magnesium, calcium, and most micronutrients reflect their lower mobility in the vine and the smaller demand of the developing fruit for these elements. A mass-flow vascular transport model has been developed to predict the relative importance of the phloem and xylem supply for nutrient accumulation by the fruit.<sup>52</sup> The model indicates that transport to the fruit is principally by the phloem, except for calcium, manganese, and zinc, which are transported almost exclusively by the xylem.

## **B. NUTRIENT DISORDERS**

### **1. Potassium Deficiency**

The most significant nutrient disorder affecting kiwifruit vines in New Zealand in recent years has been a deficiency of potassium.<sup>132,149</sup> This deficiency appears most commonly in orchards approaching maturity and beginning to produce large quantities of fruit. The high incidence of potassium deficiency reflects the large quantity of this element that is removed from the orchard in fruit and inadequate applications of potassium in fertilizer.<sup>132,149</sup> As potassium deficiency can be detected readily by leaf analysis and corrected with fertilizer,<sup>149</sup> this disorder is now much less common in New Zealand. Maximum fruit yields were associated with potassium concentrations in the leaves in excess of 25 g kg<sup>-1</sup> dry weight 6 weeks after bud break.<sup>149</sup> The average fruit weight decreased from 107 g on healthy vines to 90 g on the severely deficient vines.

### **2. Nitrogen Deficiency**

Recent studies suggest that nitrogen deficiency of kiwifruit vines is more common than has been thought previously.<sup>134,138,150</sup> Maximum fruit yields were associated with concentrations of nitrogen in the leaves of 42 g kg<sup>-1</sup> dry weight at 6 weeks after bud break and 25 g kg<sup>-1</sup> dry weight at 12–20 weeks after bud break. A 50% reduction in photosynthetic rate has been measured for leaves from nitrogen-deficient kiwifruit vines.<sup>63</sup> One reason for the incidence of this deficiency is the large requirement for nitrogen in the developing framework of the kiwifruit vine.<sup>133,143</sup>

Minor nitrogen deficiencies are difficult to detect unless leaf samples for analysis are taken very early in the growing season.<sup>132</sup> Detection of nitrogen deficiency early in the season enables correction of the disorder while the canopy and fruit growth can still respond to an improvement in the nitrogen status of the vine.<sup>46,150</sup>

### **3. Other Nutrient Deficiencies**

Production losses have also been associated with deficiencies of magnesium<sup>151</sup> and manganese.<sup>152</sup> In New Zealand, manganese deficiency has been most easily overcome through reducing the pH of the

soil below 6.8.<sup>152</sup> In California, zinc deficiency is reported to be common,<sup>153</sup> while iron and manganese deficiencies are widespread in parts of Italy.<sup>154,155</sup> However, the effects of these disorders on fruit production have not been measured.

#### 4. Nutrient Toxicities

Instances of excess nutrients affecting productivity have also been measured. Kiwifruit vines are especially sensitive to excess boron. Large reductions in fruit yield have been reported where the concentrations of boron in the leaves exceeded  $80 \mu\text{g g}^{-1}$  dry weight and associated concentrations of hot water-soluble boron in the topsoil were greater than  $0.5 \mu\text{g g}^{-1}$  dry weight.<sup>156</sup> Typically the concentration of boron in the leaves of high producing kiwifruit vines in New Zealand ranges from 40 to  $50 \mu\text{g g}^{-1}$  dry weight.<sup>132</sup>

Suggestions that kiwifruit vines are sensitive to chlorine toxicity<sup>157</sup> have not been supported by direct experimentation. Where in excess of  $1.2 \text{ t ha}^{-1}$  of chlorine has been applied in one application in spring with equivalent quantities of nitrogen to kiwifruit vines in the field, there was no indication that chloride ions adversely affected the vines despite the concentrations in the soil being up to 10–15 times those usually found in commercial kiwifruit orchards in New Zealand.<sup>146,158</sup> In a long-term study with field-grown kiwifruit vines, nitrogen deficiency has been associated with the appearance of leaf chlorosis and necrosis and increased concentrations of chloride in the leaves despite the concentrations of chloride in the soil remaining relatively constant at about  $60 \text{ mg kg}^{-1}$ .<sup>150</sup> These changes in the composition of kiwifruit leaves and appearance of symptoms are typical of those as nitrogen concentrations vary in the vine.<sup>146</sup> Hence the suggestion that these leaf symptoms indicate chlorine toxicity<sup>157</sup> does not appear to be valid.

Kiwifruit vines are generally tolerant of relatively high concentrations of soluble salts in the root zone, with the exception of sodium. Severe damage to kiwifruit vines has resulted from the use of irrigation water containing sodium concentrations that ranged from 230–860  $\text{mg l}^{-1}$ .<sup>132</sup> This sensitivity to sodium, rather than chlorine, largely accounts for their sensitivity to saline irrigation water.<sup>132,159</sup> Where exceptionally large quantities of soluble fertilizer (up to  $10 \text{ t ha}^{-1}$  of a 12:10:10 N:P:K mixture) have been used to increase the soluble salt level in the root zone to high levels (the electrical conductivity of the soil was increased to over  $2 \text{ d sm}$  at  $25^\circ\text{C}$ ), there was a marked increase in the number of buds that developed in spring, along with flower numbers, and root growth.<sup>158</sup> Measurements at harvest showed that fruit yields were doubled for the high fertilizer treatment compared to the control vines which received typical annual inputs of fertilizer. The results from this study suggest that osmotic effects may play an important part in the bud-breaking process in spring.

A feature common to all mineral nutrient disorders of kiwifruit vines is that the loss of productivity results primarily from a reduction in fruit numbers.<sup>11</sup> The average weight of individual fruit from affected and unaffected vines has been found to be similar in most cases.

#### C. EFFECTS OF MINERAL NUTRITION ON FRUIT QUALITY

A feature of fruit from kiwifruit vines is their ability to be stored for remarkably long periods (6–8 months) at low temperatures ( $-0.5$  to  $0.5^\circ\text{C}$ ) before being ripened to an edible state.<sup>1</sup> Various claims have been made, however, about the extent to which mineral nutrition influences the post-harvest storage of kiwifruit. In the specific case of nitrogen, results from the long-term study of responses to nitrogen fertilizer have shown no significant effect on fruit quality with fertilizer inputs ranging from 0–200  $\text{kg ha}^{-1} \text{ year}^{-1}$ .<sup>150</sup> Applying even greater quantities of nitrogen ( $1400 \text{ kg ha}^{-1}$ ) just before bud break, had no effect on the long-term storage of the fruit.<sup>158</sup> In a survey of the relationship between vine nitrogen status and post-harvest fruit quality for kiwifruit growing in Italy, no relationship could be found between the concentration of nitrogen in the leaves sampled mid-season and flesh firmness of the fruit after harvest.<sup>160</sup> These results fail to support an earlier claim that nitrogen may be linked to a more rapid deterioration of fruit in storage and with a higher incidence of *Botrytis* infection.<sup>161,162</sup> It would appear that the detrimental effects of nitrogen fertilizers on the post-harvest storage characteristics of kiwifruit have been confounded by other factors. For example, the small but significant decrease in fruit firmness attributed to an increase in the nitrogen concentration in the fruit was confounded by the use of ammonium sulfate as the source of nitrogen.<sup>163</sup> An even greater change in the concentration of manganese than nitrogen was measured in these fruits, as resulted from the acidification of the root zone through the use of this form of nitrogen. Consequently, the extent to which nitrogen fertilizer was having a direct effect on fruit quality or an indirect effect through changes in the acidity of the root zone remains

Table 5 Relationship between mineral composition and postharvest fruit disorders

| Nutrient element | Botrytis infection (%) | Soft fruit (%) | Surface pitting (%) |
|------------------|------------------------|----------------|---------------------|
| Potassium        | 0.133                  | -0.013         | 0.048               |
| Nitrogen         | 0.076                  | -0.019         | -0.122              |
| Chlorine         | 0.048                  | -0.130         | 0.058               |
| Calcium          | -0.077                 | -0.045         | -0.009              |
| Phosphorus       | 0.053                  | -0.028         | 0.114               |
| Sulfur           | 0.077                  | -0.021         | -0.084              |
| Magnesium        | 0.098                  | 0.085          | 0.064               |
| Sodium           | 0.038                  | -0.074         | -0.086              |
| Iron             | -0.027                 | 0.051          | 0.054               |
| Boron            | 0.151                  | 0.059          | -0.047              |
| Copper           | 0.100                  | 0.021          | -0.085              |
| Zinc             | 0.011                  | 0.145          | -0.057              |
| Manganese        | 0.017                  | 0.029          | 0.078               |

Note: The values in the table are correlation coefficients (r). Significant values for r were  $p(0.05) = 0.156$ .

uncertain. Similarly an earlier report of a reduction in storage life of kiwifruit,<sup>164</sup> was associated with the abnormal practice of applying nitrogen in late summer/early autumn when vine growth had largely ceased.<sup>9</sup> In New Zealand it is general practice to apply most, if not all of the annual requirement of nitrogen before or during the first 10 weeks after bud break in spring.<sup>11</sup>

Recently the relationship between the mineral composition and post-harvest disorders of kiwifruit was investigated using a large sample of fruit (1660) from 166 commercial orchards in the major kiwifruit growing districts of New Zealand. Included were examples of fruit that had softened prematurely and/or were infected with *Botrytis* while in storage and fruit with no storage disorders.<sup>165</sup> There were no clear relationships between the mineral composition and the incidence of soft fruit or *Botrytis* infection. The correlation coefficients rarely exceeded 0.1 for any of the individual nutrient elements (Table 5). There was also little evidence to suggest that nitrogen or calcium was more strongly associated with post-harvest fruit disorders than any other mineral nutrient in the fruit. Principal component analysis of the results indicated that nutrient elements could be separated into two distinct groups. The first group, comprised of nitrogen, phosphorus, sulfur, potassium, and copper, behaved in the opposite manner to the second group of elements, which were equally strongly linked together and were comprised of calcium, manganese, and zinc. Hence the effect of an individual element cannot be separated from that of the other elements present in these groupings.

The absence of any obvious relationship between calcium and post-harvest fruit disorders of commercially grown fruit was consistent with earlier findings where no relationship was found between total calcium concentrations in the fruit or young leaves and the firmness of the fruit during storage.<sup>166,167</sup> Calcium concentrations in kiwifruit ( $0.5\text{--}3.7\text{ g kg}^{-1}$  dry weight) are up to 10 times greater than those in the flesh of other fruits which often develop calcium related disorders, such as apples.<sup>168,169</sup> However, exceptionally low concentrations of calcium ( $<0.2\text{ g kg}^{-1}$  dry weight) have been measured in kiwifruit from China.<sup>165</sup> These fruit had large surface pits and necrotic tissue surrounding the vascular tissues to the seeds. A large fraction of calcium in kiwifruit has been found to be present as calcium oxalate,<sup>1</sup> but the concentration of the more soluble forms of calcium in the flesh can be at least three times greater than the total calcium concentration in apples.<sup>170</sup> The suggestion that soluble forms of calcium may reflect more closely the behavior of kiwifruit during storage than total calcium<sup>162</sup> has not been supported by direct measurement.<sup>170</sup>

No significant differences in fruit quality have been associated with potassium deficiency,<sup>132</sup> magnesium deficiency,<sup>151</sup> or manganese deficiency,<sup>152</sup> but excess boron has been associated with a significant reduction in the firmness of the fruit after only a short period in storage.<sup>156</sup>

## VII. WHOLE-PLANT EXPRESSION OF STRESS

In an earlier review,<sup>9</sup> the interactions between roots and shoots were described in terms of the acquisition of resources for growth and how these relationships changed in response to environmental stresses.

Carbon acquisition has been shown to be central to the responses of kiwifruit vines to most environmental stresses. As shown in the sections above, the gross effects of stresses on the vine are relatively easy to identify and describe. However, it is the subtle effects of these stresses that are less understood, frequently overlooked, and often these effects are attributed to other factors and confused with natural variation within the vine itself. Hence understanding the growth patterns and extent of the variation of “stress free” vines is important in examining the responses of the vine to environmental stresses.

Spatial heterogeneity of the physical, chemical, and post-harvest attributes of fruit appears to reflect effects of at least some “subtle” environmental stresses. Recent studies of this spatial heterogeneity suggest that a large fraction of the variation in fruit quality encountered in the New Zealand kiwifruit industry originates at the level of the individual vine.<sup>171</sup> For many species, differences in the physical, chemical, and post-harvest attributes of fruit can be detected when the entire population of a single plant is analyzed.<sup>172,173</sup> The recent development of a rapid method for representing in 3-dimensional space the location of each fruit<sup>174</sup> has highlighted relationships between spatial heterogeneity of fruit quality and the position of the fruit in the canopy. Fruit with above-average physical and post-harvest attributes and flavor were from parts of the canopy with high leaf area density, while fruit with less desirable attributes were from the less dense parts of the canopy close to the ground.<sup>171,175</sup> Such patterns suggest that, at least in parts of the canopy, resources for fruit growth are limited.

Of the limited number of studies where the post-harvest characteristics of the fruit from vines exposed to an environmental stress (root anoxia) have been assessed according to their position in the canopy of the vine, the results show an increase in the number of fruit with inferior attributes from the less dense parts of the canopy.<sup>128</sup> However, the apparent relationship between the temporal and spatial variation in photosynthetic activity within the canopy and fruit growth<sup>171</sup> and quality indicates that the dynamics of acquisition and allocation of resources within the vine are likely to be very complex and require further clarification.

### VIII. PROSPECTS FOR MINIMIZING STRESS

Understanding the mechanisms and environmental factors regulating the allocation of resources within the whole vine is central to identifying options for minimizing adverse effects of environmental stresses. The importance of recognizing the complex patterns that exist in the spatial arrangement of the leaves and fruit in the canopy lies in developing strategies for producing fruit of a more uniform quality. Differences in canopy architecture and management practices such as leaf pruning and fruit thinning can substantially modify the interception of radiation and allocation of resources within the vine.

For kiwifruit in New Zealand, the effect of environmental stress is usually inversely related to vine vigor. In particular, high producing vines growing on deep, free-draining soils in the Bay of Plenty region are often considered to be excessively vigorous.<sup>1</sup> These vines usually have extensive root systems,<sup>22,23</sup> but are rarely affected by water stress<sup>109,119</sup> or mineral nutrient stress.<sup>132</sup> It is likely that this “vigorous” growth of such vines is central to high rates of carbon acquisition and hence carbon allocation for fruit and root growth and tolerance of below-ground stresses. Options for minimizing stress therefore include:

- Ensuring a uniform bud break in spring. In locations where natural bud break is poor, the use of the bud breaking chemical, hydrogen cyanamide, increases the number of dormant buds that break and uniformity of shoot development.<sup>38</sup> The suppression of shoot growth by shoots that develop early can be prevented by removing the terminal bud of any early developing shoot. Such treatment can increase fruit yields by 20–40%.<sup>176</sup>
- Reducing the period over which the flowers open in spring. Hydrogen cyanamide is effective in compressing the flowering period in locations where there is a history of flowering problems.<sup>38,39</sup> A prolonged flowering period results in a population of fruit on a single vine with a wide range of physiological ages at harvest.<sup>171,177</sup> This diversity in fruit age impacts on the post-harvest storage potential of these fruit.
- Increasing the rate of leaf canopy development in spring by avoiding leaf pruning during the first 100 d after bud break and ensuring that the vine is adequately supplied with mineral nutrients, especially nitrogen. For New Zealand conditions the optimum leaf index appears to be about 3.0–3.5 m<sup>2</sup> m<sup>-2</sup>.<sup>34</sup> Although the direct effects of limited carbon acquisition may not necessarily be immediate, fruit production in the long term can be very sensitive to even subtle changes in the leaf area index. Often these changes are reflected in the production of flowers for the following season.<sup>12</sup> However, where the limitation of

carbon acquisition within any one season is sufficiently severe, especially during the first few weeks after fruit set, fruit growth can be affected directly as illustrated by the reduction in average fruit size following a reduction in total leaf area.<sup>12,178</sup>

- Increasing radiation interception by the leaf canopy. The relative importance of limitations to carbon acquisition due to radiation environment, leaf area, and the photochemical efficiency of the canopy is difficult to measure directly. Mathematical modelling, however, suggests that variations in radiation interception are relatively more important than variations in photochemical efficiency.<sup>44</sup> Minimizing shading, such as from wind shelter, provides the greatest opportunity for manipulating the radiation environment in an orchard.
- Maximizing starch reserves in the vine by avoiding overcropping or removal of too many leaves during the previous season.
- Ensuring that a large root system is maintained. Because the root system of kiwifruit vines is a poor competitor for resources of growth, indirect effects of limited supplies of these resources increase the sensitivity of the vine to below-ground stresses such as drought, anoxia, and mineral nutrient deficiencies. Increasing the size of the root system effectively increases the volume of soil explored by the roots thereby decreasing the concentration of resources required in the soil to support a given rate of uptake.<sup>141</sup>
- Reducing the dependence of the vine on irrigation by encouraging the growth of a large root system. The greater volume of soil explored by a large root system means that the transpiration requirements of the vine can be met at a greater soil moisture tension because of the overall increase in the quantity of water available to the vine.<sup>9</sup>
- Avoiding the risks of root anoxia and the adverse effects which excess water has on the storage properties of the fruit, by refraining from flood irrigation or the application of large quantities of water after infrequent intervals to slowly draining soil types.
- Improving the carbon allocation to the roots by ensuring a complete canopy and hence radiation interception at an early stage of the growing season and restricting crop load, especially on young developing vines.
- Selecting rootstocks that are better adapted to local environments. Kiwifruit production has traditionally involved 'Hayward' grafted on to seedling rootstocks or 'Hayward' grown on its own roots.<sup>10</sup> Neither root system confers any particular advantage to the 'Hayward' scion. However, the recent selection of the clonal rootstock of *Actinidia hemsleyana* ('Kaimai') for 'Hayward',<sup>179</sup> has shown what can be achieved in terms of improvements in production and fruit quality.

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## Chapter 6

# Olive

Guido Bongi and Alberto Palliotti

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## I. INTRODUCTION

### A. ORIGINS, EVOLUTION, AND GENETIC VARIABILITY OF *OLEA EUROPAEA* L.

The genus *Olea* includes at least 30–35 species that belong to the family Oleaceae, subfamily Oleoideae ( $n = 23$ ), which has been recognized as a distinct family since 1809.<sup>1,2</sup> The cultivated olive (*Olea europaea* L.) is an evergreen tree that evolved from tropical and subtropical species. The palaeontological remains of many extinct *Olea* spp. have also been found in France and Italy.<sup>3–5</sup> The area of origin of

the olive was the *Laurophyllus* forest around the Thetys.<sup>6</sup> The Tertiary Mediterranean basin was inside a tropical zone, but partial basin drying out and Pleistocene glaciation were strong natural selection criteria for a sclerophyllous plant with moderate freezing avoidance characteristics.<sup>6,7</sup> Glaciation events probably restricted the original olive population. Only populations with a capacity for freezing avoidance from  $-5$  to  $-12^{\circ}\text{C}$  survived; minima below  $-12^{\circ}\text{C}$  greatly limited the natural distribution if *Olea* species.<sup>6</sup>

Evidence of early olive cultivation at around 4800 BC were found in Cyprus.<sup>8</sup> The age of the species and its vast prehistoric range may explain its very high intraspecific variability. It has even been speculated that 'forms' hybridized under different climatic events now constitute the species *Olea europaea*.<sup>3,4</sup> According to recent results, measurable genetic variability exists among individuals of the same variety. It has been reported that some clonal characteristics persisted in trees obtained from self-rooting cuttings.<sup>5,9,10</sup>

Frost-resistant varieties are required in northern and central Italy, since damaging frosts occurred several times in the 19th and 20th centuries.<sup>11</sup> Although dry summers and mild winters provide the ideal climate for olive cultivation, summer drought limits the overall productivity. In most cases, it is necessary to improve resistance to adverse climates by breeding new varieties. Resistance is normally found in land-races with poor pomological traits.

The use of clonal rootstocks is of particular interest for stress resistance.<sup>12</sup> For example, the cv. Oblonga confers resistance to *Verticillium* wilt and may also influence fruit shape,<sup>13</sup> while *O. cuspidata* and cv. Zhongshan 80 are more tolerant to root hypoxia than other olive species and cultivars.<sup>14,15</sup>

## B. GROWTH, MORPHOLOGY, AND PHENOLOGY

Olive trees may grow to a considerable size, but a slow growth rate and longevity are characteristics of the species. Olive plants reach full size in 10 years in the southern growing area. However, because of alternate bearing and rainfall fluctuations, 30 years are required to estimate overall productivity. Shoot elongation occurs mostly in spring and correlates well with rising temperatures.<sup>16</sup> The terminal growing apices are dominant and repress axillary bud development in a basipetal direction; however apical dominance is influenced by irradiance, soil fertility and growth regulators.<sup>11</sup>

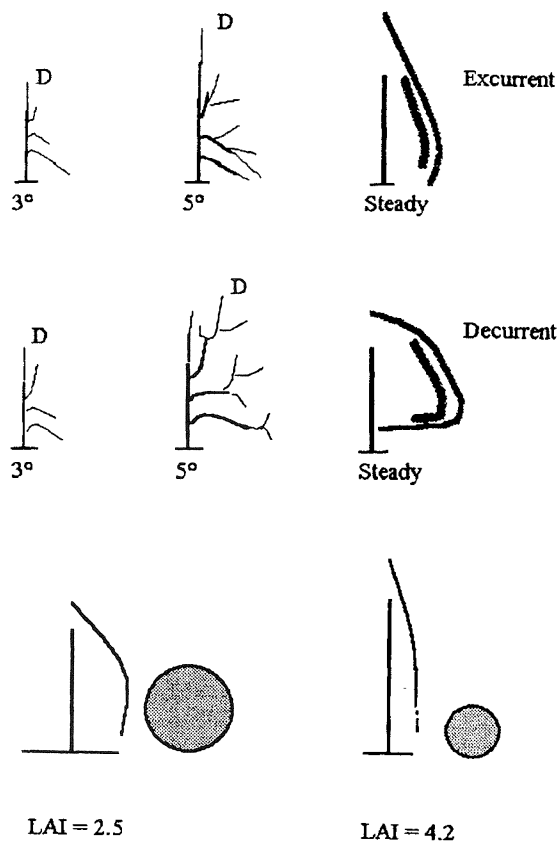
The strong dominance of a leader shoot inside a branch can originate 'decurrent' or 'excurrent' forms. When dominance control is exerted for only one season, the lateral shoots become dominant and, in the following year, the plant crown tends to an irregular sphere with basitonic multiple heads (Figure 1). When concurrent apices are removed by pruning or when the apical dominance lasts more than one season, stable excurrent forms may be maintained with a single or multiple axes. It seems that natural spindle forms, characterized by strong dominance and small basitony, have higher yields.<sup>5</sup>

Olive trees bear flowers on the lateral buds of 1-year-old wood. Apical flowering is rarely found in *O. europaea* (Figure 2) and flowering on 2-year-old shoots is uncommon. Pruning keeps the fruiting parts not too far from the roots, avoiding embolism and transport limitations, but some one-year-old wood must be preserved for flowering. Vegetative and fruiting buds are mostly located at the leaf axils. Flowering, fruit-set and fruit development processes are extremely climate-dependent.<sup>17</sup>

The flowers of olive are hermaphroditic and grouped in dichotomous panicles with 12–40 flowers, but generally set only one fruit per inflorescence. Only a few cultivars with small fruits (e.g., cv. Koroneiki) may set more than three fruits per panicle. Within each inflorescence, flowering is not synchronous (Figure 2) and early drop reflects imperfect fertilization. Olive cultivars are generally self-incompatible and pollination is wind dependent.<sup>11</sup> Mature olive trees may produce 500,000 or more flowers; however, fruit set is normally below 5%.

Successful pollination by wind requires a continuous source of pollen over the period of stigma receptivity. Some cultivars are better pollinizers than others; male sterility or high ovary abortion is present in some cultivars.<sup>11,17–19</sup> The high degree of heterosis in olive is primarily caused by its self-incompatibility,<sup>8</sup> but is also dependent upon climate.<sup>20,19</sup>

Growth and fruit development in olive also depend on climate. Environmental variability may be more important than genetic variability for several traits, including oil content and quality. The best quality oil is obtained from districts of the northern and eastern parts of the Mediterranean basin and near the margins of 'maquis vegetation'.<sup>6</sup> However, frost damage restricts further expansion northward. The chemical components (e.g., polyphenols, aliphatic alcohols, triterpenic alcohols, sterols, and triterpenic diols) that determine oil quality vary according to cultivar and year of cultivation.<sup>21</sup> Rainfall is one of the predominant environmental factors affecting oil quality. Irrigation may also affect the variability in oil quality.<sup>22</sup>



**Figure 1** Evolution of olive tree training systems. The first row presents an excurrent form with moderate basitony; D depicts the dominant shoot that maintains dominance over years, from the third to the fifth year after planting; on years 1–3 a tutor is needed. The second row reports a decurrent form with the same basitony. The last row shows how excurrent forms may give rise to an increased LAI.

## II. LIGHT

### A. LIGHT RESPONSES

Light intensity is the radiant flux of a source per steradian of spherical volume, including the source at the center (Watt per steradian). At the physiological level, the radiant flux density per leaf surface unit (Watt per unit surface,  $\text{mmol photon m}^{-2} \text{s}^{-1}$ ) is more relevant. The term 'light fluence' will be used here to indicate 'radiant flux density on the leaf surface'. The use of the term irradiance rather than fluence is technically incorrect as it apportions the fluence from all directions on a surface. A discrepancy arises because sensors used for measuring fluence density and irradiance read spherical space of  $2\pi$  or  $4\pi$  steradians, respectively, and differ in their responses. Only collimated beams at  $90^\circ$  of incidence give the same reading in both instruments. If radiation is substantially diffused, the irradiance level may reach 4 times the fluence level.

#### 1. Light Fluence Density

Light fluence is a very important factor for olive flower induction. Shading reduces flower differentiation.<sup>23,24</sup> However, shading after the period of flower induction does not influence flowering,<sup>24</sup> but can induce high morphological sterility (e.g., ovary abortion). Leaf shading or leaf removal may totally inhibit flowering.<sup>25</sup>

Light fluence incident on leaves decreases through the olive canopy and light extinction may vary according to the shape of the trees and the density of the canopy. The olive canopy is moderately dense and evergreen. The amount of leaf area per projected ground surface (LAI) often approaches 2.5. The influence of cultivars, training systems, and orchard management practices (irrigation, fertilization, pruning, etc.) on LAI is unknown. The potential production, e.g., the number of flowers per hectare, is related to the average number of new nodes per hectare. The distance between internodes is under genetic control,<sup>5</sup> and the presence of evergreen leaves inhibits growth of new nodes in shaded positions.

To evaluate the effects of plant shape and size on light extinction, it is essential to know both the LAI and the harvest-index (HI), which is the ratio between fruit production and above ground dry



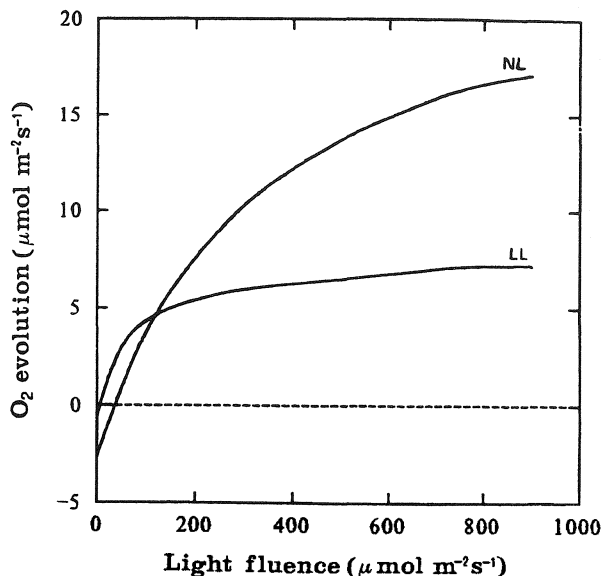
**Figure 2** Apical inflorescence (a), and 'normal' vegetative apical development at full bloom (b) on cv. Koroneiki. The plants, kept in 25-l pots, were subjected to an induction period of 8 weeks at 12/7°C (day/night). These pictures were taken after 60 days, with a day/night cycle of 22–15°C. A significant proportion of the apices (5%) were completely flowers. This is indicative of the biological presence of this flowering topology in olive plants which, if fixed in a new cultivar, may drastically change the schemes of olive growing.

matter. There is a positive effect of high LAI on olive production. The new cultivar, 'Barnea', with a tall natural spindle form produces more fruits per projected ground surface area than other cultivars.<sup>5</sup> In this case, the increased productivity is associated with the increase of LAI while HI is constant. In olive, flowering is associated with growth and the HI is inversely proportional to current season vegetative growth. Production during the subsequent year tends to be reduced as flowers originate only from one-year-old leaf axils.

Both canopy density and the light response of individual leaves also require further discussion in olive. Maximum net CO<sub>2</sub> assimilation ( $A_{\max}$ ) of olive, under optimal conditions, is lower than that of most C<sub>3</sub> species. At high CO<sub>2</sub> concentrations (15% CO<sub>2</sub>, 2% O<sub>2</sub>, 83% N<sub>2</sub>, vol vol<sup>-1</sup>)  $A_{\max}$  can be measured by O<sub>2</sub> evolution with polarographic gas phase electrodes.<sup>26</sup> Stomatal limitations to net CO<sub>2</sub> assimilation ( $A$ ) are obviated and the system becomes CO<sub>2</sub> saturated (i.e., respiration in light is minimized). In these conditions,  $A_{\max}$  is achieved and is satisfactorily described by the term 'photosynthetic capacity'. The photosynthetic capacity has been positively correlated with the rate of uncoupled electron transport from water to NADP in spinach chloroplasts.<sup>26</sup> However, similar experiments have not been performed on olive.

Olive leaves have a photosynthetic capacity not higher than 18  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$  at a fluence of 900  $\mu\text{mol quanta m}^{-2}\text{s}^{-1}$ . The low photosynthetic capacity in olive is related to leaf thickness and a low density of the photosynthetic reaction centers. Maximal rates of both electron transport in thylakoid suspensions and chlorophyll *a/b* ratios are typical of shade-adapted chloroplasts.<sup>27</sup> A substantial proportion of olive chloroplasts are dispersed in inner palisade layers and are exposed to low light levels. Up to 6 palisade layers may develop in olive leaves.<sup>27</sup>

The photosynthetic capacity of olive may be drastically reduced if leaves develop in shade, as normally exists in the canopy understory (Figure 3). The photosynthetic capacity of shade-grown leaves may be less than 30% of that of sun-grown leaves. Thus, it may be advisable to prune to enhance light penetration in the canopy. The olive LAI of 2.5 is low compared to that of other fruit crops (in *Citrus*



**Figure 3** Response of  $O_2$  evolution to light fluence in olive leaves, cv. Frantoio, developed in normal light (NL,  $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and in low light [LL, under a screen (i.e., neutral filter) of 20% light transmission]. Net exchange was determined as described by Walker (1989)<sup>26</sup> with a  $CO_2$  partial pressure of 15,000 Pa.

it may reach 10), perhaps as a consequence of the rapid reduction of the photosynthetic capacity of olive leaves kept in dim light.

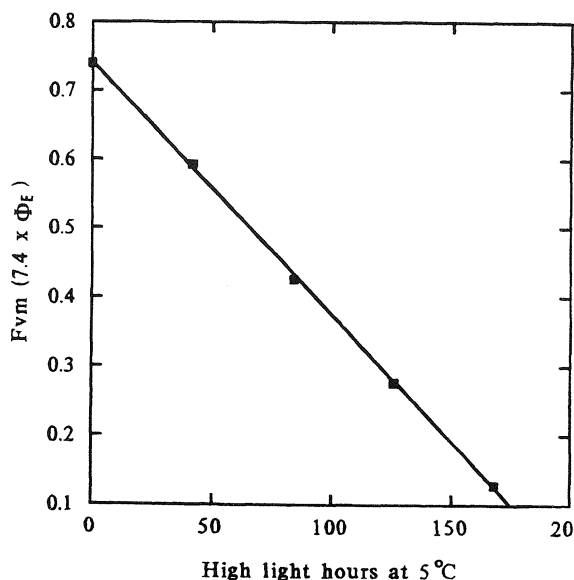
The quantum efficiency ( $\phi_e$ , i.e.,  $\text{mol } O_2 \text{ absorbed quanta}^{-1}$ ) in olive is 0.089,<sup>27</sup> compared to 0.107 for most higher plants.<sup>28</sup> The lower  $\phi_e$  for olive may be caused by respiration of inner palisade layers. Basic mechanisms of photochemistry are similar across species of higher plants; 8 photons are required for each evolved oxygen. In environmental conditions characterized by high fluence and variable temperature, a reduction in  $\phi_e$ , known as photoinhibition, may occur. Structural damage of functional components of photosystem 2 (PS2) (mostly D1 protein)<sup>28</sup> and adverse effects on oxidative processes (e.g., Calvin and glycolate cycles and peroxidases), all reduced  $\phi_e$ . A long duration may be required to achieve pre-photoinhibition values of  $\phi_e$ .

Chlorophyll fluorescence is a useful method for determining  $\phi_e$  of intact leaves in the field. The ratio of variable (Fv) to maximal (Fm) fluorescence has been linearly correlated with  $\phi_e$  and is a good determinant of photoinhibition.<sup>29,30</sup> By use of chlorophyll fluorescence measurements,  $\phi_e$  can be monitored in olive leaves conditioned to very long-term stress periods.<sup>31–34</sup> Broad-leaf evergreens are sometimes able to avoid the short-term effects of combined environmental stresses that may be lethal to the leaves of deciduous species.<sup>32</sup> However, the combination of high fluence and temperatures lower than  $5^\circ\text{C}$  for a week or more, typically induce photoinhibition in leaves located in the outer canopy (Figure 4).<sup>33</sup> Olive should not be cultivated in cool areas with a high frequency of chilling, largely due to the long time necessary to reconstitute the original  $\phi_e$ . A marked loss of productivity (50%) of olives occurs between  $41^\circ$  and  $36^\circ$  latitude north.<sup>35,36</sup>

An increase in fluence is often concomitant with a drop in absolute humidity around midday. Stomata of olive leaves close in response to low humidity which may decrease  $CO_2$  concentration in the chloroplast. Consequently, A may increase up to a fluence of  $1500 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ , but may decrease at higher fluence as a result of increases in vapor pressure deficit (VPD).<sup>37</sup>

## 2. Light Quality

Olive leaves are bifacial and morphologically heterogeneous. The adaxial surface of the leaf is noticeably darker than the abaxial surface. Baldy et al.<sup>38</sup> found that the adaxial surface absorbs more photosynthetically active radiation (PAR, 400–700 nm) than the abaxial surface. The abaxial surface reflected 20 to 40% of the PAR. Near-infrared radiation (i.e., wavelengths  $> 700 \text{ nm}$ ) are poorly absorbed and highly reflected by both leaf surfaces. The transmission of direct radiation is very low in olive leaves (i.e., less than 1% at 440 nm). The quality of transmitted light is very different from the incident light quality and has a much higher infrared/PAR ratio. The poor PAR transmission limits the photosynthetic capacity of the lower part of the olive canopy. During aging, olive leaf thickness increases, further reducing



**Figure 4** Effect of high light and low temperature on the intensity of chlorophyll fluorescence in olive leaves. Temperature was maintained steady at 5°C during the experimental period and leaves were subjected to hardening in natural light. The  $F_{vm}$  is  $F_v F_m^{-1}$ , and  $\Phi_E$  is obtained in olive leaves dividing  $F_{vm}$  by 7.4.<sup>33</sup>

light transmittance and photosynthetic capacity of leaves in the lower canopy. Diffuse light is not thought to contribute significantly to leaf photosynthesis in olive.<sup>39</sup>

### III. TEMPERATURE

#### A. THERMAL REQUIREMENTS

Temperature is the most important environmental factor limiting olive cultivation. Olive plants do not survive temperatures lower than  $-12^{\circ}\text{C}$ ,<sup>6</sup> but require a chilling period for flower bud induction.<sup>40</sup> Thus, temperature limits olive growth to areas mostly between  $30^{\circ}$  and  $45^{\circ}$  latitude.<sup>35</sup>

Olive oil production is qualitatively improved by cold winters. This may explain why 10 to 15% of olive production occurs in areas with an inherent risk of frost injury. The yearly primary production per square meter of leaf area at  $34^{\circ}$  latitude north is 50% more than at  $45^{\circ}$  due to winter growth limitations,<sup>39</sup> and to photoinhibition.

*Olea europaea* is an obligate thermoperiodic species that requires at least 10 weeks below  $12.2$  to  $13.3^{\circ}\text{C}$  for full expression of flowering.<sup>41,42</sup> The total number of chilling hours required for flowering is cultivar dependent. Cultivars acclimated to warm winters require fewer chilling hours.<sup>43</sup> Flowering is induced best when temperature fluctuates between  $2$  and  $15^{\circ}\text{C}$  for 70–80 days.<sup>40</sup> Under these conditions, flowering can be induced year-round and independently in different parts of the canopy. Temperatures constantly below  $7^{\circ}\text{C}$  or above  $15^{\circ}\text{C}$  may inhibit flower induction,<sup>40</sup> while winter temperatures above  $20^{\circ}\text{C}$  for 2–3 weeks may impede the release of flower buds from dormancy.<sup>44</sup> The hormonal status of trees also regulates the chilling requirement for flower induction. High-yield years or late harvest may increase the chilling requirement of olive.<sup>44</sup> Flower differentiation occurs at temperatures higher than those required for induction. Abnormally high temperatures in spring can impede flower development.<sup>17</sup> Self-pollination may also be limited by high temperatures during the flowering period, due to the inhibition of pollen tube growth.<sup>45</sup> Low spring temperatures prolong olive flowering up to 3 weeks,<sup>17</sup> and can also temporarily interrupt flowering or interfere with cross-pollination.

The temperature requirements of olive vary with the tissue and the phenological stage. Olive seed germination is optimized by keeping the seeds at  $10^{\circ}\text{C}$  for a month before seeding at  $20^{\circ}\text{C}$ .<sup>46</sup> However, a seeding temperature of  $25^{\circ}\text{C}$  seems to reverse the effect of a chilling treatment of less than 5 weeks. Rooting of olive stem cuttings is greatly improved when the basal temperature is kept high ( $30^{\circ}\text{C}$ ) for 15 days, and then gradually decreased from 30 to  $18^{\circ}\text{C}$ .<sup>47</sup>

Photosynthesis of olive trees saturates at different temperatures on different cultivars, and the role played by cultivar acclimation is likely to be important.<sup>48</sup>

Concentrations of metabolites in different parts of the olive tree are both seasonal and temperature dependent.<sup>49,50</sup> Starch accumulation in leaves is associated with periods of vegetative growth, principally during the spring, whereas leaf starch, soluble carbohydrates, and mannitol concentrations decrease in

summer and their depletion may be related to low metabolic activity during this period.<sup>49</sup> Leaf starch concentration also decreases in winter, but concentration of soluble sugars increases. Export of mannitol from bark to xylem is reduced by low temperatures.<sup>49</sup>

## B. THERMAL STRESS

### 1. High Temperature

The southern limit for the reproduction of olive is determined by winter temperatures, which must be lower than 14°C for 2 weeks in order to induce some flowering. Only a few cultivars, such as 'Rubra' and 'Arpa', have lower winter chilling requirement,<sup>43</sup> and these cultivars could be used in breeding programs to extend olive cultivation to warmer areas. Olive productivity is not limited by high temperatures, but very high temperatures immediately after flowering may totally eliminate the crop, as occurred in California in the spring of 1984.<sup>51</sup> Olive leaf tissue can withstand 52°C before the dissociation of protein antennas of PS2.<sup>52</sup>

Photosynthesis is generally inhibited by temperatures higher than 35°C. However, olive cultivars acclimated to high temperatures maintain 70–80% of their photosynthetic rate at 40°C.<sup>48</sup> The olive leaf cuticles underwent irreversible structural changes at temperatures higher than 55°C; in many other species this damage occurred in the interval between 40 and 50°C.<sup>53</sup>

High temperatures are frequently associated with high VPDs between leaf and air, water stress, and high light fluence; this situation is very common in the Mediterranean climate. Vapor pressure deficits between fruit and air also rises with increasing temperature and peduncle withering may produce drastic late July fruit drop.

### 2. Low Temperature

When winter temperature drops below 5°C, plants begin an acclimation process known as hardening. Hardened plants stop growing and undergo important metabolic changes. In particular, low temperatures cause the starch to be converted into soluble sugars. Starch is also reallocated and concentrated in frost-protected organs such as the roots.<sup>50</sup> A winter temperature of –12°C damaged all the aerial parts of olives. Buds and inflorescences were also particularly sensitive to spring-frost,<sup>11</sup> and during flowering, temperatures below 10°C reduced pollination.<sup>45</sup>

In all plants, ice formation first takes place in the apoplast since it is about 100 times more dilute than the symplast; the matric forces created by large molecules also contribute to a freezing point depression of the symplast. The matric forces exerted by cell wall microfibrils may inhibit the freezing of apoplastic water down to –10°C. When an ice crystal forms in the apoplast, the cell remains permeable to water and a high difference in water potential causes water loss from the symplast. For example, in *Eucalyptus* at –2°C, ice formation resulted in an osmotic potential ( $\Psi_\pi$ ) of –2.5 MPa, while at –10°C the  $\Psi_\pi$  was –11.8 MPa.<sup>54,55</sup>

It is known that olive and palm undergo deep supercooling, a freeze avoidance mechanism.<sup>56,57</sup> However, if ice formation occurs, 'water soaking' and 'leaf bending' take place upon thawing (Figure 5), due to the relative difficulty of reversing cellular plasmolysis and initiating and maintaining water uptake through membranes.<sup>58</sup> Cold-hardening for a period of 4 weeks at 5°C reduced the exotherm temperature by 2.3°C compared to unhardened leaves (Figure 6).<sup>59</sup>

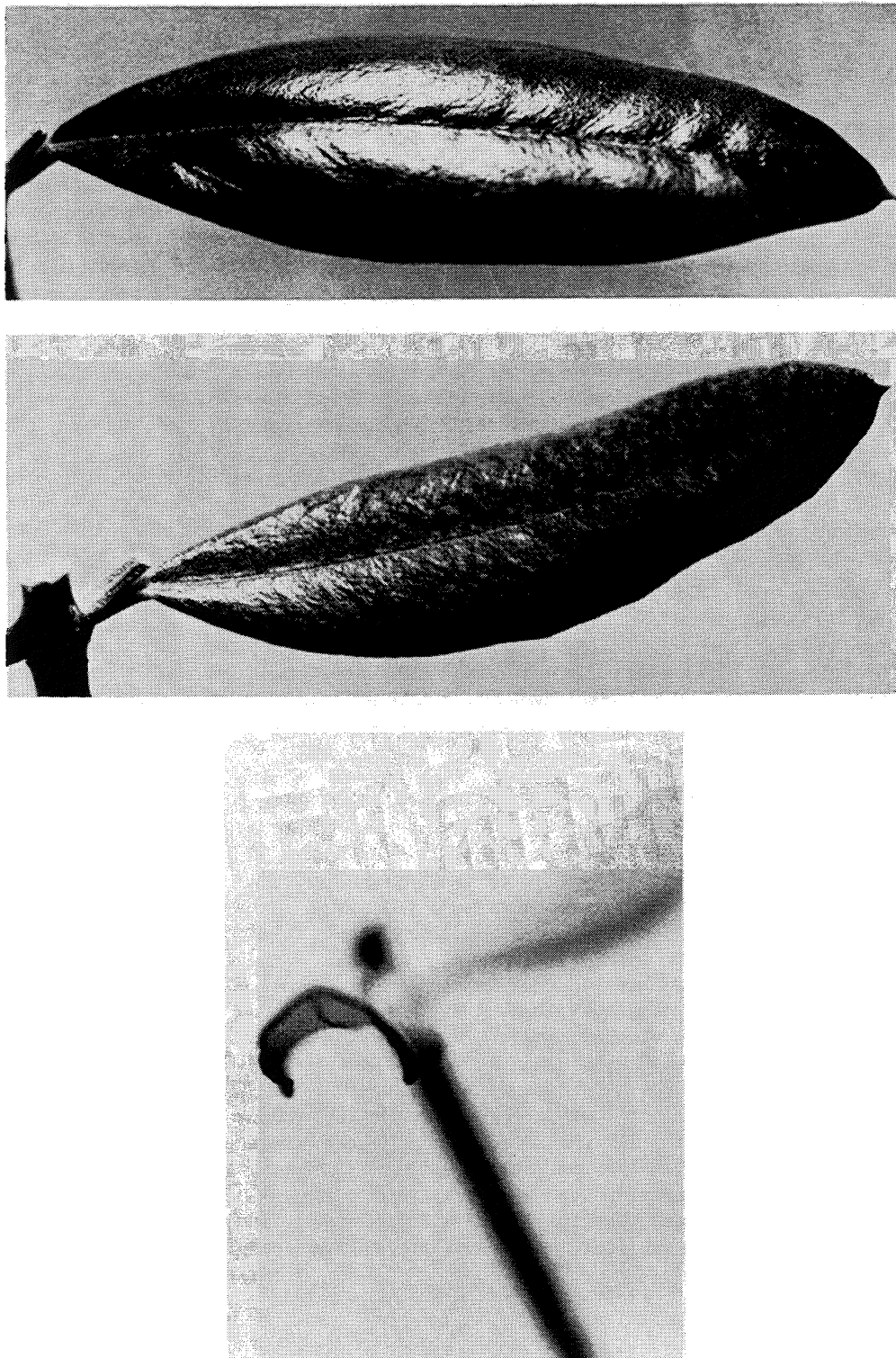
At least two classes of carbohydrates, rhamnose glycosides (i.e., verbascoside)<sup>60</sup> and sugar alcohols (i.e., mannitol)<sup>49</sup> are present in the xylem fluid of olives. Their concentration mainly increases when the winter pseudo-dormancy of roots results in a massive amount of starch deposition in xylem tissue.

Many independent traits must be combined to improve freezing resistance (e.g., fruit size, waxes, photoinhibition tolerance, etc.).<sup>61</sup> However, Roselli et al.<sup>62</sup> reported that stomatal density was lower in olive cultivars that were tolerant of cold temperatures. Thus, stomatal density may be used as a screening criterion for cold tolerance in olives.

## IV. WATER

### A. WATER REQUIREMENTS OF OLIVE

Olive is considered a drought-resistant species because it thrives in areas where water stress is frequent (Mediterranean climate). It has been postulated that the minimum water requirement for olive is 200 mm year<sup>–1</sup>.<sup>63</sup>



**Figure 5** The top picture shows the leaf of cv. Frantoio before freezing damage. If freezing occurs, upon thawing the leaf appears as in the middle picture, becoming 'water soaked' with superficial pit development and a color change which resembles a leaf kept in water for several days. The bottom picture is a side view of the middle leaf, taken several hours later. Leaf abscission occurred after 2 weeks.

## 1. Root Level

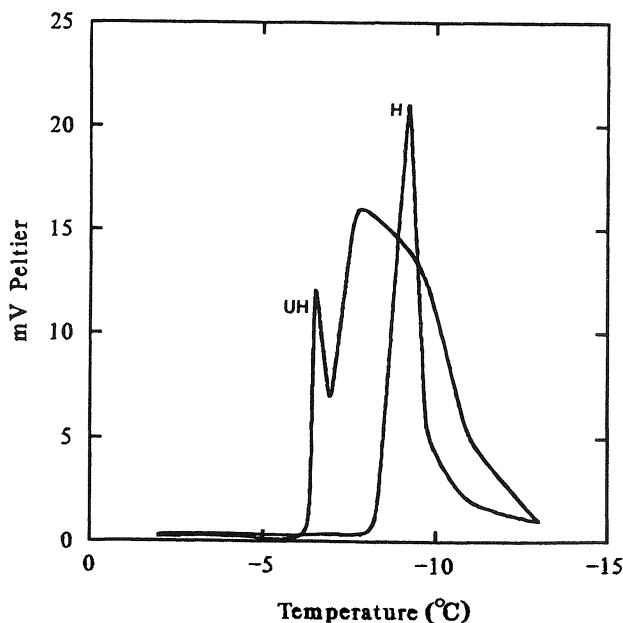
Olive trees do not have a dominant tap root. Even in small plants, the main roots almost invariably follow soil fertility channels, where lateral roots grow rapidly.<sup>11</sup> The root system is mainly confined to the top meter of soil and exceeds the projection area of the aerial parts. Olive xylopode (i.e., the tissue between the trunk and the root crown) is characterized by a stellate section and by the presence of ovular hyperplastic bodies, which contain sphaeroblasts (i.e., wartlike protuberances containing meristematic and conductive tissues).<sup>11</sup> Up to 30% of the total carbon fixed by the plant is invested in xylopodes, which are the origin of the olive adventitious root system.<sup>11</sup> This rooting habit is probably the result of sensitivity to hypoxia<sup>61</sup> and may allow for more efficient water absorption in response to light and intermittent rainfall than a deep rooting system. A drought avoidance response, on the other hand, not displayed by olive is the development of a deep root system to reach water during dry periods.

Interesting data on root distribution have been obtained from 20-year-old 'Manzanillo' trees.<sup>64</sup> The plant crown radius was 2 m, while roots extended less than 3 m and more roots were present at distances greater than 1 m from the trunk. Mean root density of irrigated and non-irrigated trees was measured in mini-rhizotrons. Using this data set the total length of living roots was calculated to be 2283 m on non-irrigated and 975 m on irrigated trees, a ratio of 2.3 between treatments. The increase in linear weight versus root length indicates that irrigation may decrease the carbon investment in roots.<sup>64</sup>

If water is supplied to trees maintained in non-irrigated conditions for a long period, care must be taken to supply water to the entire system. When the roots of the olive plants were split and irrigated at two different soil potentials ( $\Psi_{\text{soil}}$ ,  $-0.2$  and  $-1.1$  MPa), the plants grew less than plants maintained with both split roots irrigated at a  $\Psi_{\text{soil}}$  of  $-0.2$  MPa. This effect occurred even when only a small fraction of the root system was exposed to a  $\Psi_{\text{soil}}$  of  $-1.1$  MPa (Figure 7).<sup>65</sup> The leaves of the 'split-root olive plants' maintained full turgor and optimal water content, but stomatal conductance was reduced. Zhang and Davies,<sup>66</sup> obtained similar results for maize which they attributed to a large increase in the abscisic acid content in fine roots and in the transpiration stream. Thus, olive trees in the field may adapt to non-uniform soil potentials. If irrigation does not reach the entire root system of olive plants developed in non-irrigated conditions, a stress signal coming from the non-irrigated portion of the root may inhibit growth. Irrigation should therefore be a regular practice that confines the root system within a projected canopy area.<sup>67</sup>

## 2. Water Relations: Fruit and Leaf Gas Exchange

Feedback reactions between leaf conductance ( $g_s$ ) and VPD exist in leaf and fruit. We can measure water losses by  $g_s$ , since leaf porosity is much more constant than transpiration ( $E$ ). For example, in the fruits of cvs. Leccino and Dolce Agogia,  $g_s$  decreased from  $38.4 \text{ mmol m}^{-2}\text{s}^{-1}$  at 20 days after full



**Figure 6** Microcalorimetric differential traces of freezing in hardened leaves (H, 4 weeks at  $5^{\circ}\text{C}$  under natural light) and unhardened leaves (UH) of the same plant (cv. Frantoio) before the hardening. H trace shows a single peak at  $-9.0^{\circ}\text{C}$ , whereas in UH, a double heat emission with the primary peak at  $-6.7^{\circ}\text{C}$  was detected. The relative intensities are the potentials generated on a differential microcalorimeter with a matrix of 144 Peltier thermoelements. The temperature program was  $-0.05^{\circ}\text{C min}^{-1}$ .<sup>59</sup>



**Figure 7** Development of small olive plants (cv. Frantoio) grown with a small portion of the roots in drought and the rest in optimal conditions (split-roots). The roots in the left plant were maintained in uniform soil water potential of  $-0.2$  MPa, whereas, in the right one, a small portion of the roots was maintained at  $-1.1$  MPa. Turgor loss was never observed in the leaves of split-root plants, but instead stomatal closure occurred which appeared to be mediated by a translocatable signal.

bloom to  $22.4 \text{ mmol m}^{-2}\text{s}^{-1}$  at 170 days after full bloom. The leaf  $g_s$  ranged from 120 to  $190 \text{ mmol m}^{-2}\text{s}^{-1}$ .<sup>68,69</sup> The stomatal density of olive fruit is much less than that of the leaves; during ripening fruit stomata or pores gradually cover with wax and sink below the fruit surface.<sup>70</sup> Leon and Bukovac,<sup>71</sup> found 470 stomata  $\text{mm}^{-2}$  in leaves of cv. Manzanillo. Blanke and Lenz,<sup>72</sup> reported that the frequency of stomata or pores per surface unit in apple fruit was at least 30 times lower than in leaves. Large fruit with a lower surface area:volume ratio retain water more efficiently than small fruit. The following calculations are based upon an olive tree with a crown soil-projected area of  $12.5 \text{ m}^2$ , a leaf area of  $31.4 \text{ m}^2$ , and 22 kg of fruits per tree. Assuming  $g_s = 120 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$  for leaves, about 58.6 kg of water is lost daily through leaf stomata compared to about 6.5 kg from the fruit which represents 11% of the total water transpired.

### 3. From Gas Exchange to Orchard Management

Orchard irrigation schedules (called CRIS) were obtained after integrating water losses for a month under typical climatic conditions<sup>73</sup> in olive, *Prunus* and *Citrus*.<sup>65</sup> Temperatures lower than  $40^\circ\text{C}$  did not significantly affect  $g_s$ . Under this temperature,  $A_{\text{max}}$  is maintained by irrigating every 3 days. Using the CRIS model and data from measurements of leaf gas exchange, an estimate of irrigation requirements of olive orchards has been obtained.<sup>65</sup> These requirements are similar to those based on lysimetric measurements<sup>74</sup> and favorable leaf water potentials ( $\Psi$ ).<sup>75-78</sup> Evapotranspiration (ET) was comparatively low in olives ( $603 \text{ mm year}^{-1}$ ) compared to peach (with winter weeds in the orchard,  $1088 \text{ mm year}^{-1}$ ) and *Citrus* ( $940 \text{ mm year}^{-1}$ ). However, olive requires  $638 \text{ mm year}^{-1}$  water in order to avoid frequent water stress.

According to the CRIS model, in the southern Mediterranean district the volume of supplemental irrigation required to maintain the leaf relative water content deficit (RWCD) below 15% for *Prunus*, *Citrus*, and *Olea* were 561, 418, and 173 mm, respectively. Thus, olives required 3.2 times less irrigation than *Prunus* and 2.4 less than *Citrus* spp. While *Citrus* and *Prunus* may reach  $10.3 \text{ tons ha}^{-1}$  of fruit

dry matter, the 'on-year' limit for olives is 5.5 tons ha<sup>-1</sup>. Dividing the production rates by irrigation volumes, 3.17, 2.46, and 1.78 g of dry fruit matter was calculated per kilogram of water in olive, *Citrus*, and *Prunus*, respectively. Under the same conditions, the energy yields of the crop is 103.4 MJ ha<sup>-1</sup> for *Olea*, 90.5 MJ ha<sup>-1</sup> for *Prunus*, and 62.3 MJ ha<sup>-1</sup> for *Citrus*.<sup>79</sup>

When an olive orchard in a northern Mediterranean district is considered, we find that a very limited amount of irrigation is needed during summer (180 m<sup>3</sup> ha<sup>-1</sup>). The absence of supplemental water (about 288 kg tree<sup>-1</sup> year<sup>-1</sup>) may induce fruit drop. Since water turn-over time in fruit is about 1 day, only a few days with a dry soil are sufficient to induce fruit drop.

## B. RESPONSES TO WATER STRESS IN OLIVE

Water deficits are tolerated by olive for prolonged periods. Olive has evolved a series of adaptations which confer tolerance to water stress. One adaptation of olive leaves is the drastic increase in  $\Psi_{\pi}$  of water-stressed leaf cells.<sup>80</sup>

### 1. Mannitol and Osmotic Potential

Sucrose is a major solute among many higher plants, but mannitol, a polyol, predominates in olives and represents from 1/2 to 2/3 of the total soluble sugars in leaves and bark.<sup>49,50</sup> The vacuolar concentration of sucrose can reach 2 M. Above this range, the water binding capacity of sucrose may have deleterious effects. At concentrations higher than 0.5 M, carbohydrates start to bind water chemically, and the "bound" water is sequestered from physiological equilibria. This leads to substantial reductions in  $\Psi_{\pi}$  far below van't Hoff's calculations of  $\Psi_{\pi}$ . In fact, a 2 M solution of sucrose in cells may exert a  $\Psi_{\pi}$  of -13.6 MPa instead -4.9 MPa.<sup>81</sup> Many species use sugar alcohols, called polyols, instead of sucrose. Polyols are more similar to water than sucrose in terms of polarity, electroneutrality and redox potentials and tend to bind water less than sucrose. Cells with high mannitol concentrations absorb water from apoplast at very low water potentials.

Olive fruits are unable to carry out a large degree of osmotic adjustment because little mannitol is present (less than 10% of soluble sugars);<sup>82</sup> in fruits, mannitol is readily re-synthesized into fructose-6P. Mannitol has also been found in xylem sap after winter pseudo-dormancy,<sup>49</sup> and may play a role in cold hardening.

### 2. Water Content and Capacitance Effects

Olive leaves can tolerate  $\Psi_i$  near -9 to -10 MPa with full rehydration ability,<sup>80</sup> and it is difficult to establish a critical  $\Psi_i$  for growth or physiological processes. However, a stress parameter able to accurately establish if a leaf is under stress is essential. Olive leaves have been reported to absorb water from humid air (poikilohydricity).<sup>83</sup> However, poikilohydricity can only occur under very humid conditions (i.e., mean relative humidity ca. 100%) and when air temperature exceeds leaf temperature. In addition stomata must be open and  $\Psi_i$  must be near zero.

The instantaneous water potential of leaves can be obtained from the relationship  $\Psi_i = A + B e^{(-Ct)}$ , where A is a soil potential parameter, B is a constant associated with  $\Psi_i$ , C is a kinetic constant derived by the resistance offered by the hydraulic connections to water transport, and t is the time.<sup>84</sup> The transpiration rate affects both A and B parameters, and any changes in stomatal opening modifies  $\Psi_i$ .<sup>84</sup> In steady conditions, hydraulic resistances determine the  $\Psi_i$  across segments of the vascular system. If E is prevented, the plant equilibrates to the root water potential.

The large midday water potential drop found from leaves to root in olive may reflect a strong resistance to water movement. A specific hydraulic resistance of 250 MPa s m kg<sup>-1</sup> has been found in potted olive cv. Nocellara plants, whereas in many deciduous species the hydraulic resistance ranged between 35 and 4 MPa s m kg<sup>-1</sup>.<sup>85</sup> The linear pressure gradient necessary to move water was 65, 170, and 560 kPa m<sup>-1</sup> in olive primary, secondary, and tertiary stems, respectively. Values for intact field trees are not known.<sup>85</sup> Maintaining a low  $\Psi_{\pi}$  in olive leaves may be essential to drive water through the apoplast given such large hydraulic resistances.

### 3. Volumetric Elastic Modulus

Olive leaf cells have a high volumetric modulus of elasticity ( $\epsilon$ ).<sup>86</sup> This parameter represents an applied pressure divided by a fractional change in volume size,<sup>87</sup> according to:

$$\epsilon = \frac{\Delta P}{\Delta V/V} \quad (1)$$

where  $P$  is turgor pressure and  $V$  is cell volume. Note that  $\epsilon$  is a parameter that is inversely proportional to tissue elasticity.

In olive,  $\epsilon$  tends to increase under drought. At 87.5% of maximal cell volume,  $\epsilon$  of 7 and 22.5 MPa have been recorded in hazelnut and mature olive leaves, respectively.<sup>88</sup> Turgor loss for the more rigid cells of olive leaves occurred at 80% of maximal cell volume; however, positive turgor was maintained in hazelnut leaves at 66% of maximal volume. The  $\epsilon$  of young olive leaves was 8.4 MPa, indicating that tissue elasticity was reduced with leaf aging. The negative adaptation of  $\epsilon$  is typical of Mediterranean evergreens.<sup>86</sup> By contrast, succulent plants, like *Agave deserti*, displayed a decrease in  $\epsilon$  (i.e., less rigid cells) and tended to retain higher turgor pressure ( $\Psi_p$ ) under drought conditions.<sup>86</sup> Olive apparently relies more on reducing  $\Psi_\pi$  than on maintaining a low  $\epsilon$  in response to drought. A reduced  $\Psi_\pi$  (and hence  $\Psi_l$ ) facilitates the extraction of water from the soil at low soil water potentials ( $\Psi_{\text{soil}}$ ). As a consequence of the low  $\Psi_\pi$  and  $\Psi_l$  generated in the symplast, apoplastic water uptake is a rapid phenomenon in olive leaves.<sup>86,89</sup> Water-stressed olive leaves are strong sinks for water at very low  $\Psi_\pi$  values. By contrast, olive fruits are succulent bodies that have very low  $g_s$  and may even contribute to a “capacitance effect” by supplying water to leaves during midday.

#### 4. Growth Rate and Carbon Allocation

Leaf surface-based photosynthetic capacity and growth have recently been linked by an allocation function, the Carbon Molar Density ( $\rho$ )<sup>90</sup> where  $\rho$  represents the ratio of total plant carbon to total leaf area ( $\text{mol C m}^{-2}$ ).

The relative growth rate (RGR) has been related to photosynthesis,<sup>90</sup> by

$$\text{RGR} = \frac{Al(1 - \phi)}{\rho} \quad (2)$$

where  $\phi$  is the respiratory loss,  $l$  is the light period as a proportion of the day (i.e., for 12 h of day light,  $l = 0.5$ ),  $A$  is the net  $\text{CO}_2$  assimilation rate and  $\rho$  is the ratio of total carbon to photosynthetic area.

In wheat a value of  $\rho = 2.5 \text{ mol m}^{-2}$  has been obtained.<sup>90</sup> In well-watered small olive plants (cv. Frantoio)  $\rho$  was  $12.2 \text{ mol m}^{-2}$ , whereas in water-stressed olive plants  $\rho$  was  $14.9 \text{ mol m}^{-2}$ .<sup>65</sup> The RGR was  $72 \times 10^{-3} \text{ d}^{-1}$  for wheat,  $10 \times 10^{-3} \text{ d}^{-1}$  for well-watered olive plants and  $3.6 \times 10^{-3} \text{ d}^{-1}$  for olive plants, which were kept at one half of soil capacity. Therefore, the RGR for irrigated olives is about 7 times less than for wheat, due to a combination of two effects: the reduction of  $A$  because of stomatal limitation and an increase of  $\rho$ .

#### 5. Stress Caused by Waterlogging

Excessive irrigation or rainfall may result in waterlogging. Hypoxic conditions associated with waterlogged soil conditions alter root metabolism,<sup>91</sup> and, when hypoxia conditions are persistent, metabolic functions, including water and nutrient absorption and transport, are impaired.<sup>92</sup>

Olive is considered a sensitive species to root hypoxia and the sensitivity varies among cultivars.<sup>93</sup> Plants of cv. Mission died after a 30-day period of waterlogging, whereas about 50% of the cv. Kalamata plants survived a 60-day period of waterlogging.<sup>93</sup> Resistance to waterlogging in olives has been correlated with the capacity to avoid root hypoxia by producing adventitious roots close to the soil surface.<sup>93</sup> Waterlogging damage can be reduced by using resistant rootstocks, such as *Olea oblonga* and *O. cuspidata*, or resistant cultivars such as ‘Zhongshan 80’.<sup>14,15</sup> The darkening of heartwood or “duramen” has been used as sensitivity index for hypoxia in olive.<sup>15</sup> When the duramen of small potted plants darken after 10 days of waterlogging they were classified as sensitive.<sup>15</sup>

### V. NUTRIENTS

#### A. NUTRIENT REQUIREMENTS

The nutrient requirements of olive are lower than that of many other fruit trees such as peach, grape, or citrus. However, when the requirement is not met by soil supply, nutrient stress can cause major physiological changes in the plant. Olive macronutrient requirements may be satisfied by soils containing

more than 0.1% N and more than 0.03%  $P_2O_5$  and  $K_2O$ .<sup>94</sup> Other macronutrients are normally present in sufficient amounts in the soil. When nutrients in the leaves are adequate for optimal growth, the rate of fertilizer depletion is the product between RGR and the percentage of nutrients in the leaves.<sup>95</sup>

The optimal macronutrient composition of an olive leaf is 2.1% N, 0.35% P, and 1.05% K in leaf dry matter.<sup>96</sup> The optimum total (N-P-K) concentration, however, vary significantly according to soil, cultivar, plant age, and leaf age.<sup>94</sup> Bouat<sup>97</sup> reported that the total nutrient concentration decreased from 5.03% in young leaves to 2.45% in senescent leaves. However, few large scale experiments have investigated the relationship between nutrients and RGR.

## B. NUTRIENT STRESS

High concentrations of starch and soluble carbohydrates have been detected in olive leaves during spring and autumn, whereas in summer there is a reduction in starch, soluble carbohydrates and mannitol.<sup>49</sup> In winter, bark and xylem tissues are used to store mannitol and starch.<sup>49</sup> Carbohydrate concentration is more stable in roots than in shoots.<sup>98</sup> Flowering stems are stronger sinks for carbohydrates than vegetative stems.<sup>99</sup> It has been proposed that floral differentiation requires high carbohydrate and nitrogen concentrations in the leaves.<sup>100,101</sup>

When nutrients are not sufficient to support vegetative and reproductive flushes of olive trees, a series of physiological events are triggered. Vegetative growth is reduced by nitrogen deficiency. However, nitrogen excess (frequent in nurseries) favors lush growth, increases susceptibility to pathogens and impairs the physiological balance with other elements, particularly phosphorus.<sup>94,102</sup> Heavy cropping depletes the carbohydrate concentration and reduces the vegetative growth of olive trees.<sup>17</sup> Leaf concentrations of N, P, and K are high before heavy cropping.<sup>94</sup> Lateral shoot development is influenced by the N/P ratio. A high N/P ratio induced a significant reduction in lateral shoot development.<sup>103</sup> A balanced fertilization program can significantly reduce the problem of alternate bearing. Boron deficiency (below 15 ppm in leaf tissue) results in leaf chlorosis and necrosis, followed by leaf drop, bud abortion, lack of flowering, and the development of abnormal fruits.<sup>17,94</sup> Stress caused by antagonistic interactions of elements or other microelement deficiency is rare.

## VI. SALT

### A. TOLERANCE TO SALT

Olive is moderately salt tolerant, although salinity may be a problem, due to the high salt concentration in the irrigation water used in the Mediterranean area. Olive orchards growing along the coast must also cope with salt deposited by sea winds. Useful parameters for a quantitative and qualitative analysis of salinity are the total salt concentration in the irrigation water and the sodium absorption ratio (SAR, the ratio between the cation  $Na^+$  and the cations  $Ca^{2+}$ , and  $Mg^{2+}$  in the irrigation water). Olives can be irrigated with water containing up to 3200 ppm of salt with an SAR of 26 or lower.<sup>94</sup> Salt accumulates in the soil if the irrigation to evaporation ratio is low. Robinson<sup>104</sup> observed that on sand an irrigation to evaporation ratio of 1 supports olive growth when water with 1430 ppm of salt is used. When the irrigation/evaporation ratio is lower than 1, however, salt accumulates in the soil and, eventually, olives may succumb to salt toxicity. Tolerance to salt appears to be cultivar-dependent. For example, an NaCl concentration of 80 meq  $l^{-1}$  may increase or decrease the percentage of perfect flowers in different cultivars.<sup>105</sup> The growth of all cultivars tested was reduced under salt stress to varying degrees.

### B. SALINITY DAMAGE

Salinity decreases the  $\Psi_\pi$  of the soil solution and makes water absorption from the soil more difficult for olive plants.<sup>105</sup> Increasing the ionic concentrations of the nutrient solution from 43 meq  $l^{-1}$  to 69 meq  $l^{-1}$  has reduced shoot length, leaf area, root length, and rooting ability of olive cuttings.<sup>106</sup>

A reduction in growth, shoot and leaf differentiation, and total leaf area has also been induced by increasing concentrations of NaCl in the water.<sup>106</sup> The photosynthetic characteristics of salt-stressed olives did not change provided that  $Cl^-$  concentration was lower than 80 mM in total tissue water.<sup>107</sup> Above this threshold, however, a reduction in photosynthesis and stomatal closure occurred and plant morphology was altered.<sup>108</sup> It has been found that, following salt stress, stomata were also less responsive to environmental changes, particularly air humidity. Leaf thickness and plant growth was reduced; a leaf drop of 50% has also been reported.<sup>108</sup> When the  $Cl^-$  concentration approached 200 mM in tissue water, leaves became permanently desiccated.<sup>108</sup> Accumulation of  $Cl^-$  and  $Na^+$  has been reported to

decrease distally in olive leaves and to be lower in lateral shoots, stems, and roots than in leaves. There is four times less chloride accumulation in the apical leaves of a shoot compared to the basal leaves.<sup>108</sup> The salt tolerance mechanism in olives may be related to the capacity to accumulate salt in the leaf vacuoles.<sup>108</sup> By accumulating salt in the basal leaves, rather than in the apex or stems, olive plants retain their capacity to recover and grow by shedding leaves containing excess salt.<sup>108</sup>

## VII. CO<sub>2</sub>

At a high fluence level, leaf photosynthesis is limited by CO<sub>2</sub> partial pressure. In C<sub>3</sub> plants, the enzyme ribulose-bisphosphate carboxylase-oxygenase (RUBISCO) fixes CO<sub>2</sub> inside the chloroplast stroma. The steady state concentration of CO<sub>2</sub> depends on CO<sub>2</sub> in air and CO<sub>2</sub> conductance from the stomata. Conductance of CO<sub>2</sub> in intercellular spaces across membranes into cells until the CO<sub>2</sub> reaches the site of fixation may also affect the inner CO<sub>2</sub> levels. CO<sub>2</sub> concentration progressively diminishes from the ambient air to the chloroplast stroma. The chemical CO<sub>2</sub> gradient is the diffusive force which allows CO<sub>2</sub> to move from the environment to the stroma.<sup>109</sup>

A comprehensive treatment of biochemical and biophysical principles of gas exchange parameters is discussed in the Citrus chapter of Volume II.

### A. BIOCHEMICAL REGULATION LIMITED BY STOMATAL DIFFUSION

The partial pressure of CO<sub>2</sub> in the intercellular spaces in the leaf (C<sub>i</sub>) can be estimated from CO<sub>2</sub> and H<sub>2</sub>O gas exchange measurements.<sup>110</sup> In non-stressed leaves of C<sub>3</sub> plants, the ratio between intercellular and ambient CO<sub>2</sub> concentration (C<sub>i</sub> C<sub>a</sub><sup>-1</sup>) is about 0.75, with a small variance, within 0.15; this variance is associated with relative water efficiency among C<sub>3</sub> types. Note that C<sub>i</sub> is a volume-averaged value and CO<sub>2</sub> is reduced in concentration continuously as it diffuses from the stomata to the site of fixation in the chloroplast. Similarly, the accuracy of calculating C<sub>i</sub> from gas-exchange values determined with infrared gas analyzers is contingent upon homogeneous stomatal behavior. However, heterogeneous stomatal closure has been reported in olive leaves.<sup>111</sup>

Net CO<sub>2</sub> assimilation in high light and in ambient air is linked to CO<sub>2</sub> partial pressure in the chloroplast by:<sup>110</sup>

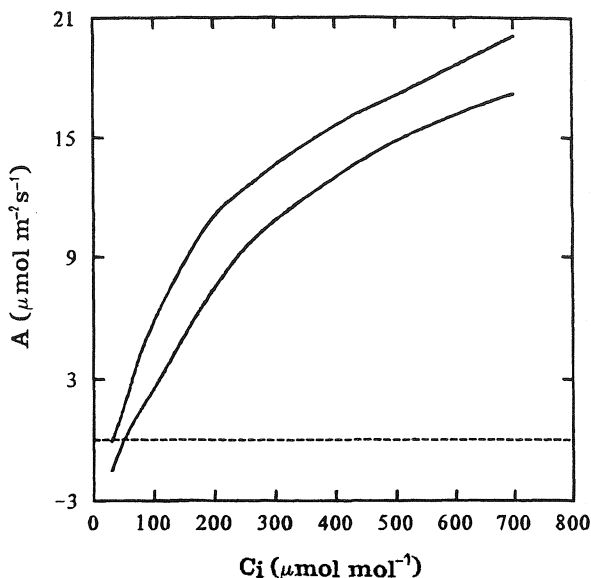
$$A = V_c \frac{C_i - \Gamma^*}{C_i + k_{ap}} - R_d \quad (3)$$

where V<sub>c</sub> is the maximal capacity of RUBISCO in the leaf exposed to saturating CO<sub>2</sub>, Γ\* is the compensation point in the absence of photorespiration, k<sub>ap</sub> is the apparent Michaelis constant of RUBISCO (including the competitive inhibition of oxygen) and R<sub>d</sub> is the respiration rate. In ambient air (0.198 mol mol<sup>-1</sup> O<sub>2</sub>) at 28°C, in 3-month-old olive leaves the V<sub>c</sub> was 75–95 mmol m<sup>-2</sup> s<sup>-1</sup>, Γ\* was 46 mmol mol<sup>-1</sup>, k<sub>ap</sub> was 720 mmol, and R<sub>d</sub> was about 1.2 mmol m<sup>-2</sup> s<sup>-1</sup>.<sup>112</sup>

Within these assumptions, the differences of A in C<sub>3</sub> plants, at constant C<sub>i</sub>, are mostly due to changes in V<sub>c</sub>; the amount of RUBISCO is proportional to total leaf nitrogen, since at least 20% of the leaf protein is in the form of RUBISCO. Therefore, if a spinach leaf with A = 35 μmol m<sup>-2</sup> s<sup>-1</sup> and an olive leaf with A = 11 μmol m<sup>-2</sup> s<sup>-1</sup> have the same C<sub>i</sub>, then the V<sub>c</sub> of the olive leaf is three times lower than the V<sub>c</sub> of spinach. This conclusion is supported by the low nitrogen concentration of olive leaves. Photosynthesis of non-stressed olive leaves with a C<sub>i</sub> of 200 mmol mol<sup>-1</sup> is about 11 mmol m<sup>-2</sup> s<sup>-1</sup>, but the most accurate C<sub>i</sub> determinations never gave less than 240 mmol mol<sup>-1</sup>, with an ambient value of 330 mmol mol<sup>-1</sup>.<sup>112</sup> Most of the <sup>14</sup>CO<sub>2</sub> in olive is fixed by the Calvin cycle and employs the glycolate pathway, with a significant proportion (10%) of photorespiration through alanine.<sup>112</sup>

### B. INTERACTIONS WITH WATER CONTENT, HUMIDITY, AND NITROGEN

The effect of drought on leaf gas exchange of 4-month cv. Verdiale has been studied (Figure 8). The CO<sub>2</sub> response of leaves that reached turgor point loss at 20% RWCD (i.e., Ψ<sub>l</sub> = -1.9 MPa) was slightly different from the controls at 4% of RWCD. There was a limited loss (24%) in negative biochemical capacity associated with an osmotic adjustment (i.e., Ψ<sub>π</sub> varied from 1.3 to 1.9 MPa). Field values of A were reduced by 76% and stomatal conductance to CO<sub>2</sub> (g<sub>s</sub>') fell from 0.212 to 0.086 mol m<sup>-2</sup> s<sup>-1</sup> and C<sub>i</sub> diminished to 120 mmol mol<sup>-1</sup>. Thus, stomata may play a major role in controlling photosynthesis



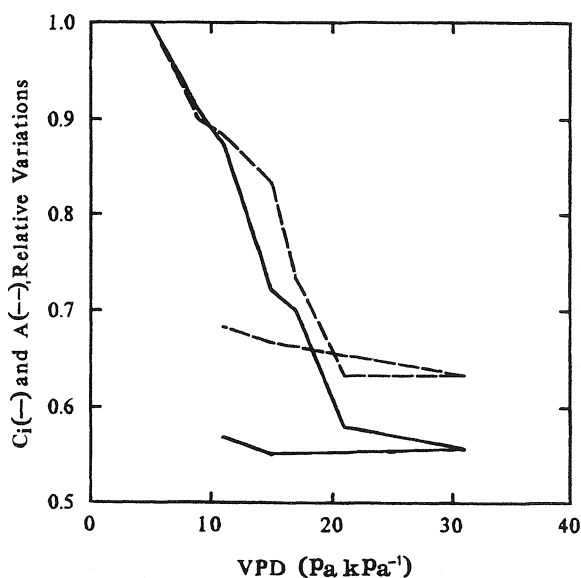
**Figure 8**  $\text{CO}_2$  response curves corrected for stomatal conductance, and hence expressed in substomatal  $\text{CO}_2$  molar fraction ( $C_i$ ). The upper curve is for leaves in full turgor, whereas the lower one is for leaves which lost 20% of maximal water content at a turgor pressure near zero. The conspicuous reduction in photosynthesis ( $A$ ) is due mostly to a  $C_i$  drop, from 260 to 150  $\mu\text{mol mol}^{-1}$  and, to a lesser extent, to biochemical factors associated with a reduced  $\Psi_\pi$ .

under drought,<sup>112</sup> but these data should be viewed with caution due to the possibility of stomatal heterogeneity.

An increase in VPD caused a marked reduction in  $A$  and  $C_i$  in greenhouse olive plants (Figure 9).<sup>107</sup> The reduction was also associated with reduction of  $g'_s$ . As reducing the VPD neither restored the original  $A$  and  $g'_s$  nor increased  $C_i$ , the responses to VPD appear to be irreversible. Extensive stomatal heterogeneity with closed patches of stomata was also observed after a high VPD treatment,<sup>111</sup> but heterogeneity ceased if the treatment duration was longer than 30 min.

### C. DOWN REGULATION CASES

The relationship between  $A$  and  $V_c$ , may be obviated in many cases by phosphate limitations caused by export of photoassimilates from chloroplasts to cytoplasm, and by starch accumulation inside chloroplasts.<sup>113</sup> The photosynthetic rate is reduced also after increasing  $\text{CO}_2$  partial pressure, light, or decreasing  $\text{O}_2$  concentration.<sup>113</sup> Such reduction is often termed "down regulation" because it does not depend on stomatal closure, but instead may depend on photoinhibition, phosphate starvation, low temperature inactivation of phosphate chloroplast turnover or photosynthate accumulation inside leaf cells.<sup>113</sup> Treat-



**Figure 9** Leaf-air vapor pressure difference (VPD) noticeably affects photosynthesis ( $A$ ). The time course was 20 min for each VPD, starting from  $A$  and  $C_i$  equal to unity: when VPD was again lowered, instability of  $C_i$  was generated. A subsequent  $^{14}\text{CO}_2$  experiment confirmed the presence of heterogeneous stomatal closure.<sup>111</sup>

ments, such as girdling, that limit photosynthate translocation in olives have the side effect of blocking photosynthesis.<sup>114</sup>

## D. CO<sub>2</sub> UPTAKE AND WATER LOSS

### 1. Biochemical Models of Water Use Efficiency

The ratio of <sup>13</sup>C to <sup>12</sup>C in plant tissue has been employed for assessing water use efficiency. Isotope discrimination of <sup>13</sup>C/<sup>12</sup>C ( $\Delta$ ) is a measure of the difference in the ratio of <sup>13</sup>C/<sup>12</sup>C in plant tissue compared to air.<sup>115,116</sup> Carbon isotope discrimination is measured in a stable isotope ratio analyzer from isotopic ratios in leaf cellulose and air as:

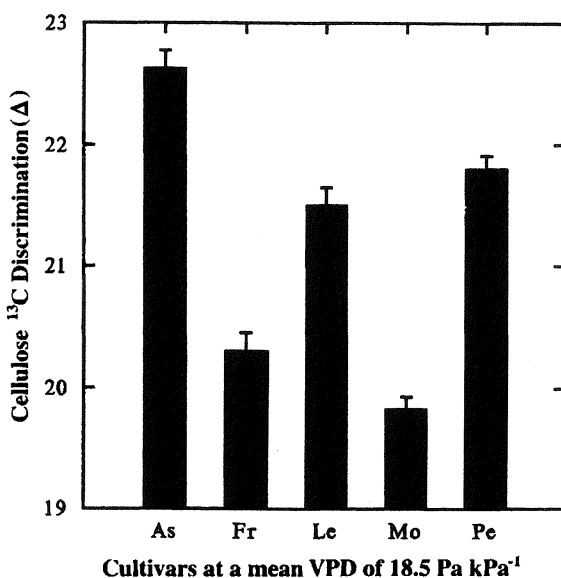
$$\Delta = \frac{R_{\text{air}}}{R_{\text{leaf}}} - 1; \quad R_{\text{air,leaf}} = \frac{{}^{13}\text{C}(\text{mol})}{{}^{12}\text{C}(\text{mol})} \quad (4)$$

$R_{\text{air}}$  and  $R_{\text{leaf}}$  are the molar ratios of carbon isotopes (<sup>13</sup>C/<sup>12</sup>C) in the air and in the leaf. About 1.1% of the carbon in air is naturally <sup>13</sup>C. Farquhar et al.<sup>116</sup> found that in C<sub>3</sub> plants the observed variances of  $\Delta$  were linked to C<sub>i</sub> C<sub>a</sub><sup>-1</sup> variance. Discrimination originates from a diffusional effect produced by the laminar flow within stomata ( $\Delta = 4.4 \times 10^{-3}$ ) and by the smaller reactivity of RUBISCO for <sup>13</sup>CO<sub>2</sub> ( $\Delta = 27 \times 10^{-3}$ ) compared to <sup>12</sup>CO<sub>2</sub>. The total "isotope" effect depends on C<sub>i</sub> C<sub>a</sub><sup>-1</sup> according to:

$$\Delta \cdot 10^3 = 4.4 + (27 - 4.4) \frac{C_i}{C_a} \quad (5)$$

Cellulose is the material used most frequently for  $\Delta$  determinations.<sup>115,117</sup> Leaf cellulose does not change in composition with respect to the Calvin cycle metabolites, and may be conveniently purified by nitric acid digestion.<sup>117</sup> Another useful characteristic is that cellulose synthesis occurs predominantly when the leaf is at its maximal photosynthetic capacity and is minimal under stress. Consequently,  $\Delta$  is an indicator of the differences in the stomatal regulation during plant growth. Figure 10 reports the leaf cellulose  $\Delta$  values recently obtained in five olive cultivars in an environment with a mean VPD of 18.5 Pa kPa<sup>-1</sup>. Fruit-bearing olive shoots had a  $\Delta$  of  $21.64 \times 10^{-3}$  in 'Frantoio' and of  $21.76 \times 10^{-3}$  in 'Ascolana';  $\Delta$  of non-fruiting shoots were  $20.29 \times 10^{-3}$  and  $21.28 \times 10^{-3}$ , respectively.<sup>118</sup> The presence of fruits results in significant differences in  $\Delta$ .

From the relationship given for the C<sub>i</sub> calculation,<sup>119</sup> the following parametric link among A, E,  $\Delta$ , and C<sub>i</sub> C<sub>a</sub><sup>-1</sup> results:



**Figure 10** Field experiment of olive cultivars, with a midday mean VPD of 18.5 Pa kPa<sup>-1</sup> when new shoot formation took place, it clearly showed genetic differences in cellulose <sup>13</sup>C discrimination against air CO<sub>2</sub> ( $\Delta \cdot 10^3$ ). The acronyms are: As, Ascolana; Fr, Frantoio; Le, Leccino; Mo, Moraiolo, and Pe, Pendolino. Bars represent 1 SE.

$$\text{WUE} = \frac{27 - \Delta \cdot 10^3}{22.6} \frac{\text{Ca}}{1.6 \text{ VPD}} \quad (6)$$

The estimated WUE (water use efficiencies) were  $2.16 \times 10^{-3}$  and  $3.48 \times 10^{-3}$  mol C mol  $\text{H}_2\text{O}^{-1}$  for 'Ascolana' and 'Moraiole', respectively (Figure 10).

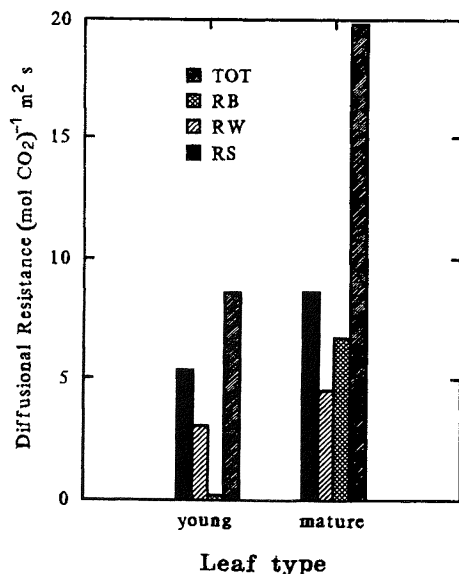
## 2. Complete Gas Diffusion Paths in Leaves

The  $\text{CO}_2$  concentration in chloroplast stroma ( $C_c$ ) in olive is noticeably different from  $C_i$  calculated from gas-exchange measurements.<sup>112</sup> The inverse notation of conductance, resistance, is more appropriate here because, in 'in-series' resistance circuits, like the one we are now introducing, total resistance is the sum of resistances to  $\text{CO}_2$  transfer. It should be kept in mind that up to this point the parameter  $C_i$  that results from the difference  $\text{Ca} - [\text{A } r_s]$ , was being applied.<sup>110</sup> The relationship between WUE,  $C_i$ , and  $\Delta$ , which considered  $C_i$  not as a volume-averaged  $\text{CO}_2$  concentration in leaf intercellular spaces but as the actual partial pressure of  $\text{CO}_2$  in the chloroplast stroma, has been successfully used on glycophytic plants.<sup>116</sup> In olive and in most "hypostomatous plant species", a corrective term must be incorporated due to a conspicuously high diffusive resistance between stomata and stroma. Several measurements indicate that internal diffusive resistance may be equivalent in magnitude to stomatal resistance in mature leaves of all woody species studied.<sup>120,121</sup> For hypostomatous leaves, the total resistance to  $\text{CO}_2$  ( $r_{tc}$ ) pathway from chloroplast to stroma is  $r_{tc} = r_s + r_b + r_w$ , where  $r_s$  is stomatal resistance, the  $r_b$  is microboundary layer resistance, and  $r_w$  is the sum of remaining diffusion resistances between stomata and stroma.

The diffusion equilibrium becomes  $C_c = \text{Ca} - [\text{A } r_{tc}]$ ; total resistance  $r_{tc}$  is expressed for  $\text{CO}_2$  transfer. The reason for this correction arose after applying on-line isotope discrimination to olive.<sup>122,123</sup> On-line discrimination, a technique to measure the instantaneous values of  $\Delta$ , involves determination of  $\Delta$  of the air surrounding the leaf in a gas exchange cuvette.<sup>120</sup> By contrast, carbon isotope discrimination for structural carbohydrates corresponds to integrated or long-term values.<sup>122</sup> For mature olive leaves the cellulose discrimination was within the limits for a typical  $\text{C}_3$  plant, whereas the on-line  $\Delta$  value fell below  $12 \times 10^{-3}$ , a value more typical for a CAM plant.<sup>122</sup> Cellulose was formed while leaves were young, indicating a change in  $\Delta$  with ageing in olive. Stomata were invariably closed at night and  $\text{CO}_2$  fixation in malate was never detected in olives. Cellulose discrimination and on-line  $\Delta$  were similar for young leaves, but there was a significant difference in  $C_i$  values when they were calculated from leaf gas exchange determinations compared to  $C_i$  determinations predicted from the relationship between  $\Delta$  and  $C_i$ .<sup>123</sup> Bongi and Hubick<sup>123</sup> calculated that  $r_b + r_w$  was three times higher in young olive leaves than in wheat, and proposed that internal restriction to  $\text{CO}_2$  diffusion into the chloroplast was responsible for high  $r_w$ . Packing of palisade cell layers called 'scala' are present in olive leaves,<sup>124</sup> that may produce a longer path for  $\text{CO}_2$  from stomata to the chloroplast envelope. Further restrictions to the  $\text{CO}_2$  pathway are caused by dense thick cell walls and the presence of trichomes on the abaxial leaf surfaces.<sup>71,125</sup> In summary, diffusive resistances, other than stomatal, may considerably limit photosynthetic capacity in olive leaves.

Using the carbon isotope discrimination method, the  $r_b + r_w$  has been estimated to be  $3.2 \text{ mol}^{-1} \text{ m}^2 \text{ s}$  in peach and  $7.6 \text{ mol}^{-1} \text{ m}^2 \text{ s}$  in *Citrus paradisi* and *Macadamia* spp.<sup>120</sup> In mature olive leaves a  $r_b + r_w$  of  $11.2 \text{ mol}^{-1} \text{ m}^2 \text{ s}$  has been calculated.<sup>123</sup>

When trichomes of mature olive leaves were removed,  $r_b + r_w$  decreased from  $11.2$  to  $4.5 \text{ mol}^{-1} \text{ m}^2 \text{ s}$  (Figure 11). Therefore,  $r_b$  makes a large contribution to  $r_{tc}$ . When  $r_b$  was calculated as the difference between  $r_{tc}$  with and without trichomes, it was  $6.7 \text{ mol}^{-1} \text{ m}^2 \text{ s}$ . The advantage of disposing of a barrier outside the stomata in olive leaves, can be derived from the diffusion theory.<sup>119</sup> In turbulent air, the diffusivity ratio for  $\text{H}_2\text{O}$  vapor and  $\text{CO}_2$  is 1.37, whereas the laminar flow produced by the chemical gradients inside the stomata results in a diffusivity ratio of 1.6. The 0.23 difference in diffusivity allows 14% more  $\text{CO}_2$  uptake than  $\text{H}_2\text{O}$  loss; hence WUE increases.<sup>119</sup> Ying et al.<sup>14</sup> found a large genetic variation on  $r_b$  in olive leaves; cv. B-114 had the highest  $r_b$  and more than 8 layers of trichomes, but only 25% of the abaxial surface of cv. ZS-586 was covered with trichomes. The abaxial surface of the leaves was silver-white on cv. B-114, but pale-green on cv. ZS-586. Other genotypes displayed a range of 17 color gradations.<sup>14</sup>



**Figure 11** The evolution of strong diffusive resistance in young (2-months-old) and mature (1-year-old) leaves of cv. Verdiale. The use of on-line discrimination recorded a great increase in  $rb$ , the resistance to transfer of  $\text{CO}_2$  through external boundaries among leaf types due to the build-up of multiple trichome layers. TOT indicates the total resistance to  $\text{CO}_2$  transfer, which should be employed to calculate the partial pressure in the chloroplasts ( $C_c$ ), according to  $C_c = C_a - [A \text{ TOT}]$ ;  $C_a$  is the molar fraction of  $\text{CO}_2$  outside the boundary layer.

## VIII. CONCLUSIONS

Olive has developed adaptations to environmental stress consistent with evolution in a Mediterranean climate. The mechanisms are, however, poorly understood. The performance of a genotype is a cumulative response to various environmental variables and the interaction with environmental variables. The simultaneous occurrence of two or more stresses is generally more deleterious than the occurrence of an isolated stress and makes interpreting stress effects more complex. The low growth rate and photosynthetic capacity of the olive should be considered an adaptation to the environment. Moreover, most olive cultivars which are considered resistant to environmental stresses also exhibit poor horticultural performance.

Morphological features of the olive leaf (size, thickness, anatomy of the mesophyll), limit the exchange of water vapor and  $\text{CO}_2$  between leaf and atmosphere, which reduces evapotranspiration and may substantially reduce photosynthesis because of carbon starvation in the stroma. Water stress induces a change in carbon partitioning used for root formation in water stressed plants, thereby reducing the carbon available for photosynthetic end-product formation and canopy growth.

The tolerance of olive to salt is associated with salt accumulation in leaf cells, which inhibits photosynthesis and eventually causes leaf drop only in the leaf population proximal to the roots.

Photoinhibition is limited by low efficiency of the PS2 reaction centers in the adaxial surface of the leaf. Multiple palisade layers in the leaf mesophyll creates a low light environment, reduces the electron transport rate and the photochemical efficiency of photosynthesis, yet protects the apparatus from photoinhibition. Abaxial leaf surfaces reflect a greater percentage of incoming solar radiation than the adaxial leaf surface, also minimizing the deleterious effects of a high light/variable temperature habitat prevalent in Mediterranean regions.

Supercooling and winter pseudo-dormancy confer a slight to moderate level of cold hardening (i.e., down to  $-12^\circ\text{C}$ ); however, genotypic variation in cold hardiness does occur. Conversely, olive does have a cold requirement to insure adequate flowering and high qualitative and quantitative oil characteristics of the fruit.

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## Pear and Quince

Peter D. Mitchell, Ian Goodwin, and Peter H. Jerie

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### I. INTRODUCTION

Both pear and quince belong to the Rosaceae family and along with the apple and some lesser known fruits, the subfamily Pomoideae. The pear belongs to the *Pyrus* genus of which there are at least 22 primary species. Present day pear varieties belong to those from the West (the European or French pears) or those from the East (the Oriental, Chinese or Asian pears). The European pears have evolved from *Pyrus communis* (Linnaeus), whereas of the 13 species native to China significant cultivars have been derived from *P. pyrifolia* (Nakai), *P. ussuriensis* (Maxim), and *P. bretschneideri* (Rehder).<sup>1</sup> Hybrids of *P. pyrifolia* × *P. ussuriensis* are also common. *P. pyrifolia* because of its fire blight tolerance has also been crossed with *P. communis*, the 2 common varieties of which are 'Keiffer' and 'LeConte'. Over time, thousands of varieties have been selected and bred, there being almost 3,500 in China alone.<sup>1</sup>

Among temperate fruits, pear is only surpassed by apple in economic importance and is widely distributed throughout the temperature zones. Commercial plantings are still expanding and production of European pears are a significant export industry in many countries, particularly in the Southern hemisphere. From the multitude of varieties several high quality broadly adapted varieties, Bartlett, Anjou, Comice, Bosc, and Packhams form the bulk of these commercial plantings.

It is only in the last 10 or so years that the Western world has shown interest in Oriental pears. This began with cultivars of *P. pyrifolia* often referred to as the Nashi or Japanese pear, Nashi being the word for pear in Japanese. It is now produced commercially in New Zealand, Australia, and the U.S.A. There is also interest in other species of Chinese pear.

The quince, *Cynodia oblonga* (Miller) though ancient and spread widely has not achieved great economic importance. Botanically the quince can be divided into 3 sub-species; *C. oblonga piriformis* (pear quince), *C. oblonga malformis* (apple quince), and *C. oblonga lusetanian* (Portugal quince). The Chinese quince *Chaenomelia sinensis* is also an edible fruit but not well known in Western culture. Within the above species and sub-species of quince there are a number of popular varieties and some areas of commercial production in Greece and Italy. Generally, however, quince is of little commercial value and there has been little research into its management and physiology. Notwithstanding the above, quince is very important horticulturally as a dwarfing rootstock for pear and has been so used for centuries, however, most quince rootstocks lack the adaptability generally associated with pear and are more prone to environmental stress.

Pear is well adapted to many of the environmental stresses experienced in its native range. The wide geographical range of commercial cultivation is evidence that species of pear evolving in nature or varieties of pear developed by breeding are adapted to a wide range of climatic and edaphic conditions. Nevertheless, the productivity of pear in all regions is limited by one or more often, several environmental stresses. An understanding of the environmental factors such as irradiance, temperature, and water on physiology can improve yield and fruit quality in current areas of production and may facilitate the further expansion of pear to new geographical regions. There is ample justification for further research in the area of stress physiology, because despite the economic importance of pear surprisingly little information concerning physiology appears in the literature.

## II. IRRADIANCE

### A. PHOTOSYNTHESIS

There have been very few experiments dealing with photosynthetic characteristics of *Pyrus* leaves; virtually no experiments have been performed for whole tree canopies. The light saturation curve has been estimated from intact leaves of *P. communis* (cv. Bartlett) in a laboratory experiment under varying light intensities.<sup>2</sup> The light saturation curve was hyperbolic with a light saturated net CO<sub>2</sub> assimilation (A) occurring at a photosynthetic photon flux (PPF) of approximately 1100  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . The light saturation curve, however, varies between pear species and varieties.<sup>3</sup> Measurements were made on detached leaves of *P. serotina* (cvs. Chojuro, Suishu, and Doitsu), *P. communis* (cv. Bartlett), and *P. betulaefolia*. All differed in A response to PPF. For example *P. communis* (cv. Bartlett) increased to near maximum  $A = 19.0 \mu\text{mol m}^{-2}\text{s}^{-1}$  at  $\text{PPF} = 400 \mu\text{mol m}^{-2}\text{s}^{-1}$  whereas *P. serotina* (cv. Suishu) increased slowly to  $A = 11.7 \mu\text{mol m}^{-2}\text{s}^{-1}$  at  $\text{PPF} = 1200 \mu\text{mol m}^{-2}\text{s}^{-1}$ . Other workers have measured variation in response of photosynthesis to light between hybrids of *P. pyrifolia*,<sup>4</sup> varieties of *P. communis*,<sup>5</sup> and pears of different derivation.<sup>6</sup>

Under orchard conditions maximum photosynthesis ( $A = 18.9 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) of attached *P. communis* (cv. Bartlett) leaves occurred at 0830 hr with slow decline for the remainder of the day.<sup>2</sup> Light saturation ( $\text{PPF} = 830 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) was slightly below that measured in the laboratory ( $\text{PPF} = 1100 \mu\text{mol m}^{-2}\text{s}^{-1}$ ). A similar decline in photosynthesis after the morning has been measured in apples.<sup>7</sup> Leaf water potentials, however, were much more negative at dawn ( $-1.2 \text{ MPa}$ )<sup>2</sup> than the  $-0.46 \text{ MPa}$  reported at dawn at the same location for regulated deficit irrigated trees receiving 25% of normal irrigation.<sup>8</sup>

When leaf gas exchange characteristics were measured on 11 species of field-grown fruit crops, *P. communis* cv. Flordahome had an intermediate A rate relative to the other species and similar to apple.<sup>9</sup> Net CO<sub>2</sub> assimilation was  $11.8 \mu\text{mol m}^{-2}\text{s}^{-1}$  at a PPF of  $2049 \mu\text{mol m}^{-2}\text{s}^{-1}$ , an air and leaf temperature of 30.0 and 29.7°C, respectively, and a vapor pressure deficit of 3.5 kPa. Transpiration rate (E) was  $5.7 \text{ mmol m}^{-2}\text{s}^{-1}$ .

The single leaves of these experiments represent only a minute portion of the entire canopy and photosynthesis within the tree is highly complex. While it has been estimated that only 15 to 20% of the trees canopy may be light saturated,<sup>10</sup> the influence of alternating sunflecks, leaf orientation, a possible increase in apparent quantum yield of shade grown leaves and other dynamic factors must be considered in an assessment of whole tree photosynthesis.

### B. SHADING

The adverse effect of shading on fruit size and quality of pear has been demonstrated. Individual branches of 35-year-old 'Bartlett' pears were covered with shade cloth to give 30, 50, 65, and 82.5% shade.<sup>11</sup> Fruit under all shade treatments at harvest were smaller and of lower quality than non-shade

cloth-covered fruit. Size, total, and soluble solids were inversely related to shade levels in a linear manner and firmness was proportional to shade level. Shade also reduced specific leaf weight in a curvilinear manner with the biggest reduction (12.5%) between 0 and 30% shade with little further response past 50%. Shade-induced differences in fruit characteristics may have been largely due to differences in maturity. Although fruit may often ripen earlier in the top of the tree, the apparent influence of light on such responses could be influenced by positional effects within the tree, fruit maturing earlier as distance from tree base increases.<sup>12</sup> Shading also decreased specific leaf weight on young *P. pyrifolia* trees however dry matter production only decreased relative to a control treatment (full sun) when radiation on the shaded treatment decreased by 30 to 40% of the control treatment.<sup>13</sup>

Within well-trained pear trees shading is mainly intermittent and cloud and wind may also result in fluctuating irradiance. Net CO<sub>2</sub> assimilation rate of pear leaves exposed for 80 seconds to 100, 66, 33, and 10% full sun (100% PPF =  $2049 \pm 1.48 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) declined from 12.2 to 7.3 at 33% then to  $1.8 \mu\text{mol m}^{-2}\text{s}^{-1}$  at 10%.<sup>14</sup> Recovery was rapid and short term shading did not affect photosynthetic capacity. Transpiration rate declined from 5.9 to  $4.8 \text{ mmol m}^{-2}\text{s}^{-1}$  between 100 and 10% full sun while stomatal conductance ( $g_s$ ) was not affected by temporary shade ( $227$  and  $231 \text{ mmol m}^{-2}\text{s}^{-1}$  at 100 and 10% full sun, respectively). Water use efficiency (A/E) was thus low at 10% full sun. Pear leaves can therefore be considered as non-sun tracking having stomatal apertures independent of short term changes in irradiance.<sup>15</sup> The above lack of stomatal response to intermittent shade was consistent with slow changes in  $g_s$  measured by Yamamoto et al.<sup>16</sup> as light levels rose and fell, however, in this experiment stomatal movement was more sensitive to light when leaves reached full size than at an earlier or later stage of growth.

### C. LIGHT AND FRUITING

The importance of maintaining an open canopy to intercept maximum sunlight has been demonstrated for pear trees;<sup>17,18</sup> photosynthetic activity was 15 to 33% higher on dwarf trees on quince rootstock due to better light interception than on larger trees.<sup>18</sup> However, in Italy, mechanical pruning of 'Abbe Fetel' and Passe Crassane pear trees over a five-year period did not reduce yield despite the development of a dense crown which resulted in poor light interception.<sup>19</sup> Nevertheless, yield could not be maintained on ultra-high density pear ( $4 \times 0.5 \text{ m}$ ) presumably due to poor light penetration;<sup>20</sup> fruit set only at the crown and though fruit set was less at this spacing than at a wider spacing, fruit size was smaller.

Timing of adequate light penetration into the canopy is also important. Pears typically fruit on spurs and the formation of flower buds depends on light received by the spur leaves. The irradiance level 50 to 70 days from full bloom is generally considered critical for successful bud initiation. The level of irradiance required to promote successful bud initiation is not known for pear although 30% of full sun has been suggested for apple.<sup>10</sup> Maximum shoot growth of pear in a high density planting has occurred 40 to 60 days from full bloom<sup>21</sup> and the control of shoot growth at this time is important for fruit set and improved light penetration. For example a reduction in vegetative growth was probably responsible for a greater set response to regulated deficit irrigation (RDI) at  $0.5 \times 4 \text{ m}$  compared to  $1 \times 4 \text{ m}$  tree spacing.<sup>20</sup> RDI, an irrigation technique meant to limit shoot growth early in the season is reviewed in Section IV.A.

## III. TEMPERATURE

### A. HIGH TEMPERATURE

#### 1. Summer Temperatures

High summer temperatures generally do not restrict the geographical range of pear and quince, however, they can have a negative impact on vegetative and reproductive growth.

Under conditions of high irradiance the temperature of plant tissue can be elevated considerably over air temperature. This is particularly true with darkly colored and or bulky tissue with low rates of transpiration. A threshold for the coagulation of protein for pear fruit has been reported to be 65°C, compared to 63°C for apple, and 50°C for peach.<sup>22</sup> Although leaf temperatures are seldom more than 5°C higher than air temperature, bark temperatures as high as 56°C have been recorded at air temperatures of 45.6°C.<sup>23</sup> Such air temperatures can occur in early spring in hot climates before the tree canopy is fully developed. Branch and trunk tissue may die and productivity may decline though the tree generally survives. Trunks can be painted white to minimize damage due to high or fluctuating temperature.

Though it is generally accepted that pears thrive in relatively hot climates, high temperatures can slow fruit growth, and temperatures above 24°C may delay ripening on some varieties.<sup>24</sup> Such varieties could only be suited to cooler climates. Nevertheless, greater growth and earlier ripening of 'Bartlett' pears have been reported where overhead sprinklers were used to hold air temperatures below 32°C.<sup>25</sup> After 50 minutes of continuous sprinkling air temperature was lowered 3.5 to 4.5°C, leaf temperature 7°C and internal fruit temperature 7 to 7.5°C. The fruit matured 7 days early and were 15% larger at harvest than a control treatment, though all treatments received ample water and were harvested at the same time. Under Australian conditions, pear fruit expand predominantly at night and high daytime temperatures would appear to delay the onset of the diurnal growth cycle.<sup>26</sup> Overhead sprinkling for temperature control has not been used commercially on pear probably due to high costs and management problems; wet leaves increase the risk of fungal disease while wet soil interferes with vital spray operations. Also, treatments which simply advance ripening are not of great advantage to the canning fruit industry. An optimum temperature for fruit development may exist for pear, however, even within varieties there is probably a wide range of temperatures over which pears will develop and mature well. Nevertheless, there are localities around the world renowned for their pears (e.g., the Goulburn Valley of Northern Victoria, Australia and Medford, Oregon). Such areas generally have warm to hot summer daytime temperatures. Localities with mean summer temperatures below 18°C are not suitable for Bartlett pear, and the firmest and best flavored pears are grown in areas much too hot for good apple flavor.<sup>24</sup>

Fruit development periods of pears and other fruits from 7 different localities in North America have been evaluated over a 9-year period.<sup>27</sup> Heat units were calculated as day degrees by averaging the maximum and minimum temperatures for each day and subtracting 10°C then summing these values over the period between blossoming and harvest. At the temperature extremes of this comparison were Kentville (772 ± 31 heat unit) in Nova Scotia and Vineland, Ontario (1150 ± 34 heat unit) in Canada. However, time to maturity was approximately the same 115.9 ± 1.34 and 117.2 ± 1.70 days, respectively, though both blossoming and harvest were 10 days earlier in the warmer regions. The pears from Nova Scotia were of good quality but required heavier thinning to produce fruit of acceptable size. Lower heat units apparently slowed growth but not maturity. Over 6 of the sites, fruit development period for 'Bartlett' pear ranged from 106.5 ± 2.00 to 117.2 ± 1.70 days. 'Bartlett' pears at Tatura in the forementioned Goulburn Valley of Southern Australia also have a similar fruit development period ranging from 110 to 120 days with heat units approximating 930.

## 2. Winter Dormancy Temperatures

The major factor limiting the expansion of pear production to warm regions is exposure to insufficient chilling temperature during the winter.

Deciduous fruit trees, including pear, in temperate climates enter a period of rest or dormancy in autumn and remain dormant. Rest is broken either at the accumulation of sufficient cold, by a lapse of time or both. Where dormancy is ended before the accumulation of sufficient cold fruit bud opening is delayed and leaf and flower buds open asynchronously, followed by flower abscission and poor fruit set.

In spite of research over many years the concept of "rest" in fruit crops is still far from being fully understood. The general approach to measuring accumulated cold is either to record hours of cold above 0°C and below some base temperature (e.g., 7.5 or 10°C) or by recording chilling units where temperature around 6°C are weighted higher.<sup>29</sup> Though the latter approach is widely favored, high correlations were obtained by both methods when 48 pear varieties and species were tested for chill requirement in Southern England.<sup>30</sup> Varieties were grouped into 5 dormancy classes with hours of accumulated cold (between 0 and 10°C) ranging from 850 to 2600 hours. The species *P. betulaefolia*, *P. calleryana*, and *P. serrulata* were ranked at the bottom of the 850 hour class, whereas *P. communis* cv. *Fleurissant Tard* required 3000 hours to break dormancy. In Table 1, abstracted from Speigel Roy and Alston data,<sup>30</sup> seven common varieties are grouped into their allotted dormancy class together with the mean accumulated hours of chilling recorded for each class.

The site specificity of a given chill hour accumulation can be illustrated by referring to conditions in the Goulburn Valley of Victoria, Australia. *P. communis* cvs. William Bon Chretien (syn. Bartlett) and Packham Triumph are the two major varieties. From the data in Table 1, only in the coldest winter would 'Packham Triumph' receive sufficient chilling whereas 'William Bon Chretien' would not be considered suitable for the area. For example, in 1990 both spur and lateral buds of 'Packham Triumph' growing in the Goulburn Valley, broke rest at approximately 60 to 70 days prior to full bloom after

Table 1 Chilling requirements in Southern England of some common pear varieties

| Class | Variety                              | Chill units | Hours between 0–10°C | Hours below 7.2°C |
|-------|--------------------------------------|-------------|----------------------|-------------------|
| 1     | Josephine                            | 891         | 857                  | 617               |
| 2     | Doyenne du Comise Conference         | 1422        | 1412                 | 1159              |
| 3     | Packham Triumph                      | 1808        | 1912                 | 1624              |
|       | Buerre Hardy                         |             |                      |                   |
|       | Old Home                             |             |                      |                   |
|       | William Bon Chretien (syn. Bartlett) |             |                      |                   |

From Spiegel-Roy, P. and Alston, F. H., *J. Hort. Sci.*, 54, 115, 1979. With permission.

the accumulation of 464 hours below 7°C. This compared with 1159 hours below 7.2°C in Table 1. In addition, flower and leaf buds may vary greatly in chilling requirements. On 'William Bon Chretien' large differences seemed to exist between spur and lateral buds. Spur buds broke rest after 464 hours below 7°C at 70 to 80 days prior to full bloom, however, lateral buds required 623 hours and did not break rest till 40 to 50 days prior to full bloom indicating that reproductive and vegetative chilling requirements are quite different for 'William Bon Chretien'. The chilling requirements for the same variety in Southern England (Table 1) was 1624 hours below 7.2°C, while in Utah (USA) a statistical process of analyzing temperature and blossom dates over several years estimated 1100 to 1200 chill units for 'Bartlett' pear.<sup>31</sup>

The effect of post dormant temperatures on time of blossoming is also variety dependent. Spiegel-Roy and Alston<sup>30</sup> determined that varieties with a high chill requirement also had a high post dormant heat requirement (number of days at 15°C required for 50% bud break). Accumulated growing degree hours above 4.5°C (GDH°C) from end of dormancy to 80% full bloom were also recorded. Though for early and late flowering varieties GDH°C correlated well with chill and post dormant heat requirement, the correlation was poor for intermediate varieties. GDH°C from the completion of rest to full bloom has been estimated by a statistical method and validated in the field in Utah, USA for 'Bartlett' at 5644 GDH°C.<sup>31</sup>

Post dormant temperatures have been manipulated to delay blossoming by evaporative cooling<sup>32</sup> or to advance blossoming by plastic enclosures.<sup>33</sup> A potential may also exist to manipulate bloom date with chemical control of the cyanide-sensitive respiration pathway. Differences in chilling requirements and post dormant GDH°C between *Pyrus* species have been related to the mechanism controlling respiration of dormant buds. Respiration of *P. calleryana* buds, which blossom earlier, were more resistant to cyanide inhibition than buds of *P. communis*.<sup>34</sup> However, chemical control has not been investigated and the nature of bud respiration is not yet fully understood.

The concept of dormancy in deciduous fruit trees and its relationship to required cold is a highly pertinent topic given the forecast of imminent global warming. Improved methods of estimating effective chilling and post dormant requirements seem necessary. Optimum temperatures for chilling may vary between variety. Moreover, in the more temperate fruit growing areas where daytime winter temperatures rise to 10 to 15°C and fall to near or below 0°C at night the importance of day temperature outside the recognized chilling range needs to be understood. The latter seems highly important for it is in these regions that global warming will have the greatest impact on the production of pear and other temperate fruit crops.

## B. LOW TEMPERATURES

### 1. Hardiness

As with other fruit crops, cold temperatures limit pear production to the temperate latitude. However, even within these zones, periodic freezes cause massive losses to the fruit industry. Larsen<sup>35</sup> in his introduction to a *Symposium on Cold Hardiness, Dormancy and Freeze Protection of Fruit Crops* claimed that "the economic losses from freeze damage to America's fruit industry exceeds the loss from insect, disease, rodents and weeds combined." Due to limited cold hardiness *P. communis* in North America is exclusively limited to the middle regions. Yet *P. ussuriensis* which is considered as being very cold hardy can exist in Siberian winters where temperatures are maintained at –50°C over long

periods. The same species, however, lacked hardiness under much milder conditions in Oregon<sup>36</sup> indicative of the complex relationship of cold hardiness in the genus *Pyrus*.

Devoid of extraneous ice nucleators, water can be supercooled to  $-38^{\circ}\text{C}$  without freezing. Pear along with other hardy fruits contain supercooled water in vegetative and reproductive tissue. Cold hardiness to  $-38^{\circ}\text{C}$  was not reached in laboratory tests on a wide range of *Pyrus* species.<sup>37</sup> In this experiment the most hardy species was *P. caucasica*; visual stem damage being observed at  $-33^{\circ}\text{C}$  and measured by electrical conductivity damage occurred at  $-37^{\circ}\text{C}$ . Stem tissue of *P. ussuriensis*, however, was no more hardy than *P. communis*. This was not surprising given that the tested twigs were sampled from a collection of pear species in Oregon far from the Siberian habitat of *P. ussuriensis*. *P. ussuriensis* during dormancy has probably acclimated to supercool to close to  $-40^{\circ}\text{C}$  in its native habitat. Its survival depends on low chilling requirement as this can only be achieved during a short spring season when temperatures rise above  $0^{\circ}\text{C}$  (i.e., temperatures below  $0^{\circ}\text{C}$  are not thought to contribute to chilling units). In the warmer regions of Oregon dormancy may be broken for varieties with low to moderate chilling requirements in late winter and be damaged during late winter or early spring freezes at temperatures no lower than  $-9$  to  $10^{\circ}\text{C}$ .<sup>36</sup>

Similarly, freezes in late autumn before the tree is fully acclimated will result in damage. Though comprehensively reviewed, the process of acclimation is poorly understood.<sup>38</sup> Attempts to explain cold hardiness have generally considered the plasma membrane as the site of critical freezing injury. However, altered cell wall properties particularly changes in extra-cellular polysaccharides and deposition of callose in the cell wall have been associated with cold acclimation at  $2^{\circ}\text{C}$  of suspension cultured pear.<sup>39</sup>

Any condition which prolongs growth in late autumn such as high N levels, continued irrigation, vigorous rootstock, etc. will delay cold acclimation. Both trunk and lower branches are most susceptible to damage at these times.<sup>23</sup>

## 2. Blossoming Temperatures

As anthesis approaches buds of pear are at risk once temperatures drop to below  $0^{\circ}\text{C}$ . Damage can range from slight to drastically reduced fruit set and loss of the entire crop. Fruit can also be malformed, e.g., neck thickening or fruit elongation. As with wood damage at harsher temperatures, blossom damage rises when abnormally late winter warmth stimulates bud activity after chilling requirements are met.

The principal methods of frost protection, heaters, overhead irrigation, and wind machines, may increase average orchard temperatures by 1 to  $2^{\circ}\text{C}$ . The former is more reliable but expensive to operate. For instance, from estimates made by Gerber,<sup>40</sup> depending on conditions and placement, a heating system to be effective would need to produce 1.5 to 5 thousand kilowatts per hour per hectare to raise temperatures by 2 to  $3^{\circ}\text{C}$ . This could require up to 100 heaters per hectare within the orchard and individual heaters per tree on the orchard periphery, each burning up to 4.5 l of fuel per hour.

Critical temperatures have been defined as the lowest temperature that can be endured by buds, flowers, or fruit for 30 minutes without injury. Hardiness decreases with bud development. For example, critical temperatures for pear taken from the National Weather Service in the USA<sup>41</sup> in 1970 varied from  $-3.9^{\circ}\text{C}$  as the blossom buds become exposed following scale separation to  $-2.2^{\circ}\text{C}$  at full bloom and  $-1.1^{\circ}\text{C}$  post bloom. Values were given for intermediate stages<sup>42</sup> but varied between locality.<sup>43-46</sup> Critical temperature are extremely variable at bud break though they became more constant at and after full bloom.<sup>45</sup> Also, the stage of bud development will vary within an orchard and within a tree, the exact stage is hard to define. Differences in critical temperature also occur between localities,<sup>41,45,46</sup> probably due to preconditioning of climate and microclimate. Another problem exists in relating tissue temperature to that of the surrounding air, given temperature variation within the tree associated with height and exposure.

The duration of and rate of freezing are important determinants of injury to fruit buds. For 'Bartlett' pear, freeze damage (i.e., internal tissue browning) for all stages of blossom development increased with up to 30 minutes exposure to critical temperature, but except for the small fruit stage, little further damage was measured beyond 60 minutes. Damage was greater at a rate of  $-2.5^{\circ}\text{C hr}^{-1}$  compared to  $-1.9^{\circ}\text{C hr}^{-1}$ .<sup>42</sup> Evaporative cooling via overhead irrigation has also been used to delay bud break of pear by 14 days, however fruit size was decreased and maturity delayed.<sup>32</sup>

Lindow<sup>47,48</sup> reduced frost damage on 'Bartlett' pear from  $-3^{\circ}\text{C}$  frost by spraying antagonistic bacteria to eliminate ice nucleation active bacteria (INA) that prevent supercooling beyond  $-2^{\circ}\text{C}$ .<sup>47,48</sup> Results from further experiments indicated that although the absence of INA bacteria decreased frost injury of excised fruitlets, damage was not reduced on orchard trees.<sup>49-51</sup> Similarly, excised flower buds free from

INA bacteria supercooled to  $-5^{\circ}\text{C}$ , a temperature 2 to  $3^{\circ}\text{C}$  lower than attached buds. The difference between intact and excised flower buds and fruitlets has been attributed to the overriding effect of ice formation initiated within the woody tissue spreading to the developing flowers and fruit.<sup>52</sup> An exception was a radiation frost when the developing flowers and buds cooled faster than adjacent woody tissue because of direct radiation to the sky.<sup>52</sup> Ice formation would be initiated in the blossom buds first, which could be prevented in the absence of INA bacteria. Proebsting and Gross<sup>49</sup> suggested that this occurred in Lindow's experiments during a mild radiation frost of  $-3^{\circ}\text{C}$ . Similar frosts were not observed over 6 years in their experiment.<sup>49</sup>

Blossom damage will drastically reduce fruit set. High and low temperatures in the 10 days post bloom have also reduced fruit set of 'd'Anjou'<sup>53</sup> and 'Tsakoniki'<sup>54</sup> pear. During this period increased yield was positively related to temperature less than  $19^{\circ}\text{C}$ <sup>53</sup> and rapid pollen tube growth was recorded at  $20^{\circ}\text{C}$ .<sup>54</sup> However, at lower temperatures the pollination period is lengthened<sup>54</sup> and under favorable circumstances (low humidity) pollination could proceed at temperatures as low as  $10^{\circ}\text{C}$ .<sup>55</sup> Bee activity declines below  $13^{\circ}\text{C}$  and could be the limiting factor influencing set at low temperatures.<sup>55</sup>

### 3. Species Differences

As previously mentioned pear species are native to a wide range of latitudes from the sub Arctic to near tropical latitude. Thus it is not surprising that wide ranges of temperature tolerances exist across species.<sup>56</sup> *P. calleryana*, *P. pashia*, and *P. kawakami* are all classed as being highly tolerant to heat and susceptible to cold. *P. calleryana* is a popular vigorous stock in warm areas, while *P. pashia*, besides being a common stock in the Indian sub-continent has cultivars suited to hot climates. On the other hand *P. ussuriensis* is tolerant of winter cold but not of summer heat. Fortunately *P. communis* (common pear) is heat tolerant and moderately cold tolerant as is *P. betulaeifolia*, a commonly used stock.

The prime economic importance of these different temperature traits relates to matching rootstock species to climatic zones to facilitate production of popular commercial varieties. The variation in intraspecific cold tolerance provide a rich gene pool for increasing temperature tolerance of both rootstock and scions. For example, hybrids of *P. ussuriensis*  $\times$  *P. communis* have been bred for greater cold hardiness,<sup>57</sup> however, their use has been limited to the northern plains of America and Russia due to poor fruit quality.

Wide variation in intraspecific and interspecific chilling requirements also exists for germination of seed.<sup>58</sup> Trees grown from these seeds with a high chill requirement would also have a longer chilling requirement to break rest according to the general statement of Vegis.<sup>59</sup>

Different rootstock species may also influence the level of cold hardness of the scion. In Oregon, pear trees on *P. serotina* and *P. ussuriensis* stocks were damaged more in a cold winter than trees on *P. communis*, though no damage occurred below the union on all three stocks.<sup>60</sup> Observations of differential hardiness associated with rootstock have been observed elsewhere,<sup>61</sup> and is partly a consequence of the growth characteristic induced by different stocks (e.g., delayed defoliation reducing acclimation).

Nevertheless, there is good evidence for winter chilling characteristics being translocated across the union.<sup>57</sup> For example, 'Bartlett'/*P. calleryana* had lower chilling requirement to break rest than 'Bartlett'/*P. communis*.<sup>62</sup> Westwood<sup>61</sup> discussed the possible movement of hardiness promoters and/or inhibitors across the graft union. Both the wide range of graft compatibility and the wide variation in cold hardiness led Westwood to conclude that *Pyrus* species could be used to test any general theory "of the origins, movement and fate of hardiness promoters and inhibitors".<sup>58</sup> Unfortunately, little progress has been made in this area.

### C. TEMPERATURE EFFECTS ON QUINCE

As with other environmental factors there is little documented evidence on the effect of temperature on quince. As a rootstock for pear it is generally considered to have a low tolerance for cold and heat, however hardier strains such as the Causacian Quince and Fonteray Quince are graded as being moderately tolerant to cold.<sup>56</sup>

In spite of the above, quince generally grows well over a range of cool to hot climates. The buds have a low chilling requirement and flower early and evenly where winters are warm. Conversely, where winters are cold and long, flowering is delayed and only occurs on terminal buds after considerable growth has been made. Reduction in yield by frost is thus rare.<sup>63</sup>

## IV. WATER STRESS

Water stress is a subjective term as it is difficult to quantify exactly when a plant water deficit (which terrestrial plants experience on a daily basis) may be sufficiently great to qualify as plant moisture stress. A slight water deficit is normal in most plants, and for pear there is no evidence that such deficits suppress short- or long-term productivity. Moreover, moderate deficits at specific times have been associated with increased yield.<sup>20,64-66</sup>

Pears are grown in a range of climates from cool humid areas where irrigation is either absent or supplementary, to arid zones where commercial yield is entirely dependent on irrigation. In humid areas frequent irrigation has often resulted in variable yield responses. This could relate to variations in environmental conditions (vapor pressure deficit and/or soil) influencing plant water status as in both humid and arid areas the water status at a specific phase of seasonal growth can be more important than actual deficit level. For instance, water deficit prior to harvest are likely to decrease fruit size and yield, whereas a similar deficit early in the season may reduce vegetative growth without decreasing yield or ultimate fruit size.

### A. REGULATED DEFICIT IRRIGATION

RDI was developed in Australia in 1978 at Tatura (36° 26'S, 145° 16'E) on a medium to heavy duplex soil type to control vegetative growth in high density peach trees,<sup>64</sup> and was then extended to high density 'William Bon Chretien' (syn. 'Bartlett') pear trees.<sup>20,65,66</sup>

RDI involves limiting the supply of water to fruit trees during the period of rapid shoot growth, which for both peach and pear is from early to mid season while fruit growth is slow. In experiments at Tatura, Australia early irrigation was withheld to dry the soil after winter and spring rain. Cumulative net evaporation (class A pan evaporation (E) less rainfall) from full bloom was used to determine irrigation commencement (a cumulative deficit of 125 to 150 mm). This resulted in low soil matric potentials in the area of maximum root concentration in the tree line of  $-1.25$  to  $-2.61$  MPa at 1.0 m spacing and  $-1.80$  to  $-1.94$  at 0.5 m spacing (Table 2).<sup>67</sup>

When irrigation commenced, two RDI treatments based on replacing 20 and 40% of E were compared with a control treatment (100% E).

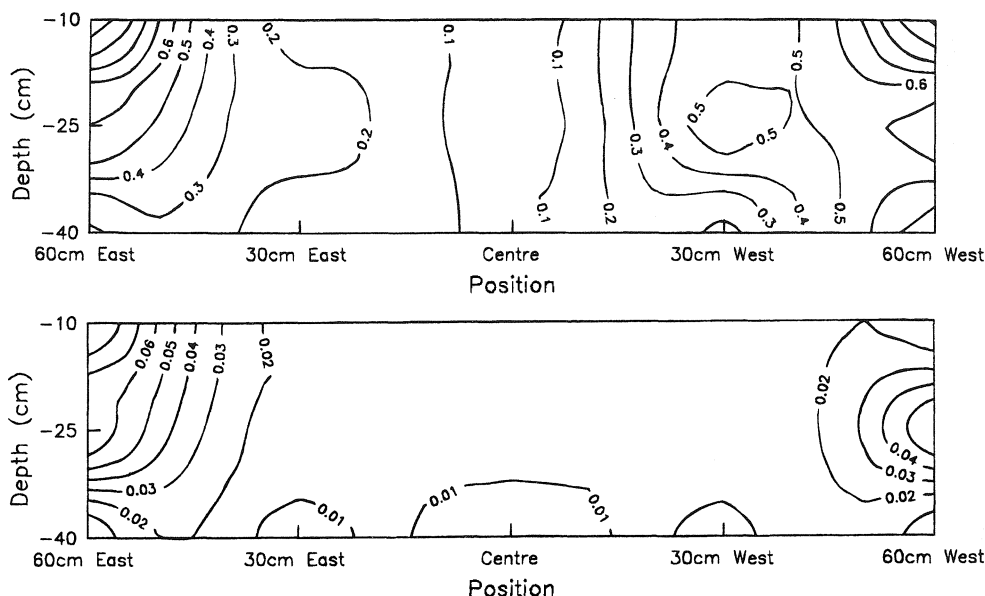
The influence of withholding irrigation followed by irrigation at low levels using trickle irrigation had two effects on soil moisture. First, as trees were irrigated at 1 or 2 day intervals the wetted volume of soils under the 20% treatment was reduced relative to the control (Figure 1)<sup>67</sup> and second, within this wetted volume soil matric potential (SMP) fluctuated between  $-0.4$  and  $-0.1$  MPa before and after irrigation. The control treatment wet a much larger volume of soil at a SMP between  $-0.04$  and  $-0.01$  MPa.

'Bartlett' on vigorous *P. callyerana* D6 stock in Australia required a considerable level of deficit irrigation at 40 days from full bloom to control shoot growth when the potential for rapid shoot growth was at its highest. Despite high soil moisture deficits, leaf water potentials ( $\Psi_l$ ) did not approach those measured under drought conditions in Washington<sup>68</sup> (see Section IV.F).

RDI had major effects on shoot growth, fruit size, and number and these results are included in the following discussion on the effects of water deficit on these components of tree growth.

**Table 2 Soil matric potential (MPa) at the end of the withholding irrigation period from a grid of gypsum blocks located midway between two trees (i.e., Center) and at 30 and 60 cm each side of the tree line (i.e., East and West)**

| Tree Spacing (m) | Depth (cm) | East  |       | Center | West  |       |
|------------------|------------|-------|-------|--------|-------|-------|
|                  |            | 60 cm | 30 cm |        | 30 cm | 60 cm |
| 0.5              | 10         | -1.35 | -1.72 | -1.80  | -0.58 | -1.16 |
|                  | 25         | -1.35 | -1.20 | -1.94  | -0.47 | -0.40 |
|                  | 40         | -0.35 | -0.37 | -0.91  | -0.41 | -0.50 |
| 1.0              | 10         | -0.61 | -0.51 | -1.25  | -1.35 | -0.57 |
|                  | 25         | -0.81 | -0.84 | -2.61  | -2.08 | -0.63 |
|                  | 40         | -0.51 | -0.48 | -0.61  | -0.54 | -0.48 |



**Figure 1** Contour diagram across the tree line of soil matric potential (SMP) distribution after irrigation joining points of equal SMP (MPa) from a gypsum block grid under trees irrigated at (top) 20 and (bottom) 80% replacement of evaporation during the RDI period.<sup>67</sup>

## B. VEGETATIVE GROWTH

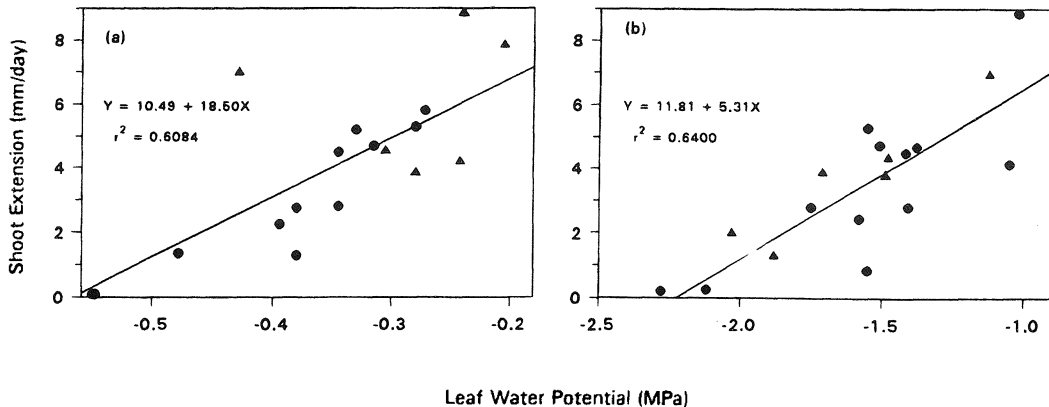
In general, shoot expansion of most cropping pears is at its maximum 40 to 60 days from full bloom and then declines as the fruit begin rapid growth. Cell expansion and cell division in the growing shoot and developing leaves are both linked to the essential components of growth; cell hydration and cell turgor. So within these distinct flush periods shoot growth and leaf expansion can be reduced by a water deficit. Given ample water availability and temperatures, terminal shoots can again grow strongly after harvest. The mechanism behind these distinct periods of growth is not fully understood. Presumably it is carbohydrate/hormone driven.

On young trees vegetative growth lays the foundation for future cropping, while on mature trees a large healthy canopy allows for maximum radiation to sustain maximum photosynthesis. The majority of pear varieties fruit on spurs and a large percentage of the current seasons growth is removed at pruning. Moreover, a dense canopy will reduce the irradiation level within the tree interior and when shoot growth is less vigorous more photoassimilate will be available for fruit growth.<sup>8</sup>

The threshold  $\Psi_1$  at which stomata closed was greater on terminal than on basal pear leaves.<sup>16</sup> For apples, it has been shown that young leaves due to a lower solute content lose turgor before mature leaves at a given  $\Psi_1$  thus slowing growth.<sup>69</sup> Osmoregulation, which is an adaptive mechanism to maintain turgor necessary for growth and stomatal opening for photosynthesis at a lower  $\Psi_1$  than would otherwise be possible, is more prevalent in mature rather than young leaves. For pear, both osmoregulation<sup>70</sup> and maintenance of photosynthesis at low  $\Psi_1$  has been shown to occur. Due to the greater sensitivity of young leaves to stress, significant reductions in cell elongation can occur at relatively high  $\Psi_1$  before photosynthesis in mature leaves is reduced. Goode<sup>71</sup> quotes numerous cases of shoot growth reductions on deciduous fruit trees at low moisture deficits. In RDI experiments, shoot extension of pear was linearly related to dawn and midday  $\Psi_1$  and growth was depressed at relatively high  $\Psi_1$  (Figure 2).<sup>8</sup>

Similarly shoot extension of *P. communis* (cv. Anjou) was less on a treatment receiving 100% replacement of E fortnightly (normal irrigation) compared with a wet treatment receiving 125% of E weekly.<sup>72</sup> In this experiment a comparatively small soil water deficit ( $-0.035$  and  $-0.012$  MPa for the normal and wet treatments, respectively) was measured.

Thus, pear vegetative growth and the structure of the tree framework can be manipulated by variations in soil moisture. In arid areas water can be applied by irrigation to achieve a desirable balance of vegetative and reproductive growth, although RDI is not successful in regions with abundant rainfall during the growing season.



**Figure 2** Influence of leaf water potential ( $\Psi_l$ ) on shoot growth of 'Bartlett' pear trees at dawn (a) and midday (b). ( $\Delta$ )  $\Psi_l$  on 11 Nov. cf. shoot growth between 7 and 15 Nov. ( $\bullet$ )  $\Psi_l$  on 20 Nov. cf. shoot growth between 14 and 21 Nov. From Chalmers, D. J., Burge, G., Jerie, P. H. and Mitchell, P. D., *J. Amer. Soc. Hort. Sci.*, 111, 904, 1986. With permission.

### C. FRUIT GROWTH

There are three important concepts concerning the relationship of water deficits to fruit growth. First, fruit growth rate can decline at a relatively low moisture deficit.<sup>72</sup> Second, increasing soil drying may not further decrease fruit growth rate.<sup>72</sup> Third, a relatively large increase in growth rate is possible following the relief of water deficits.<sup>64-66</sup>

In a field experiment, Brun et al.<sup>72</sup> measured considerable loss in pear fruit size over 8 days on a dry treatment, however, in the next 13 days without irrigation growth rate did not decline further. In the first 8 days,  $\Psi_l$  at midday fell from  $-0.9$  to  $-1.4$  MPa ( $-0.9$  to  $-1.0$  MPa, respectively, on a wet control) and in the next 13 days continued to fall to  $-1.8$  MPa. Leaf conductance of shaded leaves followed a similar pattern falling from  $67$  to  $36$   $\text{mmol m}^{-2}\text{s}^{-1}$  ( $76$  to  $54$   $\text{mmol m}^{-2}\text{s}^{-1}$  on the wet treatment) and then fell to  $18$   $\text{mmol m}^{-2}\text{s}^{-1}$ . These measurements were taken in mid season, however, similar fruit growth responses have been measured early in the season under RDI in 1984,<sup>65</sup> and in other years (unpublished). Likewise, Richards et al.<sup>73</sup> measured fruit diameter of *P. pyrifolia* (cv. Nijissike) fruit using a Linear Variable Differential Transformer (LVDT) and found that a water deficit lengthened the period of daily shrinkage and rehydration, and thus delayed the commencement of growth till late in the evening. This pattern was established early in the season (SMP of  $-0.1$  MPa), and there was no marked tendency for the pattern to alter as the soil dried. The above three examples emphasize the importance of duration in addition to the level of water stress in determining total loss in fruit size. They also suggest some level of drought adaptation to water deficits that develop slowly which has been suggested for apples.<sup>74</sup>

Three possible mechanisms of plant adaptation to water deficits have been described by Turner.<sup>75</sup> Each is discussed in relation to pear:

1. The ability of a plant to complete its life cycle before serious soil and plant water deficits develop (i.e., drought avoidance). There is no evidence that pears can avoid water stress by early fruit maturation.
2. The ability of a plant to endure low tissue water potential as a result of a water deficit. Mechanisms in this category include desiccation tolerance and turgor maintenance by osmotic adjustment, increase in cell wall elasticity or decrease in cell size. As mentioned previously there is some evidence that mature leaves can osmotically adjust to maintain photosynthesis. There is also some evidence to support osmotic adjustment in the pear fruit to maintain turgor for maximum growth.<sup>76</sup> In most cases, however, fruit growth is slightly retarded from a water deficit during the slow fruit growth stage. Despite a decline in fruit growth rate during this stage, dry weight continues to accumulate<sup>77</sup> as has been reported in grapefruit<sup>78</sup> and apples.<sup>79</sup> The accumulation of the products of leaf photosynthesis by the fruit may also help to prevent a negative feedback on leaf photosynthesis. When water stress is relieved and  $\Psi_l$  and turgor increase, fruit growth accelerates which is facilitated by the increase in solute concentration that occurred during the water deficit. The increase in turgor allows the fruit to grow during the day whereas normally the fruit would shrink.<sup>76</sup> Such compensatory growth has been

measured in all RDI experiments as stress imposed by RDI is relieved.

3. The ability of a plant to endure water deficits while maintaining a high tissue water potential. The two mechanisms in this category are a reduction in water loss (by stomatal control, loss of leaf area or reduction in absorbed radiation) and/or maintenance of water uptake. Less and smaller leaves throughout the canopy could reduce leaf area and water loss. This would certainly seem to apply to pear in the RDI experiments where in the early stages of fruit growth, canopy growth is gradually reduced. An increase in root depth and density has also been suggested<sup>9</sup> which would help maintain water uptake during water deficits and could also enable root systems to extract more water when stress is relieved.

Adaptations to moderate levels of stress could explain the lack of fruit response to irrigation in humid climates where stress is moderate or intermittent,<sup>80,81</sup> and why in arid areas precisely scheduled irrigation may not dramatically increase yield. However, in the 3 to 4 weeks prior to harvest, the acceleration of fruit growth following improved water status is not sufficient for pear fruit growth to catch up. Indeed growth is so rapid during this stage that minor water deficits can permanently suppress fruit size. For example, similar sized fruit at day 116 from full bloom differed by approximately 15 g at day 144 on a treatment replacing 100% of E fortnightly, relative to a treatment replacing 120% of E weekly. At day 135 midday  $\Psi_l$  of shaded leaves was  $-0.5$  MPa more negative on the 100% treatment and leaf conductance of shaded leaves, which had not previously differed, was  $31.2 \text{ mmol m}^{-2}\text{s}^{-1}$  less.<sup>72</sup>

The timing of irrigation relative to the fruit growth cycle is thus probably more important than precise scheduling according to soil water deficits. In Australia, pear trees are usually irrigated more frequently in the period of high demand 3 to 4 week prior to harvest. Though harvest usually coincides with the hottest weather and a fully grown canopy, growth stage alone could impose a higher rate of water use (i.e., evapotranspiration per mm E) as in peach.<sup>82,83</sup> Chalmers et al.<sup>84</sup> found that transpiration rate of peach leaves correlated with assimilate demand by the fruit. In this regards pears, like peaches, accumulate assimilate and grow rapidly near harvest. A percentage decline in cell expansion during the RDI period has a small impact on final fruit size, relative to a similar percentage loss in fruit growth just prior to harvest.<sup>82</sup>

In general, temporary water deficits in humid areas on medium-to-heavy soil types may have minimal effect on final fruit size and yield of pear, except when deficits occur close to harvest. When grown on shallower, lighter soils a sustained water deficit will substantially decrease yield and tree health. In arid areas irrigation should be aimed at maintaining the maximum potential fruit growth rate, consistent with maintaining the maximum yield and fruit quality. Nevertheless, when tree vigor is high resulting in reduced irradiation within the canopy, less irrigation early in the season may increase yield and fruit size. This would be particularly so in high density planting on medium-to-heavy soil types.

#### D. CROP LOAD

Crop load has a major influence on final fruit size of pear and thinning may be necessary. On 'William Bon Chretien' (syn. 'Bartlett') pear in Australia, however, fruit number at harvest virtually determines canning yield, maximum canning size being restricted to diameters of  $<65$  mm. In the absence of thinning, fruit number at harvest generally relates to bud initiation, bud development, and condition at blossoming and fruit set. Water deficit at these times will affect crop load.<sup>85,86</sup> Water deficits at 70 to 80 days<sup>85</sup> and at 75 to 90 days from full bloom<sup>86</sup> have increased fruit set the following year on apple and pear, respectively, presumable by increasing bud initiation. The major responses to RDI (up to 60 to 70 days from full bloom) have involved increased fruit set<sup>20</sup> and blossom density.<sup>65</sup> By contrast, fruit number on container-grown pear trees was increased by irrigation<sup>87</sup> while moderate levels of water stress ( $\Psi_l$  of  $-1.8$  and  $-2.1$  MPa at midday)<sup>88</sup> during rapid fruit growth (at 70 to 115 days from full bloom), and presumable bud initiation, coincided with decreased fruit set in the following year.<sup>88</sup>

A severe water stress during bloom is generally considered detrimental to fruit set<sup>89</sup> and critical periods prior to and during bloom for pear and other deciduous fruits have been proposed.<sup>90</sup> However, rapid shoot growth can also be antagonistic to fruit set and in humid areas, dry sunny conditions after blossoming could favor fruit set with cool moist conditions favoring shoot growth. In arid areas the necessity to irrigate provides the opportunity to manipulate both fruit set and shoot growth.

Data concerning the effect of climate and management on bud initiation and development is limited. It has been stated that stress may concentrate and localize the movement of carbohydrates and endogenous growth substances favoring flower bud formation whereas high transpirational rates may enable rapid

movement and dispersal of the same growth substance.<sup>91</sup> On young expanding trees the above creates a dilemma. Long-term productivity relates to maintaining a certain level of vegetative growth and minimizing the water deficit. In the short term, however, on mature dense plantings the success of RDI emphasizes the value of moderate levels of stress at critical times.

## E. QUALITY AND DISORDERS

Quality of pears is generally determined by sugar content and storage life, however, other factors such as texture, firmness, flavor and color are important. Soil water availability and climatic factors may influence the above parameters. However, as with other fruits, water may be an indirect cause of loss in quality. For instance, water supply will influence mineral composition and excess water in the vegetative stage limits light penetration.

Goode<sup>92</sup> cites various authors with conflicting data on the effect of water supply on fruit quality. For example, better keeping quality of pear<sup>93,94</sup> has been attributed to irrigation, however, the storage life of 'Bartlett' though not 'Buerre Bosc' was best when grown in dry compared to wet conditions.<sup>95</sup> Similarly, higher sugar contents have been attributed to favorable irrigation regimes<sup>96</sup> and poor flavor to dry conditions,<sup>95</sup> however, the flavor of 'Anjou' pear was improved by a water deficit near harvest.<sup>97</sup> Such conflicting reports probably relate to the poorly understood interactions of plant water status with stages of growth and other environmental variables.

The three common disorders associated with high water status (black-end, cork spot and alfalfa greening) are nutrition-mediated, and are greatly influenced by rootstock and scion. All reflect the balance of Ca and other minerals (e.g., K and N) in the fruit. Alfalfa greening and cork spot were positively correlated with increased irrigation and fruit K and N concentrations but negatively correlated to fruit Ca.<sup>88</sup>

## F. DROUGHT TOLERANCE

Large water deficits can kill pear trees,<sup>98</sup> however, they can also survive extreme levels of water stress. Pear trees (cvs. Bartlett and Anjou) growing in 1.5 m deep fine sandy loam with 8% available water survived a whole season without irrigation (net E = 712 mm).<sup>68</sup> Fruit shrivelled and return bloom was delayed and reduced, as was fruit set. During the drought period,  $\Psi_l$  of shaded leaves fell to a minimum of -4.5 MPa. At the same sight the minimum  $\Psi_l$  of shaded leaves from droughted peach trees which later died was -3.9 MPa. Heavy winter pruning, lighter summer pruning and thinning improved productivity of the trees exposed to severe drought. In another experiment defruited peach trees used 50% of the water of fruited trees in the rapid stage of growth,<sup>84</sup> although similar results have not been reported for pear. When water stress is extreme heavy thinning and summer pruning of pear trees will ensure some level of commercial yield.

The drought tolerance of many pear varieties has been assessed in Russia.<sup>98,99</sup> The leaves of the drought-resistant varieties had a higher water retaining capacity during summer drought, and detached leaves lost water slower than drought susceptible varieties. This would suggest different levels of stomatal control between varieties and could reflect environmental pre-conditioning at their place of origin or genetic variability.

Similarly, the tolerance of rootstocks to dry conditions could relate to such pre-conditioning and/or variability in rooting characteristics. In Oregon, Lombard and Westigard<sup>56</sup> categorized the drought tolerance of pear and quince rootstocks from high to low as follows: *P. betulaefolia*, *P. calleryana* = *P. communis*, *P. ussuriensis* = *P. salicifolia*, *C. oblonga*. In Australia the *P. calleryana* D6 rootstock is recognized as being more drought tolerant than *P. communis*<sup>101</sup> and *P. salicifolia* outperformed *P. communis* in Russia and was claimed to be tolerant of drought, extreme temperature, and saline conditions.<sup>101</sup> Drought tolerance relates in part to genotype and rooting depth but may also be influenced by climate and edaphic pre-conditions.

## G. FLOODING

"Pears grow in wet low land" (from Shi Jing a book written about 1000 B.C. in China).<sup>102</sup> Quince and pear are generally regarded as the most flood-tolerant fruit tree species.<sup>103-107</sup> Mature pear in Oregon flooded from April to August showed minimal damage, however, tree vigor declined after a second flooding two years later.<sup>108</sup> Despite generalization of extreme waterlogging tolerance, differences exist within and between pear and quince.<sup>56,109-112</sup> Observations have separated pear rootstock in order of decreasing tolerance: *P. betulaefolia*, *P. calleryana* = *P. communis*, *P. ussurienses*, *P. pyrifolia*.<sup>56</sup> Clones

of 'Bartlett' and 'Anjou' and crosses within the *P. communis* species were also ranked. Furthermore Province Quince was rated equivalent to *P. betulaefolia* with Quince A less tolerant. Conversely quince stocks have been shown to be poorly tolerant.<sup>112</sup> This could relate to the known incompatibility of quince with pear and associated double stress. Quince may also be less tolerant to *Phytophthora*.

The above observed difference has been confirmed by controlled pot experiments.<sup>109-111</sup> The flood tolerance of container-grown fruit tree species based on growth, leaf gas exchange, and survival was ranked as follows: *P. betulaefolia* > *P. calleryana* = *C. oblonga* > *P. communis* cv. Bartlett > *P. communis* cv. OH × F97 = *P. pyrifolia* = *P. ussurienses* = *Malus domestica* > *Prunus persica*. *P. betulaefolia* was placed among the most flood tolerant mesophytic tree species having exhibited 100% survival after 20 months of flooding despite months of midday soil and air temperatures above 27 and 33°C, respectively. *P. communis* cv. OH × F97 but not cv. Bartlett defoliated after one month.<sup>109</sup> In the above experiment oxygen diffusion rate (ODR) stabilized after 30 days around  $5 \times 10^{-8} \text{ g cm}^{-2} \text{ min}^{-1}$ , a level similar to that measured after two months of flooding in an established orchard.<sup>113</sup> Rootstock selection is thus important for pears growing on heavy soil and or those prone to flooding.

One of the earliest physiological responses to flooding is a reduction in leaf conductance.<sup>110,111</sup> Measurements of leaf conductance have reflected differences in flooding tolerance between pear species and other fruits and was greater in spring than in autumn. The mechanism for flood induced stomatal closure is still unresolved<sup>114</sup> but it occurs independent of changes in  $\Psi$ .<sup>115</sup>

The decrease in leaf conductance on pear coincided with a simultaneous decline in root hydraulic conductivity.<sup>111</sup> Whether ABA is involved as a signal agent for stomatal closure of flooded pear trees is not known.<sup>111</sup> Nevertheless, in flooded soil, reduced stomatal aperture would seem to be an adaptive response to maintain leaf turgor under conditions of increased root resistance to water flow.<sup>111</sup>

The reasons for waterlogging tolerances of many *Pyrus* species is not clear. The movement of O<sub>2</sub> from shoot to root has been proposed as an adaptive mechanism to waterlogging.<sup>116</sup> Hypertrophied lenticels were more pronounced on pear and quince under flooded soil conditions<sup>109</sup> and movement of O<sub>2</sub> from shoot to root via lenticels has been proposed.<sup>115-117</sup> For many species, hypertrophied lenticels at or below the water line could also serve as exit points for toxic metabolites.<sup>118</sup> Rowe and Beardsell<sup>103</sup> dismissed O<sub>2</sub> transport from shoot to root as contributing to waterlogging tolerance of woody species including pear because of the limited shoot and root lengths through which O<sub>2</sub> may diffuse. Also Andersen et al.<sup>110</sup> found no evidence of aerenchyma on anaerobically-treated *P. betulaefolia* and *P. communis*. An alternative explanation for the flood tolerance of pear and quince could relate to the limitation of ethanol production by metabolic control over glycolysis (i.e., regulation of the Pasteur effect).<sup>119,120</sup>

Poor tree performance following waterlogging is generally associated with root death following oxygen deficiency or the build up of phytotoxins. However, sustained anaerobic conditions can markedly alter soil chemical and physical properties. For example, pear trees are susceptible to Mn toxicity<sup>121</sup> and sustained flooding can increase the availability of Mn to toxic levels by reduction of manganic ion to soluble manganous. Similarly Fe toxicity can also occur and S, Ca, Mn, N, Zn, Pb, and Co have been found more available after flooding.<sup>122,123</sup> Denitrification occurs in waterlogged soil and pH can change. These soil nutrient changes may affect tree vigor of waterlogging-tolerant fruits such as pear and quince even if root O<sub>2</sub> deficiency did not interfere with nutritional uptake. However, West and Nicholson,<sup>124</sup> found that after 20 days of flooding, container grown pears exhibited a decline in leaf concentration of K, Ca, Cu, and Zn. This decline was probably associated with interference to nutritional uptake, since on removal of flooding Ca and Cu rapidly equilibrated to the level of a non-flooded control with similar tendencies for K and Zn. Levels of leaf Mn and Fe did not rise. Uptake of Mn and Fe could be more related to greater soil concentrations of these two elements in soluble form under anaerobic conditions which may only occur under sustained flooding. Soil physical properties will also change as wet soil conditions combined with heavy orchard traffic compact soil and limit root growth. Though pear and quince may not die under waterlogged conditions numerous associated factors can combine to limit vigor and health. Fortunately pathogen invasion under wet conditions is not common on the above two species.

## V. SALINITY

Though Bernstein<sup>125</sup> showed a yield reduction for pear of 10% at an electrical conductivity of a saturated soil extract (ECe) of 2.5 dS m<sup>-1</sup> there is little available data for pear and quince on the effect of sustained

high salinity levels in the soil profile. In Australia with mounting pressure to use moderately saline water for irrigation, 40 year old 'William Bon Chretien' (syn. Bartlett) pears were irrigated with five ranges of salinities from 0 to 2.7 dS m<sup>-1</sup> over 10 years.<sup>126</sup> Despite soil E<sub>Ce</sub> under the higher salinity levels stabilizing by year 4 at around 4.0 dS m<sup>-1</sup>,<sup>127</sup> there was no effect on yield until year 8. In year 7, leaf Cl and Na rose sharply after harvest while midday A rates and g<sub>s</sub> were reduced with high salinity (2.7 dS m<sup>-1</sup> treatment). Under this treatment in years 8 and 9 yields declined and 40% of the trees died. The yield reduction in year 9 coincided with a reduction in fruit number. However, in previous years, though fruit number was not measured, there were more undersized fruit at the high salinities with yields similar between treatments.<sup>126</sup> This infers a greater fruit number at the higher salinity levels. For canning pears, total tonnage depends largely on fruit set not fruit size. Salinity effects on productivity are therefore minimal, however, with increasing soil salinity, eventually yield and fruit number declines rapidly and death may follow.<sup>126</sup>

It is now well recognized that the effect of salinity increases under waterlogged conditions. Leaf chloride levels rose sharply on pear trees having access to a saline water table and waterlogged by successive irrigations.<sup>128</sup> Trees partially defoliated and yielded small fruit. Waterlogging in winter had no such effect.<sup>108</sup> In the pot experiment of West and Nicholson<sup>124</sup> where pear trees were flooded with saline water for 20 days, the combination of waterlogging and salinity also markedly depressed shoot growth rates.

These results pose problems of long-term management of pears in a saline environment (i.e., above a saline water table). While in the absence of spring and summer waterlogging, pears may produce profitability above a salty water table, long-term effects maybe more insidious. As toxic ion concentrations rise in both soil and plant, tree productivity will decline. In the heavy soils common to pear, leaching to remove salt build up poses the threat of waterlogging and rise in damage levels. Maintaining the water table below a level where toxic ions will not encroach significantly into the rootzone may be the only answers. Given the apparent slow nature of salt damage on pear this approach will require regular and careful monitoring of Cl and Na uptake and subsequent effects on tree performance.

## VI. CONCLUSIONS

In compiling this chapter two things were obvious. First, the pear adapts well to a range of adverse conditions. Second, recent literature of environmental stress of pear is scarce. Perhaps the former predisposes the latter. Minimum winter temperatures are probably the major environmental limitation, a problem remaining complex and poorly understood. More importantly, freezing injury and chill and dormancy requirements require more study given present predictions of global warming. Large areas of pears, some comparatively new, may be at risk if mean temperatures rise 2 to 3°C. What seems needed is not detailed lists of chilling requirements for countless varieties but a better understanding of the relationship of temperature to dormancy.

As with other fruits most future pear plantings will be at higher density. This may increase environmental stress as temperature and humidity within the planting increase, light penetration to the lower canopy becomes more uneven, and water use of the dense canopy higher. None of these effects will be unique to pear. However, they could pose more of a problem on pear given the absence of suitable dwarfing rootstocks, the vigorous nature of many of the recognized rootstocks and the early flush period of shoot growth common to most European pears.

The success of the previously mentioned RDI experiment of pear at Tatura (a 20% yield increase over a 100 tonne/ha crop) shows what can be achieved by manipulations of the orchard environment. Even so it is still not clear as to what physiological plant responses increased yield. Similarly there are numerous accounts of increased yield from high density systems and pear plantings have been prominent in this regard. Claims based largely on yields are made for better and more efficient systems. Much less attention has been given to the more difficult problem of how and why yield and efficiency increased or in other words how man can manipulate the environment for his betterment.

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## Chapter 8

# Persimmon

Alistar D. Mowat and Alan P. George

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## I. INTRODUCTION

The cultivation and climatic requirements of persimmon have been extensively covered by previous authors.<sup>1-7</sup> These reviews have shown that persimmon can be cultivated over a wide range of climatic environments, from temperate through tropical zones. This review describes the ecophysiology of persimmon and discusses the environmental limitations to production.

### A. ORIGIN AND DISTRIBUTION

Persimmon is a member of the genus *Diospyros* containing over 400 species<sup>8</sup> which occur predominantly in tropical and subtropical environments. Species tend to be evergreen, but several species are deciduous and adapted to warm temperate climates. *Diospyros kaki* L. is the major commercial species. Other species, *D. virginiana* L., *D. lotus* L., *D. oleifera* Cheng, *D. digyna* Jacq., and *D. blancoi* A. DC., are of relatively minor economic importance.

The mountains of central China are the center of origin and primary center of diversity for *D. kaki*, and Japan is a secondary center.<sup>9</sup> The wild form of persimmon, *D. kaki* var. *sylvestris* Makino grows in mountain areas in central and western China to an altitude of 1150 m.<sup>10</sup> *D. kaki* is hexaploid ( $2n = 90$ )<sup>11</sup> and the wide diversity in fruit shape and form suggest probable allopolyploid origins.<sup>12</sup> Morphological, geographical, and cytological evidence suggests that *D. oleifera* (syn. *D. roxburgia* Carriere) is a parent of *D. kaki*.<sup>13</sup> The origin of the other parental species is not known but it could be *D. hexameria* Wu, a species closely related to *D. oleifera* from southern China that has a ribbed fruit.

Persimmon has been cultivated in China for several thousand years, where over 2000 cultivars have been selected.<sup>14</sup> *D. kaki* was introduced to Japan about 1300 years ago.<sup>15</sup> In Japan two distinct forms have been selected, astringent and non-astringent, the latter having a much lower concentration of water-

Table 1 Climatic characteristics of persimmon-growing locations

| Sites                 | Latitude | Mean monthly temperature |              | Mean annual rainfall (mm) |
|-----------------------|----------|--------------------------|--------------|---------------------------|
|                       |          | Minimum (°C)             | Maximum (°C) |                           |
| Batumi, Georgia       | 41.37 N  | 2.0                      | 25.0         | 100                       |
| Fukushima, Japan      | 41.31 N  | −3.0                     | 30.5         | 1455                      |
| Pulsan, South Korea   | 35.06 N  | −3.0                     | 30.5         | 1380                      |
| Nara, Japan           | 34.41 N  | −0.5                     | 32.0         | 1375                      |
| Xian, China           | 34.16 N  | 2.5                      | 31.5         | 100                       |
| Los Angeles, U.S.     | 34.00 N  | 8.0                      | 28.0         | 380                       |
| Haifa, Israel         | 32.49 N  | 9.5                      | 32.0         | 670                       |
| Cairo, Egypt          | 30.03 N  | 5.0                      | 35.5         | 25                        |
| Chang sha, China      | 28.10 N  | 6.0                      | 30.0         | 140                       |
| Homestead, U.S.       | 25.29 N  | 12.0                     | 32.5         | 1570                      |
| Canton, China         | 23.08 N  | 8.5                      | 32.5         | 1580                      |
| Mackay, Australia     | 21.10 S  | 16.8                     | 27.4         | 1694                      |
| Limeria, Brazil       | 22.34 S  | 13.0                     | 30.0         | 150                       |
| Nambour, Australia    | 26.40 S  | 16.0                     | 29.0         | 1800                      |
| Santiago, Chile       | 33.16 S  | 3.0                      | 29.0         | 35                        |
| Loxton, Australia     | 34.38 S  | 4.0                      | 31.0         | 274                       |
| Kerikeri, New Zealand | 35.12 S  | 10.0                     | 20.0         | 1650                      |
| Hastings, New Zealand | 39.39 S  | 7.5                      | 19.5         | 770                       |

soluble tannins.<sup>4,10</sup> Persimmon can be further subdivided into pollination constant and pollination variant types.<sup>10</sup> The pollination constant astringent (PCA) form is the oldest and comprises almost all the Chinese cultivars and several Japanese cultivars. Pollination variant astringent (PVA) and non-astringent (PVNA) forms originated in Japan about 1200 years ago and exhibit flesh darkening when pollinated. The flesh darkening reaction is associated with a low ascorbic acid content in the flesh,<sup>16</sup> high polyphenol oxidase activity,<sup>17</sup> and ethanol production in seeds.<sup>18</sup> The pollination constant non-astringent (PCNA) persimmon is the most recent form, originating approximately 500 years ago in Japan.<sup>19</sup> It was derived from PCA cultivars, but has a different tannin composition.<sup>20</sup> The PCNA form is generally free of astringency at harvest; post-harvest treatments to remove astringency are not required.

The distribution of persimmon to countries outside Asia has occurred within the last 150 years. Commercial cultivation occurs between latitudes 45° north and south of the equator (Table 1). Over one million tonnes of persimmon are produced annually from an area of approximately 235,000 hectares.<sup>21</sup> The major producers are China, Japan, Brazil, Korea, and Italy. Minor producers include Israel, U.S.A., New Zealand, Australia, Spain, Georgia, Egypt, and Chile.

## II. PHENOLOGY

The growth cycle of persimmon is described in Figure 1. The phenological sequence of development is; (1) bud burst; (2) shoot elongation; (3) cessation of shoot growth; (4) full bloom; (5) fruit growth; (6) floral bud development for the subsequent season; (7) resting of floral bud development; (8) fruit maturation; and (9) leaf-fall.<sup>22</sup> This sequence of development is specific to cultivar, environment, tree condition, and management practices.

### A. VEGETATIVE DEVELOPMENT

Trunk and branch cambial activity begins at bud-burst and continues for 24 weeks.<sup>23</sup> Shoots, emerging from buds that developed the previous season, cease growing before full-bloom. Conditions that stimulate vigor (i.e., juvenility, low crop load, hard pruning, excess nitrogen, and soil moisture) can induce a second flush of the terminal buds of current season growth. Shoots emerging from older buds, a result of hard winter pruning, limb breakage, or frost damage, are generally vigorous and cease growth late in the season. In Japan, canopy development reaches a maximum approximately 75 days from budbreak<sup>24</sup> and the leaves are present on the tree for 170–200 days.

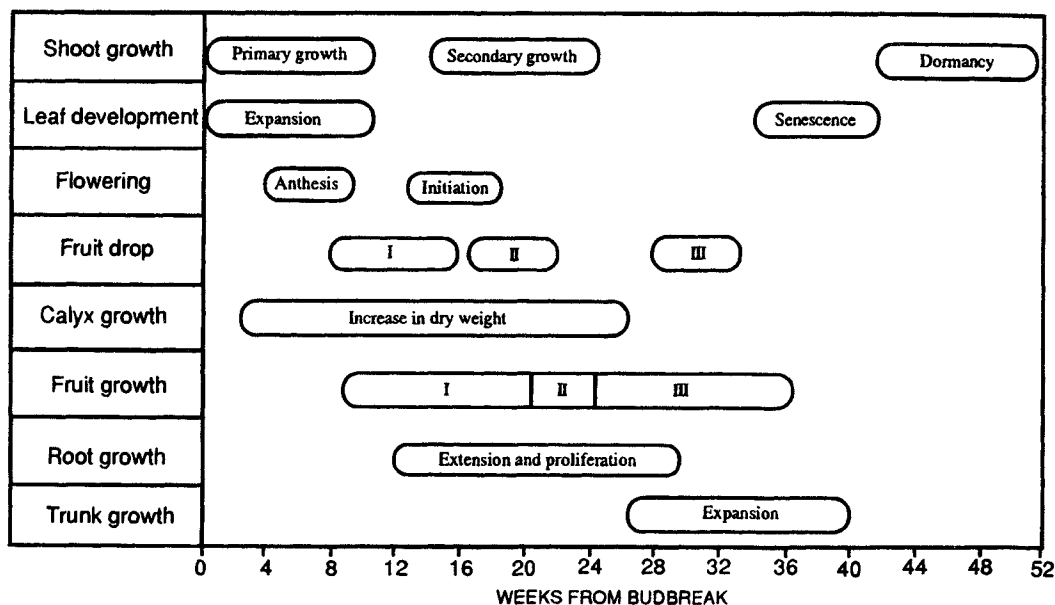


Figure 1 The phenology of persimmon.

Trunk and branch expansion occur over the latter part of the growing season. Trunk expansion is sensitive to competition from the fruit. In Queensland, Australia, the relative increase in butt cross-sectional area for a range of cultivars was found to decline as the annual yield increased.<sup>25</sup> Since fruit harvest generally occurs near or at leaf fall there is no opportunity for post harvest accumulation of reserves in heavy cropping years.

In bearing trees the biomass is distributed between the trunk and branches, leaves, fruit, and roots. A Japanese study, on 9-year-old bearing persimmon, found the proportion of biomass (DM) contained by specific organs was as follows: leaves 11.4%, fruit 14.6%, one-year-old shoots 3.3%, trunk and branches 38.4%, fine roots 1.7%, and other roots 30.5%.<sup>26</sup> The biomass associated with new tissue was 52.2% of the total biomass. In 25-year-old bearing 'Fuyu' persimmon the distribution of new tissue biomass (DM) between specific organs was as follows: leaves 23.2%, fruit 29.2%, trunk, branches, and shoots 28%, and roots 19.6%.<sup>27</sup> The ratio of shoot biomass (including trunk and branches) to the root biomass may vary with tree maturity and bearing. The shoot to root ratio of 3-year-old persimmon trees, on a dry weight basis, was 0.73<sup>28</sup> compared with a ratio of 1.29 in 9-year-old bearing trees.<sup>26</sup> Root growth may be more affected by the partitioning of resources to fruit than shoot growth. Bearing may affect the total amount of biomass contained in vegetative organs. In water culture studies, the new tissue biomass of vegetative organs was 40–50% lower in bearing trees in comparison to non-bearing trees.<sup>29</sup>

Root growth occurs in one or two flushes over the growing season. In Japan root flushes occurred from mid-summer to autumn in bearing trees.<sup>30</sup> In Queensland, Australia, the timing of the root flush occurred in late spring/early summer and appears to be influenced by shoot and fruit growth cycles.<sup>31</sup> Peak root growth tends to occur between the spring vegetative flush and fruit growth. The effect of soil temperature on persimmon root activity, although not studied, may be an important factor in explaining differences in the timing of root growth between temperate and sub-tropical environments.

## B. REPRODUCTIVE DEVELOPMENT

Flower evocation begins after a terminal bud has formed on the current seasons growth and the production of new leaf primordia within the bud has ceased.<sup>32</sup> Shoots terminating early in the growing season have a greater ability to differentiate flower buds than those terminating in the mid or late part of the growing season.<sup>33</sup> Only the sepals and petals differentiate prior to the winter rest period and all other development occurs in the spring.<sup>34</sup>

The tree has a tip bearing habit with flowers occurring in the more basal nodes of current season shoots. The flowering habit is complex, ranging from dioecious to monoecious.<sup>35</sup> Most commercial

cultivars are pistillate or pistillate-sporadically monoecious, though several androdioecious and tri-monoecious cultivars exist.<sup>36</sup> Fruit can be set parthenocarpically, but this is dependent on cultivar and environment.<sup>37</sup> If suitable cultivar and environment combinations are not present pollinators will be required to ensure reliable fruit set. The flower is pollinated by insects, with the European honey bee being the predominant pollinator.<sup>38,39</sup> The transfer of pollen between male and female flowers by insect activity can be poor<sup>40</sup> and flowers may require hand pollination.<sup>41</sup> Fruit drop can occur in two to three phases after fruit set.<sup>42,43</sup> Competition between fruit and shoots causes seedless fruit to fall in the first two phases of drop while fruit and root competition can cause both seeded and seedless fruit to abscise in a third phase of drop.

### C. FRUIT DEVELOPMENT

The fruit of persimmon is botanically a berry<sup>44</sup> consisting of a parenchymatous mesocarp surrounded by an epicarp, covered by a cuticle.<sup>45</sup> Fruit mass and size curves follow a sigmoid<sup>39</sup> or double sigmoid growth pattern,<sup>5,36,46</sup> consisting of two active stages of growth, stage I and stage III separated by a less active stage (stage II) (Figure 2). Fruit development ranges from 120–190 days, depending on cultivar and environment; and the duration of stages I, II and III is 60–100, 20–40 and 40–50 days, respectively. Growth stage I is thought to be associated with cell division/differentiation and growth stage III with cell expansion/maturation. The significance of growth stage II is not clear, but it does not appear to be related to seed development as the growth curves of seed bearing and seedless cultivars are similar.<sup>36,47–49</sup> Growth stage II may reflect a change point between cell division/differentiation and cell expansion/maturation. Therefore the duration of stage II may simply reflect the influence of genetic, physiological, or environmental factors on the duration of stage I and the start point of stage III. Seed growth is completed by the end of stage I, after which physiological changes associated with seed coat coloring and endosperm hardening occurs.<sup>47</sup> Calyx growth commences before flowering and is completed by the end of stage II. At full bloom the calyx may comprise more than 50% of the flower weight,<sup>5</sup> and though the calyx can assimilate carbon,<sup>50</sup> it is not known if the calyx is a significant source of photosynthates for the developing fruit. The calyx is an important gas exchange organ for the fruit,<sup>50</sup> since fruit lack stomata or lenticels and is covered by a layer of wax.<sup>36</sup> The calyx has a major influence on fruit growth and development. Removal of the lobes of the calyx or damage by agrochemicals and disease can enhance fruit drop and reduce fruit size and soluble solids.<sup>51,52</sup>

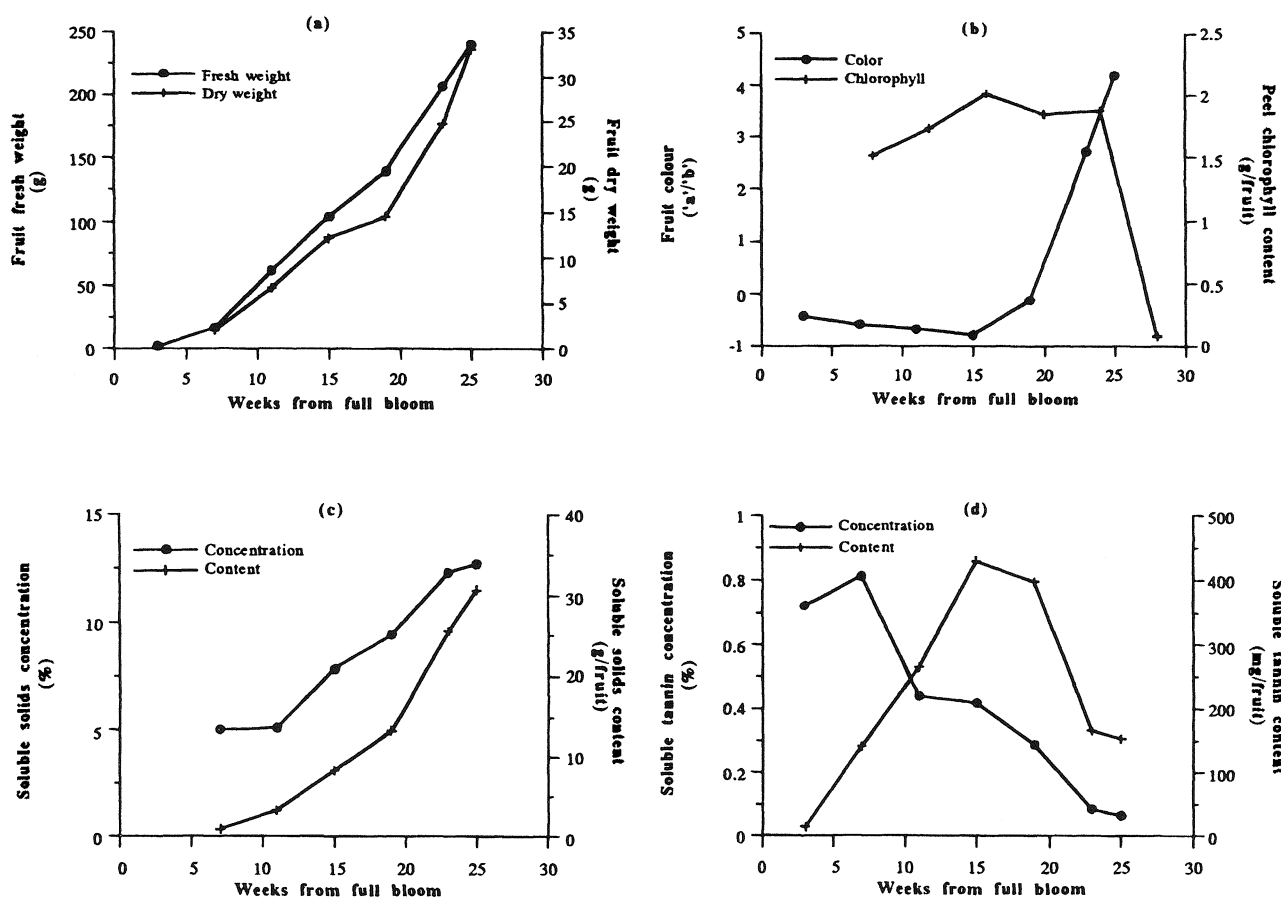
Soluble sugars accumulate in the fruit by translocation<sup>53</sup> of sucrose where it is hydrolyzed to fructose and glucose.<sup>54</sup> The rate of sugar unloading in the fruit is controlled by fructose invertase activity and varies with fruit age.<sup>55</sup> The sugar composition of mature ripe fruit is ca. glucose (48%), fructose (49%) and sucrose (3%).<sup>56</sup> Fruit color increases with maturation as a result of chlorophyll degradation and carotenoid synthesis.<sup>57</sup>

Water-soluble tannin is contained in specialized tannin cells dispersed within the parenchyma of the fruit mesocarp.<sup>36</sup> In astringent cultivars, tannin cells enlarge from flowering until stage III while in PCNA cultivars they cease growth at the end of stage I.<sup>58</sup> Tannin accumulation stops when cell growth ceases because of pore closure in the cell wall.<sup>49</sup> Loss of astringency in PCNA cultivars is a combination of two processes, first a dilution of soluble tannins, and second the coagulation (i.e., polymerization) of soluble tannins into an insoluble form. Astringent cultivars require treatment to remove astringency.

### D. PRODUCTIVITY

The productivity of mature orchards is moderate compared to other fruit crops, ranging from 8.6–25 t ha<sup>-1</sup>.<sup>36,59</sup> The factors limiting the productive potential of persimmon have not been adequately defined. Productivity could have a genetic component. Productivity differences have been reported between cultivars under a range of environmental conditions.<sup>60–64</sup> Cultivars can differ in their precocity and parthenocarpic setting ability.<sup>25,37</sup> Bud mutations of cultivars can also differ in productivity.<sup>65</sup> ‘Supahiratanenashi’, a dwarf bud mutation of ‘Hiratanenashi’, has been found to have lower vigor, earlier bearing, and higher yields than ‘Hiratanenashi’.<sup>66</sup>

Detailed studies on the physiological differences between a dwarf bud mutation and the original cultivar could provide a better understanding of the factors influencing persimmon productivity. In Japan, a number of studies between a dwarf bud mutation of ‘Nishimura wase’ and ‘Nishimura wase’ have been carried out on 20-year-old trees planted at the same density. The dwarf strain produced twice the yield on a canopy volume basis but only the same yield as ‘Nishimura wase’ on a yield per unit of land area basis.<sup>67</sup> As the canopy volume of the dwarf strain was 83% smaller than ‘Nishimura wase’



**Figure 2** Seasonal changes in fruit composition (cv Fuyu): (a) fresh and dry weight; (b) color and peel chlorophyll content; (c) soluble solids concentration and content; and (d) soluble tannin concentration and content.

then the yield per unit of land area could be increased by planting the trees at a higher density. The improvement in productivity of the dwarf strain could be attributed to a number of factors. Improved partitioning between vegetative and reproductive growth could be another factor influencing productivity. The dwarf form had 80% less wood than 'Nishimura wase'. The percentage of current season growth to total wood weight was 6.3% for the dwarf form and 1% for 'Nishimura wase'. As the net CO<sub>2</sub> assimilation (A) rate of a tree is strongly affected by the ratio of the non-photosynthetic system to the photosynthetic system<sup>68</sup> then the dwarf strain could have a higher A rate through a reduction in total respiration of non-photosynthetic organs. The leaves of the dwarf strain also had a higher set CO<sub>2</sub> assimilation rate, smaller leaf size, thicker leaves, and contained higher levels of chlorophyll and nitrogen than 'Nishimura wase'.<sup>69</sup> Shoots on the dwarf strain ceased growth earlier in the season than those on 'Nishimura wase'.<sup>70</sup> The dwarf strain had a higher flower density fruit set than 'Nishimura wase'.<sup>71</sup>

Rootstocks and interstocks can also influence persimmon productivity.<sup>72,73</sup> Persimmon is generally cultivated on seedling rootstocks from a range of species. In California, 'Haichiya' was found to be lower yielding on *D. lotus* than other rootstocks.<sup>72-74</sup> The main cause of low yields was an excessive fruit drop associated with high tree vigor rather than low flower density. The development of clonal rootstocks in persimmon has been limited by suitable propagation techniques.<sup>75</sup> In Japan, fruit yield of trees on dwarfing rootstocks was higher than on standard rootstocks on a canopy volume basis but not on a canopy area basis.<sup>76</sup> Shoot growth was shorter on the dwarf trees in comparison to standard trees, although the graft union of the dwarf trees showed abnormal thickening and stock over growth.

Persimmon is prone to fluctuations in bearing. Bearing can range from biennial to much longer cycles. In Japan, persimmon was found to have an alternate bearing cycle of 4.2 years.<sup>77</sup> This contrasts with a biennial bearing habit of 'Pomelo IAC 6-22' in Brazil.<sup>78</sup> Fluctuation in bearing could be caused by over cropping or through environmental influences. Overcropping during the 'on' year results in competition for assimilates between fruit and shoots.<sup>78-80</sup> The low carbohydrate status of a tree in an 'on' year can reduce flower evocation<sup>81</sup> and may also cause pre-bloom flower bud abscission in the following season. In New Zealand, persimmon often shows a longer fluctuation in bearing that could be associated with a shortage of reserves. Where cropland is used to control tree vigor, a high cropland in one season can stimulate flower initiation by causing shoots to cease growth early and subsequently cause heavy flowering and cropping in the second season. A heavy crop carried in the second season may then deplete tree reserves leaving limited resources for shoots, trunk and roots. This may then reduce flower evocation or cause pre-bloom flower abscission. Longer bearing cycles may also occur as a result of a slow depletion of reserves by a succession of heavy crops.

Environmental factors can influence bearing by affecting assimilation or through physical damage of reproductive organs. Flower evocation and fruit drop are particularly sensitive to environmental stress.<sup>42,81</sup> Flower buds and fruitlets can be prone to damage from cold, hail, and wind.<sup>82-84</sup>

Management factors influencing productivity include plant density, training system, pruning and crop thinning. In Japan, the yield per unit of land area of 'Matsumoto wase Fuyu' was found to increase with increasing planting density until full canopy closure was reached.<sup>85</sup> Training systems such as the 'Y' and palmette have been developed to improve the productivity of persimmon (Photo 1). In Japan, a 'Y' training system was found to increase the yield per tree and per trunk cross sectional area, and



**Photo 1** Persimmon trained on a Y trellis to improve light distribution within the canopy.

reduce fluctuation in annual yields in comparison with the traditional open vase training system.<sup>86</sup> Renewal pruning can increase persimmon productivity by stimulating new replacement growth from old wood.<sup>87,88</sup> In comparison, a lack of pruning may cause a decline in productivity. This could be due to a reduction in flower evocation. In unpruned trees, flower evocation occurs mainly on the tips of bearing shoots where competition from fruit for assimilates can be high. Productivity of persimmon can increase with fruitload.<sup>89</sup> However, as fruit weight is negatively correlated with fruit load then the marketable yield per tree tends to be lower than the maximum potential yield per tree.<sup>89,90</sup> Biennial bearing can be reduced by thinning fruit to an optimum cropload that is based on shoot type and leaf number.<sup>91</sup> Phytotoxicity from agrochemical sprays can reduce productivity by stimulating fruit drop.<sup>42,92</sup> Fruit drop may occur as result of a loss of leaf surface through spray damage or as a stress response.

Nutrition can improve persimmon productivity by increasing tree size or reducing fruit drop.<sup>42,93,94</sup> The response of persimmon to nutrition is dependent on the initial nutritional status of the tree and applications of additional nutrients may have no effect on productivity.<sup>95</sup> In New Zealand, leaf nitrogen levels can be high ( $>2\text{ g kg}^{-1}$  DM) when persimmon is cultivated on high fertility soils. Additional applications of nitrogen under these conditions can reduce productivity by stimulating vigor and enhancing fruit drop or reducing flower evocation by stimulating secondary growth flushes. In Japan, annual yields can fluctuate on soil types that stimulate tree growth.<sup>96</sup>

Pest and disease problems can reduce persimmon productivity via damage to the root system,<sup>97,98</sup> a reduction in leaf area,<sup>99,100</sup> a loss of flowers/fruit,<sup>101</sup> or a reduction in fruit size. Pest damage may have an adverse effect on physiological processes in the plant. In Georgia, an infestation of citrus white fly on persimmon was found to reduce photosynthesis, leaf carbohydrate and protein content and enhance respiration.<sup>102</sup>

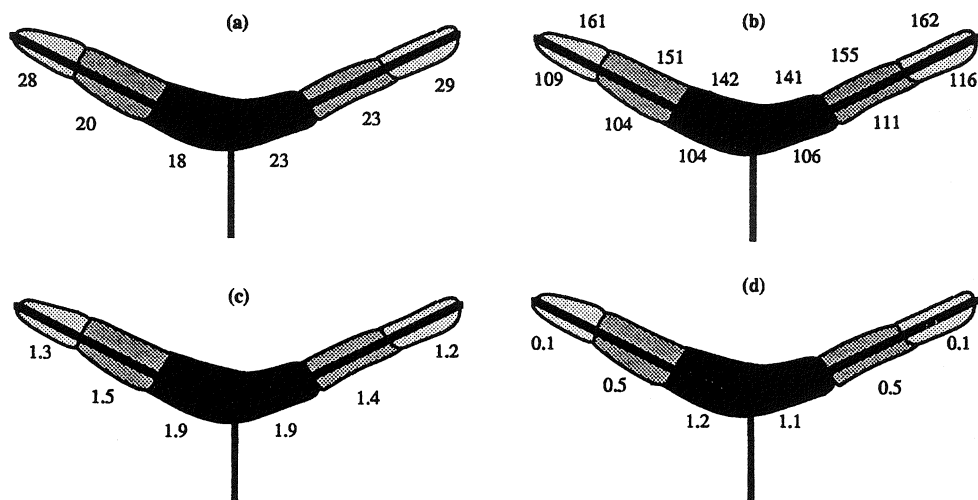
### III. IRRADIANCE

Irradiance affects photosynthetic activity, productivity, and fruit quality of persimmon. Climate, shelter height, proximity of adjacent trees, and the canopy density all influence the radiation environment.

#### A. PHOTOSYNTHESIS

Photosynthetic activity increases with leaf age. In Japan photosynthetic activity reached a maximum ca. 85 days after bud-break, then declined slowly through the growing season until ca. 50 days before leaf fall when it declined rapidly.<sup>102,103</sup> Initially, the photosynthetic rate of the leaf is related to the development of palisade and spongy mesophyll tissue.<sup>102</sup> Leaf thickness differs between cultivars, and photosynthetic activity is highest in cultivars with thick leaves.<sup>104,105</sup> Leaves in the lower part of the canopy have a higher photosynthetic activity than those in the upper part during leaf expansion.<sup>103</sup> This could be due to the high nitrogen content of lower canopy leaves increasing the rate of leaf development,<sup>106</sup> or to photoinhibition caused by high irradiance levels in the upper canopy. The light environment of individual leaves changes with canopy development which results in higher photosynthetic activity in the upper part of the canopy compared with lower parts.<sup>103</sup>

Net  $\text{CO}_2$  assimilation decreases as irradiance falls from light saturation. In a Japanese study, photosynthetic activity decreased as irradiance declined from light saturation at  $720\text{ }\mu\text{mol m}^{-2}\text{s}^{-1}$  ( $A = 7.9\text{ }\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$ ) to light compensation of  $90\text{ }\mu\text{mol m}^{-2}\text{s}^{-1}$ .<sup>107</sup> Fluctuating irradiance on exposed persimmon leaves can cause a rapid decline in  $A$ . Net  $\text{CO}_2$  assimilation of 'Fuyu' decreased from  $7.8\text{ }\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$  in full sun [photosynthetic photon flux (PPF) =  $2106\text{ }\mu\text{mol m}^{-2}\text{s}^{-1}$ ] to  $0.2\text{ }\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$  in heavy shade (PPF =  $211\text{ }\mu\text{mol m}^{-2}\text{s}^{-1}$ ), followed by a rapid recovery in full sun to  $7.4\text{ }\mu\text{mol m}^{-2}\text{s}^{-1}$ .<sup>108</sup> The irradiance efficiency (IE = total radiation at leaf surfaces/total radiation at soil surface of area occupied by leaf surface  $\times 100\%$ ) of the canopy reaches a maximum (IE = 90%) at approximately the same time as the cessation of canopy leaf development (leaf area index = 1.9).<sup>24</sup> At full canopy development, differences in leaf area index and shoot composition within the canopy (Figure 3) can expose leaves to lower than optimum levels of irradiance.<sup>104</sup> Leaves in shaded parts of the tree are characterized by low specific leaf weights, low nitrogen contents and low dry weights. The decline in late season photosynthetic activity could be due, in part, to low irradiance, falling temperatures, leaf aging, senescence, or a reduction in leaf nitrogen content. In the subtropical environment of southeast Queensland, Australia, irradiance and temperature conditions after harvest are sufficient to maintain high photosynthetic activity ( $8\text{--}12\text{ }\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$ ).<sup>110</sup> Declining leaf nitrogen could also lower photosynthetic rates, since a large portion of organic nitrogen is in the form of ribulose biphosphate



**Figure 3** The influence of canopy location (shaded areas denote upper, middle, and lower parts of the canopy) on: (a) PAR (percent of full sun); (b) specific leaf weight ( $\mu\text{g mm}^{-2}$ ) (above and below canopy surface); (c) leaf area index; and (d) ratio of nonfruiting to fruiting shoots.

carboxylase/oxygenase. Also, late season nitrogen applications can improve assimilate translocation to the fruit and delay leaf-abscission.<sup>111</sup>

## B. EVOCATION AND FRUIT SET

Irradiance can influence the productivity of persimmon by affecting flower evocation and fruit set. Evocation and fruit set have been positively correlated with the total hours of irradiance over late summer and spring, respectively.<sup>112</sup> The reduction in the shoot carbohydrate content caused by lower irradiance<sup>113</sup> can adversely affect evocation.<sup>81</sup> Low irradiance from cloud cover and artificial shade stimulated fruit drop.<sup>39</sup> In Queensland, a low irradiance of  $29.4 \text{ mol m}^{-2} \text{ day}^{-1}$  or less, can significantly increase fruit drop over the post-flowering period and less than  $12.6 \text{ mol m}^{-2} \text{ day}^{-1}$  can prevent fruit set.<sup>114</sup> Unpollinated fruit are more susceptible to fruit-drop than pollinated fruit,<sup>37,115,116</sup> as the presence of seed increased fruit sink strength.<sup>117</sup> Fruit set of cultivars with a high parthenocarpic ability may be adequate without pollination when grown in regions with high irradiance hours or days following flowering.<sup>37</sup> However, in regions with low levels of irradiance after flowering, pollination is needed to control fruit drop. Fruit drop during and after flowering is due to severe assimilate competition between shoots and fruit as the sink strength shifts from vegetative to reproductive organs.<sup>118,119</sup> A reduction in photosynthetic activity, due to low irradiance, reduces the assimilate pool for competing sinks. The effect of low irradiance can also be localized within a tree, as fruit on shoots growing in shaded areas of the canopy are more prone to drop than fruit on exposed shoots.<sup>114</sup>

## C. FRUIT QUALITY

The quality of fruit from a given tree can be location dependent. Fruit in exposed parts of the canopy are of larger size, better colored, higher in soluble solids, and lower in astringency than fruit from lower or interior parts of the canopy.<sup>106,109,117</sup> Pruning has been effective in improving light distribution within the tree and has increased fruit quality.<sup>106,120,121</sup> It is not clear if irradiance affects fruit quality by influencing the A rate of adjacent leaves and the calyx and/or through the thermal effects of direct radiation. Fruit weight and soluble solids could be influenced by irradiance through changes in the assimilate supply of adjacent leaves. Fruit size can be reduced by shading the calyx or entire fruit over the first 40 days of fruit development.<sup>114</sup> Irradiance influences fruit temperature. In Japan, fruit exposed to full sun were  $6.5$  to  $11^\circ\text{C}$  higher than shaded fruit.<sup>122</sup> Fruit color, soluble solids, and astringency were also affected by temperature,<sup>123,124</sup> (and by the thermal effects of irradiance). An irradiance level of 25 to 30% of full sun was adequate for inducing the red peel color of mature fruit associated with lycopene development.<sup>122</sup>

Alternatively, fruit can be injured by high irradiance levels. Sunburn severely reduces fruit quality and can be a major quality defect in Australia.<sup>25,125</sup> Sunburn affects exposed parts of the fruit by bleaching the surface and causing localized damage to fruit tissue. Sunburn occurs through the final stages of fruit development and damage appears to be less in seasons of low irradiance.<sup>31</sup> The exposure of fruit to ultraviolet radiation can cause black spots to develop on immature fruit.<sup>126</sup>

## IV. TEMPERATURE

### A. GROWTH AND DEVELOPMENT

Persimmon has a relatively low chilling requirement for dormancy release compared to other deciduous fruit crops, and has been successfully cultivated in areas with low winter chilling,<sup>127–129</sup> including the tropics.<sup>130,131</sup> Some reports however, suggest that the tree does not thrive in tropical lowland environments,<sup>132,133</sup> though it may not be due to a lack of chilling. Chilling requirements differ between cultivars and those with higher chilling requirements, are grown at higher elevations in the tropics than those with lower requirements.<sup>134</sup>

The physiological basis of dormancy and the degree of chilling needed to satisfy dormancy in persimmon is not clearly defined. Shanks<sup>135</sup> noted that a rest period of 800–1000 hours below 7°C was adequate to permit normal bud-break and subsequent vegetative and reproductive growth. In Queensland, Australia, persimmon can be grown satisfactorily in regions which receive 100 hours of chilling below 7°C. However, more uniform and rapid bud-break occurs in regions which receive greater than 300 hours of chilling. The use of 7°C as a base temperature for persimmon may be inappropriate, as dormancy can be satisfied by a mean minimum temperature of 14°C.<sup>136</sup> Root temperature rather than bud temperature may be the more important factor in defining the chilling requirements, as detached shoots break bud with minimal exposure to chilling.<sup>137</sup> Root temperature could influence the initiation of growth through the conversion of starch to sugars in roots and then subsequently affecting the rate of water uptake. In a controlled environment study, root temperature was found to influence the time of bud-break. A moderate root temperature (13°C) promoted bud-break, which was delayed by high (23°C) and low (7°C) temperatures.<sup>138</sup>

Once chilling requirements have been satisfied, the cumulative daily mean air temperature, above 10°C, required for bud-break and anthesis is 90 and 300 degrees, respectively.<sup>139</sup> Raising soil temperatures by clear polyethylene mulches can advance bud-break, and root and shoot growth.<sup>140</sup> Temperature influences the amount of time between bud-break and anthesis. In a controlled environment, simulated low spring temperatures (17/12°C day/night) delayed this period by 28 days and increase flower size at anthesis by 60% in comparison with a higher temperature (27/22°C day/night); suggesting that cool temperatures can increase cell division cycles.<sup>137</sup>

Temperature over the flowering period can influence the duration of flowering. In southeast Queensland, flowering is concentrated over a 7–10 day period and temperatures average 21°C. In contrast, cooler spring temperatures (14°C) in New Zealand extended the length of flowering to 14–28 days. Temperature also influences the length of the fruit development period. Fruit development of the non-astringent cultivar 'Fuyu' often takes 24 to 27 weeks under ambient conditions in Australia. However, when the tree is grown at a constant temperature of 25°C, fruit development can be as short as 20 weeks.<sup>139</sup> Fruit quality and composition are also influenced by temperature. Fruit quality, based on fruit weight, peel color, soluble solids and soluble tannins, was highest when the day/night temperature during stage II and stage III respectively was 25/25 and 25/20°C, compared to higher (30/30°C) and lower temperatures (15/15°C).<sup>139</sup>

### B. LOW TEMPERATURE STRESS

*D. kaki* is cold tolerant and may survive temperatures, down to –18 to –20°C.<sup>141,142</sup> However, in regions where winters are mild, the tree can be injured by a 3 h exposure to –7°C.<sup>143</sup> In Korea, frost injury of vegetative and floral buds increased with lowering temperature, with 10% injury at –10°C to 75% at –17°C, and 100% at –20°C.<sup>82</sup> The duration of cold can also influence the severity of frost injury. Dormant trees can be killed by exposure to –7°C for more than 30 days, but injury to vegetative buds occurred after 15 days at –7°C.<sup>144</sup> Tree and wood age can influence the sensitivity of the tree to low temperatures. Mature trees are more resistant to freezing temperatures than younger trees<sup>142</sup> as older wood is hardier than younger wood.<sup>82</sup> Severely frost-injured trees recover rapidly over the following season by producing vigorous shoots from adventitious and dormant buds in the trunk and major branches.<sup>135,142</sup>

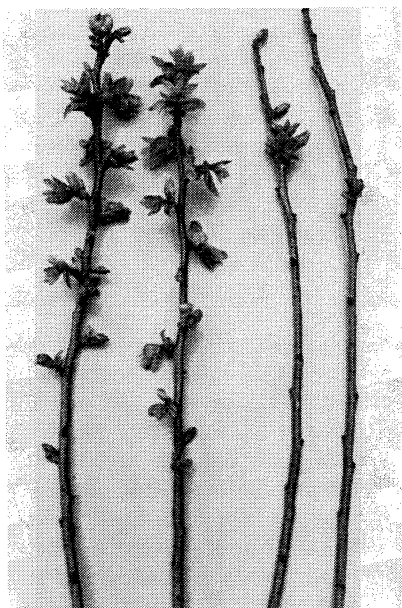
A history of heavy cropping or poor growing conditions over previous seasons increases the risk of severe frost injury.<sup>129</sup> Freeze resistance of the woody parts of the tree could be associated with carbohydrate reserves, as fruiting suppresses starch accumulation of shoots and branches.<sup>80</sup>

Cold tolerance in persimmon also has a genetic basis, with cultivars differing in cold tolerance.<sup>135,145</sup> The introduction of cold tolerance genes into *D. kaki* has been achieved by intra-specific hybridization with *D. virginiana*, in combination with backcrossing to high quality cultivars.<sup>146-148</sup>

Cold tolerance is also influenced by rootstock. In temperate regions, persimmon is cultivated on *D. lotus* and *D. virginiana* rootstock,<sup>14,132,149</sup> while the less hardy *D. kaki* and *D. oleifera* rootstocks are generally restricted to warm temperate and subtropical regions. In regions subject to freezing winter conditions, persimmon is grafted well above the ground on *D. lotus* and *D. virginiana*.<sup>129,149</sup> Persimmon on *D. virginiana* was found to be more frost resistant than those on *D. lotus*.<sup>142</sup> The cold tolerance of *D. virginiana* could be due to this stock being better adapted to alternating warm/cold cycles and not initiating cambial activity as readily as *D. kaki*.<sup>129</sup> The physiological basis of cold tolerance within the deciduous species of *Diospyros* has not been adequately investigated and warrants further investigation. It is not clear if different rootstocks impart cold tolerance by causing early cessation of shoot growth and subsequent shoot hardening during the growing season or through other mechanisms that induce and maintain deep dormancy within the top growth during the winter months. Temperatures over the dormant season could be a significant factor for inducing dormancy, as trees exposed to temperatures below 0°C over dormancy have a delayed bud-break in comparison to trees exposed to temperatures above 0°C.<sup>150-152</sup>

Newly emerging and expanding vegetative and reproductive buds are most sensitive to cold (Photo 2). In Japan severe damage to vegetative and floral buds of 'Fuyu' occurred after exposure to -3°C for 1 hour.<sup>153</sup> Low spring temperatures influence fruit set by affecting flower development and pollination. In Japan abnormal embryo development occurs when flower differentiation is exposed to a mean temperature of 15°C or lower during the time between bud-break and anthesis.<sup>154</sup> Fruit set is reduced because abnormal embryos are not capable of producing viable seeds and pollen tube growth is inhibited by temperatures of 15°C or lower.<sup>155</sup> As persimmon flowers are naturally pollinated by European honey bees and other bee species, low temperatures during flowering may also reduce pollinator activity and pollination effectiveness.

Temperatures over the latter stage of the growing season affect maturation and senescence. When fruit are exposed to lower temperatures (14°C) during fruit growth stage III, rapid chlorophyll degradation occurs in the peel,<sup>156</sup> unmasking the carotenoids that produce the typical orange/red color of a mature fruit. In temperate regions, frost (<-3°C) in autumn can cause premature leaf fall and frost damage to fruit. The symptoms of frost damage to fruit include surface pitting, rupturing of flesh cells, and



**Photo 2** The effect of prebud burst frost damage on persimmon buds (right: undamaged buds; left: damaged buds).

fruit softening. Ethylene production from damaged leaf tissue and defoliation can also cause fruit softening and can lead to abscission of undamaged fruit within the canopy.<sup>157</sup>

Mature fruit can be stored at low temperatures ( $-1$  to  $1^{\circ}\text{C}$ ) for 3 months under controlled atmosphere (CA) or modified atmosphere (MA) storage.<sup>36</sup> However, chilling injury can occur during low temperature storage, reducing the effective storage life.<sup>158–162</sup> Chilling injury of mature fruit has also been reported to occur when fruit are held at temperatures below  $13^{\circ}\text{C}$  for extended periods.<sup>163</sup> Symptoms of chilling injury include changes in odor, flavor, texture, and flesh color.<sup>160</sup> The sensitivity of the fruit to chilling injury is influenced by maturity, seasonality, and storage environment.<sup>163,164</sup>

### C. HIGH TEMPERATURE STRESS

Persimmon can be successfully cultivated in desert regions<sup>165</sup> where air temperatures reach  $48^{\circ}\text{C}$ .<sup>166</sup> However, under hot dry conditions unprotected young trees can be killed by sunburn.<sup>1</sup> Persimmon trees are more resistant to summer heat than apple, pear, and grape, tolerating temperatures up to  $50^{\circ}\text{C}$ , and have a high optimum night temperature for vegetative growth ( $32^{\circ}\text{C}$ ).<sup>167</sup> However, high temperatures may reduce A and the optimum leaf temperature for maximum A was reported at  $20^{\circ}\text{C}$ .<sup>107</sup> High day/night temperatures ( $32/27^{\circ}\text{C}$ ) have induced excessive vegetative growth and increased flower and fruitlet abscission.<sup>137</sup> The influence of temperature on flower and fruitlet abscission may be due to high temperatures causing an increase in shoot to fruit competition and a reduction in carbon assimilation.

Fruit quality and composition are affected by high temperature stress. Fruit growth is sensitive to high temperatures during growth stage II. A temperature of  $30^{\circ}\text{C}$  or greater extended the duration of stage II and delayed maturation in comparison to fruit temperatures of  $20^{\circ}\text{C}$ .<sup>139,156</sup> Persimmon growing in hot, dry climates can have a flatter fruit shape when compared to fruit from cool, damp climates.<sup>168</sup> Temperature can have a negative effect on fruit soluble solids, as fruit exposed to high temperatures ( $30^{\circ}\text{C}$ ) during stage III have a lower soluble solids than fruit exposed to lower temperatures ( $15^{\circ}\text{C}$ ).<sup>124</sup>

High temperatures during growth stages II and III are important for causing natural astringency loss in PCNA cultivars.<sup>123</sup> However, the mechanism for natural loss of astringency has not been clearly defined. It is known that soluble tannins coagulate in the presence of acetaldehyde to form insoluble tannins<sup>169</sup> and that acetaldehyde accumulates in the tannin cells of fruit exposed to high temperatures ( $>25^{\circ}\text{C}$ ) during growth stage II.<sup>139</sup> PCNA cultivars would require exposure to anaerobic conditions during fruit development since acetaldehyde accumulation occurs during anaerobic respiration.<sup>170</sup> A study on seasonal changes in the internal gas composition of persimmon fruit has shown that internal oxygen levels drop from approximately 5 to 1% v/v during stage II for a short period.<sup>171</sup> The cause of this phenomena is unknown but may be associated with an increase in resistance to oxygen diffusion into the fruit by cuticular wax formation. When changes in cuticular resistance to oxygen are coupled with an increase in oxygen demand through the effect of high temperature on fruit respiration,<sup>51</sup> then it is possible that persimmon fruit increase the proportion of anaerobic/aerobic respiration. Excess exposure to anaerobic conditions may reduce internal fruit quality, as fruit exposed to high temperatures ( $30^{\circ}\text{C}$ ) during growth stage III can contain brown specks in the flesh.<sup>172</sup>

Thus, the natural loss of astringency in PCNA cultivars, by soluble tannin coagulation, could be associated with two factors: (1) early cessation of tannin cell development coinciding with changes in cuticular resistance to oxygen diffusion; (2) mid summer temperatures inducing anaerobic conditions within the fruit.

## V. WATER

Persimmon is adaptable to regions with a wide range of soil moisture regimes, including drought prone environments,<sup>165,166</sup> the humid tropics<sup>173</sup> and high rainfall areas in warm temperate zones (Table 1). The response of persimmon to water is dependent on the organ or tissue and the phenological stage of development.

### A. DROUGHT STRESS

Persimmon seedlings show greater sensitivity to water stress than apple, peach, or grape seedlings.<sup>174,175</sup> The rate of water loss from the tree is influenced by soil moisture, leaf area, and environmental conditions.<sup>176</sup> Growth of seedling persimmon can be poor in soils with low moisture.<sup>177</sup> The concentration of roots in persimmon orchards is greatest within 200–300 mm of the surface,<sup>178,179</sup> and changes in soil moisture in the upper soil layers (100–150 mm in depth) can have a major influence on persimmon

tree development and fruit yield.<sup>180</sup> Water stress influences the productivity of persimmon by adversely affecting vegetative growth, fruit set, and fruit development. Water stress affects shoot development,<sup>1</sup> reducing the potential bearing surface and leaf area for the present and following seasons crop. Severe water stress during flowering can stimulate fruit drop,<sup>181,182</sup> and cause a reduction in yield. During fruit growth, water stress can reduce fruit weight and increase soluble solids,<sup>183</sup> by either concentrating soluble solids and/or by retarding of shoot growth and increasing assimilate partitioning to the fruit.

Rootstock can influence the tolerance of persimmon to low soil moisture, as the drought tolerance of *D. kaki* and *D. virginiana* is higher than *D. lotus*.<sup>184</sup> In southern China, persimmon can be successfully cultivated in drought prone regions when it is grown on a *D. oleifera* rootstock. Biological characteristics differ between rootstocks,<sup>185</sup> but the physiological basis of drought tolerance between species is presently not well understood.

Mineral nutrition can be influenced by moisture stress. In extremely dry summers, leaf symptoms associated with magnesium deficiency can occur on fruiting trees.<sup>186</sup> A moderate moisture stress was found to improve the leaf nitrogen content of persimmon in comparison with a higher and lower moisture stress.<sup>175</sup> Manganese toxicity causes 'green blotch', a physiological disorder of the fruit peel.<sup>187</sup> A high calcium to manganese ratio can ameliorate the severity of manganese toxicity.<sup>188</sup> In soils prone to 'green blotch' the severity of the disorder is increased by low transpiration rates reducing the calcium supply to the fruit. Because the major period of calcium uptake coincides with fruit growth stage I,<sup>47</sup> the calcium content of fruit may be reduced by water stress occurring over this growth stage.

Plant water relations within the persimmon tree have received limited attention. The stomatal conductance and transpiration ratio of persimmon is low to moderate (207 mmol m<sup>-2</sup> s<sup>-1</sup> and 1.4 mmol CO<sub>2</sub> mol H<sub>2</sub>O<sup>-1</sup>, respectively) in comparison with other fruit crops.<sup>108</sup> Persimmon appears to be very sensitive to water stress with stomatal conductance falling rapidly with only slight increases in leaf water potential from 0.2–0.6 MPa.<sup>189</sup>

## B. WATERLOGGING STRESS

Persimmon has been reported to grow in wet sites on heavy soils.<sup>1</sup> However, the drainage of the soil is more important than soil type,<sup>190</sup> because the growth of persimmon seedlings is retarded when soils are maintained at a high moisture content throughout the year.<sup>174</sup> The rootzone is predominantly found in the upper soil layer,<sup>178,179</sup> and growth can be retarded when the water table rises to <350 mm below the soil surface for extended periods.<sup>191</sup> Tree growth and fruit yield can be poor when grown under waterlogged conditions (soil moisture tension < 2 kPa) for 80% of the year. In contrast, moist soils (soil moisture tension > 2 kPa for 50% of the year) enhance tree growth and yield.<sup>180</sup> Waterlogged soils may cause damage to root systems by oxygen deficiency as a result of changes in the redox potential.<sup>192</sup> Persimmon seedlings were found to exhibit normal root growth down to a soil oxygen concentration of 5% v/v,<sup>193</sup> and have been reported to tolerate a lower soil oxygen concentration (1% O<sub>2</sub>) than apple, pear, and peach seedlings.<sup>194</sup> Persimmon may have a greater resistance to Fe<sup>++</sup> and H<sub>2</sub>S injury than fig, peach, and pear.<sup>192</sup>

Waterlogging can reduce the yield of persimmon by increasing fruit drop<sup>181</sup> and by reducing fruit size. Techniques such as forced soil aeration by compressed air have been found to be effective in increasing the soil oxygen concentration and improving shoot growth and the soluble solids content of fruit.<sup>195</sup>

## C. HUMIDITY STRESS

Fruit staining, a physiological disorder, significantly reduces the external quality of persimmon. This disorder is characterized by dark staining of the surface of ripe fruit and may also have a cloudy, fine crazing, or smudged appearance. Staining develops over the final stages of maturation and is associated with a high relative humidity (>90% RH) over the 2 months prior to harvest.<sup>196</sup> During fruit enlargement, cuticular cracks can form which extend into sub-epidermal cells.<sup>197</sup> Cuticular cracks occurring in stage I of fruit growth form a protective suberized cell layer, but cracks occurring in stage III form no protective layer.<sup>198</sup> The severity of cuticular cracking can differ between cultivars and is related to differences in fruit growth patterns and cuticle thickness.<sup>199</sup> The incidence of cuticular cracking increases with irrigation and other factors stimulating excessive fruit growth during stage III.

The presence of unprotected cuticular cracks can provide entry to fruit tissue by pathogens, pesticide sprays and water under conditions of high relative humidity or rainfall. Pesticides and rainwater cause black stains by the oxidation of polyphenolic compounds in exposed epidermal and sub-epidermal



**Photo 3** Plastic covers to reduce the effect of water on the fruit surface.

cells.<sup>126,200</sup> Anthracnose (*Glomerella cingulata* Spaulding et Schrenk) and alternaria (*Alternaria* sp.) can invade the fruit through cuticle cracks under conditions of high humidity. Water can also cause physical damage to the fruit surface by osmosis drawing water into exposed sub-epidermal tissue, resulting in localized splitting of the cuticle and subsequent fruit softening. Cultivars with a high soluble sugar concentration (i.e., >16% soluble solids) are more prone to this disorder than those with lower soluble solids.<sup>201</sup> This is consistent with the disorder having an osmotic component. The change in turgor pressures in localized regions of water absorption may exceed the strength of the cuticle or of cell walls in sub-epidermal regions.

Staining can be reduced by lowering within-canopy humidity through summer pruning, the application of protective calcium and plastic polymer sprays to cuticular cracks, and the exclusion of water from the fruit surface by bagging or growing trees under plastic covers (Photo 3).<sup>201,202</sup>

## VI. WIND

Wind can modify the surrounding thermal environment of a tree and temperatures of specific plant organs. In temperate zones, the amount of heat units over the growing season can be marginal for growth and development. Wind during the period between bud-break and anthesis can delay flowering and reduce leaf size by lowering orchard temperatures. Fruit development can also be delayed by wind cooling exposed fruit. In areas prone to wind, natural and artificial wind breaks are used to raise orchard temperatures<sup>203</sup> and reduce the effects of wind damage.<sup>204</sup>

Wind can cause physical damage to plant organs. Persimmon leaves are large (70–100 cm<sup>2</sup>) and prone to damage. Physical damage of emerging shoots and leaves, by spring winds, reduces the potential bearing surface and leaf area in an orchard. Bacterial blast (*Pseudomonas syringae* van Hall) and grey mold (*Botrytis cinerea* Persoon) can enter leaf tissue through wind damaged leaves and shoots causing further loss in leaf area. Persimmon is also prone to branch and trunk breakage in strong winds. The trees require staking when young and the development of a strong branch framework to reduce tree damage by wind in future years. Salt laden wind can cause injury and leaf fall in persimmon<sup>205</sup> when the salt content on leaves reaches 0.3 mg/cm<sup>2</sup>.<sup>206</sup>

The loss of leaf area by wind damage in the early stages of fruit growth can cause fruit drop, while damage in later stages reduces the soluble solids content of fruit.<sup>84</sup> A premature loss of leaf area lowers the carbohydrate status of a tree and reduces flower evocation and fruiting in the following season. Wind rub can be major cause of fruit blemish. Trellising of trees and the use of wind breaks have been effective in reducing the incidence of wind rub in New Zealand orchards (Photo 4).

Persimmon pollen can be carried great distances by wind,<sup>207</sup> but it is not effective in transferring pollen to female flowers.<sup>208</sup> Some air movement around persimmon is beneficial. Wind can lower relative humidity in and around the tree, and subsequently reduce humidity related problems. Low wind flows of 2 l<sup>-2</sup> dm<sup>-2</sup> min<sup>-1</sup> can enhance photosynthetic activity in persimmon.<sup>107</sup>

## VII. CONCLUSIONS

Persimmon will grow under a wide range of environmental conditions, but when grown as a fruit crop, production and market needs tend to restrict the suitable environmental range. The length of the growing



**Photo 4** An artificial windbreak with natural shelter in the background.

season required to mature fruit, rather than winter temperatures, may be the major limitation to persimmon cultivation in cool temperate climates. The recent selection of early ripening cultivars<sup>148</sup> may expand the range of persimmon cultivation to climates with a short growing season. Frost damage during the growing season can adversely affect plant growth and fruiting in temperate regions. Areas prone to frost damage over the growing season may require frost protection by using overhead irrigation, wind machines, or careful site selection.

The low dormancy requirement of many persimmon cultivars allows the tree to be grown in the tropics. However, careful selection of site would be necessary to minimize the affect of environmental stress on productivity, fruit quality, and tree health.

The productivity of persimmon is very sensitive to assimilate supply during the period from flower evocation to fruit set.<sup>81,209</sup> Environmental factors that reduce photosynthetic activity including low irradiance, high temperatures, drought stress, and defoliation by wind may all have a deleterious effect on fruit set and fruit development. Techniques to minimize stress include the use of pruning and training systems to improve light distribution in the canopy, pollination to increase fruit sink strength, irrigation, and the use of windbreaks. The quality and composition of fruit can also be affected by factors influencing photosynthetic activity. Temperature can affect flower and fruit growth, color development, and fruit astringency.<sup>139</sup> High temperature stress during flower development reduces flower size and over growth stage II, delays maturation, and reduces fruit size. The cultivation of non-astringent cultivars is unsuitable in climatic regions with low summer temperatures, as the fruit can remain astringent at harvest. Fruit temperature can be increased by exposing fruit to full sun, or by raising ambient temperatures through the use of shelter and plastic covers.<sup>123,202,210</sup> However, excess exposure of fruit should be avoided in areas with high irradiances as this can cause blemishes through sunburn and fruit spotting<sup>59,127</sup> (see Section III.C, Irradiance). Wind, humidity, rainfall, and hail over fruit development can also cause blemish through physical damage and cuticular cracking.<sup>31,83,127,196,200</sup>

Opportunities exist for reducing some of the present environmental limitations to persimmon cultivation by better understanding the whole plant effects of a particular environmental stress. Carbon assimilation and allocation within a persimmon tree has received little attention, though this process appears to be very sensitive to irradiance, temperature, and drought stress. The recent development of models describing seasonal changes in the tree and canopy structure of mature persimmon trees, and the radiation flux at leaf surfaces within the canopy<sup>23,211,212</sup> will assist in better understanding whole plant interception of light. The use of phenological approaches to describe and quantify whole plant responses to stress could also assist in better defining the effect of environment on the growth and development of persimmon.<sup>22,213,214</sup> Plant improvement could be used to select cultivars with high A rates and better partitioning. A dwarf bud mutation of the cultivar Nishimura wase has been shown to have thicker leaves and higher photosynthetic activity on a leaf area basis than the original form of Nishimura wase.<sup>67</sup> The selection of dwarf cultivars with lower wood to leaf biomass ratio may increase carbon gain through a reduction in whole plant respiration. The selection of rootstocks that improve plant water relations may increase tolerance to conditions of drought or flooding and may serve to maximize carbon gain under a range of climatic and edaphic conditions. The selection of cultivars and rootstocks with improved

partitioning could improve productivity and fruit quality, reduce fluctuations in bearing and enhance fruit set under adverse conditions.

Expansion of the area of persimmon under cultivation is occurring outside the major production areas. This has been due to consumer demand for "out of season" fruit in traditional markets and an increasing demand for exotic fruit in non-traditional markets. Knowledge and management of environmental stress, particularly in areas of marginal adaptation, will be critical in meeting these market demands and for minimizing production failure.

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## Chapter 9

# Stone Fruit

James A. Flore

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## I. INTRODUCTION

When does the environment limit yield, fruit quality, and/or longevity of stone fruit, and which environmental conditions are most limiting? Clearly, these questions cannot be resolved unless one has a thorough understanding of the crop, coordination of growth and development in that crop, and the impact of the environment on the physiology of the plant. Herein, the effect of light, water, and temperature and other environmental inputs are reviewed in relation to carbon assimilation and the longevity and productivity of *Prunus*. Emphasis is on cherry and peach, the principles, however, can be applied to most stone fruit crops in different locations.

The reader is referred to several reviews and books on *Prunus* growth and physiology, or on environmental physiology for more information.<sup>1-5</sup>

### A. BOTANICAL DESCRIPTION, ORIGIN, AND HABITAT

Stone fruit are members of the Rosaceae, subfamily Prunoidea.<sup>1</sup> The genus *Prunus* includes peach, nectarine, plum, cherry, apricot, and many species used as rootstocks. The basic chromosome number varies from 16 to 176. Stone fruit may be deciduous or evergreen. The fruit is classified as a drupe, and is usually one seeded. Fruit growth is described as double sigmoidal, with rapid growth during cell division, followed by a period of slow growth during pit hardening, and then a period of rapid cell enlargement.<sup>6</sup>

Commercially important species of *Prunus* originated between eastern Europe and western China. They have a broad range of adaptability to environmental stress and wide distribution between the latitudes of 30–40° where light levels are high, skies are clear, and seasons are long and dry. In humid environments *Prunus* spp. are sensitive to a broad range of diseases. Compared to apple, stone fruit generally are less winter hardy and bloom earlier than apple, thus limiting their range of commercial importance. They are considered to be more sensitive than apple to high water tables, and require sites that have good water and air drainage, or must be grafted (e.g., plum) to rootstocks that allow them to tolerate anoxic conditions.

## II. GROWTH AND DEVELOPMENT

In relation to many other fruit trees, *Prunus*, particularly cherry, peach, and nectarine, have a shorter life cycle. *Prunus* generally bear fruit at an early age, and the fruiting period lasts 5–35 years. Each stage of plant growth and development is strongly limited by the environment which can have a major effect on survival and development (Table 1).

Time to establish full canopy varies with species (peach is generally faster than cherry), and location. For example, peach canopy development in Michigan may require 4–6 years and only 3–4 years in California. Most stone fruit have the potential to fruit the year after planting. However, the primary objective during this period is to maximize vegetative growth to fill the allotted space in the orchard. For many crops (i.e., apple, pear), it is recognized that cropping is essential for growth control. In cherry, for example, cropping may not be desirable until trees are 6 or more years of age when the trunk diameter is large enough to allow for mechanical harvesting. The strategy during this phase of

**Table 1 Life cycle phases for *Prunus* and major environmental constraints during each phase**

| Species                            | Phase of development      |                           |                     |                                    |
|------------------------------------|---------------------------|---------------------------|---------------------|------------------------------------|
|                                    | Propagation               | Canopy development        | Maturity cropping   | Senescence                         |
| <b>Duration in years</b>           |                           |                           |                     |                                    |
| Peach                              | 1–2                       | 3–6                       | 3–25                | >25                                |
| Plum                               | 1–2                       | 5–10                      | 5–35                | >35                                |
| Apricot                            | 1–2                       | 3–6                       | 3–35                | >35                                |
| Cherry                             | 1–2                       | 5–10                      | 5–35                | >35                                |
|                                    | Management strategy       |                           |                     |                                    |
|                                    | Promote vegetative growth | Promote vegetative growth | Reproductive growth | Environmental or biological stress |
| <b>Major environmental factors</b> |                           |                           |                     |                                    |
|                                    | Nutrition H               | Water M                   | Irradiance H        | Temperature H                      |
|                                    | Water H                   | Nutrition M               | Temperature H       | Water H                            |
|                                    | Soil pests H              | Pest control H            | Water M             | Pest H                             |
|                                    | Foliage pests H           | Site selection H          | Nutrition M         |                                    |
|                                    | Weed control H            | Temperature H             | Pest control M      |                                    |

Note: H = high; M = moderate; L = low.

development is to fill canopy space and promote vegetative growth followed by reproductive bud development.

Cold temperatures during dormancy and in the spring are the most limiting factor for fruit trees grown in regions near the latitude range for peach and cherry. Nearer the equator the opposite is true and inadequate cold temperature for chilling is a problem. A plant architecture that maximizes light interception and minimizes shading is particularly important to conserve moisture during the fruiting stage unless irrigation is provided as in many arid regions of the world. Soil moisture during the growing season may also be a major limitation. When grown in the northern U.S., temperature is the main problem affecting tree longevity, while biological stress is more important in areas with milder temperatures.

## A. ANNUAL LIFE CYCLE OF MATURE TREES

Several physiological, developmental, and growth processes are initiated at different times during the annual cycle for stone fruit. Periods of initiation and maximum activity are highly dependent upon the species and the cultivar, the location, crop load, and the environment. Since it is difficult to develop a common generic model that describes each cultivar at each location, this section will emphasize sour cherry in Michigan conditions as an example (Figure 1). Similar models could or have been developed for other *Prunus* spp.<sup>7,8</sup>

### 1. Vegetative Growth

Root growth development occurs before shoot development. A bimodal periodicity of root growth occurs for many fruits crops, characterized by a flush of growth in the spring prior to vegetative bud break and again in the fall when vegetative growth has stopped.<sup>9</sup> The common explanation for this observation is that the above and below ground parts of the tree are in competition with one another for resources, and that the above ground parts have priority. The few studies that have been conducted on the seasonal root growth periodicity in *Prunus* spp. do not support the observation that root growth stops during periods of high sink demand by the above ground part of the plant. Atkinson and Wilson<sup>10</sup> reported a single peak of growth for 'Merton Glory' sweet cherry that extended from May until mid-July or mid-August for F12/1 and Colt rootstocks, respectively, in southeast England. Beckman<sup>11</sup> found that *Prunus mahaleb* L. and *P. avium* L. cv. Mazzard rootstocks displayed a marked reduction in root

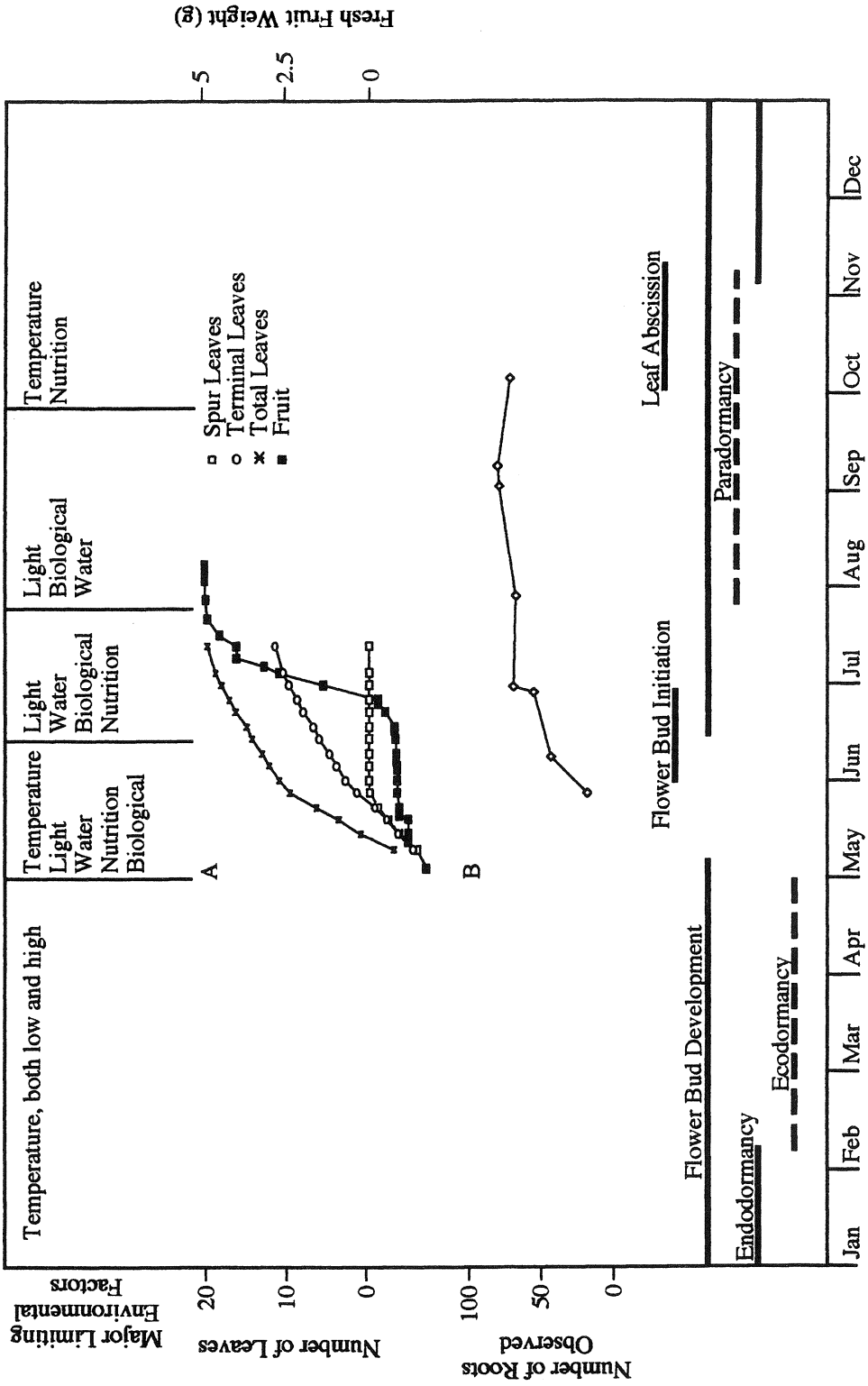


Figure 1 Vegetative and reproductive growth and the important environmental limitation during the annual growth cycle of mature 'Montmorency' sour cherry under Michigan conditions. (A, from Eisensmith et al.,<sup>14</sup> B, from Flore et al.<sup>12</sup>)

growth potential during first leaf expansion but recovered later in the season. Williamson and Coston<sup>12</sup> demonstrated that maximum root growth occurred for peach during the summer, after the cessation of shoot growth but prior to abscission. Recently, using a minirhizotron camera to observe root growth of sweet cherry ('Emperor Francis' on Giessen 148/1 rootstock), Flore et al.<sup>13</sup> observed a single peak of root activity that extended throughout the summer period. Most of these studies have been conducted on young non-bearing trees, thus there is a need for further study to determine if there is preferential partitioning of carbon to roots or arboreal plant parts during different phases of growth, or in response to different types of environmental stress.

After sufficient chilling temperatures have occurred to release dormancy, the initiation of bud growth in the spring is a temperature dependent process. Accumulation of heat is generally calculated in terms of the number of growing degree days (GDD) or of growth degree hours (GDH). Eisensmith et al.<sup>14,15</sup> found that sour cherry leaf emergence was highly correlated with degree-day accumulation at a base of 4°C, and that shoot extension ceased about 350 (20–23 days) and 850 (55–65 days) degree-days after first leaf emergence for spur and terminal shoots, respectively. Leaf size increased linearly with degree-day accumulation until full expansion. This approach has also been used for peach.<sup>16</sup>

Vegetative and reproductive buds may have different chilling requirements or different temperature thresholds for growth. Vegetative and reproductive buds do not always break at the same time. At locations nearer the equator reproductive growth usually occurs first, followed by vegetative growth, but may coincide with vegetative development at distances farther from the equator.<sup>17,18</sup> Temperature is locally perceived by buds; and has been shown not to be affected by soil temperature. In an attempt to delay bud break, Hammond and Seeley<sup>19</sup> modified soil temperatures around roots of peach and cherry prior to anthesis, but there was no advance or delay of bud development from any of the treatments except when the soil was frozen.

Vegetative bud development depends upon the temperature to which each bud is exposed. Buds on apple<sup>20</sup> or cherry<sup>21</sup> can be locally affected by mist cooling, which may delay bud break up to 3 weeks. On the other hand, localized heat can accelerate bud break and growers are placing plastic bags over dormant buds to advance their development.<sup>22</sup> Terminal buds outside the bag were unaffected.

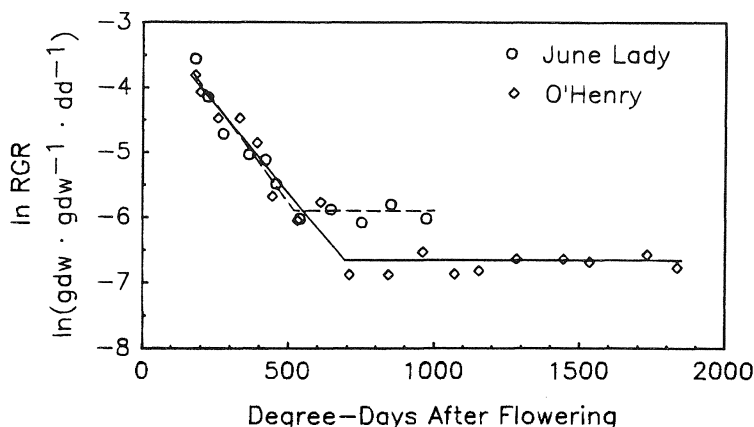
Foliage development of *Prunus* can be classified as either terminal shoots or as lateral shoots, and/or spurs. The proportion of each depends on the species, the cultivar, the degree of fruiting, and tree vigor. Peach and cherry have simple buds, either vegetative or reproductive. Flower buds are found in the lateral position on shoots and spurs; the proportion between shoots and spurs is variety and age dependent.<sup>23</sup> As vigor decreases the number of nodes that have flower buds increases and the number of spurs decreases.<sup>24</sup> A similar response occurs in peach under drought.<sup>25</sup>

Foliage and fruit development may be in competition for the same carbon resources early in the season.<sup>8,26,27</sup> In sour cherry, vegetative growth is greatest during stage I and early stage II of fruit growth, and is completed by fruit harvest. In contrast to cherry, terminal growth on shoots and laterals of peach progress throughout the summer, often setting terminal bud during periods of environmental stress at or just before harvest, and resuming shortly after the stress has been eliminated. Once the terminal bud is set, shoot growth does not stop. Shoot and trunk growth of *Prunus* will continue to grow in girth until leaf fall. This initial phase of vegetative development is primarily driven by increasing temperature, but sustained growth is contingent upon internal factors (e.g., degree of competition and environmental factors such as soil moisture, vapor pressure deficit, light, temperature, and nutrition).

## 2. Reproductive Growth

The double-sigmoidal growth curve of stone fruit has been described as having three stages: stage I, the period of cell division; stage II, the slow growth phase that coincides with the period of pit hardening; and stage III, the period of cell enlargement.<sup>6,28</sup> It has been estimated that 50–80% of peach and cherry fruit growth may occur during stage III. More recently, DeJong and Goudriaan<sup>8</sup> have reevaluated the double-sigmoidal growth pattern for peach and have related the relative growth rates of the fruit to degree-days after flowering (Figure 2). Their results indicated that there were actually two physiologically distinct phases of sink activity instead of the three stages that are traditionally recognized, and that the traditional stage II of fruit growth is apparently a function of the timing of the shift between these two phases.

They also showed that each of these phases were linearly related to degree day accumulation using an upper and lower threshold of 35 and 7°C, respectively. The slopes of the relationships are similar between growth and degree days between varieties, but the transition points occurred at different points



**Figure 2** Relative fruit growth rates of 'Spring Lady' under California conditions. Reprinted with permission from DeJong, T. M. and Goudriaan, J., *J. Am. Soc. Hortic. Sci.*, 114, 800, 1989.

after flowering. Stages of fruit development for 'Montmorency' sour cherry can also be predicted by degree day accumulations.<sup>7</sup>

Fruit of sour cherry 'Montmorency' accumulated 164 mg (7.5 mg/day), 28.9 mg (2.4 mg/day), and 320 mg (15.2 mg/day) of carbohydrate during stages I, II, and III, for periods of 22, 12, and 21 days of growth, respectively.<sup>26,27</sup> Haun and Coston<sup>29</sup> predicted daily growth and development of peach leaves and fruit to different environmental factors. They found that maximum and minimum temperature, soil moisture, and age were among the most important variables affecting leaf and fruit growth.

Under Michigan conditions flower bud initiation for sour cherry and peach occurs from 3–4 weeks after bloom through terminal bud set and does not seem to be influenced by photoperiod.<sup>1,30</sup> For other stone fruit in locations around the world, flower bud initiation can range from 3–4 weeks after bloom until just after terminal bud set, or fruit harvest.<sup>1</sup> Location, cultivar, and cultural practices can have a profound effect on the time of initiation within a given year. The initial change from vegetative to the reproductive stage in sour cherry under Michigan conditions is evident 4 weeks after anthesis, sepal primordia form by July 30 and petal primordia are evident by August 15.<sup>30</sup>

### 3. Dormancy

*Prunus* vegetative and reproductive buds go through three distinct stages of dormancy, and Lang<sup>31</sup> has defined those stages as follows. During paradormancy, buds are dormant from the inhibitory influences of other plant parts. Endodormancy is related to factors inside the affected structure, and during ecodormancy, the dormant structure has the capability to resume growth once favorable environmental conditions are met. Endodormancy cannot be broken until a certain chilling requirement has been met. During dormancy, chilling is an important limiting factor at latitudes near the equator. At distances farther from the equator, cold temperature injury to the buds and tree is more important (see next section for a discussion of cold hardiness).

### 4. Storage Carbohydrates

Storage carbohydrates are necessary to sustain growth under periods of stress, during dormancy, and are important during initiation of growth in the spring. Nonstructural carbohydrates of stone fruit change quantitatively and qualitatively during the season.<sup>17,32</sup> Nonstructural carbohydrates in sweet cherry consist mainly of starch, sorbitol, sucrose, fructose, glucose, and raffinose. Keller and Loescher<sup>17</sup> reported that total nonstructural carbohydrates (TNC) were the highest at leaf abscission. Shortly before budbreak, TNC decreased in all perennial tissues except the spurs where they increased. TNC then increased slowly once provided with current year's assimilate until fruit harvest, after which they accumulated at a higher rate. Starch was the most common storage material, sucrose the most predominant soluble carbohydrate during dormancy and sorbitol the most common soluble carbohydrate during spring bud break. Keller and Loescher<sup>17</sup> speculated that if flower buds developed earlier than vegetative buds as they do in the northwest U.S., then flower development must rely upon TNC reserves until enough photosynthetic leaf area was present to provide sufficient photosynthate.

Kappes<sup>27</sup> found that for sour cherry, net export from a terminal shoot did not occur until 17 days after leaf emergence when the shoot was approximately one quarter (27%) of total dry matter accumulation. Under simulated conditions, Johnson and Lakso<sup>33</sup> found that spurs and shoots on apple did not begin to export carbon to the rest of the plant until 15–25 days after budbreak, and that short shoots began earlier than long shoots.

The amount of storage TNC is dependent upon the duration of the foliage in the fall between harvest and leaf fall. Respiration rate during the winter months has also been negatively related to yield the next season.<sup>34</sup> Both of these processes are temperature dependent. In the spring the plant must rely on carbohydrate storage until it becomes a net assimilator. During this period there are considerable demands on storage carbohydrate from roots, leaves, and developing fruits. Therefore environmental conditions at and immediately after bud break are important in determining current carbohydrate supply. Light and temperature are the most critical. During stage II of fruit development, demand for carbohydrate by the fruit decreases<sup>8,27</sup> and most of the carbon produced is partitioned into vegetative growth. Environmental constraints on carbon assimilation and supply could be limiting at the end of stage II and the beginning of stage III of fruit growth if sink activity is greater than the daily supply of carbon. (See Section VI.C.1 for a discussion on deficit irrigation.) Moreover, light, temperature, and evaporative demand are at their peak this period. Demands for carbohydrate at this time include: fruit enlargement and flower bud development; if carbon is limiting, it could affect flower bud initiation or development.

After harvest, carbohydrate demands are reduced considerably especially if new vegetative growth has ceased. Biological stress, such as leaf damage due to disease or insects, remain important because damage to leaves, or loss of leaves, can reduce the amount of storage carbohydrate available for next season's growth. There is a positive relationship for the length of time between harvest and leaf abscission and fruit production the following year.

### III. PHOTOSYNTHESIS

#### A. INTRODUCTION

The process of photosynthesis is fundamental to plant productivity, and any factor or stress that limits this process may potentially reduce yield. However, only under certain circumstances does photosynthetic rate limit yield.<sup>3,35</sup> It was proposed<sup>35</sup> that photosynthetic potential in fruit crops is under two forms of control: (1) environmental, which influences physical and biochemical reactions directly and/or by affecting the development of the leaf and the manufacture of photosynthetic machinery available to convert CO<sub>2</sub> to carbohydrate; and (2) through sink demand which controls photosynthetic rate through some type of feedback signal from the sink itself. (See Reference 3 for an in-depth discussion.)

Scurlock et al.<sup>36</sup> presented an equation with four factors that define the quantitative relationship between photosynthesis and plant productivity, where biomass gain (Pn) is affected by the quantity of incident light (Q), the proportion of the light that is intercepted by the plant ( $\beta$ ), the efficiency of photosynthetic conversion of the intercepted light into biomass ( $\epsilon$ ), minus respiratory losses of biomass (R).

$$Pn = Q \cdot \beta \cdot \epsilon - R \quad (1)$$

The quantity of the incident light is determined by the location, day of the year (day length), and length of the season, and cannot be easily manipulated unless the plants are grown in a controlled environment facility supplemented with artificial light. The efficiency of light interception  $\beta$  is directly related to the development, magnitude, and duration of foliage, as well as the light absorption characteristics of the individual leaves. Light absorption characteristics of individual leaves can be optimized by changing canopy structure, tree architecture, and planting system, and likely has a greater effect on biomass productivity than any other factor.

Efficiency of energy conversion ( $\epsilon$ ) refers directly to the photosynthetic process, and is most usually reported as a rate of CO<sub>2</sub> fixed per unit area, per unit time. Flore and Lakso<sup>3</sup> have suggested units for expression that shall be used throughout the text (Table 2).

The  $\epsilon$  is fairly constant and not of great concern unless the leaf is below light saturation, which may occur either in the interior of the canopy or under environmental stress.

Carbon loss due to dark respiration: can range from 10–20% of maximum net photosynthesis; is temperature dependent, has  $Q_{10}$  that range from 1.8–2.1;<sup>37</sup> and can account for a substantial loss in

Table 2 Suggested items, units, and abbreviations for reporting gas exchange parameters

| Term  | Abbreviation | Units  |
|---|--------------|--|
| Net carbon dioxide exchange (i.e., photosynthesis or assimilation rate) | A            | $\mu\text{mol m}^{-2}\text{s}^{-1}$            |
| Gross carbon exchange   | $A_g$        | $\mu\text{mol m}^{-2}\text{s}^{-2}$            |
| Long term dry weight (24 h; net assimilation rate or crop growth)       | C            | $\text{kg dry matter m}^{-2} \text{ day}^{-1}$ |
| Transpiration (water loss by the leaf)                                  | E            | $\text{mmol m}^{-2}\text{s}^{-1}$              |
| Conductance   |              |  |
| $\text{H}_2\text{O}$  | g            | $\text{mmol m}^{-2}\text{s}^{-1}$              |
| $\text{CO}_2$   | $g'$         | $\text{mmol m}^{-2}\text{s}^{-1}$              |
| Leaf  | $g_l$        | $\text{mmol m}^{-2}\text{s}^{-1}$              |
| Stomata   | $g_s$        | $\text{mmol m}^{-2}\text{s}^{-1}$              |
| Temperature   |              |  |
| Air   | $T_a$        | C  |
| Leaf or other plant surface   | $T_l$        | C  |
| Partial pressure of water vapor   | e            | kPa  |
| Vapor pressure gradient (leaf to air)                                   | VPG          | kPa  |
| Leaf area (single surface for photosynthesis)                           | L            | $\text{m}^2$                                   |
| Respiration   |              |  |
| Dark  | $R_d$        | $\mu\text{mol m}^{-2}\text{s}^{-1}$            |
| Photorespiration  | $R_i$        | $\mu\text{mol m}^{-2}\text{s}^{-1}$            |
| Concentration of $\text{CO}_2$  |              |  |
| Air   | $C_a$        | $\mu\text{mol mol}^{-1}$                       |
| Internal  | $C_i$        | $\mu\text{mol mol}^{-1}$                       |
| Photosynthetic photon flux (incident)                                   | PPF          | $\mu\text{mol m}^{-2}\text{s}^{-1}$            |
| Quantum flux of photons (absorbed)                                      | Q            | $\mu\text{mol m}^{-2}\text{s}^{-1}$            |

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carbon. Other than leaves and fruit, few studies have characterized respiration on woody plants (see Chapter 2 for references) or on the effect of temperature on respiration rates of woody plants. It has been estimated that 40–60% of gross photosynthesis of cool temperate forests is lost due to respiration.<sup>38</sup> Grossman and DeJong<sup>39</sup> have reported  $Q_{10}$  of approximately two for leaves and stems of peach between 20° and 30°C, with lower values for leaves above 30°C. They reported that the specific respiration rate at 20°C of leaves and stems declined rapidly from the spring to a constant rate by summer, and that although trunk biomass accounted for 80–90% of above-ground vegetative biomass, trunk respiration accounted for only 8–12% of above-ground diurnal respiration. They speculated that the large demand for carbohydrate imposed by the respiratory need of vegetative and reproductive organs, rather than a reduction in photosynthesis supply lead to source limited fruit growth.

It has been suggested that reducing dark respiration will increase biomass accumulation. Small adjustments in rate or  $Q_{10}$  probably would have little effect on carbon balance over the year, however, length and temperature of the night period and/or the dormant period would likely have a greater influence.

Re-examination of Equation 1 then would lead us to conclude that for *Prunus* the greatest gains in productivity would be achieved by increasing light interception, while optimizing environmental factors that affect the development of photosynthetic machinery rather than affecting the photosynthetic process directly. Current environmental and preconditioning effects of the environment will be discussed in the following sections.

## B. PHOTOSYNTHETIC CHARACTERISTICS OF STONE FRUIT

The net photosynthetic (A) characteristics of *Prunus* have been described in several studies (Table 3) and are typical of  $C_3$  plants. It is interesting to note that four of the five *Prunus* species, except apricot, have similar values. Maximum values of A ( $A_{\max}$ ) ranged from a low of 13.3  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in peach to a high of 21.5  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for sour cherry.<sup>3</sup>

DeJong<sup>40</sup> found that A, expressed on a leaf area basis, mesophyll conductance ( $g_m$ ), and leaf conductance ( $g_l$ ) to water vapor, were all linearly related to leaf nitrogen content. Leaf intercellular  $\text{CO}_2$  ( $C_i$ )

**Table 3 Reported and calculated gas exchange characteristics for peach, sweet cherry, sour cherry, plum, and apricot**

| Parameter   | Peach          | Sour cherry    | Sweet cherry   | Plum      | Apricot       |
|---|----------------|----------------|----------------|-----------|---------------|
| Maximum A at 350 $\mu\text{l l}^{-1}\text{CO}_2$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) | 13.3 $\pm$ 3.8 | 21.5 $\pm$ 6.2 | 17.9 $\pm$ 5.3 | 20.6      | 7.0 $\pm$ 0.1 |
| Carboxylation efficiency ( $\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )                            | 0.1–0.08       | 0.1–0.09       | 0.1–0.08       | 0.1–0.08  | —             |
| Apparent quantum yield ( $\mu\text{mol CO}_2$ fixed/mol PPF)  | 0.04–0.03      | 0.06–0.05      | 0.05           | 0.04–0.06 | 0.02–0.04     |
| Light compensation point ( $\mu\text{mol quanta s}^{-1} \text{ m}^{-2}$ )                               | 20–30          | 15–30          | 25–30          | 15–30     | 25–40         |
| CO <sub>2</sub> compensation point ( $\mu\text{l l}^{-1} \text{CO}_2$ )                                 | 66             | 40–60          | 56             | 61        | 69            |
| Net carbon exchange per unit of N ( $A_N$ nmol CO <sub>2</sub> mg N <sup>-1</sup> s <sup>-1</sup> )     | 6.39           | —              | 6.75           | 6.17      | 3.76          |

Data from References 3 and 40.

concentrations decrease slightly with increasing A rate and leaf N content, indicating that A rate was not being restricted by low  $C_i$  or  $g_i$  with lower assimilation capacity. Maximum A per unit of N was 6–7 nmol CO<sub>2</sub> mg N<sup>-1</sup> s<sup>-1</sup>. DeJong<sup>40</sup> and DeJong and Doyle<sup>41</sup> argue that photosynthetic rates expressed in terms of CO<sub>2</sub> fixed per unit of leaf N are just as valid as those expressed on a leaf area basis.

### C. SPECIES AND CULTIVAR DIFFERENCES

There is little genetic variation of A in *Prunus* reviewed in this chapter. Among the deciduous temperate fruits,  $A_{\text{max}}$  of sour cherry and sweet cherry rank near the highest, followed by peach which is similar to apple. DeJong<sup>40</sup> reported that the mean  $A_{\text{max}}$  rates of peach and cherry, as well as other *Prunus* except apricot, were very similar. Early reports indicated that peach had low photosynthetic rates. However, recently reported values were comparable to or higher than apple (18.0 vs. 15.7  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). Flore and Sams<sup>42</sup> reported differences between sweet and sour cherry and between different clones of sour cherry, and noted that spur type selections often had higher rates of A than the standard variety 'Montmorency'. Differences of this magnitude have also been shown for apple by Looney.<sup>43</sup> Respiration (R) could influence the overall carbon balance of the plant, especially if temperatures during the dormant period are high. Genetic variation for R exists in other plants but we know of no studies of this type for *Prunus*. It is a question that needs resolution. In comparison to other factors, genetic variation in  $\epsilon$  and R likely has little practical effect on fruit production in *Prunus*.

### D. LEAF AGE

Photosynthesis increases with leaf expansion and reaches a peak just before full development, then remains steady for a period of time before declining.<sup>3,44</sup> Roper and Kennedy<sup>45</sup> found that chlorophyll, stomatal conductance ( $g_s$ ), and quantum efficiency increased in sweet cherry as leaves expanded to a leaf plastachron index of 10, then remained constant until senescence. Andersen and Brodbeck<sup>46</sup> noted that  $g_s$  to water vapor approached maximum values in peach before  $A_{\text{max}}$  was reached. Net CO<sub>2</sub> assimilation and water use efficiency were greatest for recently expanded leaves and gradually declined with leaf age after full expansion. Leaf water potential ( $\Psi_l$ ) was similar for all leaf ages under field conditions. Leaf dry weight and chlorophyll per leaf increased with leaf age after expansion. Diurnal patterns of  $g_s$ , transpiration (E), and  $\Psi_l$  were similar for expanded spring- and summer-flush leaves. Minimum  $\Psi_l$  during midday (i.e., -2.4 MPa) were not associated with reduced  $g_s$ .

Normal decline in A after full leaf expansion can be ameliorated by the presence of fruit,<sup>47–49</sup> by decapitation or debudding,<sup>50</sup> by defoliation in sour cherry,<sup>51</sup> or by summer pruning.<sup>52,53</sup>

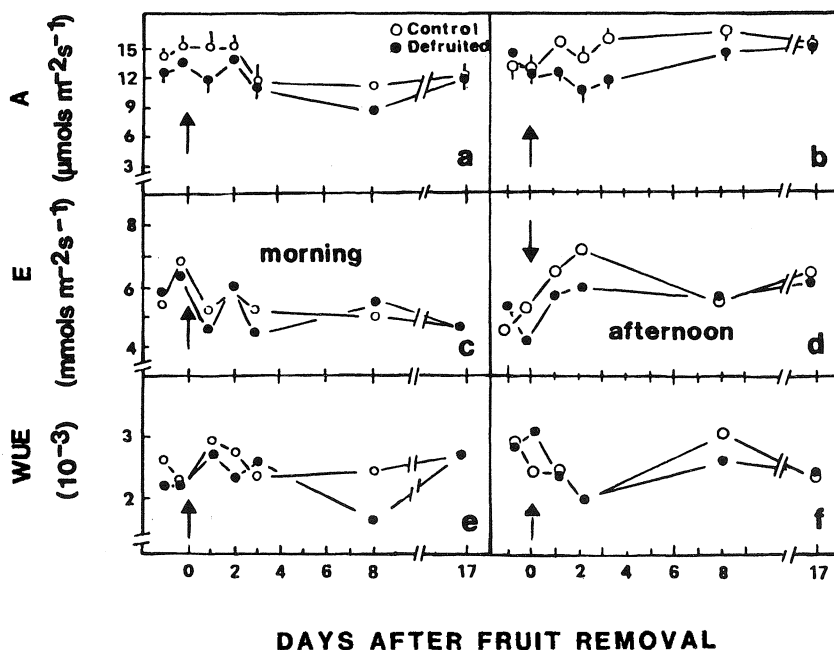
### E. SEASONAL INFLUENCE

Several whole season studies have been conducted on stone fruit. Usually single leaf or branch measurements are made at predetermined intervals, then are used to calculate an estimated seasonal profile.

Crop load and seasonal differences can affect this pattern. Sams and Flore<sup>44</sup> showed two very different patterns of  $A$  for sour cherry on the same trees in 1978 and 1979. They concluded that the differences were due in part to different crop loads (one heavy and the other light), and rate of leaf emergence and canopy development due to very warm vs. cool temperatures during the spring. There was a strong positive correlation between  $A$  and leaf emergence rate when vegetative growth was rapid under warm conditions, but not when conditions were cool which resulted in slow leaf emergence rates. Chalmers et al.<sup>54</sup> found that daily  $A$  rate for peach was closely related to demand, time of year, and location in the canopy.

## F. SINK ACTIVITY

Increased sink activity, either reproductive or vegetative or reduction in source supply, has been associated with an increase in rate of photosynthesis (see review by Flore and Lakso<sup>3</sup>). Direct positive effects of fruit sink strength for stone fruit have been shown for peach<sup>55-57</sup> and sour cherry,<sup>48</sup> for defruited cherry and plum,<sup>49,58</sup> and for defoliation.<sup>51,59</sup> DeJong<sup>56</sup> found that  $A$  and  $g_i$  were 11–15 and 30% higher, respectively, for fruiting compared to defruited trees. Minor changes in  $g_m$  and leaf nitrogen content were observed. It was concluded that the fruit effect on  $A$  was primarily related to stomatal behavior. The results of this study clearly indicate that the presence of fruit influenced stomatal regulation relative to plant water status in mature peach trees. Fruited trees maintained higher  $g_i$  for a given  $\Psi_i$  than in the de-blossomed trees. These data indicate that fruit may have specific influences on stomatal regulation in bearing trees rather than a more generalized “feedback inhibition” involving  $CO_2$  metabolism. Gucci et al.<sup>49</sup> investigated a possible feedback regulation of  $A$  by starch accumulation in defruited field grown sweet cherry. Defruiting decreased  $A$  by 43% and increased leaf starch content by 59% within 24 hours. Similar results were obtained with sour cherry<sup>48</sup> and by calculation from  $A/C_i$  curves, the stomatal contribution to the decrease of  $A$  from defruiting ranged from 32–40% in a controlled environment and from 25–45% under field conditions. There was a larger difference in  $A$  in the afternoon compared to the morning for both plum and sour cherry<sup>48,49</sup> (Figure 3). The large non-stomatal contribution to the



**Figure 3** Changes of leaf photosynthetic rate ( $A$ ), transpiration ( $E$ ) and water use efficiency ( $WUE$ ) of fruiting and defruited plum trees during stage II of fruit development in the morning and in the afternoon in 1987. Symbols are means  $\pm$  SE of 18–24 replicates (SE bars not shown if smaller than the symbol). Arrows indicate the date of fruit removal (16 June). Reprinted with permission, Gucci, R., Xiloyannis, C., and Flore, J. A., *Physiol. Plant*, 83, 497, 1991.

decrease of A after harvest and the changes in starch levels supported the hypothesis that defruiting results in end-product inhibition of photosynthesis.

Layne<sup>59</sup> altered assimilate supply in sour cherry trees by whole-plant partial defoliation or by continuous illumination.<sup>60</sup> Partial defoliation resulted in a photosynthetic enhancement within one day that was attributed to higher  $g_i$ , higher estimated photochemical and carboxylation efficiencies and higher ribulose-1,5-bisphosphate (RuBP) regeneration rates. Stomatal limitation to A increased from 20–35% within 24 hours, but fell back to predefoliation levels by day 3. The increase in A was associated with reduced carbon partitioning to starch and increased partitioning to sucrose and sorbitol. Photosynthetic enhancement was maintained over a 32 day period and senescence was delayed. Continuous illumination resulted in an inhibition of A within 24 hours that was attributed to lower  $g_i$ , lower estimated photochemical and carboxylation efficiencies and lower RuBP regeneration rates. Another study<sup>51</sup> demonstrated that photosynthetic compensation occurred in response to a partial reduction in leaf area in sour cherry. The threshold level of leaf area removal before A was significantly reduced by 20% defoliation. Carboxylation efficiency increased at 10 or 20% defoliation, and there was no significant increase in  $g_i$  or change in stomatal limitation to A. These studies are consistent with a type of feedback inhibition controlling A.

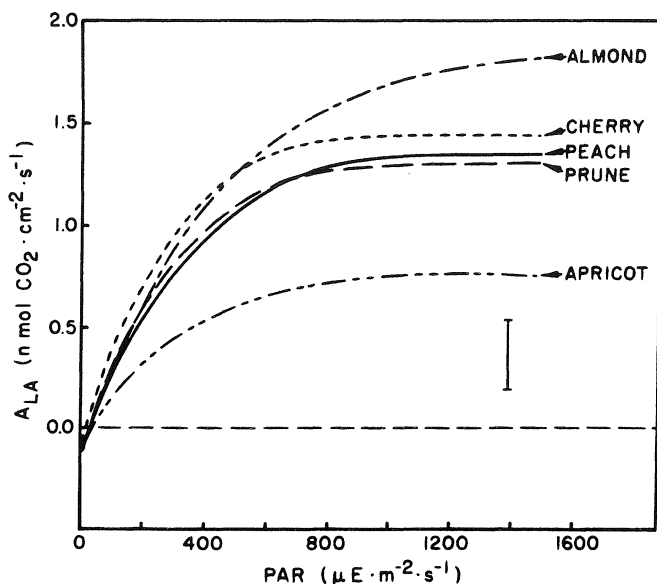
Maximum potential for efficiency of conversion can be affected by the environment, either by affecting the process directly as is the case for temperature, CO<sub>2</sub> concentration, light, and humidity, or longer term by affecting the development of the leaf and the amount of photosynthetic machinery present. Since A is influenced by many factors, such as season, age of tissue, fruit load, and environment, it seems dangerous to try to draw any conclusions concerning overall efficiency of conversion of energy without extensive studies.<sup>42</sup>

## IV. IRRADIANCE

The importance of light to stone fruit crop productivity has been the subject of several recent studies. Irradiance influences the energy balance of the plant, the photosynthetic capacity of the leaves and whole tree, and may influence responses that are either photomorphogenic (non-time-dependent) or photoperiodic (time-dependent). The amount of irradiation received by a plant is dependent upon the intensity and the duration of photosynthetic active radiation (PAR). The factors are predetermined by latitude, elevation, and slope of the site. In addition, light interception and shading within and between trees depends upon the degree of foliage development, tree shape and size, foliage density, and the geometry of the orchard. For many crops light interception has been positively related to dry matter production and yield.<sup>61</sup> Few studies have been conducted on stone fruit but in a preliminary report, Flore and Layne<sup>62</sup> found a linear relationship between yield and light interception for 8-year-old 'Montmorency' sour cherries when fruit set was high, with a strong tree shape interaction ( $r = 0.81$  for triangular shaped trees, and  $r = 0.4$  for rectangular shaped trees). Additionally, earlier high yields in terms of tree age have been found to be associated with high tree density, the implication being that light interception is maximized early in the development of the orchard.

### A. PHOTOSYNTHETIC RESPONSE

Light is the main driving force for photosynthesis, while temperature, water, CO<sub>2</sub>, and humidity play regulatory roles. Typical asymptotic photosynthetic response curves to increasing photosynthetic photon flux (PPF) have been reported for stone fruit with saturation occurring between 400–800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .<sup>55,63–65</sup> Apparent quantum efficiencies (Q) vary from 0.04–0.06  $\mu\text{mol CO}_2$  fixed/mol PPF (Table 3) for sun grown leaves. There seems to be little genetic variation for this trait when trees are grown under similar nonstress conditions. DeJong<sup>40</sup> compared photosynthetic responses in light for five *Prunus* spp., and although not reported, it appeared from his data that Q were about the same among species except apricot which was considerably lower. Light compensation points were similar (15–30  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), however saturation points differed, and ranged from 20% for sweet cherry to 40–50% for peach and other species (Figure 4). Sams and Flore,<sup>63</sup> and Kappel and Flore<sup>64</sup> have reported similar values for 'Montmorency' sour cherry, and 'Redhaven' peach, respectively. It is interesting to note that a small change on the lower part of the curve can result in a major change in A, while above saturation changes in PPF have little effect. Light response curves for whole canopies or branches often do not show a point of saturation (Figure 5). We did not find a point of saturation when using a whole plant chamber on mature sour cherry grown in a hedge row situation. Lack of saturation in a hedge row is not surprising



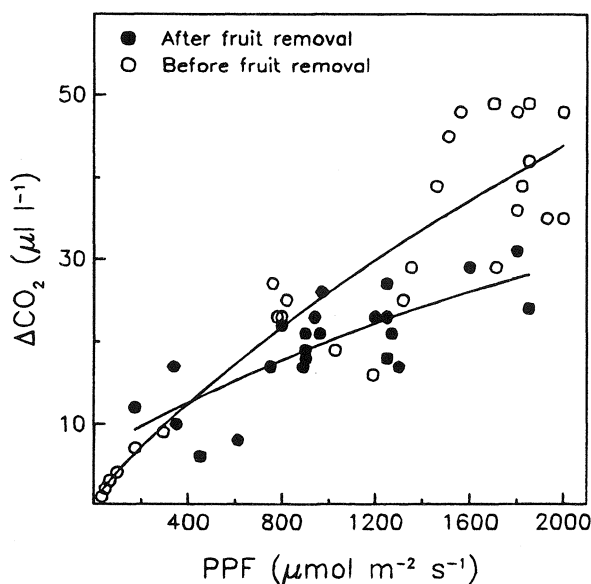
**Figure 4** Relationship between net  $\text{CO}_2$  assimilation ( $A_{LA}$ ) and level of photosynthetically active radiation (PAR) for 5 *Prunus* species. Each curve represents the mean response of 3 individual leaves for a given species. Reprinted with permission, DeJong, T. M., *J. Am. Soc. Hortic. Sci.*, 108, 303, 1983.

because of inter- and intra-tree shading. Leaves in the interior receive irradiance levels less than saturation, and may be exposed to levels near the compensation point.

Photoinhibition<sup>66</sup> may occur after several days of cloudy cool conditions followed by high light. In a preliminary experiment on sweet cherry grown under high light, then transferred to the dark at 5°C for 4 hours, followed by normal temperatures (20°C) for the rest of the dark period (10-hours total) and high light intensity,  $A$  dropped significantly for a period of several days,<sup>67</sup> and was associated with damage to PSII. This situation may occur under field conditions in the spring when temperatures are low, growth has started, and is followed by clear sunny days. This needs further study.

## B. ADAPTATION TO SHADE

Adaptation to shade or sun during or after leaf development is well documented for several species (see Flore and Lakso<sup>3</sup> for review). In general leaves developed under shade are thinner, less dense, have fewer layers of palisade cells, more intracellular spaces, have lower  $A_{max}$ , lower compensation



**Figure 5** Whole cherry tree photosynthetic response to increasing PAR grown in a hedge row, before and after fruit harvest. From Flore, J. A., unpublished data, 1993.

**Table 4 Available percent of full sunlight in cherry tree canopies after full foliage development at different locations within the tree, under sunny conditions**

| Distance from apex of canopy (m) | Available light (% full sun) distance from tree center (m) |     |     |     |     |     |       |
|----------------------------------|--|-----|-----|-----|-----|-----|-------|
|                                  | 1.5  | 1.0 | 0.5 | 0.0 | 0.5 | 1.0 | 1.5   |
|                                  | North  |     |     |     |     |     | South |
| 1.0                              | 36   | 10  | 5   | 5   | 6   | 6   | 58    |
| 2.0                              | 39   | 5   | 4   | 4   | 4   | 6   | 32    |
| 3.0                              | 4  | 2   | 3   | 4   | 3   | 5   | 5     |
|                                  | West   |     |     |     |     |     | East  |
| 1.0                              | 35   | 18  | 15  | 5   | 10  | 10  | 43    |
| 2.0                              | 21   | 7   | 8   | 4   | 4   | 6   | 14    |
| 3.0                              | 13   | 5   | 3   | 4   | 3   | 3   | 8     |

*Note:* Data are the means of three tree replications, determined between 1200 and 1400 hrs, August 25, 1978, standard 'Montmorency' 11-year-old, planted 24' × 20'. Reprinted from Flore, J. A., *Annu. Rep. Mich. St. Hortic. Soc.*, 111, 161, 1981. With permission.

points, and lower light saturation points. For fully expanded leaves, A rate was correlated to previous exposure, and shade induced loss of A was not readily reversible by re-exposure of the leaves through summer pruning or canopy manipulation. Peach<sup>64</sup> and sour cherry<sup>63,68</sup> responded in a similar manner in that  $A_{max}$ , light saturation point and light compensation points were reduced with no change in quantum efficiency when leaves developed in shade. Leaf thickness, leaf density, and chlorophyll a/b were decreased while leaf area and chlorophyll (on a dry weight basis) increased. In both species, leaves continued to thicken after full expansion, and as a consequence, shading had a similar but greater effect on leaves that were in the bud stage at the time of shading. Shading also increased shoot length and decreased shoot diameter.

### C. LIGHT DISTRIBUTION AND LEVELS IN TREE CANOPIES

Light interception and distribution depend on the leaf area index (LAI) or density of the foliage, the spacial distribution of leaves, and the shape and color of individual leaves. The penetration of light into a canopy decreases logarithmically with LAI from the top of the canopy to the bottom, and can be defined using Beers law with the following equation reported by Jackson,<sup>69</sup>

$$I_t/I_0 = e^{-kL} \quad (2)$$

where  $I_0$  = incident light above the canopy,  $I_t$  = light under the canopy,  $L$  = leaf area index, and  $k$  = the extinction coefficient for visible radiation. Reported  $k$  values range from 0.33 to 0.77 for apples, with means of 0.43,<sup>70</sup> 0.56,<sup>71</sup> and 0.60.<sup>72</sup> Recalculating the data in Kappel et al.,<sup>73</sup> for different training systems of peach,  $k$  ranged from 0.27 to 0.34 for peach. For sour cherry we have calculated a  $k$  of 0.33 for non-hedged trees (LAI of 6.2).<sup>74</sup>

The characteristic growth habit of peach and sour cherry may result in a mantle of dense foliage on the perimeter of the tree. This is more pronounced on sour cherry than peach, depends on the variety, the degree of spurs vs. long shoots, and is enhanced by summer hedging or topping. We have characterized light distribution in four different types of sour cherry orchard designs of different spacing, different tree shape, plus and minus summer hedging.<sup>62,75-77</sup> Regardless of system, light levels decreased rapidly from the exterior to the interior of the tree (see Table 4). Summer hedging increased the density of the foliage on the perimeter of the tree and caused a greater decrease in available light 0.5 m from the exterior of the canopy (Table 5). Triangle-shaped trees had higher light levels in the top of the tree (Table 6). Regardless of system, the available percent of full sunlight was often less than 20%. Leaf area index of non-hedged control trees and summer hedged trees for a period of 3 years were 6.2 and 7.5, respectively. It was concluded that: (1) foliage, and therefore shade, was fully developed within 60-65 days from bloom (see Section II.A.1, on foliage development); (2) triangular shaped trees in a N/S orientation had better light distribution in the top and center of the canopy when compared with standard non-hedged trees; and, (3) repeated hedging increased leaf density on the exterior of the tree

Table 5 Influence of summer hedging on light intensity in hedge row 'Montmorency' cherry tree canopies

| Pruning <sup>a</sup> system | Canopy position | Sunlight (% sky) |                  |      |
|-----------------------------|-----------------|------------------|------------------|------|
|                             |                 | Date             |                  |      |
|                             |                 | 5/5              | 7/1 <sup>b</sup> | 8/29 |
| Control                     | N               | 52               | 69               | 52   |
|                             | W               | 82               | 60               | 6    |
|                             | S               | 50               | 56               | 4    |
|                             | E               | 41               | 52               | 67   |
|                             | 3m              | 89               | 94               | 46   |
|                             | 2m              | 63               | 78               | 12   |
| P-1 <sup>c</sup>            | 1m              | 61               | 47               | 9    |
|                             | N               | 43               | 22               | 4    |
|                             | W               | 82               | 60               | 6    |
|                             | S               | 50               | 39               | 27   |
|                             | E               | 41               | 52               | 67   |
|                             | 3m              | 68               | 71               | 10   |
| P-3 <sup>d</sup>            | 2m              | 64               | 29               | 5    |
|                             | 1m              | 14               | 59               | 5    |
|                             | N               | 84               | 16               | 7    |
|                             | W               | 68               | 14               | 5    |
|                             | S               | 69               | 18               | 6    |
|                             | E               | 27               | 15               | 8    |
|                             | 3m              | 55               | 37               | 3    |
|                             | 2m              | 57               | 24               | 9    |
|                             | 1m              | 55               | 20               | 3    |

<sup>a</sup>Trees summer-pruned three 3 weeks prior to harvest. <sup>b</sup>Readings taken under cloudy conditions (320  $\mu$ E).

<sup>c</sup>Summer pruned in 1976, 1977. <sup>d</sup>Summer pruned in 1974, 1975, 1976, 1977.

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causing increased internal shading. Since currently there are no commercial plantings of sour cherry on dwarfing rootstocks, summer hedging is the only practical way to control tree size in a dense planting. Therefore it is necessary to supplement repeated hedging with dormant pruning to open "windows" of light into the interior of the tree.<sup>77</sup>

Kappel et al.<sup>73</sup> studied light levels in four different peach hedgerow canopies: oblique fan (OF), canted oblique fan (COF), modified central leader (MCL), and open center (OC). They found little

Table 6 Available percent of full sunlight in tapered cherry tree canopies after full foliage development at different locations within the tree, under sunny conditions

| Distance from apex of canopy (m) | Available light (% full sun) distance from tree center (m) |     |     |     |       |
|----------------------------------|--|-----|-----|-----|-------|
|                                  | 1.0  | 0.5 | 0.0 | 0.5 | 1.0   |
|                                  | West   |     |     |     | East  |
| 1.00                             |  | 40  | 19  | 76  |       |
| 2.00                             |  | 44  | 5   | 12  |       |
| 3.00                             | 17   | 4   | 10  | 8   | 10    |
|                                  | North  |     |     |     | South |
| 1.00                             | 70   | 83  | 19  | 100 | 97    |
| 2.00                             | 47   | 5   | 5   | 50  | 53    |
| 3.00                             | 8  | 6   |     | 15  | 4     |

Note: Data were determined between 1200 and 1400 hrs, September 11, 1980, 'Montmorency' spaced 20'  $\times$  12'. Reprinted from Flore, J. A., *Annu. Rep. Mich. St. Hort. Soc.*, 111, 161, 1981. With permission.

difference in light level in the canopy due to canopy training system except at 1 m above the ground. Hedging increased light in the interior of the canopy, but this advantage was lost by the end of the season. Mean LAI for these canopies were 4.57 for OF and 2.92, 3.30, and 2.96, respectively, for COF, MCL, and OC. Values below 30% full sun were rare, even in the center of the tree. As canopy depth increased, absorption of radiation of all wavelengths decreased, but not equally. Light wavelengths of 400 nm penetrated peach canopies the least. Thus interior leaves were exposed to a higher ratio of near infrared to red light than occurs in direct sunlight. We have found similar results for cherry,<sup>74</sup> and these results agree with those reported for apple.<sup>79</sup>

Light distribution and levels in peach canopies seem then to be highly dependent on tree vigor, crop load, duration of season, degree of pruning, and orchard system. When peach was grown in a non-hedgerow system, under a traditional open center training system, light levels were greatest at the tree perimeter, lowest midway between the periphery and the trunk, and intermediate at the center.<sup>80</sup> Light levels were very low at the tree center in mid-July, prior to pruning and topping, regardless of treatment (4–15% full sun). Summer pruning increased light penetration in the center of both ‘Loring’ and ‘Cresthaven’ trees while summer topping only improved it in ‘Cresthaven’. The authors concluded that this was probably because topping stimulated lateral shoot growth in ‘Cresthaven’ more than in ‘Loring’. This indicates that there may be strong cultivar differences in response to summer pruning and topping, and that regrowth is likely to be highly dependent upon timing. Also climate, variety, and vigor can affect light distribution.

#### D. MORPHOLOGICAL RESPONSE

Leaf adaptation to shade has been reviewed. In general, as shade increases, vegetative morphology of the tree changes to facilitate light harvesting. In shade, leaves are larger, flatter, thinner, and have more chlorophyll per unit weight or area. In addition, shoots are longer and thinner, leaf area and the number of lateral shoots and internodes are shorter, and whole tree dry weight is decreased.<sup>65,68,73,75,77</sup>

#### E. REPRODUCTIVE RESPONSE

Shade affects reproductive development of the current crop for peach and cherry (reduced color, reduced soluble solids, smaller fruit, delayed maturity, delayed abscission, reduced fruit set) and affects flower bud formation and fruit set the following year.<sup>65,68,73,75,76,81,82</sup> Timing of shade can influence the response. Shading had a profound effect on fruit maturation in sour cherry<sup>62,76</sup> as indicated by color and fruit retention force of the fruit. Fruit in the interior of the tree were often greener and harder to remove than those on the exterior. The degree of response depends on variety and on crop load (leaf to fruit ratio). Similar results have been reported for peach.<sup>65,73,80,81,83</sup> As load increases, shade delays maturity to a greater extent than for trees with a low crop. In a differential shading study, Marini et al.<sup>84</sup> found that time of shading was important for ‘Biscoe’ peach and that shading during the final swell of fruit development had the greatest effect on fruit weight and quality, while shading during stage II had little effect.

Light levels have also been associated with flower bud initiation in cherry. Through shading and correlations studies in the orchard, we have found that 15–20% of full sun is needed for flower bud formation in sour cherry.<sup>68,75</sup> Fruit set in large trees is adversely affected by levels of light below 20%.

Wood and bud hardiness are also influenced by shade. Cold hardiness of wood and buds during the acclimation period in the fall for ‘Redhaven’ and ‘Montmorency’ trees grown in pots was reduced as much as 9°C due to shading. Hardiness decreased as shading increased from 37% of full sun to 9%, and was associated with a decline in storage carbohydrate.<sup>85</sup> Shading whole peach trees also reduced hardiness during the acclimation period by 1–2°C.<sup>86</sup>

Light thresholds for optimum growth and production have been developed for apple (see review by Jackson<sup>69</sup>). Herein we present our estimate of threshold values for sour cherry.<sup>75,76</sup> Note that these are based on Michigan conditions and may need to be adjusted for areas that receive greater or lesser amounts of incident solar radiation or have longer or shorter growing seasons (Table 7).

### V. TEMPERATURE

#### A. VEGETATIVE AND REPRODUCTIVE GROWTH

Temperature above freezing is the main regulator of metabolic and therefore growth processes in the plant. It is the driving force for bud break, and is closely correlated with vegetative and reproductive growth, as well as fruit maturity. Young and Werner<sup>87</sup> found that chilling temperatures of the roots were

Table 7 Summary of the effect of shading on the morphology and fruiting of sour cherry

| Parameter                   | Response to shading | Light threshold <sup>a</sup><br>(% full sun) |
|-----------------------------|---------------------|--|
| Leaf size                   | +                   | 36   |
| Leaf thickness              | —                   | 36   |
| Leaf chlorophyll (mg/gm)    | +                   | 36   |
| Stem length                 | +                   | 21   |
| Stem diameter               | —                   | 21   |
| Flower bud formation        | —                   | 20–25  |
| Fruit set                   | —                   | 10   |
| Fruit retention force       | +                   | 36   |
| Fruit color                 | —                   | 36   |
| Hardiness                   | —                   | 21   |
| Maximum photosynthetic rate |                     | 36   |

<sup>a</sup>Highest percent of sky value at which a significant effect was observed. Reprinted from Flore, J. A., *Annu. Rep. Mich. St. Hortic. Soc.*, 111, 161, 1981. With permission.

not required for the onset of growth for peach, although chilling the rootstock delayed budbreak. By contrast, chilling temperatures are required to terminate dormancy of shoot buds (followed by a period of warming). The reader is referred to several models that have been proposed to predict the chilling requirement necessary to end rest for peach and cherry for an in-depth discussion.<sup>88–91</sup> The range of chilling hours (total number of hours below 45°F) requirement for peach, sour and sweet cherry are 100–1100, 600–1500, and 500–1300, respectively.<sup>2</sup> Once endodormancy is completed, budbreak is regulated by temperature. The amount of heat required varies with the species, the physiological condition of the plant, the stage of development, and geographic location of the trees.

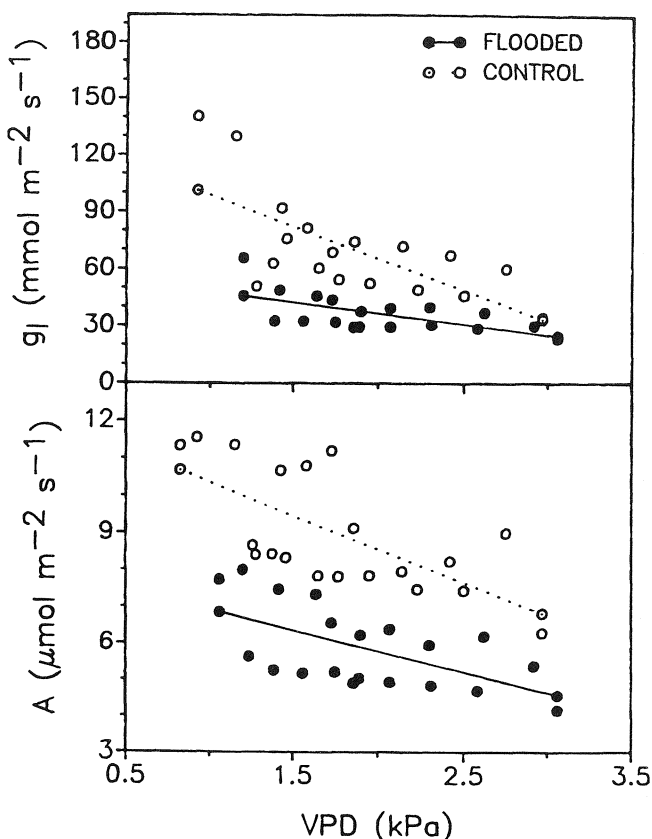
## B. GAS EXCHANGE AND RESPONSE TO TEMPERATURE AND HUMIDITY

*Prunus* spp. exhibit a typical parabolic relationship between photosynthesis and temperature, with a flat response between 17° and 30°C.<sup>63,92</sup> Cherry had higher A at low temperatures than peach, while the converse is true at high temperatures. A true high temperature threshold has not been well established for two reasons. First, under field conditions plants can adapt to higher temperatures.<sup>93–95</sup> Lange et al.<sup>95</sup> demonstrated that under desert conditions, apricot exhibited characteristic seasonal shifts in temperature optimum for A. Second, unless vapor pressure of water is controlled in assimilation cuvettes, vapor pressure deficits (VPD) between the leaf and air increase with increased temperature. Vapor pressure deficits greater than 1.5 kPa have been shown to cause stomatal closure and decreased photosynthesis in sour cherry.<sup>96,97</sup> The decrease in A in response to temperature could in part be due to the direct effect of low humidity on the stomata, and in turn, affect A. A typical response to VPD when temperature is held constant was demonstrated for control and flooded cherry trees as shown in Figure 6.

With the advent of portable photosynthetic equipment, it is now possible to measure A in the field throughout the growing season. Often under field conditions, A of *Prunus* is still 50–70% of maximum when temperatures are between 35° and 38°C.<sup>98,99</sup> It is doubtful that an upper threshold for *Prunus* can be fully characterized without taking into consideration preconditioning. The genotypic potential for preconditioning and adaptation are not known, but warrants further study.

## C. LOW TEMPERATURE RESPONSE

Parker<sup>100</sup> has indicated that cold temperature is the single most important factor limiting the range and distribution of plant species. Peach and cherry are no exception and seem especially vulnerable. Examples include the late November freeze of 1950 in the Midwest which killed most of the peach trees in the region, and the November 1955 and December 1964 freezes in the Pacific Northwest which killed hundreds of thousands of fruit trees. Fluctuation in yield due to frost are also common and are probably the single most important marketing problem for the sour cherry industry in Michigan.



**Figure 6** Stomatal conductance to water ( $g_i$ ) and net  $\text{CO}_2$  assimilation rate ( $A$ ) as functions of vapor pressure deficit (VPD) in sour cherry trees after 5 days of flooding (all regressions significant at  $p < 0.01$ ). Fitted lines—control:  $g_i = 131.9 - 33.3 \cdot \text{VPD}$ ,  $r^2 = 0.47$ ; flooded:  $g_i = 59.4 - 11.4 \cdot \text{VPD}$ ,  $r^2 = 0.37$ ; control:  $A = 12.2 - 1.8 \cdot \text{VPD}$ ,  $r^2 = 0.45$ ; flooded:  $A = 8.1 - 1.1 \cdot \text{VPD}$ ,  $r^2 = 0.35$ . Reprinted with permission from Beckman, T. G., Perry, R. L., and Flore, J. A., *Hort Science*, 27, 1297, 1992.

#### D. TYPES OF COLD DAMAGE

Cold damage can be manifested in several ways: either as damage to buds, flowers or fruits, or as damage to the regenerative tissue of the tree itself. Tree damage has been termed crown injury, crotch injury, sunscald, bark splitting, southwest injury, or black heart. Several reviews have been written on the mechanisms of cold damage, we will summarize them briefly, but refer the reader to the following for an in-depth discussion.<sup>101–106</sup> It is generally thought that death to stone fruit trees occurs either by extracellular or intracellular freezing. In extracellular freezing, ice forms on the surface of cells or between the protoplast and the cell wall. Because of differences in osmotic potentials ( $\Psi_\pi$ ), water moves through the plasma membrane to the ice crystal, causing dehydration, and if severe plasmolysis follows, this can cause injury and permanent damage. When intracellular ice forms within the cell, the cells are killed due to the destruction of membranes.

The ability to resist cold below the normal freezing point of water is called supercooling.<sup>107</sup> Ice does not form until a small volume of liquid crystallizes (see Ashworth<sup>107</sup> for a thorough discussion). Ashworth<sup>107</sup> has reviewed many factors which affect the ability of a plant tissue to supercool and form ice; among them are: specimen size, cooling rate, surface moisture, presence of ice nucleation active bacteria, intrinsic ice nucleating agents, tissue moisture content, tissue structure, and the cell wall. It is generally now accepted that ice crystallization is a prerequisite for injury, and is particularly important in plants which lack tolerance to ice formation.<sup>107</sup> For these plants, the temperature of ice formation is associated with lethal damage,<sup>103</sup> however, the temperature at which ice crystallization occurs is not constant, nor is it necessarily just at or below  $0^\circ\text{C}$ . The importance of supercooling and ice formation to survival of wood and stems seems to be different from that of buds. In many deciduous woody plants, plant death and ice nucleation occurred at the same temperature in living xylem tissues that supercooled.<sup>107</sup> It has been hypothesized that intracellular ice formation was responsible for cell death. However, when ice formed in overwintering buds, a single nucleation event resulted in freezing of an entire flower resulting in death. Tissue structure has been implicated as being responsible for differential

ice formation and spread of ice within plant tissues. It is clear that there is segregation of ice when overwintering buds are frozen. Theories to explain the compartmentalization include: the presence of bud scales<sup>108</sup>; that the scales contain intrinsic ice nucleating agents<sup>108</sup>; tissue water potentials are different; and there are differences in bud morphology and vascular development.<sup>109</sup> Quamme and Gusta<sup>108</sup> presented compelling evidence that the supercooling of flower primordia within dormant peach buds is dependent on water migration from the base of the flower primordium to preferential sites of freezing in the flower bud scales and pith during the initial stages of freezing.

Trunk splitting is manifested by a vertical split in the tree trunk extending through the bark and cambium into the sapwood, and is a serious problem for many trees species in temperate regions. It has a serious debilitating or even lethal effect on the tree. This problem has been studied extensively, and results from measurements indicate 17–20°C differences of temperature within the trunk tissue on clear sunny days.<sup>110</sup> Norris et al.<sup>110</sup> concluded that this type of injury was mainly due to differences in thermal expansion, and noted significant differences among the bark, sapwood, and heartwood, as well as thermal coefficients of expansion in both tangential and radial directions.

Winter injury that causes death of the bark (cambium, phloem, or cortex) or sap wood (xylem parenchyma and pith) at or near ground level is less well explained, and is thought to be caused by freezing death of the tissues. Some trees may survive damage to the phloem and xylem during the winter, but seldom survive if the cambium around the tree is substantially damaged. Layne and Flore<sup>111</sup> showed that if the trunk was injured to the cambium in a band 10 cm in length, 75% around the circumference of the tree, it could survive but not if damage was more extensive. White paint applied to the trunk and scaffolds can minimize cold damage to stone fruit in the colder temperate region.

## E. COLD ACCLIMATION, DEEP WINTER HARDINESS, AND DEACCLIMATION

The hardiness cycle for stone fruit is usually divided into 3 stages: acclimation, deep winter hardiness, and deacclimation. Depending on the location and the cultivar, each of these phases can have more or less importance in the survival of the buds and the tree. Acclimation or hardening coincides with cessation of growth in late summer or early fall.<sup>106,112</sup> Leaves provide substrate, receive signals, and promote hardiness. It has been postulated that a hardiness promoting factor is produced in the leaves which is responsible for the first phase in the acclimation process. This process is thought to be induced by photoperiod in some plants, is reversible, and the stimulus is translocatable.<sup>113</sup> Although short days have been implicated as the trigger, they are not effective during spring growth, and some plants will acclimate in the fall regardless of photoperiod.<sup>106,113</sup> Once induction has occurred, high temperature will not reverse it. The hardiness factor does not seem to be genotypically specific. In peach, the youngest leaves seem to be the most active in promoting hardiness development.<sup>114</sup>

A second phase of acclimation is usually induced by frost or low temperature, which causes the plant to go through a further hardening process. As temperature drops, plants become more hardy, the process is reversible and seems to be quantitative. There may be a third transition to deeper hardiness induced by very low temperature (−30° to −50°C) in some species.

There are differences among species in developing bud hardiness in the fall. Once hardening occurs it does not remain constant. Apple will dehardens when exposed to warm temperatures and rehardens when exposed to low temperatures. The degree of rehardening seems to be dependent upon the stage of dormancy, and the length of time that they are exposed to warm temperatures. As dormancy proceeds toward spring, the capacity to rehardens decreases, and after a certain point they are permanently dehardened.<sup>115</sup> Andrews and Proebsting<sup>116</sup> found that sweet cherries developed the capacity to deep supercool 1–2 weeks earlier than peach. Increase and decrease in hardening follows temperature fluctuations. Cherry lost 6.1°C in hardiness when exposed to 24°C for 4 hours, while cherry and peach rehardens at a rate of 1.9°C, and 2.2°C per day, respectively, if temperatures are below −1.1°C.<sup>117</sup> The dehardening-rehardening cycle is not completely reversible, and dehardening occurs faster than hardening. Peach loses the capacity to rehardens after rest is complete and some after bud development has occurred.<sup>112</sup>

Synchronization of hardiness does not occur equally in all parts of the plant in the fall. It coincides with cessation of growth and begins in the periphery of the tree, first and last in the trunk.<sup>112,118</sup> In Michigan it has been reported<sup>119</sup> that the apical part of peach shoots are hardier than the base early in the acclimation period, however, this reverses later in the season. Not only do different organs and tissues acclimate at different rates, but their overall sensitivity to cold is different. In general, roots are more sensitive than shoots, fruit buds are more sensitive than shoots, and shoots are the most hardy. The cambium is generally the most sensitive tissue in the shoot.

Dehardening is strictly related to temperature. As buds develop, they are more vulnerable to frost, which can be identified by stage of phenological development. Killing temperatures ( $LD_{50}$ ) for 'Montmorency' sour cherry buds rise rapidly as buds swell in the spring, reaching  $-5^{\circ}\text{C}$  just before separation of bud scales and  $-3^{\circ}\text{C}$  at full bloom.<sup>120</sup> They seem to lose hardiness in the water stage, then regain some protection in the next stage when air insulates the pistle from the rest of the flower. Similar responses are found for the other stone fruit as they develop.

## F. SPECIES, VARIETY, AND ROOTSTOCK

Plant genotype is the most important factor in determining the potential for cold tolerance.<sup>112</sup> Cultural and environmental factors can only modify this potential. It has long been recognized that there is a wide tolerance to cold within the genus *Prunus*, and between cultivars within a species. Scion hardiness is also influenced by rootstock.<sup>121-127</sup> It is generally accepted that within *Prunus*, tolerance to cold from most to least occurs as follows: *P. domestica* > *P. cerasus* > *P. avium* > *P. armeniaca* > *P. persica*.<sup>128-130</sup> Within a species rootstock can play a large role. Layne<sup>130</sup> classified the following rootstocks as: very hardy (Siberian C, Tzim Pee Tao, Chui Lum Tao); medium hardy (Bailey, Harrow Blood), medium tender (Yeh Hsiemtung Tao, Sinung Chui Mi, Rutgers Red Leaf); and tender (Gold Drop, Lemon Free, and Elberta).

Resistance to cold stress is a complex phenomenon involving several genes and is expressed through a multiplicity of physiological processes. Among them are carbohydrate production and acclimation, cessation of growth, acclimation, deep winter hardiness, super cooling, length of endodormancy, deacclimation, and bloom date. As a result, it is difficult to predict how a certain scion/rootstock combination will perform in a new combination or environment. Traditionally, hardiness has been evaluated during test winters or to determine which cultivars survive after being subjected to very cold temperatures sometime during the dormant season, and then by ranking the cultivars according to their survival rate in the spring. This technique has several deficiencies, among those are that no two seasons are ever exactly alike either in regard to cultural and environmental preconditioning, or in terms of the time and degree of the cold event.<sup>118</sup> In recent years researchers have been using artificially controlled events to evaluate cold hardiness in an attempt to decrease that component of variability that is associated with the cold event. Some of these tests have been conducted at the peak of winter dormancy in an attempt to characterize maximum winter tolerance to cold, but Howell<sup>131</sup> would argue that in order to fully characterize tolerance to cold, one must assess tolerance to cold at 2 to 4 week intervals throughout the acclimation, deep winter hardiness, and deacclimation stages.

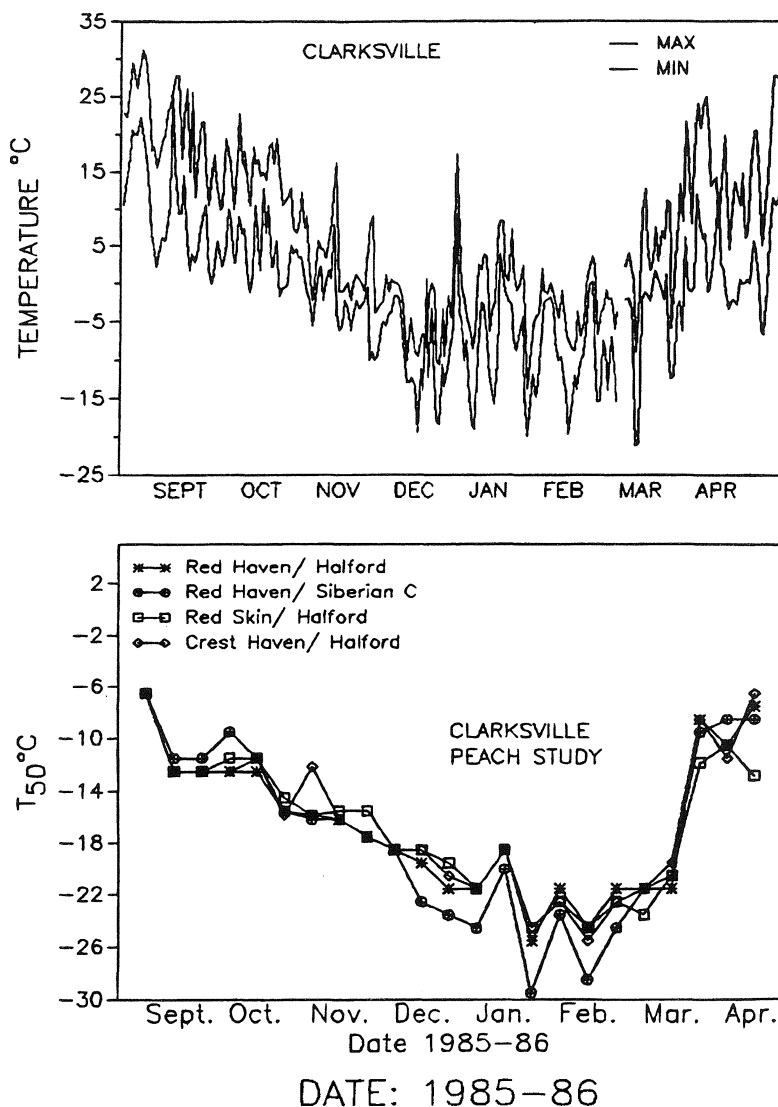
The effect of season, variety, and rootstock can be illustrated by an experiment where we compared the hardiness of 'Redhaven', 'Redskin', and 'Cresthaven' on 'Halford' and 'Siberian C' rootstock in Michigan throughout the dormant season (Figure 7). The scions, rootstocks, and their combinations differ in response depending on the season.<sup>132</sup> 'Redhaven' on 'Halford' was harder than 'Redhaven' on 'Siberian C' on September 10, 1985, but this relationship was reversed by November 19, 1985. In addition 'Siberian C' was several degrees harder than 'Halford' by the end of December.

Thus the rootstock scion combination should be matched for the particular climatic situation. If acclimation in the fall is important then a combination which assures early development of hardiness is probably most desirable and may be more important than midwinter hardiness. On the other hand, in more northern climates, midwinter hardiness might be the most important factor in relation to survival of the tree. The length of endodormancy is also important. If the chilling requirement is too low, then active growth may resume too early in the spring and a warm period during the winter could trigger active growth, making the tree more vulnerable to cold. This illustrates two points: (1) that hardiness ranking depends upon the time and stage of development, and (2) that a test winter, or controlled freezing test at one time during the winter may not adequately describe tolerance to cold in a scion/rootstock combination for a certain climate.

## G. CULTURAL AND ENVIRONMENTAL FACTORS

A healthy tree will better resist cold damage than a tree that is in low vigor, or one that has been under environmental or biological stress. Cessation of growth which coincides with the trigger for the first stage of the hardening process is desirable, but should not result in growers inducing early bud set by early defoliation, by water stress or poor nutrition. These are all detrimental to cold tolerance.

Circumstantial evidence indicates that a certain minimum level of carbon assimilation is necessary for maximum winter hardiness. Levels of carbohydrate in peach buds and shoots have been positively



**Figure 7** Maximum and minimum temperatures at the Clarksville Horticultural Research Station, Clarksville, MI (top) and  $T_{50}$  values for Redhaven/Halford, Redhaven/Siberian C, Red Skin/Halford and Crest Haven/Halford during the dormant period, 1985-86. Reprinted with permission from Flore, J. A., Howell, G. S. Jr., Gucci, R., and Perry, R. L., *Compact Fruit Trees*, 20, 60, 1987.

correlated with cold hardiness.<sup>126,133</sup> Cold acclimation is an active process and requires energy to occur. However, this does not necessarily mean that an increase in carbohydrate will increase hardiness, or that sugar or polyols are the hardiness promoting factor. It is likely that some minimum level of carbohydrate is required to attain maximum hardiness, beyond which no additional benefit can be derived. The same cannot be said for the hardiness factor produced by the leaf and translocated to the rest of the tree as more research is needed in this area. Important factors related to carbohydrate accumulation and cold hardiness are outlined in the following sections.

### 1. Defoliation and Duration of Foliage

Early cold acclimation is often associated with early defoliation and low vigor. However, duration of foliage on the tree should be maximized and early senescence avoided. Howell and Stackhouse<sup>134</sup> showed that early defoliation in sour cherry due to pathogens or by artificial means decreased hardiness the

following spring. Regression analysis of Cooper's data on peach<sup>135</sup> revealed a positive relationship between later leaf abscission and percent bud mortality the next spring, while Flore et al.<sup>132</sup> did not find a correlation between hardiness and percent leaf abscission in the fall for peach in a rootstock trial.

Early defoliation has been considered as an indicator of early acclimation to cold damage, and there is very good evidence that actively growing shoots are less hardy than those that have stopped growing. However, we should not equate early defoliation with adequate vigor and health of the tree. Clearly active growth in the fall does not allow for sufficient acclimation in time to resist cold temperatures. By contrast premature leaf abscission should not be encouraged since this might result in a carbohydrate limitation, and once abscission occurs, the acclimation factor present in the leaves is no longer available to the rest of the plant.

## 2. Light

Light is important in cold acclimation and winter resistance process. Acclimation in many plants is triggered by day length. It is also necessary for adequate carbohydrate assimilation and translocation in trees. Cultural practices which reduce exposure of leaves to light presumably affect hardiness by their influence on carbon assimilation. Shading studies on potted trees of peach and cherry<sup>85</sup> and on field grown trees<sup>132</sup> indicated that there was a decrease in hardiness with increasing shade, which was also associated with a decrease in shoot carbohydrate content.

## 3. Nutrition

Any nutritional factor that is limiting enough to show deficiency symptoms will generally decrease winter hardiness. A review of the effect of mineral supply on cold hardiness has been published by Levitt,<sup>136</sup> and here we will only place emphasis on nitrogen because of its influence on tree vigor, acclimation, and hardiness.

Late applications of N have generally been discouraged because of their possible stimulation of growth. However, later applications after active growth has stopped, or which have prolonged foliage health have been associated with higher yields in stone fruit. Savage<sup>137</sup> showed that N applied after harvest in the fall on peaches in Georgia prolonged tree life over applications in the Spring. Fall N seems to delay leaf fall and may help increase the duration of foliage. Savage<sup>137</sup> speculated that this might also delay the emergence from rest the next spring.

## 4. Fruiting

Crop load decreases cold tolerance.<sup>118,138</sup> The fruit on the tree are the primary sink for carbon produced by photosynthesis. Overcropping reduces vegetative growth, vigor, and decreases storage carbohydrate. In grape vines, excess cropping reduced cold resistance in cane and bud tissues.<sup>139</sup> We have found that non-thinned peach trees are similar in hardiness to shaded trees, which are less hardy than thinned fully exposed 'Newhaven' peach. Heavy crop load is generally not a problem on cultivars that mature their fruit early in the season, but may be a problem with the later maturing varieties of peach and plum in extreme climates where seasons are short. Once the optimum crop load has been determined for a given cultivar, excessive cropping should be prevented.

## 5. Pruning

Pruning may affect cold hardiness positively by increasing the level of light in certain areas of the tree, or negatively by reducing carbon production, by removing leaf area, by reducing uptake of water and nutrients (root pruning), or by stimulation of shoot and cambium activity. For the purposes of this review, pruning terms will be defined as follows: summer pruning = selective removal of shoots or branches during the growing season; dormant pruning = the same as summer pruning, except that shoots are removed during the dormant season before active new growth; and summer or dormant hedging or topping = the indiscriminate removal of all branches within a plane either in the summer or dormant period.

Reports relating cold tolerance to the time and degree of pruning have been inconsistent. In general the earlier that pruning occurs in the dormant period, the more negative the effect on cold hardiness. Dormant pruned trees often defoliate slightly earlier than summer pruned trees, but the onset and duration of dormancy seem to be just about the same. Pruning just prior to the occurrence of low temperatures tends to increase injury.<sup>1,140</sup> Therefore in extreme climates it is often recommended that growers prune their hardest varieties first on their best sites followed by the less hardy varieties.

When compared to dormant, summer pruning reduces total shoot growth, decreases shoot diameter, increases lateral shoot growth, and flower bud density is decreased while lateral branching is often increased.<sup>52</sup> The earlier in the season that summer pruning or hedging is conducted the greater the reduction in current season growth. Marini<sup>141</sup> found that summer pruning in late July slightly delayed defoliation of mature 'Sunqueen', while Hayden and Emerson<sup>142</sup> found that summer hedging hastened defoliation. Summer pruning may induce late fall growth which does not have an adequate period of time to acclimate before the first cold temperatures. Early dormant pruning can influence the cold resistance of cambial tissue close to the cut surface and can affect the resistance of shoots and buds if inadequate healing does not occur.<sup>105</sup> In general, summer pruning or hedging may reduce cold hardiness of peach.<sup>141,143</sup>

When considering if summer pruning will have an effect on cold hardiness, timing is especially crucial. If done too early in the season, it will reduce leaf area for carbon production and have a negative effect; if done too late it will also have a negative effect by stimulating shoot growth and delaying dormancy; and if done very late in the season, the tissue may not have an adequate time to heal. In Michigan, we recommend that summer pruning coincide with final swell of fruit growth. During this period, most of the carbon will be partitioned to fruit growth and shoot growth will usually only be slightly stimulated. Unless the variety is particularly late in maturing, this should give adequate time for the foliage to produce carbohydrate for the next year. Clearly in our studies<sup>52,105</sup> during the acclimation period shoots from summer, pruned peach were 1–3 degrees less hardy than dormant-pruned trees. In many years this difference may not be significant, but in Michigan, where cold periods can occur in the late fall and early winter, this is a very critical period of time. The benefits of summer pruning in terms of increased fruit quality and reduced pruning costs the following spring must be considered in relation to the possible negative effect on winter hardiness.

## 6. Water Content, Irrigation, and Ground Cover

Water content of the tissue is often negatively correlated with hardiness.<sup>144,145</sup> Irrigation and rain may influence cambial activity in the fall, and the heat holding capacity of the soil. Adequate water should be supplied to promote good vigor since reduced vigor often results in lower hardiness. Layne and Tan<sup>146</sup> found that irrigation reduced peach tree mortality on sandy soils, presumably due to decreased winter injury. A similar response was observed in several cherry orchards in northern Michigan in 1988 when conditions were much hotter and drier than normal.<sup>147</sup> In areas where rainfall is high in the late summer or fall, cover crops might be sown to compete with the trees and hasten acclimation. However, in experiments at Clarksville Horticultural Research Station, Clarksville, MT in 'Newhaven' with sorghum sown on July 1 or August 1, we found no benefit and in some cases found that the cover crop reduced hardiness.<sup>148</sup>

In areas where irrigation is used, water should be reduced in late summer and early fall to stop tree growth, then increased near the time of defoliation to assure that the soil is wet to slow the rate of drop in temperature of the soil to prevent cold injury to the roots.<sup>112</sup> Ground cover from best to worst for spring frost protection would be wet soil > mulch > herbicide strips > sod cover.

## VI. WATER

After irradiation, water is the second most important factor limiting growth of *Prunus* during the summer period. Several excellent reviews have been recently published concerning the effect of drought<sup>2,4,149</sup> and flooding<sup>150,151</sup> on trees. Since we have covered the effects of humidity under Temperature, examples of drought and anoxia on stone fruit will be stressed in this section. In this review emphasis will be on: vegetative, reproductive, and physiological response to drought and anoxia; current theory concerning irrigation scheduling and strategy, and the importance of root restriction and root zone wetting on management decisions.

### A. CULTIVAR AND SPECIES AND ROOTSTOCK DIFFERENCES

Water use and sensitivity to drought differs within and between species in the genus *Prunus*. Faust<sup>2</sup> has classified fruit trees according to their relative requirement for water and Kenworthy<sup>152</sup> has ranked them according to drought tolerance, while Rieger and Dummel<sup>153</sup> have made a comparison of morphological and physiological characteristics for different species within the genus *Prunus* (Table 8).

Table 8 Relative water use and sensitivity to drought within the genus *Prunus*

| Relative response | Water requirements <sup>a</sup><br>most to least                                   | Tolerance <sup>b</sup> to drought<br>most to least   | Habitat <sup>c</sup> dry to wet  |
|-------------------|--|--|--|
| Greatest          | Quince<br>Pear<br>Plum<br>Peach<br>Apple<br>Sweet cherry<br>Sour cherry<br>Apricot | Pear<br>Prune<br>Apple<br>Grape<br>Walnut<br>Plum<br>Almond<br>Citrus<br>Peach<br>Cherry<br>Olive<br>Apricot | Nevada desert almond<br>Western sand cherry<br>Beach plum<br>Peach<br>Sierra or Pacific plum<br>Nanking cherry |
| Least             |  |  |  |

<sup>a</sup>According to Faust.<sup>2</sup> <sup>b</sup>According to Kenworthy.<sup>152</sup> <sup>c</sup>According to Rieger and Dummel.<sup>153</sup>

Drought tolerance in *Prunus* from most to least is as follows: plum > almond > peach > sweet cherry > sour cherry > apricot. However, there is a high degree of diversity in tolerance to drought and anoxia within and among *Prunus* spp.<sup>150,153</sup> Many *Prunus* spp. are graft compatible. For example, a plum rootstock could be grafted with a peach or apricot cultivar to improve its tolerance to drought or flooding. There seems to be a greater diversity to anoxia than drought and the reader is referred to the recent book edited by Rom and Carlson<sup>154</sup> for a comprehensive discussion of rootstocks for each species.

### 1. Peach Rootstocks

Peach, interspecific peach hybrids, plums, plum hybrids, and other *Prunus* species have been used as rootstocks for peach. There are few examples of wide tolerances to drought for peach. Couvillon et al.<sup>155</sup> reported that peach trees on their own roots were able to withstand greater levels of water stress than trees propagated on 'Lovell', 'Nemaguard', or 'Halford' seedling rootstocks. In a rootstock trial for peach in Illinois, Kjellgren and Taylor<sup>156</sup> concluded that there were no major differences for cv. Redhaven own rooted, or on cvs. Halford, Amandier, Damas, or Lovell, but that St. Julien had lower  $g_i$  and greater hydraulic resistance than the others. They also noted considerable differences in plant size, so it is difficult to know if differences in drought tolerance were due to the rootstock or to size of the plant.

Peach rootstock response to anoxia is diverse. Layne<sup>130</sup> classified resistance to waterlogging from most to least as follows: **very good**, 'Damas GF 1869'; **good**, cvs. St. Julien No 1 and 2, St. Julien GF 655.2; **moderate**, wild peach, cvs. Nemaguard, GF 305, Brompton, Prunier GF 43, GF 677; and **low**, peach, apricot and almond seedlings. However, Chaplin et al.<sup>157</sup> reported tolerance of peach rootstocks from most to least as follows: 'Rutgers Red Leaf', 'New', 'Siberian C', 'Harrow Blood', and 'Lovell'. Rom and Brown<sup>158</sup> reported that 'Halford' and 'Lovell' were more sensitive to waterlogging than 'Nemaguard'. It is agreed that almond and apricot are among the most sensitive of all species in the Rosaceae family.<sup>150</sup> Through the correct choice of rootstock, the grower can utilize a wide range of sites with different soil moisture characteristics.

### 2. Cherry Rootstocks

There is little reported genotypic diversity among cherry rootstocks for drought tolerance, however, trees on mahaleb are usually more vigorous than mazzard under dry conditions.<sup>128</sup> The opposite seems to be true in wet soils where mazzard survives longer. Tolerance to anoxia has been ranked from most to least as: *P. cerasus* L. > *P. avium* > *P. mahaleb* by Norton et al.,<sup>159</sup> while Beckman<sup>160</sup> has ranked cherry rootstocks as follows on the basis of A and shoot extension: M × M 2 least sensitive; mahaleb, 148/1, colt, mazzard, Montmorency, M × M 60, 148/9, 195/1, 195/2 as sensitive, and 196/4, M × M 39 as most sensitive. It must be pointed out that in comparison to rootstocks available for peach and plum, all cherry rootstocks are relatively sensitive to anoxia.

### 3. Apricot and Plum Rootstocks

There seems to be little diversity in response to drought or flooding for apricot and the important aspects concerning plum have already been discussed. We refer the reader to Okie<sup>161</sup> and Crossa-Raynaud and Audergon<sup>129</sup> for an in-depth discussion. In conclusion, under flooding conditions, plum and prune are the most tolerant, followed by Japanese plum, sour cherry, sweet cherry, with peach and apricot being the most sensitive.<sup>150</sup>

## B. GENERAL CONSEQUENCES OF DROUGHT

The physiological control of water status in temperate fruit crops has been recently reviewed by Jones, Lakso, and Syvertsen,<sup>4</sup> and the influence of water and anoxia on photosynthesis and stomatal conductance has been covered by Flore and Lakso.<sup>3</sup> Herein, the consequences of drought and anoxia on vegetative and reproductive growth and physiological process in *Prunus* are reviewed with emphasis placed on sensitivity, and how water can be managed to improve yield.

### 1. Diurnal Changes

Diurnal changes in physiology and growth in *Prunus* are well documented. Stomata open in response to light (maximum  $g_i$  levels are similar to those for A or approximately at PPF of 500–800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). As a consequence, the negative  $\Psi_i$  that develop within the leaf and stem are thought to follow  $g_i$  and are not the cause of stomatal closure unless the trees are under moderate to extreme stress.<sup>3,4,46</sup> Diurnal shrinkage in fruit, trunks, and scaffolds can be noted in *Prunus* in response to diurnal changes in water potential, and some have suggested that the degree of diurnal shrinkage can be used as a measure of plant water status and thus could be used to schedule irrigation.<sup>162–164</sup>

### 2. Shoot and Leaf Expansion

Shoot and leaf expansion are among the most sensitive plant parameters to  $\Psi_i$ . Andersen and Brodbeck<sup>46</sup> found that as water deficits developed, shoot and leaf expansion were inhibited prior to reductions in A or  $g_i$ . They concluded that a moderate level of water stress could reduce the rate of vegetative growth of peach trees without a reduction in carbon assimilation. This would be consistent with the results found in deficit irrigation experiments (see next section).

### 3. Leaf Gas Exchange

The influence of water status on  $g_i$  and A have been reviewed by Flore and Lakso.<sup>3</sup> Values of  $g_i$  for *Prunus* are between 150 to 400  $\text{mmol m}^{-2} \text{s}^{-1}$  and are typical of most fruit crops. For different species, reported values are: apricot, 108–440  $\text{mmol m}^{-2} \text{s}^{-1}$ ; peach, from 60 to 280  $\text{mmol m}^{-2} \text{s}^{-1}$ ; and plum and cherry, 280  $\text{mmol m}^{-2} \text{s}^{-1}$ , converted from  $\text{mmol}$  according to Nobel.<sup>165</sup> Previously it was thought that  $g_i$ , and therefore A, were almost entirely dependent upon  $\Psi_i$  and loss of turgor,<sup>3</sup> however, in recent research, it has been shown recently that *Prunus* undergo adaptation to drought, one method being osmotic adjustment.<sup>46,166,167</sup> Thus, keeping turgor potential high and stomata open even at very negative  $\Psi_i$ .

Stomatal conductance is strongly coupled to A in *Prunus*<sup>96</sup> and is responsive to vapor pressure gradients above 1.5 kPa for cherry, however peach was not affected until  $\Psi_i$  greater than  $-2.0$  MPa were reached. Photosynthesis was not affected adversely until these levels of stress were reached. Therefore under field conditions, it seems that  $g_i$  and A are not affected until more severe stress conditions are imposed.

Recently it has been suggested that ABA is produced in the root in response to drought or anoxia and that it is transported to the leaves where it plays a regulatory role in the control of  $g_i$  and A (see review by Flore and Lakso<sup>3</sup>). Neri and Flore<sup>168</sup> have shown in split root studies with peach that ABA increased with soil drying, but  $g_i$  or A did not decrease until several days after leaf and shoot growth were affected. There was an increase in hydraulic conductivity of the dry roots.

In non-irrigated peach trees, ABA concentration increased sharply after mid-summer; this was associated with a decrease in  $g_i$  and  $\Psi_i$ . ABA concentrations in leaves from irrigated and non-irrigated trees increased as  $g_i$  decreased, however in stressed trees, high levels of ABA in the morning were not associated with closed stomata.<sup>169</sup> Stomatal conductance and A were inversely related to  $\Psi_i$ , when drought studies were conducted on peach grown in pots.<sup>170</sup> However, there was no 'threshold value' for  $g_i$ , as it decreased gradually as  $\Psi_i$  became more negative.

Stomatal conductance and  $A$  are both affected by flooding in fruit crops.<sup>150</sup> Recently in a very sensitive crop, sour cherry, Beckman et al.<sup>97</sup> showed that  $A$  was inhibited 24 hours after flooding was imposed, and that nonstomatal factors contributed greatly to the inhibition (Figure 8).

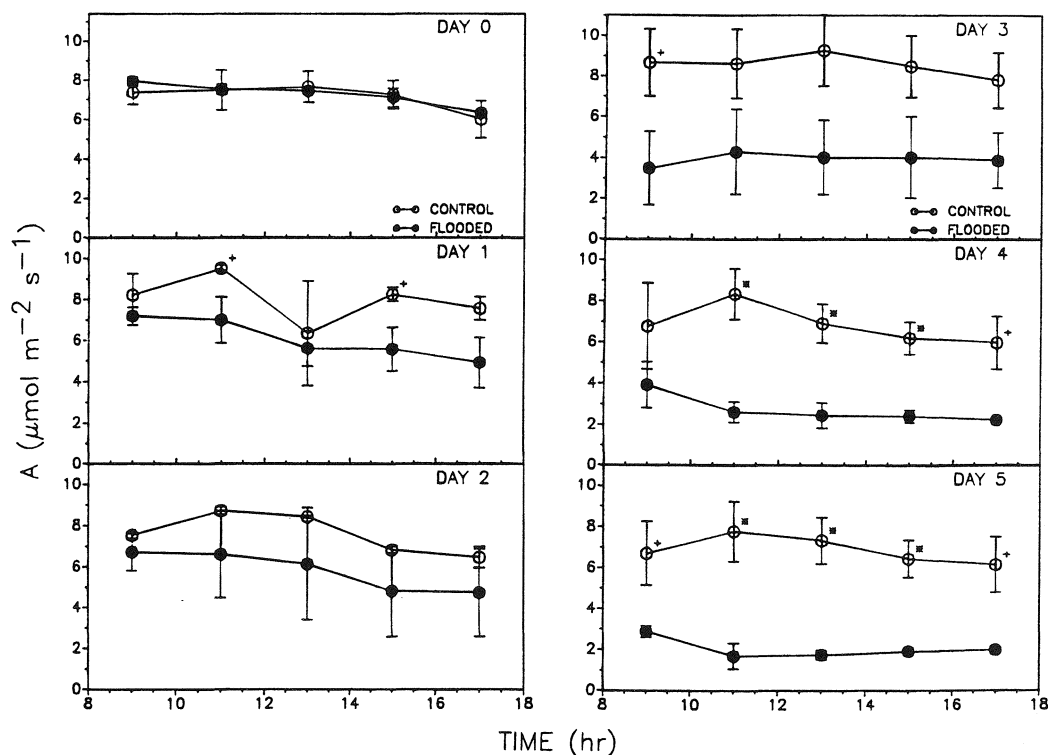
The effect of a mild water stress was investigated for container grown sour cherry. Under optimum conditions, there was a strong relationship between  $A$  and  $g_s$ . Stomata of plants subjected to a low level of stress were more responsive to VPD and seemed less responsive to  $\text{CO}_2$  gradient than on highly stressed plants. Stomatal aperture decreased in response to increased external  $\text{CO}_2$  concentration, and the degree of response varied with stress. Water use efficiency of sour cherry increased under mild stress conditions.<sup>96</sup>

Leaf water potential of container grown peach was also correlated with  $g_s$ ,  $A$ , and VPD. Maintenance of soil moisture slightly above field capacity (FC) for even short periods may decrease  $A$  as compared to maintaining soil moisture slightly below FC. Decreasing the soil water potential from  $-0.05$  MPa to the permanent wilting point resulted in decreased photosynthetic rates.<sup>171</sup>

#### 4. Water Use and Dry Matter Production and Partitioning

There is a direct relationship between water use and dry weight increase in peach. A functional equilibrium may exist between water usage and growth increment, which is mediated through the capacity of the root system to increase its water uptake as the demand/supply ratio increases.<sup>172,173</sup> The use of deficit irrigation, and root restriction as a means to control growth without a negative effect on fruiting are based in part on this premise.

Dry matter partitioning between different plant parts is influenced by drought, and is dependent on season, competition between different organs, and the presence or absence of fruit. Personal observations<sup>18</sup> would indicate that for stone fruit, the order of dry matter partitioning in relation to drought seems to follow the following pattern. Early in the season roots have preference, followed by vegetative shoot growth until the end of pit hardening. During final swell of fruit growth, fruit have preference. In



**Figure 8** Effects of 1 to 5 days of flooding on net  $\text{CO}_2$  assimilation ( $A$ ) of sour cherry trees. Data points are means of two plants/time  $\pm$  SD [\*], \* indicate significance at  $p = 0.10$  and  $0.05$ , respectively, otherwise nonsignificant, F test]. Reprinted with permission from Beckman, T. G., Perry, R. L., and Flore, J. A., *Hort. Sci.*, 27, 1297, 1992.

general, as soils dry, partitioning to roots increases, and roots develop at greater depths in the soil profile.<sup>13,174</sup> Root growth can also be locally stimulated by water, and often there will be large masses of fine roots near the source of water. Under areas of high rainfall, roots will proliferate in the soil where moisture is favorable. In orchard systems sod cover may restrict the growth of roots, presumably due to competition for water and fertilizer. Layne et al.,<sup>174</sup> in studies on irrigation in a mature peach orchard found that the total number, and the number of small diameter roots were highest in nonirrigated plots, and that they decreased with increasing levels of irrigation.

## 5. Sensitivity of Vegetative Growth to Drought

Shoot growth, leaf growth, leaf emergence, shoot diameter, and trunk diameter are all adversely affected by drought or anoxia. Generally in order of sensitivity to drought, leaf growth is the most sensitive followed by shoot growth, leaf emergence and shoot or trunk diameter. This pattern was confirmed in experiments on peach under a rapid (zero water vs. control) or a slow water stress situation (watering at 50 or 25% of control).<sup>164</sup> Growth characteristics were observed several times per week and the occurrence of a statistical difference between treatments was used to determine sensitivity to stress. Processes that were most to least affected by drought were: leaf growth > shoot extension > leaf emergence > trunk diameter >  $\Psi_i$  >  $g_i$ . Similar results have been observed with sweet and sour cherry.<sup>13</sup> In recent experiments on nonfruiting 2-year-old 'Cavalier' on 148/1 rootstock grown in a rain exclusion shelter, it was observed that the first response to a slow stress drought was an increase in root numbers, followed by a decrease in shoot growth, trunk growth,  $A_i$ , and  $g_i$ .<sup>13</sup>

Changes in trunk, scaffold, and shoot growth occur daily in response to changes in diurnal  $\Psi_i$ , but are somewhat dependent upon the level of drought, daily evaporative demand, the location on the tree, and the presence or absence of fruit. Diurnal shrinkage of trunks, shoots, and fruits have been reported for peach,<sup>162</sup> and 'Montmorency' sour cherry.<sup>163</sup> Daily shrinkage is proportional to the period of evaporation following irrigation and the magnitude and duration of daily shrinkage in peach is increased with fruit load.<sup>175</sup> Seasonal increase in trunk or scaffold diameter may be used as a tool to determine the amount of water stress the tree has undergone during the growing season.

A positive turgor potential  $\Psi_p$  is necessary for cell expansion and is often correlated with  $g_i$  and  $A_i$ . The turgor potential at a given  $\Psi_i$  is a function of  $\Psi_\pi$  in the cell. Increasing  $\Psi_\pi$  in response to lower water potential is a mechanism that has been observed in other plants. Osmotic adjustment has been confirmed for leaves and roots of cherry<sup>167,176</sup> and leaves of peach.<sup>46,166</sup> Jones et al.<sup>4</sup> have hypothesized that sorbitol may be an important osmolyte contributing to osmotic adjustment in fruit trees. Ranney et al.<sup>167</sup> suggests that the possibility exists to select superior drought resistance cultivars on the basis of their ability to osmotically adjust.

## 6. Response to Extreme Stress

Under arid conditions, water is supplied by irrigation during the growing season. Proebsting<sup>177,178</sup> has studied the effect of extreme water stress on the survival of peach, cherry, and plum. Peach was grown without irrigation and received only 86-mm rainfall during the growing season under Washington State conditions.<sup>177</sup> Trees died after experiencing  $\Psi_i$  below  $-3.0$  MPa in July and August. Defoliation began in July, fruit growth was decreased, and fruit flavor was astringent. Flower buds did not differentiate. Heavy pruning ("dehorning") delayed the appearance of drought symptoms until very late in the season and resulted in 100% tree survival. Heavy thinning in early June did not affect current season's symptoms but reduced dieback and death of trees.

Under similar conditions Proebsting et al.<sup>178</sup> subjected mature bearing cherry and prune trees to very low rates of irrigation and observed their response in the year of application and the following year. Trees were trickle irrigated daily or weekly at 100, 50, or 15% of  $E_c$  (evaporation adjusted to the area of the tree canopy). The  $\Psi_i$  reached as low as  $-2.8$  MPa for prunes in late July and August. Growth of fruit and vegetative parts were reduced by severe stress, but the trees survived on 15%  $E_c$ . Prunes recovered to normal yield and growth by the second year after treatment. Peripheral branches of cherries died back during the year of treatment and in the following year. Cherries grew and fruited normally by the third year, but had a reduced bearing surface area.

## C. MANAGEMENT OF WATER

### 1. Deficit Irrigation

Chalmers and his co-workers<sup>179,180</sup> have proposed that timing amount of irrigation can control vegetative growth in peach without a decrease in fruit yield or quality. They proposed that under Australian arid

conditions irrigation is needed early in the life of the tree to fill in allotted space. Once this has been achieved, vegetative growth during the current season can be controlled by timing of irrigation. Adequate irrigation is needed during the early part of the season when canopy and fruit cell division are occurring, but once stage II of fruit growth begins, most of the carbon and water are needed for vegetative development. Water is again needed during final swell, and at that point the fruit will compete strongly for water and photosynthate. Water may be withheld after harvest to reduce vegetative growth and pruning costs. Increased yields resulted from increased fruit growth (relative to the control) after the level of irrigation was raised to the control level following a period of reduced irrigation.<sup>179,181</sup> There was an interaction between water, tree density, and tree age. They hypothesize that spacing and water supply interact synergistically to reduce vegetative growth and increase fruit growth.

There is a strong physiological relationship between size of the root system and vegetative framework above ground,<sup>182</sup> and the root to shoot rate remains relatively constant over a broad range of conditions.<sup>172,173</sup> Since root growth can be controlled by both drip irrigation and row spacing, the result is control of vegetative growth without inhibiting fruit growth. Is this concept economically feasible? Girona et al.<sup>183</sup> pointed out that when growers receive a premium for large fruit and water is relatively cheap, the risk/reward ratio does not favor deficit irrigation on late maturing tree fruit.

Since stone fruit may mature a crop early in the season (55–65 days for cherry), or in the first third to half of the season under California conditions, the question of after harvest requirements for irrigation is an appropriate one for growers. This is especially important in arid areas with long growing seasons where the interval between harvest and leaf fall may be a period of months. Early reports on stone fruit have indicated that postharvest water stress can have a detrimental effect on flower bud development and subsequent fruiting in apricot,<sup>184,185</sup> but little effect on vegetative tree growth.<sup>186</sup>

Johnson et al.<sup>25</sup> determined the long-term response of early maturing peach to postharvest water deficits under California conditions. They found that flower, fruit density, and the occurrence of double fruit were greater in the dry treatment than the control. After normal hand thinning, yields and fruit size were not affected over a 4-year period. Vegetative growth was reduced, but there was no indication of a decline in vigor. A well-timed irrigation before carpel differentiation reduced the occurrence of double fruit. This management strategy could reduce water use while preserving marketable yields.

Three levels of postharvest irrigation on peach production under California conditions were investigated by Larson et al.<sup>187</sup> Control trees were irrigated at 3-week intervals after harvest, the medium-treatment received one, and dry-treatment trees received no irrigation. The seasonal increase in trunk radius of the dry treatment trees was reduced by 33% relative to either wet or medium treatments. The amount of daily trunk radial shrinkage was inversely proportional to irrigation level. Dormant pruning weights were less in dry treatments, return bloom was greater, and fruit set was increased in the dry treatments. After fruit thinning, there were no significant differences among treatments for fruit yield or fruit size, but fruit maturity was slightly delayed in the dry treatment.<sup>187</sup>

## 2. Methods to Determine Water Stress and Schedule Irrigation

The quantification of plant stress or the scheduling of irrigation can be based on physical (soil moisture, VPD, evapotranspiration), morphological (leaf growth, fruit growth, shoot growth, stem growth), or physiological (water potential, stem water potential, stomatal conductance, photosynthesis, chlorophyll fluorescence) factors.

Stem  $\Psi$  has been found to be a sensitive and reliable indicator of water stress in prune trees<sup>188</sup> under California conditions. However, Garnier and Berger<sup>189</sup> demonstrated that  $\Psi_i$  in peach trees was only slightly affected during a drying period and concluded  $\Psi_i$  was not very sensitive to irrigation, and that stomatal closure acted as a regulator of  $\Psi_i$  while soil water status was a strong regulator of stem  $\Psi$ . Xiloyannis et al.<sup>169</sup> found that in peach trees irrigated at 50% ET,  $\Psi_e$  and  $g_i$  were slightly affected compared with trees irrigated at 100% ET, and strong differences in  $\Psi_i$  were only found with non-irrigated trees.

In a study comparing drought resistance among *Prunus* species from divergent habitats, Rieger and Dummel<sup>153</sup> demonstrated that photosynthesis decreased linearly with stem  $\Psi$  in all species tested, however, the stem  $\Psi$  at which A reached zero was not constant.

Shoot and leaf elongation rates were exponentially dependent on  $\Psi_p$  and were reduced drastically below 1.0 and 0.7 MPa, respectively.<sup>46</sup> As leaf water deficits developed, shoot and leaf expansion were inhibited prior to a reduction in  $g_i$  or A. Thus, a moderate level of water stress can reduce the rate of vegetative growth of peach trees without concomitant reductions in carbon assimilation. It seems,

therefore, that  $\Psi_i$  is not the most sensitive parameter to stress, and that stem water potential or pre-dawn  $\Psi_i$  (which is ca. equal to stem water  $\Psi$ ), would be the matter of choice.

Irrigation based on soil water content or using estimates of evapotranspiration have been used extensively for stone fruit. However, one major limitation in the use of both is that they are not directly related to the occurrence of plant water stress. Worthington et al.<sup>190</sup> have shown that the crop coefficient (amount of water loss in relationship to Epan) for 5-year-old mature peach may vary (0.31 to 0.98) during the season, and that it is very dependent upon crop load and leaf age. Soil moisture values used to indicate irrigation requirements may not be critical values for the plants under all atmospheric conditions, nor do we know where and at what depth to measure soil moisture, especially in glacial till soils where soils can vary greatly within a short distance.

Infrared thermometry has been used to estimate the water use of peach trees<sup>191</sup> by measuring the temperature of the leaves. Leaves not under water stress with open stomata should be significantly cooler than leaves with closed stomata due to high heat of vaporization of water, and the leaves will be cooler than stressed trees. Monitoring foliage temperature minus air temperature may be used to determine water use, and schedule irrigation in peach orchard systems, however modification may need to be made, especially under high VPD. At VPD greater than  $-2$  kPa, stomatal response to VPD introduces a curvilinear response which must be taken into consideration.

Estimating sap flow using the heat balance technique on woody stems is a recent technique that is gaining in interest. In this method, the sap velocity is estimated from the time required for a heat pulse, injected into the xylem to travel a finite distance downstream. Several variations of this method have been tried.<sup>192-195</sup> Good agreement between estimates made with this method and E determined by lysimeters has been reported for trees,<sup>194-196</sup> but Shackel et al.<sup>197</sup> have reported substantial errors on peach under field conditions. However, depending on the accuracy needed and the ability to substantiate results, this seems to be a promising technique for the future.

### 3. Root Zone Wetting

Several split root studies have shown that a proportion of the root system was able to supply the water needs of the tree, and restriction to greater than 50% of the root system was required before there were major effects on shoot system. Tan and Buttery<sup>170</sup> found that watering 50% of the root system could meet the entire need of the plant. That suggested that drip irrigation could be an effective means of applying water to peach. Proebsting et al.<sup>198</sup> found that the effect of restricted irrigated soil volume was similar to that of deficit irrigation. Increasing root:shoot ratios by adjusting the soil volume or by pruning the shoot always increased  $g_i$ . Williamson and Coston<sup>12</sup> restricted peach root growth using several different techniques and evaluated the effect of two levels of irrigation on growth. They concluded that the effects of irrigation rate on vegetative growth were small compared to differences among planting treatments which restricted root volume.

## D. FLOODING

Flooding has negative effects on most growth and physiological process of woody plants.<sup>149-151,199,200</sup> The response is clearly due to a lack of oxygen, early symptoms are similar to drought, and death often occurs without diseases if the species is flood sensitive.

### 1. Species and Rootstock

*Prunus* are generally considered to be quite sensitive to anoxia. Rowe and Beardsell<sup>199</sup> ranked waterlogging tolerance of fruit trees and from that ranking *Prunus* sp. would be classified as follows: moderately tolerant, plums (*P. domestica* L. and *P. cerasifera* L.); sensitive, plum (*P. salicina* Lindl.); very sensitive, cherry, apricot, and peach. It is generally accepted that tolerance to waterlogging is mainly determined by rootstock and not the scion.<sup>150,199,201,202</sup> According to Schaffer et al.<sup>150</sup> almond and apricot are the most sensitive, followed by peach, cherry, plum, and prune.

Although not considered the most tolerant of fruit species to flooding, *Prunus* spp. exhibit a wide range of diversity, and due to graft compatibility allow for this trait to be transmitted via rootstock to the more sensitive species.<sup>150,158</sup> Schaffer et al.<sup>150</sup> have rated the relative tolerance of *Prunus* species to flooded soil conditions and we refer the reader to their review article for a more thorough discussion of species and cultivar differences. Tolerance may range from several months for plum and prune rootstocks<sup>203</sup> to less than 5 days for peach<sup>157</sup> and cherry.<sup>160,204</sup>

## 2. General Responses

Soil flooding results in low oxygen levels, and soils may be oxygen depleted within 1 day of waterlogging.<sup>205</sup> Oxygen diffusion rates are inhibited and rates below  $0.2 \mu\text{g O}_2 \text{ cm}^{-2} \text{ hr}^{-1} \text{ min}^{-1}$  have been correlated with reduced hydraulic conductivity and/or growth in peach.<sup>201</sup> Inhibition of shoot, leaf, and/or root growth have been reported in response to flooding for peach<sup>158</sup> and cherry.<sup>160,204</sup> Plant metabolism can also be affected (see Schaffer et al.<sup>150</sup> for a thorough review).

Growth and survival is dependent upon the time of flooding; with flooding during the growing season having a greater effect than during the dormant period.<sup>158,160,204</sup> Cyanogenic glycosides are common in tissues of *Prunus* spp. and Rowe<sup>206</sup> observed that under an aerobic stress, detached roots of these species evolved phytotoxic amounts of hydrogen cyanide. Additionally, Rowe and Catlin<sup>200</sup> have demonstrated that differential sensitivity of peach, apricot, and plum was correlated with cyanogenic glycoside content of the root tissue, and has been related to their ability to metabolize prunasin.<sup>203</sup>

## 3. Gas Exchange

The mechanisms by which anoxia inhibits  $A$  and  $g_s$  in fruit crops is not fully understood. Short-term effects include a decrease in  $A$  and  $g_i$  and an increase in root resistance to water flow. Typically, hydraulic conductivity of the root system is reduced<sup>150,202,207</sup> followed by typical water stress symptoms (more negative  $\Psi_i$ , lower  $g_s$ , and reduced shoot growth). Using  $A/C_i$  curves to partition out stomatal vs. biochemical limitations, and using a bioassay system, Beckman et al.<sup>97,160</sup> presents evidence that toxins produced by the root under anaerobic conditions contributed to the nonstomatal inhibition of photosynthesis in sour cherry. The identity of the toxin or inhibitory compound is not known, although ABA is known to increase in concentration in roots of pea in response to flooding.<sup>208</sup> This raises the possibility that  $g_s$  was not the major factor in reducing  $A$ .

The hydraulic conductivity of the root system is disrupted soon after flooding is imposed. This could result in more negative  $\Psi_i$  and an indirect effect on  $A$  through inhibition of  $g_i$ . Although this occurred in cherry, Beckman et al.<sup>209</sup> concluded that if inhibition of  $A$  occurred prior to stomatal closure it was in part due to an unknown signal from the root.

Our current understanding of anoxia on the mechanism of photosynthetic inhibition in *Prunus* is not complete. There is likely more than one cause, and the appearance of a toxin or lack of growth regulator produced in the root, followed by a disruption of hydraulic conductivity, is consistent with observed responses.

## VII. OTHER ENVIRONMENTAL FACTORS

### A. SALINITY

*Prunus* spp. are generally considered to be sensitive to salinity compared to most fruit crops.<sup>210-212</sup> Salt can be a problem in certain arid regions (Middle East, North Africa, Arizona) where rainfall levels are low. Bernstein et al.<sup>210</sup> demonstrated that six different varieties ('Golden Blush' peach, 'Texas' and 'Nonpareil' almonds, 'Santa Rosa' plum, 'French Improved' plum, and 'Royal' apricot) of stone fruit on Lovell rootstock were sensitive to moderate levels of salinity ( $\text{EC}_i = 0.9 \text{ mmhos}$ ), and determined that 50% of the response was due to chloride injury and 50% due to the increase in  $\Psi_\pi$  of the soil. Salt tolerance of all six varieties was similar except that the apricot was more sensitive than the others. When compared to 'Lovell' rootstock, 'Shalill' had higher chloride accumulation and less growth in peach and almonds; the Yunnan root increased chloride accumulation and toxicity in apricots, while the 'Mariana' reduced chloride accumulation and improved growth in plum and prune.

### B. AIR POLLUTION

Ozone inhibited growth and photosynthesis of almond, plum, apricot, and pear linearly with increasing concentration<sup>213</sup> while peach and cherry are unaffected. Apricot cultivars differed in their sensitivity, 'Nonpareil' was most sensitive, 'Butte', 'Carmel', and 'Sonora' were intermediate, and 'Mission' was unaffected.<sup>214</sup> Exposure of 'Casselman' plum to increased atmospheric ozone partial pressure ( $-0.44$  to  $0.111 \mu\text{Pa} \cdot \text{Pa}^{-1}$ ) over two growing seasons reduced  $A$ , caused premature leaf fall, decreased trunk growth, and reduced yield. Symptoms appear as either flick or stipple on the upper surface of the leaves,<sup>215</sup> and chlorosis and abscission may occur.

Fluoride causes injury to leaves and fruit of many stone fruit<sup>215</sup> species. Sensitive species show leaf necrosis at concentrations of 0.5 ppm or less. A disorder in peach known as soft suture is associated

with fluoride. Heggstad<sup>215</sup> considered *Prunus* as among the most sensitive species to fluoride injury, and ranks apricot as highly sensitive, prune (*P. domestica*), peach, and mahaleb cherry as sensitive, while sweet cherry, oriental flowering cherry, and myrabalam plum (*P. cerasifers*) are moderately tolerant.

Sulfur dioxide and acid rain are major air pollutants near industrial areas that affect vegetation. Zimmerman and Hitchcock<sup>216</sup> demonstrated that when plants were exposed to SO<sub>2</sub> plants of 0.2 to 1.1 ppm for 2 to 8 hours, apricot was only slightly affected, while Italian prune showed moderate phytotoxicity. Acid rain does not seem to have a direct effect of foliate, but may be a problem indirectly by lowering soil pH to 3 or less.<sup>217</sup>

## VIII. CONCLUSIONS

The questions raised in this chapter indicate definite needs for future research. In the author's opinion the following questions need to be resolved.

1. Since we are dealing with a perennial plant, any environmental or biological limitation that occurs in one season can have a profound effect on future seasons growth and yield. The effect may be obvious as would be the case with winter injury to the trunk of a tree, or it might be quite subtle, as is the case with premature defoliation. At present we do not have a "currency" within the plant that we can measure that will indicate that future effect. Research is needed in this area. What variable should be measured when should it be measured, and how can the variable be related to plant performance?
2. Quantitative data on the interaction between multiple environmental stresses and between environmental and biological stress are needed. For example how much damage can a tree sustain from an insect before economic damage results, and what effect would water stress have on this threshold.
3. The development of good predictive models that can help us anticipate the effect of an environmental constraint so that changes in management might be initiated to maximize future production have just begun to be developed. This area needs considerable emphasis in the future.
4. Are some stresses desirable? Is it possible to precondition a plant with an initial stress, or simulated stress, to increase the plants resistance to a future stress? How universal is this response?

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# Strawberry

Kirk D. Larson

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## I. INTRODUCTION

The modern cultivated strawberry (*Fragaria x ananassa* Duch.) is the most widely distributed fruit crop world wide due to genotypic diversity and a broad range of environmental adaptation.<sup>1-3</sup> World production of strawberries is increasing. The major strawberry producing countries are the United States, Poland, Japan, Italy, Spain, the former USSR, Republic of South Korea, and Mexico,<sup>4</sup> with Europe accounting for nearly half of the world's production. In the United States, California produces over 75% of the commercial crop, followed by Florida, Oregon, Michigan, Louisiana, and Washington. Many cultivars have specific regional adaptation due to critical photoperiod and temperature requirements,<sup>5</sup> and strawberry cultural systems are highly variable.<sup>2,3,6</sup>

### A. ORIGIN AND GENETICS

*Fragaria x ananassa* is a monoecious octoploid hybrid of two largely dioecious octoploid species, *F. chiloensis* (L.) Duch. and *F. virginiana* Duch.<sup>2,6</sup> Some strawberry cultivars also derive from a subspecies of *F. virginiana*, *F. virginiana glauca* Staudt.<sup>2,3,6</sup> Hybridization of *F. chiloensis* and *F. virginiana* occurred spontaneously in Europe in the 1700s when female plants of *F. chiloensis* of Chilean origin were grown in proximity to male *F. virginiana* plants of North American origin.<sup>2,3,6</sup> Since that time, extensive

hybridization between the parent species and their descendents has occurred, making *F. x ananassa* a highly variable, highly heterozygous species.

There is a wide range of morphological and physiological characteristics among individual strawberry cultivars, with considerable variation in environmental responses.<sup>2,3,7,8</sup> The progenitor species of *F. x ananassa* exhibit considerable ecological variability, due in part to dioecy.<sup>9,10</sup> *F. chiloensis*, which is indigenous to Chile, Hawaii, and the Pacific coast of North America, typically has thicker leaves, more leaf mesophyll tissue and higher net CO<sub>2</sub> assimilation rates (A) (on a leaf area basis) than *F. virginiana*, a native of eastern and central North America.<sup>2</sup> *F. chiloensis* generally is considered more tolerant of drought and salinity, but less tolerant of heat and cold, than *F. virginiana*.<sup>2</sup>

Strawberry cultivars in the eastern and northern United States may have a larger proportion of *F. virginiana* than *F. chiloensis* characteristics, probably as a result of selection in an environment best suited to that species.<sup>2</sup> Modern-day California cultivars may have a relatively larger percentage of germplasm derived from *F. chiloensis* than cultivars developed in other parts of the United States.<sup>11</sup> Present-day cultivars can be grouped according to geographic origin, with the greatest genetic differences occurring between those cultivars developed in California and those developed outside of California.<sup>12</sup> Based on genetic differences, cultivars developed outside of California can be grouped into two geographical regions, a western or northern group, and a southern or eastern group. Thus, physiological differences among cultivars are partly due to the extent to which individual parent species or clones have contributed to a particular genotype.<sup>2</sup>

In addition to *F. x ananassa*, the genus *Fragaria* includes at least eleven other species, including diploids, tetraploids, octoploids, and a hexaploid.<sup>2,3,6</sup> Many of these species have been cultivated at one time or another, and some are still grown on a limited basis.<sup>6</sup> Environmental physiology studies of *Fragaria* have often focused on species other than *F. x ananassa*, and thus do not necessarily describe the physiological responses of the modern cultivated strawberry.

## B. BOTANY

The anatomy, morphology, and growth habit of the strawberry plant have been described in detail in numerous publications.<sup>2,7,13–20</sup> In brief, the plant is a determinate perennial in which the stem is compressed into a rosetted crown,<sup>6</sup> with internodes about 2 mm in length.<sup>7</sup> Axillary buds in the leaf nodes of the crown either remain dormant, or develop into branch crowns, or stolons (runners), depending on prevailing environmental conditions. Inflorescences form terminally, and vegetative growth is continued by the uppermost axillary bud of the crown, resulting in a sympodial growth habit. Although the strawberry is often referred to as an herbaceous perennial,<sup>7,15,21,22</sup> aging results in lignification of the crown, producing a hard, woody tissue.<sup>6</sup> With time, extensive branch crown development produces a structure resembling a highly compacted tree scaffold,<sup>6,8</sup> with certain physiological responses to the environment similar to those of deciduous fruit trees.<sup>6</sup> However, vegetative and reproductive growth of strawberry are more sensitive to environmental conditions, particularly photoperiod and temperature, than most other fruit crops.<sup>3,6–8</sup> Studies concerning the environmental physiology of strawberries must be interpreted carefully due to the genetic diversity in strawberry, and to the variability in environmental response among cultivars.

This chapter discusses the effects of light, temperature, water, and other environmental factors on the growth and development of the modern, cultivated strawberry, *F. x ananassa*. The discussion also includes other *Fragaria* species, particularly when pertinent citations are unavailable for *F. x ananassa*.

## II. IRRADIANCE

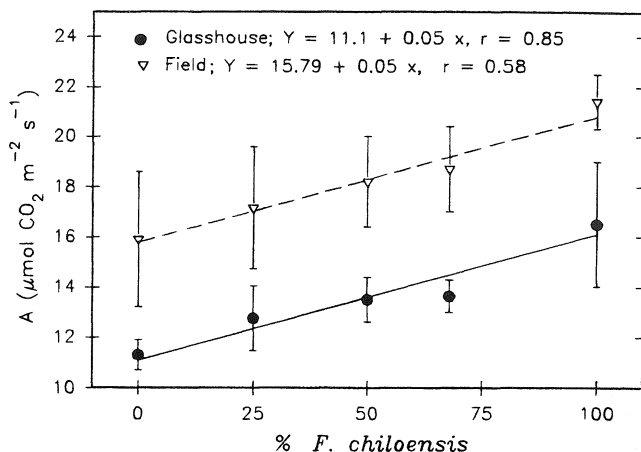
### A. IRRADIANCE LEVEL

In their natural habitats, the progenitor species of *F. x ananassa* are found in divergent light environments. *F. virginiana* is generally considered an understory species, although it occurs infrequently in mature forests,<sup>23–25</sup> whereas *F. chiloensis* is native to high light environments typical of beaches or alpine regions.<sup>26,27</sup>

#### 1. Leaf Gas Exchange

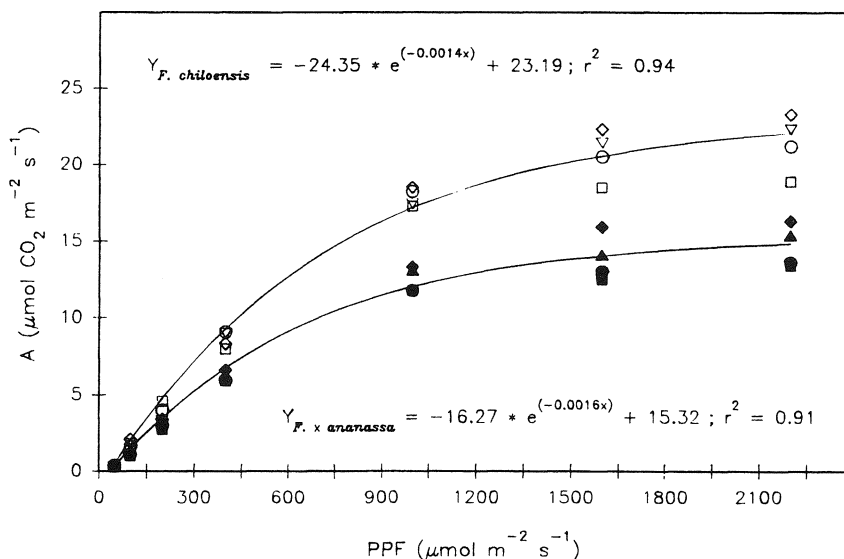
For *F. x ananassa* cultivars, A ranges from about 10 to 23  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ,<sup>28–31</sup> which is intermediate between A of *F. virginiana* (7–15  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and that of *F. chiloensis* (15–30  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ).<sup>24,25,29–33</sup> There is a positive correlation between A and the percentage of *F. chiloensis* germplasm

**Figure 1** Influence of percentage of *Fragaria chiloensis* genetic contribution on net CO<sub>2</sub> assimilation (A) in breeding populations of *F. chiloensis* and *F. x ananassa*. Symbols represent mean A  $\pm$  SE. Redrawn from Hancock, J. F., Flore, J. A., and Galletta, G. J., *Scientia Hort.*, 40, 139, 1989.



in *F. x ananassa* cultivars (Figure 1).<sup>30</sup> The greater A of *F. chiloensis* compared to *F. virginiana* or *F. x ananassa* may be due to thicker leaves and greater amount of leaf mesophyll tissue for *F. chiloensis*.<sup>2,29</sup>

Several studies have been conducted on the effects of irradiance level on A in strawberry, often with differing results. Campbell and Young<sup>34</sup> reported that light saturation for A of 'Quinault' strawberry plants occurred at a photosynthetic photon flux (PPF) between 600 and 800  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ . Similarly, light saturation for A for glasshouse-grown 'Elsanta' plants occurred at about 700  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ , with a light compensation point for A at about 50  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ,<sup>35</sup> and A of 'Earliglow' strawberry plants increased with increasing light intensity, reaching a maximum rate at a PPF between 600 and 800  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ .<sup>36</sup> However, Van Elsacker et al.<sup>37</sup> reported that light-saturated A of leaves of glasshouse-grown 'Primella' strawberry plants occurred at a PPF between 400 and 600  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ , whereas Cameron and Hartley<sup>29</sup> reported that A of four cultivars in a glasshouse increased with increases in PPF up to about 1000  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ , or greater (Figure 2). In a growth chamber, light-saturated A of leaves of 'Bogota' plants occurred at about 50 klx.<sup>38</sup> Although kilolux is a photometric rather than radiometric measurement, 50 klx represents about one half of full sunlight, or approximately 1000  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ .



**Figure 2** Influence of photosynthetic photon flux (PPF) on net CO<sub>2</sub> assimilation (A) for *Fragaria chiloensis* (open symbols) and *F. x ananassa* (closed symbols) genotypes. Different symbols within a species represent different genotypes. Redrawn from Cameron, J. S. and Hartley, C. A., *HortScience*, 25, 327, 1990.

Differences in the reported values for photosynthetic light saturation of strawberry may be cultivar, season, or leaf age dependent.<sup>24</sup> Measurement conditions, or environmental preconditioning, particularly in regard to light, temperature, nutrients, and ambient CO<sub>2</sub> concentration, may also account for some of the observed variability in photosynthetic light saturation. For example, light saturation studies by Campbell and Young<sup>34</sup> used plants preconditioned at 21°C and a PFF of 300  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ , whereas Cameron and Hartley<sup>29</sup> used plants maintained at 25.6°C and a PFF of 1100  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ .

Thus, photosynthetic light saturation in strawberry appears to occur at about one third to one half of full sunlight. Although cultivated strawberries are typically grown in well-illuminated sites where radiant energy is non-limiting, interplant competition for light, especially in mature, matted row production systems or in nurseries, could have adverse effects on whole plant A and productivity.<sup>33</sup>

## 2. Growth and Development

Light is a major environmental factor regulating plant growth and development of *Fragaria* species. Increased irradiance level resulted in increased leaf, root, and crown dry weights,<sup>36,39</sup> stamen development,<sup>40,41</sup> fruit set,<sup>40-43</sup> yield,<sup>36</sup> fruit size,<sup>42</sup> stolon formation,<sup>39,44-46</sup> and stolon dry weight.<sup>39</sup> Although constant shading at 40% of ambient sunlight reduced fruit yield and leaf and crown dry weights, fruit yields and root dry weights increased when shading was applied during the period of stolon formation.<sup>36</sup> Constant shading, or shading during stolon development, either had no effect on stolons or resulted in reduced stolon formation, whereas petiole length and leaf size increased while leaf dry weight decreased. Shading during the spring growth and fruiting period delayed fruit maturity 5 to 7 days. However, shade-induced reductions in irradiance level resulted in decreased air, plant, and soil temperatures, which may also have affected plant growth and development.<sup>36</sup> Thus, shading during a relatively cool year resulted in decreased plant growth and dry weights, but had no effect on fruit yields the following spring.<sup>39</sup>

Ferree and Stang<sup>36</sup> acknowledged the difficulty in defining the specific cause of the shading responses due to the close relationship between light and temperature. Interpreting the effects of irradiance level on strawberry physiology and morphology is often difficult, particularly under field conditions, due to irradiance level, temperature, and photoperiod interactions. Dennis et al.<sup>44</sup> considered that the effects of irradiance on stolon formation were mainly quantitative, and that photoperiod was the most important factor affecting plant response.

Maximum A ( $A_{\text{max}}$ ), on a leaf area basis, leaf thickness, specific leaf weight, and mesophyll cell volume of *F. virginiana* all increased with increasing total daily PPF,<sup>47-50</sup> and total daily PPF had a greater effect on these variables than peak PPF.<sup>49</sup> Jurik et al.<sup>24</sup> observed differences in leaf expansion rates and leaf longevity for *F. virginiana* plants maintained under different PPFs. Leaves from plants maintained in high (678  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ) and low (64  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ) light environments completed leaf expansion in 14 and 19 days, respectively, and had median life spans of 51 and 79 days, respectively. For all plants,  $A_{\text{max}}$  was achieved within 3 days of cessation of leaf growth, with a gradual reduction observed starting 4 to 7 days later. Although  $A_{\text{max}}$  on a leaf area basis was similar for leaves that developed in high and in low light,  $A_{\text{max}}$  was reached earlier, and declined more rapidly for leaves that developed in high-light. High-light plants had higher light compensation points, greater specific leaf weight (SLW), and thicker leaves with more mesophyll cell area and less air space than plants grown in low light. Changes in leaf anatomy and A were observed for developing leaves when plants were transferred from one light environment to another, indicating a potential for adaptation to changing light environments. This adaptive potential decreased with leaf expansion and increasing leaf age. Light-saturated A in *F. vesca* occurred at PPFs between 400 and 600  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ; A, specific leaf weight, leaf thickness, flowering, stolon production, and biomass all increased with increasing irradiance level.<sup>47</sup>

Strawberry seed germination is promoted by exposure to light, and germinating seed should be left uncovered.<sup>2,6,51,52</sup> The physiological mechanism underlying light promotion of strawberry seed germination has not been elucidated.

## B. PHOTOPERIOD

Strawberry cultivars are often categorized on the basis of photoperiodic responses, particularly in regard to floral induction and flower bud initiation. Leaf size, petiole length, and stolon development are also highly sensitive to photoperiod and temperature. In many cultivars there are strong photoperiod  $\times$  temperature interactions in which temperature modifies the photoperiodic response.<sup>8,26,44,46,53-58</sup> Although

vegetative and reproductive responses of strawberry plants to photoperiod and temperature are well documented, the physiological processes that regulate these responses have not been elucidated.

Most strawberry cultivars are classified as 'short-day' (SD) (also known as 'single cropping', 'Junebearing', or 'neverbearing') types, in which floral induction occurs with photoperiods of less than about 14 hrs. However, most SD cultivars exhibit a *facultative* SD response, in which floral induction will occur more or less continuously regardless of daylength, provided that temperatures are less than about 16°C.<sup>5,8,26,59</sup> Thus, although SD cultivars may have different critical photoperiods,<sup>26</sup> and a few SD cultivars are obligate single-croppers that have only one short fruiting season per year,<sup>2</sup> most will bloom independently of daylength with moderately cool temperatures. It is uncertain whether an obligate single-crop bearing habit is an inherent varietal characteristic, or is the result of excessive vegetative vigor due to winter chilling<sup>26,60-63</sup> (see Section III).

A second photoperiodic group of strawberries is comprised of the everbearing (EB) cultivars, also referred to as day-neutrals (DN), that generally flower continuously regardless of daylength. Although temperature also modifies the photoperiodic response of this second group of cultivars, they are less sensitive to high temperatures than SD cultivars. Some authorities recognize three groups, distinguishing between EB and DN cultivars on the basis of long day (LD) flower promotion in EB cultivars and no daylength effect in DN cultivars.<sup>26,54</sup> However, others consider the division between these photoperiodic types to be subjective and ill-defined.<sup>6,7</sup> In reviewing the work of Durner et al.,<sup>54</sup> Galletta and Bringham,<sup>6</sup> noted similar floral development patterns for all photoperiodic types in response to a given photoperiod × temperature regime. They concluded that the major difference among photoperiodic groups was a decreasing sensitivity to high temperatures from SD to EB to DN. Thus, flowering in strawberries ranges in a continuous gradient from obligate single-cropping ('Fairfax') to facultative short-day through the various degrees of everbearing or day neutral.<sup>62,64</sup>

Photoperiodic effects on flowering of strawberries were first reported by Sudds,<sup>65</sup> who observed increased flowering under an 8-hr photoperiod compared to a normal midsummer photoperiod of about 15 hrs in Pennsylvania. Darrow and Waldo<sup>26</sup> recognized that temperature was probably as important as photoperiod in regulating plant growth. At temperatures above 16°C, the critical photoperiod for floral initiation was 10 hrs or less, whereas at lower temperatures initiation occurred with photoperiods longer than 10 hrs. Dormancy or rest in some cultivars was considered to be caused by a combination of short photoperiods and low temperatures.<sup>26</sup> This rest period was broken by exposure to freezing temperatures, or, in some cultivars, simply by increasing the daily photoperiod (see Section III).

For plants maintained with LD (15-hr photoperiod) but for which varying percentages of leaf area were maintained with SD (10-hr photoperiod), floral initiation was directly proportional, and stolon development inversely proportional, to the percentage of total leaf area exposed to SD.<sup>57</sup> Entire plants maintained under LD failed to bloom, but flowers were produced in runner plants under LD with the attached mother plants under SD (inductive) conditions.<sup>57</sup> These experiments were considered to be indicative of a flowering stimulus that was produced in the leaves and translocated from the mother plant to the stolon under the appropriate photoperiodic conditions<sup>57</sup>. Other studies, however, failed to confirm the presence of a translocatable flowering stimulus.<sup>7,66-69</sup> The discrepancies among studies are difficult to explain, but may be due to cultivar differences, or differences in plant preconditioning.<sup>66</sup>

Flowering in strawberry was observed to occur under the following photoperiodic regimes: short light period (10 hr) with long dark period (14 hr), short light and dark periods (10 hr), and long light and dark periods (14 hr).<sup>57</sup> Floral inhibition only occurred when the daily light period was longer than the daily dark period (14 and 10 hrs, respectively). Based on this and other studies, it was hypothesized that a flower-inhibiting substance was produced in the leaves during the light period; flowering only occurred if the inhibitor was depleted during the subsequent dark period.<sup>57</sup> Thus, the duration of the dark period, rather than the light period, was considered to be the factor controlling floral initiation.<sup>57</sup> However, Vince-Prue and Guttridge<sup>70</sup> hypothesized that strawberry floral initiation was not promoted by SD conditions *per se*, but by a floral inhibitor produced under LD conditions. Thus, rather than SD stimulation of flowering, the absence of LD conditions releases strawberry from floral inhibition.<sup>8</sup>

Flowering has been observed to occur under continuous light,<sup>8,71</sup> in apparent contradiction to most studies of photoperiodic regulation of floral induction in strawberry. This phenomenon may have resulted from the type of light source used,<sup>71</sup> or from an unrecognized stress.<sup>8</sup>

Defoliation<sup>72</sup> and paired receptor-donor (plants joined by a stolon) experiments<sup>66-69,73</sup> demonstrated translocation of a floral inhibitor and the promotion of vegetative growth in donor plants maintained under LD or night interruption conditions to receptor plants maintained under SD (inductive) conditions.

Floral initiation in response to defoliation varies with photoperiodic type. Summer defoliation of a SD cultivar failed to promote floral initiation, whereas defoliation of an everbearing cultivar enhanced floral initiation.<sup>74,75</sup> Moore<sup>76</sup> reported yield reductions following defoliation, and suggested that leaf pruning eliminated the source of a floral-promoting substance. In another study, defoliation resulted in increased fruit production due to an increase in the number of crowns initiating bloom.<sup>77</sup> In this case, increased bloom was attributed to the removal of the source of a floral-inhibiting, growth-promoting substance located in the leaves.

Borthwick and Parker,<sup>78</sup> using daylength extension and night interruption, found that floral initiation was regulated by the duration of the dark period rather than by the length of the light period, and that flowering was, at least in part, phytochrome-mediated. This was evidenced by the fact that floral initiation occurred under 8- and 11-hr photoperiods, but was inhibited by a 3-hr night interruption, or by photoperiods of 14 hrs or greater.

Photoperiod has a marked effect on strawberry vegetative growth and morphology, in that stolon formation, petiole length and leaf area increase with increasing photoperiod.<sup>5,13,14,79-82</sup> Photoperiodic effects on stolon formation are cultivar-specific; 'Missionary' was more sensitive to LD or night interruption than 'Sparkle' or 'Tennessee Beauty'.<sup>81</sup> Maas and Cathey<sup>82</sup> reported that stolon formation in response to supplemental lighting varied with the photoperiodic type of the cultivar; with exposure to LD, stolon development was greatest for a SD cultivar, was intermediate for an EB cultivar, but did not occur for a DN cultivar, although an increase in crown branching was observed.

Regardless of plant preconditioning, the period of cell division in expanding strawberry leaves increases with increasing photoperiod. Cell numbers per leaf, leaf size, and petiole length all increase with LD, whereas with SD, cell division ceases shortly after leaf emergence, resulting in fewer cells per leaf, and smaller leaves with shorter petioles.<sup>13,79,80</sup> The effect of photoperiod is mainly due to an increase in cell number, rather than an increase in individual cell size.<sup>13,79</sup> Cell division in higher plants is promoted by gibberellic acid (GA),<sup>83</sup> and attempts have been made to explain photoperiodic regulation of strawberry growth and development on the basis of GA or other hormonal activity. Exposure to LD or to exogenous gibberellic acid (GA<sub>3</sub>) elicited similar responses, i.e., floral inhibition, and increased stolon formation, petiole length and leaf size.<sup>7,84-86</sup> Furthermore, GA-like activity has been observed in strawberry tissue extracts,<sup>60,87,88</sup> and GA activity increased in strawberry plants exposed to LD or night interruption.<sup>89</sup> However, exogenous gibberellins applied in the absence of LD or chilling did not completely substitute for the endogenous factors that promoted petiole elongation.<sup>86</sup> A marked reduction in endogenous auxin at the time of floral induction in strawberry was determined to be the result of floral induction, rather than a causative factor.<sup>90</sup> Durner and Poling<sup>55</sup> suggested that floral initiation in strawberry is regulated by two substances, a reproductive growth promoter produced under SD conditions, and a vegetative growth promoter produced under LD or night interruption conditions. Production of these substances is proportional to the amount of leaf area exposed to SD or LD conditions, and translocation via the stolon occurs only from older to younger plants.<sup>55</sup>

Cold damage to strawberry plants maintained in the dark was greater than that of plants maintained under a 12-hr photoperiod, suggesting a light requirement for development of cold-hardiness in strawberry.<sup>91</sup> Other studies show that for some plants, including strawberry, translocatable, cold-hardiness promoters are produced in the leaves under SD conditions.<sup>92-94</sup> Thus, the observed lack of cold-hardiness in non-illuminated strawberry plants may have resulted from non-inductive photoperiodic conditions, rather than a lack of exposure to light per se.

## C. PHOTOPERIOD × TEMPERATURE INTERACTIONS

Floral *induction* refers to the processes that occur in a leaf upon exposure to the environmental conditions that result in the eventual production of a flower bud; floral *initiation* refers to the physiological and anatomical changes that occur at a meristem in response to floral induction; and floral *differentiation* refers to the events that occur in the meristem from initiation through anthesis.<sup>95</sup>

There is a strong relationship between photoperiod and temperature in the regulation of strawberry reproductive and vegetative responses. Darrow<sup>53</sup> found that SD conditions favored floral initiation and inhibited stolon formation, regardless of temperature. However, the optimal temperature for floral initiation or stolon development was photoperiod dependent (Table 1). Under SD conditions, floral initiation from November through March was greatest at 21°C, intermediate at 15.6°C, and lowest at 12.8°C. There was no stolon initiation at any temperature. With a 14-hr photoperiod, the optimal temperature for floral initiation was 15.6°C, followed by 12.8 and 21°C. There was a five-fold increase

**Table 1 Influence of temperature and photoperiod on stolon and flower development in strawberry**

| Treatments    |                  | Stolons (S) and flower panicles (F) produced per month |    |     |    |     |    |     |    |     |    |       |     |
|---------------|------------------|--|----|-----|----|-----|----|-----|----|-----|----|-------|-----|
| Temp.<br>(°C) | Photo-<br>period | Nov  |    | Dec |    | Jan |    | Feb |    | Mar |    | Total |     |
|               |                  | S  | F  | S   | F  | S   | F  | S   | F  | S   | F  | S     | F   |
| 21            | 16 hrs           | 91   | 2  | 95  | 0  | 27  | 0  | 40  | 0  | 59  | 12 | 312   | 14  |
|               | 14 hrs           | 66   | 5  | 27  | 0  | 7   | 1  | 4   | 10 | 6   | 24 | 110   | 40  |
|               | Ambient          | 0  | 24 | 0   | 41 | 0   | 74 | 0   | 61 | 0   | 81 | 0     | 281 |
| 15.5          | 16 hrs           | 57   | 5  | 15  | 0  | 0   | 0  | 0   | 11 | 0   | 38 | 71    | 54  |
|               | 14 hrs           | 19   | 13 | 4   | 7  | 0   | 0  | 0   | 24 | 0   | 71 | 23    | 115 |
|               | Ambient          | 0  | 26 | 0   | 16 | 0   | 14 | 0   | 53 | 0   | 70 | 0     | 179 |
| 12.8          | 16 hrs           | 40   | 6  | 8   | 1  | 1   | 0  | 0   | 0  | 0   | 61 | 49    | 68  |
|               | 14 hrs           | 18   | 5  | 2   | 1  | 0   | 0  | 0   | 4  | 0   | 63 | 20    | 73  |
|               | Ambient          | 0  | 18 | 0   | 7  | 0   | 2  | 0   | 14 | 0   | 92 | 0     | 133 |

Adapted from Darrow, 1936.<sup>53</sup>

in the number of stolons produced at 21°C than at 12.8 or 15.6°C. With a 16-hr photoperiod, floral initiation during the five-month period was greatest at 12.8°C and lowest at 21°C, with stolon development inversely proportional to floral initiation. Cultivar differences were also noted, particularly in regard to floral initiation under LD conditions.<sup>53</sup> Under LD (14–16 hrs) and at 21°C, ‘Klondike’ produced only stolons, but ‘Burrill’ produced equal numbers of stolons and flower clusters, whereas at 15.6°C, ‘Klondike’ produced both flowers and stolons, and ‘Burrill’ was almost entirely sexually reproductive.

Hartman<sup>56</sup> studied floral initiation as a function of temperature and photoperiod in four cultivars. All cultivars bloomed at 15.6°C, regardless of photoperiod, and no cultivar flowered under a 15-hr photoperiod at 21°C. However, only three of the four cultivars flowered in a 10-hr photoperiod at 21°C, leading to the conclusion that temperature was as important as photoperiod in regulating floral induction in some cultivars. Similarly, for ‘Marshall’ plants maintained at 6°C, floral initiation occurred with exposure to 8-, 16-, or 24-hr photoperiods, but only occurred with 8- or 16-hr photoperiods, or an 8-hr photoperiod, for plants maintained at 10 and 14°C, respectively.<sup>46</sup> Floral initiation in ‘Robinson’ maintained at 9°C occurred with 8-, 12-, 16-, 20-, or 24-hr photoperiods, whereas at 17°C, initiation was limited to photoperiods of 12 hrs or less.<sup>59</sup> For Scandinavian cultivars adapted to long summer photoperiods, flower initiation occurred at 12 or 18°C with 10-, 12-, 14-, 16-, or 24-hr photoperiods, but at 24°C, floral initiation did not occur with photoperiods greater than 14 or 16 hrs.<sup>5</sup> The critical inductive temperature/photoperiod combination may vary among SD cultivars, but higher temperatures and longer photoperiods generally inhibit bloom and result in increased stolon development.

Although the optimal daylength for floral induction in SD cultivars appears to be between 8 and 11 hrs,<sup>6,59,78,96,97</sup> the role of photoperiod is more critical at temperatures above 15°C.<sup>8</sup> Thus, the critical photoperiod for floral induction is variously reported as between 12 and 16 hrs,<sup>59,96</sup> 12 and 14 hrs,<sup>98</sup> 11 and 14 hrs,<sup>78</sup> 11 and 15 hrs,<sup>97</sup> 13 and 15 hrs,<sup>99</sup> or 13 and 16 hrs,<sup>5,8</sup> depending on the cultivar, experimental temperature, and photoperiod. Fruiting seasons for SD cultivars tend to be longer in areas with mild winter climates (i.e., Florida and Southern California) due to a longer growing season in which photoperiods are less than 14 hrs, as well as to less winter chilling, because chilling (vernalization) can inhibit subsequent floral induction through promotion of vigorous vegetative growth<sup>7</sup> (see Temperature, Section III). In general, the critical photoperiod for inhibition of floral induction and that for promotion of vegetative growth responses such as increased petiole length, leaf size, and stolon formation are similar.<sup>5,78</sup>

Once floral induction and initiation have occurred, further development is enhanced by exposure to LD conditions.<sup>7,90,100</sup> For SD cultivars, floral cymes developing under SD conditions tend to be very large and basally branched, producing a maximum number of large fruit, but when photoperiods are lengthened, floral cymes tend to branch at a higher position and produce smaller fruit.<sup>26,101</sup> Differences in cyme morphology due to temperature or winter chilling have been observed due to vegetative growth promotion following low-temperature exposure<sup>7</sup> (see Section III).

The number of SD photoinductive cycles required for floral initiation in SD strawberry cultivars is highly variable, due to temperature × photoperiod interactions, as well as seasonal and pretreatment

factors.<sup>8</sup> The minimum number of SD cycles required for floral induction is proportional to temperature, and usually ranges between 7 and 15,<sup>46,57,59,70,90,102</sup> but may be as many as 24<sup>70,78</sup> or more, and is greater at higher temperatures. For example, with a 16-hr photoperiod, more than 16 cycles were required for floral induction at 17°C, but only 10 cycles were needed at 9°C.<sup>59</sup> Similarly, with an 8-hr photoperiod, only 10 cycles were required for floral induction at 24°C, but more than 20 cycles were required at 30°C.<sup>59</sup>

#### D. SPECTRAL QUALITY

Variations in spectral quality can affect strawberry plant physiology. Under floral inductive conditions (8-hr days), flower initiation in a SD strawberry cultivar was delayed or inhibited, and leaf petiole length increased, by extending daylength with far-red light (FR, 700–800 nm) during the first half but not during the second half of the daily dark period.<sup>70,103,104</sup> Similar responses were obtained with exposure to red light (R, 600–700 nm) during the second half, but not the first half of the dark period. Combinations of R and FR were inhibitory at either time. Stolon formation, and leaf laminae and petiole length, all increased with exposure to FR during the first half of the daily dark period, or with exposure to R during the latter half of the dark period.<sup>70,103,104</sup> Flowering was delayed when filters were used to remove R from sunlight, but filtering out both R and FR resulted in earlier bloom than in control plants.<sup>105</sup> Daylength extension with incandescent light, which emits a high proportion of FR, inhibited flowering at irradiances of 0.1 J m<sup>-2</sup> s<sup>-1</sup>, whereas fluorescent lighting, which emits little FR, did not inhibit flowering, even at irradiances of 25 J m<sup>-2</sup> s<sup>-1</sup>.<sup>59,102</sup>

Sensitivity to FR, or to R plus FR before or after the daily light period, or to R during the latter half of the dark period are typical of LD, phytochrome-mediated plant responses to spectral quality, but atypical of SD plant responses.<sup>70</sup> Based on the work with spectral light responses, strawberry exhibits spectral sensitivity patterns and processes typical of LD plants, but exhibits an opposite floral response, in that LD conditions inhibit flowering in strawberry.<sup>8,106</sup>

### III. TEMPERATURE

Strawberry growth and development are highly sensitive to variations in air and soil temperature. Simple effects of temperature as well as interactions often are cultivar and species dependent.

#### A. GROWING SEASON TEMPERATURES

##### 1. Leaf Gas Exchange

A temperature optimum of 15°C for A has been reported for 'Bogota' strawberry plants, although mesophyll conductance was highest at 20°C.<sup>107</sup> Photorespiration and transpiration (E) increased as air temperature increased from 10 to 30°C, but stomatal conductance to water vapor (g<sub>s</sub>) decreased, probably as a result of an increased vapor pressure deficit (VPD) between the leaf and air.<sup>107</sup> Van Elsacker et al.<sup>37</sup> reported a temperature optimum for A of 'Primella' strawberry to be between 15 and 25°C. Net CO<sub>2</sub> assimilation (on a leaf area basis) decreased as root temperature increased from 8 to 23°C<sup>108</sup>; however, on a whole plant basis, A increased due to increased leaf production at the higher temperatures. Transpiration and g<sub>s</sub> also increased with increasing root temperature.<sup>108</sup>

Photosynthetic temperature optima may vary among *Fragaria* species and with preconditioning treatments. For plants maintained at either 20/10°C or 30/20°C (day/night), A<sub>max</sub> for *F. chiloensis* was between 16 and 20°C.<sup>109</sup> However, for plants of *F. virginiana* and for two cultivars of *F. x ananassa* grown at 20/10°C or 30/20°C, A<sub>max</sub> was between 18–24 and 24–30°C, respectively, indicating an increase in temperature optima for A with increased growth temperature regime. For plants of *F. vesca* grown at either 10/20 or 30/20°C, A<sub>max</sub> was 15–20 and 25°C, respectively, again indicating photosynthetic acclimation to temperature.<sup>47</sup> The ability to acclimate to higher temperatures may account for the wider geographical adaptation of *F. x ananassa*, *F. virginiana* and *F. vesca* compared to that of *F. chiloensis*.

##### 2. Growth and Development

###### a. Soil Temperatures

There was no significant difference in root growth (dry weight) in 'Robinson' strawberry plants maintained at soil temperatures of 7.2, 12.8, 18.3, or 23.9°C, although there was a trend toward greater root growth with decreasing soil temperature.<sup>110</sup> The soil temperature optima for vegetative growth of strawberry appears to vary with cultivar. For example, for the cultivars 'Shasta' and 'Lassen', root dry weights were greatest with soil temperatures of 12.8 and 7.2°C, respectively.<sup>111</sup> Crown dry weights were

greatest with soil temperatures of 18.3 and 7.2°C, respectively, although leaf and total plant dry weights for both cultivars were greatest with soil temperatures of 12.8°C.<sup>111</sup> For ‘Shasta’ and ‘Lassen’, fruiting occurred only at 7.2 and 12.8°C, and was greatest at 7.2°C, while stolon development only occurred at or above soil temperatures of 18.3°C, and was greatest at 23.9°C. The use of black, polyethylene mulch increased diurnal soil temperatures at a 10-cm depth from 21 to 23°C at night, and from 27 to 30°C during the day, resulting in increased leaf elongation rates.<sup>112</sup> Voth et al.<sup>113</sup> observed a 4°C increase in soil temperature in January in southern California as a result of clear polyethylene bed mulch. For mulched plants, increased winter soil temperatures promoted plant growth, resulting in a 30% yield increase over plants on nonmulched beds.<sup>113</sup> Conversely, under high temperature conditions, opaque polyethylene or organic fiber mulches are often used to reduce soil temperatures. The influence of various bed mulches on soil temperature, and on reproductive and vegetative growth of two day-neutral cultivars, was studied during the summer in Iowa.<sup>114</sup> Soil temperatures, plant dry weights, and production were reduced, but fruit yields increased with straw or white-on-black polyethylene mulch compared to clear polyethylene.<sup>114</sup>

### ***b. Ambient Temperatures***

Nine cultivars from diverse geographical areas had high growth rates with ambient temperatures between 20 and 26°C; maximum growth rates occurred at about 23°C.<sup>115</sup> Similarly, leaf and total plant dry weights for ‘Robinson’ were greatest at 23.9°C,<sup>110</sup> but leaf development in ‘Marshall’ was greatest between 14 and 17°C.<sup>116</sup> In a short-term growth chamber study, petiole and leaf elongation rates of ‘Olympus’ strawberry increased exponentially with increasing air temperatures from 10 to 28°C, although a subsequent study of longer duration suggested that optimal temperature for leaf elongation was 22°C.<sup>116</sup> Moderate leaf production rates in the cultivar ‘Royal Sovereign’ occurred at a minimum of 5°C,<sup>13</sup> and temperatures above 35°C inhibited stolon growth, and decreased fruit fresh weight and fruit soluble solids content.<sup>6,117</sup> During periods of high temperature, evaporative cooling from mist or sprinkler irrigation can result in increased flower and fruit production, and increased vegetative growth.<sup>118–120</sup>

In general, temperature effects on shoot growth of strawberry are similar to those of other temperate fruit crops, but optimal soil temperature for strawberry root growth appears to be lower than that for many temperate fruit crops.

Temperature effects on fruit set may be cultivar dependent.<sup>121,122</sup> For example, fruit set of ‘Deutsch Evern’ was good with temperatures between 10 and 26°C, whereas fruit set did not occur below 17°C for ‘Jucunda’,<sup>122</sup> possibly as a result of low temperature-induced stamen abortion.<sup>6,121</sup> Temperatures below 15.6°C may inhibit pollen germination and pollen tube growth, resulting in misshapen fruit.<sup>123</sup> Temperature can also affect fruit set and fruit quality due to indirect effects on pollinator (bee) activity. Although the cultivated strawberry has perfect flowers and is self-fruitful, pollination is enhanced by bees.<sup>124–126</sup> Bee activity decreases at temperatures below 10°C.<sup>22</sup> Thus cool temperatures, rain, or strong winds that inhibit bee flights, and result in decreased pollination and misshapen fruit.

The length of the fruit development period decreases with increasing temperatures.<sup>2,15</sup> In Maryland, the average period from anthesis to fruit maturity is about 31 days in early spring, but can be as short as 20–25 days in late spring or summer, or as long as 60 days in autumn, due to differences in prevailing temperature and photoperiod during these periods.<sup>2</sup> For ‘Reiko’ strawberry plants maintained in a growth chamber with a 14-hr photoperiod and night/day temperatures of 17/20°C, fruit matured 29 days after anthesis.<sup>127</sup> Fruit size at harvest was negatively correlated with the prevailing soil temperature 6 weeks prior to harvest.<sup>128</sup> During the summer, a 10°C decrease in soil temperature resulted in increases of 0.9–1.6 g/berry, suggesting that mulching, shading, or irrigating the soil to decrease soil temperatures can enhance fruit size and yield.<sup>128</sup> Strawberry fruit continue to increase in size until full maturity. Fruit size was reported to increase 14% between the stages of full red color and full maturity,<sup>2</sup> and fruit size and dry weight increased exponentially up to full maturity.<sup>127</sup>

Spring or autumn frosts often result in injury to strawberry reproductive organs. Cold injury to open strawberry flowers often occurs at temperatures of about –2°C,<sup>2,129–131</sup> although flowers of several cultivars have survived exposure to –4.5°C.<sup>131</sup> Susceptibility to cold injury may vary with cultivar,<sup>131–133</sup> and with the degree of ice nucleation that occurs in the tissue.<sup>132</sup> Supercooling occurs when the temperature of a tissue or liquid decreases below the freezing point without ice crystal formation<sup>22</sup> (see Chapter 8, Volume I for a discussion of supercooling). In the absence of supercooling (i.e., with ice crystal formation in the xylem), the  $T_{50}$  (temperature required to kill 50% of the samples) for open strawberry flowers was –2.1°C.<sup>132</sup> Immature berries were more cold-sensitive ( $T_{50}$  = –1.6°C), whereas unopened flower

buds were more cold-hardy ( $T_{50} = -3.1^{\circ}\text{C}$ ) than opened flowers. Supercooling (i.e., no ice crystallization in the xylem) resulted in a  $T_{50}$  that was 1.3 to  $2.8^{\circ}\text{C}$  lower than when ice crystallization occurred, depending on the tissue. Style and receptacle tissues are reportedly more susceptible to cold injury than anthers,<sup>2,133</sup> although the opposite has also been observed<sup>130,134</sup>; this discrepancy may be due to cultivar differences.

## B. COLD HARDINESS

Strawberry species and cultivars vary in their ability to withstand low temperatures.<sup>2,130,131,135-139</sup> Although certain cultivars reportedly withstand winter temperatures of  $-50^{\circ}\text{C}$ ,<sup>2,6</sup> strawberries are generally not as cold hardy as most temperate fruit crops,<sup>140</sup> and are frequently injured by freezing temperatures.<sup>141,142</sup> For a given cultivar, severity of injury depends on plant developmental stage, temperature preconditioning, climatic conditions, plant nutritional status, soil and plant moisture status, the minimum temperature and its duration, the rate of freezing and thawing, supercooling, and the presence of snow cover or mulch and the time of its application.<sup>132,137-140,143-147</sup> For 'Catskill' strawberry plants, low temperature injury to crown tissue increased as freezing rate increased from  $1.7^{\circ}\text{C hr}^{-1}$  to  $5.6^{\circ}\text{C hr}^{-1}$ .<sup>144</sup> Crown tissue injury also increased as the duration of low temperature increased from 1 hr to 3 days.<sup>144</sup>

Studies with several cultivars have indicated that the critical low temperature for survival of dormant strawberry plants is ca.  $-12^{\circ}\text{C}$ . Harris<sup>148</sup> observed severe plant injury in four cultivars at  $-12^{\circ}\text{C}$ , and Brierley and Landon<sup>149</sup> reported injury for several cultivars following exposure to temperatures of  $-6^{\circ}\text{C}$  and mortality after exposure to  $-12^{\circ}\text{C}$ . Angelo<sup>143</sup> reported severe injury or death of plants exposed to temperatures below  $-10^{\circ}\text{C}$ . Seven cultivars were killed with temperatures of  $-12^{\circ}\text{C}$  in October or November, although some cultivars survived exposure to  $-12^{\circ}\text{C}$  in December.<sup>138</sup> For 'Blakemore' and 'Premier' strawberry plants, there was little or no plant mortality following exposure to  $-4.4$  or  $-7.8^{\circ}\text{C}$ , but considerable mortality occurred at  $-11^{\circ}\text{C}$ .<sup>146</sup> Plant mortality of dormant 'Catskill' plants increased with decreasing temperature from 0 to  $-20^{\circ}\text{C}$ .<sup>140</sup> All plants survived exposure to  $-4^{\circ}\text{C}$ , 50% died at  $-12.5^{\circ}\text{C}$ , while none survived exposure to  $-20^{\circ}\text{C}$ . However, even mild freezing temperatures ( $-4^{\circ}\text{C}$ ) resulted in abnormal plant growth. For all subfreezing (below  $0^{\circ}\text{C}$ ) temperature treatments, leaf emergence was delayed, although there was no difference among temperature treatments in leaf number after 12 weeks of growth. Exposure to subfreezing temperatures resulted in increased development of stolons and of misshapen leaves, and plants exposed to  $-12$  or  $-16^{\circ}\text{C}$  had smaller laminae. The percentage of plants that subsequently flowered and the total number of flowers per plant decreased with decreasing temperatures below  $-4^{\circ}\text{C}$ . For 'Earliglow' plants exposed to various subfreezing temperatures, there was little or no root regrowth after exposure to  $-12^{\circ}\text{C}$ , and no leaf regrowth after exposure to  $-14^{\circ}\text{C}$ .<sup>139</sup> However, 'Honeoye' plants continued to produce new leaves and roots after exposure to  $-14^{\circ}\text{C}$ .<sup>139</sup> For actively growing plants maintained for 2 weeks at fluctuating temperatures between about 1.7 and  $26^{\circ}\text{C}$ , there was no mortality for any of eight cultivars following exposure to  $-3^{\circ}\text{C}$  for 24 hrs, but mortality after exposure to  $-6^{\circ}\text{C}$  was cultivar dependent, and ranged from 0 to 100%.<sup>135</sup> All cultivars were killed with exposure to temperatures of  $-9^{\circ}\text{C}$  or lower.

Water status of strawberry plants affected plant survival under low temperature conditions. Fruit yields and total plant biomass of two strawberry cultivars exposed to subfreezing temperatures increased with decreasing soil moisture.<sup>138</sup> Similarly, for strawberry plants exposed to  $-10^{\circ}\text{C}$ , plants that were watered sparingly had greater survival than plants that received more frequent irrigation.<sup>143</sup> However, the influence of plant moisture status on cold tolerance may be cultivar dependent. Whereas hydrated (root water potential ( $\Psi_r$ ) =  $-0.3$  MPa) and dehydrated ( $\Psi_r$  =  $-1.4$  MPa) 'Earliglow' plants survived temperatures of  $-8$  and  $-12^{\circ}\text{C}$ , respectively, there was no difference in survival temperature between hydrated and dehydrated 'Honeoye' plants, which survived temperatures of  $-14^{\circ}\text{C}$ .<sup>139</sup>

Development of cold hardiness in strawberry plants occurs quickly. For 'Blakemore' and 'Premier' strawberry plants preconditioned at  $0/13^{\circ}\text{C}$  (day/night) for 0, 7, or 14 days, and then exposed to  $-7.8^{\circ}\text{C}$ , survival was greater for plants preconditioned for 7 days than for plants preconditioned for 0 or 14 days.<sup>146</sup> The resumption of vegetative growth results in a rapid loss of cold hardiness.<sup>6</sup>

## C. DORMANCY AND CHILLING

In autumn, exposure to cool temperatures and short photoperiods result in floral induction, branch crown development, reduced leaf size, and with prolonged exposure, the onset of dormancy in strawberry.<sup>8,15,26,61,150,151</sup> Unlike most temperate-zone fruit species, dormancy in strawberry is controlled solely by external conditions (ectodormancy),<sup>6</sup> such as temperature and photoperiod; dormant (resting) plants

retain green leaves, and can resume growth when environmental conditions are favorable.<sup>6,8,15,17</sup> Thus, there is no true dormancy in strawberry.<sup>152</sup> However, in the absence of sufficient chilling, dormant strawberry plants have low vegetative vigor, produce short petioles and small leaflets, have a low, compact growth habit, and yield poorly.<sup>8,15,17,26,61,153–155</sup>

Exposure to low temperatures results in vegetative invigoration, thereby reversing the effects of rest.<sup>8</sup> Complete satisfaction of the chilling requirement promoted vigorous vegetative growth, and resulted in rapid leaf production, increased petiole length, larger laminae, increased stolon formation, and an inhibition of floral induction.<sup>15,26,60,61,150,153,156,157</sup> Partial satisfaction of the chilling requirement promoted leaf production and sustained flowering, but did not promote stolon development.<sup>6,8,15</sup> The growth and fruiting response of strawberry plants for which the chilling requirement is only partially satisfied is somewhat analogous to the phenomenon of “delayed foliation” that occurs in deciduous fruit trees that receive inadequate winter chilling.<sup>6,7</sup> In such trees, vegetative growth is reduced relative to fully chilled trees, and flowering often extends through the growing season.

In the absence of low temperatures, the rest period in some strawberry cultivars can be broken by extending the daily light period.<sup>26</sup> Also, cultivars from the southern United States or similar regions grow adequately at relatively low temperatures under SD and apparently have little or no rest period.<sup>26</sup> Growth during SD of October, November, and December is considered an indication of a cultivar’s regional adaptation; most temperate-zone cultivars grow poorly at that time of year and enter a rest period, while cultivars adapted to the southern United States will grow adequately if temperatures are warm enough.<sup>26</sup> The duration of the inductive conditions required for the onset of rest has not been quantified, but may be about 4 to 6 weeks.<sup>8</sup> However, this period appears to be cultivar-dependent, and may be shorter for some cultivars.<sup>158</sup>

In Florida and certain other areas, annual strawberry production systems utilize nondormant (“green”) plants that have been exposed to SD, but that have received little or no chilling in the nursery prior to transplanting.<sup>158</sup> Transplants are usually grown in high latitude (40–45° N) nurseries and are exposed to SD in the nursery in early autumn. Although exposure to SD results in increased root carbohydrate (starch) content,<sup>159</sup> these low-chill plants have adequate vigor only if a portion of the leaves remain intact (hence the term “green plants”) during transplant and establishment.<sup>158</sup> Optimum nursery digging date for early fruit yield for such low-chilled or nonchilled plants was observed to be a photoperiodic response.<sup>158</sup> Chilling enhanced early yields for some cultivars, but only if plants were dug at or before a cultivar-specific optimum date. Digging after the optimum date resulted in decreased yields, even with a lengthy chilling period, suggesting a SD-induced dormancy.<sup>61,151,158</sup>

Annual production systems used in mild-winter areas such as California rely on cultivars that are bred and selected for growth and high yields with only partial chilling satisfaction.<sup>15</sup> In such systems, planting stock is typically produced in high-latitude (40–42° N), high elevation (>1,000 m elevation) nurseries.<sup>6,160</sup> In the nursery, exposure to high temperatures and LD during summer results in vigorous stolon production, but by late-September or mid-October, photoperiods decrease, and temperatures are sufficiently low to impart partial, but incomplete, chilling. Presumably, each cultivar has a particular photoperiodic and chilling requirement for optimal performance.<sup>158,161</sup> In the nursery, low temperatures and SD conditions reduced vegetative growth and increased stored carbohydrates in the primary roots, crown, and petioles.<sup>6,159,162</sup> Depending on the cultivar, nursery plants are dug and transplanted immediately, or given supplemental cold storage to impart added vigor.<sup>163</sup> Plants harvested at the proper time have adequate stored carbohydrates to handle the rigors of digging, transport, bare-root transplant, or supplemental cold storage, and to support rapid growth during autumn. While these plants have sufficient vigor to sustain fruit production during a 6- to 8-month fruiting season, they lack the excessive vigor that results in stolon development and inhibition of flowering.<sup>61,157,161</sup>

Bringhurst et al.<sup>162</sup> observed that the vigor response of plants exposed to a period of cold storage after digging from the nursery was equal to that of plants exposed to a similar period of chilling in the nursery. Leaves are removed when plants are dug from the nursery, thus harvested, cold-stored plants are physiologically distinct from plants left in the nursery. After a period of time, carbohydrate status of the two sets of plants should be different, since photosynthate will continue to accumulate in plants left in the nursery, whereas photoassimilate in stored plants will gradually decrease as a result of respirational losses during cold storage. The observations of Bringhurst et al.<sup>162</sup> suggest that at the time of harvesting plants for cold storage, carbohydrate levels were already adequate in both sets of plants, and that continued accumulation of photosynthate gave no advantage. They also suggest that after a

certain period of chilling, any benefit of additional chilling is due mainly to an influence on the activity or concentration of endogenous growth regulators.

In addition to stimulating vegetative growth, chilling also stimulates the emergence of previously differentiated inflorescences,<sup>8,150</sup> and results in increased peduncle, pedicel, and inflorescence branch lengths.<sup>8</sup> For dormant 'Catskill' plants, petiole length, leaf number per plant, and number of flowers per plant all increased with increasing exposure to temperatures below 7.2°C.<sup>150</sup> For 'Sovereign' plants preconditioned in SD, stored at 1.7–4.4°C for 36 or 72 days, and then forced at about 15.5°C, petiole lengths were 1.4 and 1.6 times greater, respectively, than petioles of plants that were similarly treated but that received no cold storage.<sup>61</sup> For 'Climax' plants similarly maintained, petiole lengths were 1.5 and 2.2 times greater, respectively, than petioles of nonchilled plants.<sup>61</sup>

For strawberry, reported effective chilling temperatures (the temperature required for breaking rest for resumption of vigorous vegetative growth) range from –2 to 6.5°C.<sup>60,63,153,158,164,165</sup> However, chilling temperatures of 9.5 to 10°C apparently are effective for cultivars adapted either to regions with moderate winters (i.e., California or the southern United States), or to glasshouse forcing during the winter.<sup>153,165</sup>

High temperatures, or large diurnal temperature fluctuations, may counteract the cumulative chilling influence of low temperatures in deciduous fruit species.<sup>166</sup> Tanabe et al.<sup>167</sup> studied the effect of chilling temperature regime on vegetative growth of 'Hokowase' strawberry, and on levels of endogenous growth regulators. Plants were either left in the field under natural chilling conditions, or exposed to growth chamber temperatures of 4°C day/night, 15/4°C day/night, 25/4°C day/night, or constant glasshouse temperatures of 15–25°C. Vegetative growth, calculated as the product of petiole length x laminae width, was determined for all plants during a 60-day period following temperature treatment. Vegetative growth was greatest for plants left in the field. For plants in growth chambers or in the glasshouse, vegetative growth increased with increased exposure to low temperatures; plants maintained at 25/4°C (day/night) or in the glasshouse had the lowest vigor. Vigor appeared to be correlated with concentrations of kinetin and abscisic acid (ABA), in that kinetin concentrations were greatest for field grown plants, and decreased with increased temperature regime. Conversely, ABA concentrations were least for plants in the field, and increased with increased temperature regime. Lavee<sup>168</sup> depicted similar changes in ABA and cytokinins in association with the termination of rest.

The amount of chilling required to terminate rest in strawberry is cultivar dependent.<sup>61,164</sup> Temperate-zone cultivars require longer periods of chilling to overcome rest, while subtropical cultivars require little or no chilling.<sup>8,26,61,154</sup> The duration of the chilling period required for breaking rest ranges from as little as 2 to 4 weeks for cultivars such as 'Tioga' that have a low chilling requirement, to 8 weeks or more for cultivars such as 'Red Gauntlet'.<sup>8</sup>

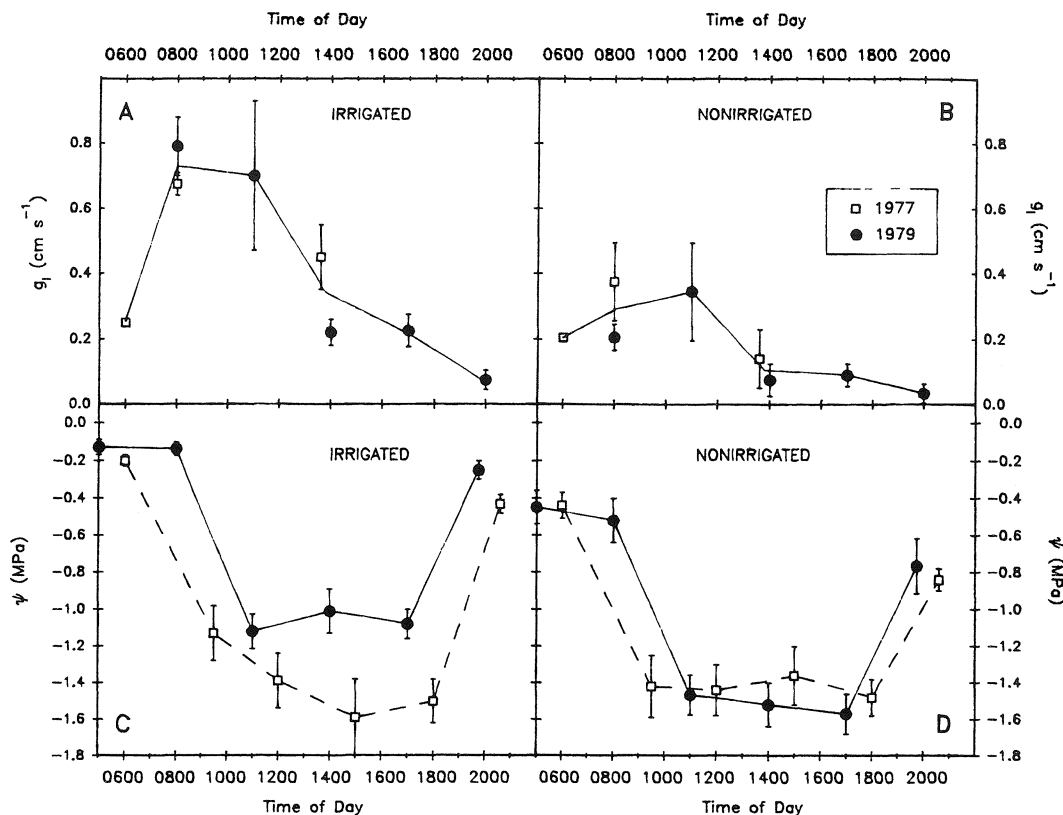
## IV. WATER

Due to an evergreen, semi-herbaceous growth habit, rapid growth rates, high fruit productivity, and a relatively shallow root system characterized by adventitious roots and rapid root turnover (see Section IV, Flooding),<sup>169,170</sup> strawberry plant growth and development are sensitive to variations in soil moisture. Growth and yield responses to soil moisture deficits and irrigation are well documented; however, relatively few studies have focused on the physiological responses of the strawberry to variations in soil moisture content or plant water status.

### A. WATER RELATIONS

Plant water status is a function of the dynamic interaction between the rates of water uptake and water loss by the plant.<sup>171</sup> Decreases in leaf water potential ( $\Psi_l$ ) in response to soil moisture deficits have been observed for strawberry<sup>172</sup>;  $\Psi_l$  may also decrease due solely to increased atmospheric VPD.<sup>173</sup> Maximum plant water status occurs pre-dawn, and determinations of  $\Psi_l$  at that time most closely reflect soil moisture status; mid-day determinations of  $\Psi_l$  are more negative, and reflect atmospheric conditions as well as plant interactions with soil moisture<sup>172,174</sup> (Figure 3).

Reductions in stomatal aperture in response to water deficits have been observed for many plant species, including strawberry<sup>172,175</sup> (Figure 3). However, leaf age and morphology, osmotic adjustment, VPD, irradiance level, and temperature may all influence  $g_s$ ,<sup>173,175</sup> and as a result,  $g_s$  is not always well correlated with plant water status. Although studies of some species indicate a  $\Psi_l$  threshold for stomatal closure,<sup>175,176</sup> other studies indicate a gradual decrease in  $g_s$  with decreasing  $\Psi_l$ .<sup>172,177–179</sup> Although the minimum  $\Psi_l$  values reported in the literature for field-grown strawberries are less negative than the



**Figure 3** Diurnal leaf conductance ( $g_l$ ) and leaf (xylem) water potential ( $\Psi$ ) for irrigated and nonirrigated strawberry plants in first-year plantings in 1977 and 1979. Graphs A and B represent  $g_l$  of irrigated and nonirrigated plants, respectively, with  $g_l$  data averaged for the two years. Graphs C and D represent  $\Psi$  of irrigated and nonirrigated plants. The symbols represent means  $\pm$  SE. Redrawn from Renquist, A. R., Breen, P. J., and Martin, L. W., *Scientia Hort.*, 18, 101, 1982.

minimum values reported for most woody fruit species, the diurnal patterns of  $\Psi_l$  and  $g_s$  for strawberry appear similar to the general diurnal patterns of other fruit species.

Renquist et al.<sup>172</sup> observed diurnal fluctuations in  $\Psi_l$  for irrigated and nonirrigated 'Olympus' strawberry plants during two years (1977, 1979) in the field in Oregon, and during one season in a glasshouse. In the field, regardless of irrigation treatment, there was a typical mid-morning decrease in  $\Psi_l$ , with a minimum  $\Psi_l$  value between late morning and late afternoon, and a gradual increase in  $\Psi_l$  after about 1700 hrs (Figure 3). Predawn  $\Psi_l$  was greater for irrigated than for nonirrigated plants ( $-0.18$  and  $-0.4$  MPa, respectively), reflecting the higher soil moisture content for that treatment. Also, for nonirrigated plants,  $\Psi_l$  decreased more rapidly in the morning, and increased more slowly in the evening than that for irrigated plants.<sup>172</sup> As a result of lower irradiance levels and a moderated environment in the glasshouse,  $\Psi_l$  of irrigated glasshouse plants was less negative throughout the day, and increased more rapidly in late afternoon compared to that of irrigated plants in the field.<sup>172</sup> After a 3-day drying cycle in the glasshouse, minimum  $\Psi_l$  was  $-2.3$  MPa, which was more negative than minimum  $\Psi_l$  values for nonirrigated plants in the field, presumably due to the smaller rooting volume for nonirrigated glasshouse plants.

For irrigated and nonirrigated 'Olympus' strawberry plants,  $g_s$  ranged between about 45 and 360  $\text{mmol m}^{-2} \text{s}^{-1}$ , and 45 and 180  $\text{mmol m}^{-2} \text{sec}^{-1}$ , respectively (Figure 3).<sup>172,176</sup> Throughout most of the day,  $g_s$  of irrigated plants was 2 to 4 times greater than that of nonirrigated plants. For all plants,  $g_s$  was greatest between 0800 and 1100 hr, and then decreased steadily over the remainder of the day.<sup>172,176</sup> A close relationship between  $g_s$  and  $\Psi_l$  was not observed; maximum  $g_s$  often occurred when  $\Psi_l$  was at or near the minimum value.<sup>172</sup>

Darrow and Dewey<sup>180</sup> observed differences between irrigation regimes in regard to diurnal patterns of stomatal aperture in leaves of strawberry plants. For nonirrigated plants, stomata only opened slightly for a brief period in early morning, and were closed for the remainder of the day. For irrigated plants, 80% of the stomata were visibly open at 0900 hr, 25% were open at 1300 hr, 50% were open at 1500 hr, and all had closed at 1700 hr. For 'Bogota' strawberry plants maintained in growth chambers,  $A$ ,  $g_s$ , and  $E$  remained relatively constant ( $16 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ,  $225 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ , and  $4.0 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ , respectively) for  $\Psi_i$  values between  $-0.4$  to  $-1.0$  MPa, but decreased sharply as  $\Psi_i$  decreased below  $-1.0$  MPa.<sup>181</sup> Net  $\text{CO}_2$  assimilation,  $g_s$  and  $E$  all approached zero as  $\Psi_i$  decreased below  $-2.4$  MPa. In contrast, Renquist et al.,<sup>172</sup> working with plants in the field and in growth chambers, found that  $g_s$  decreased gradually over a wide range of  $\Psi_i$ , with no sharp decrease in  $g_s$  at a single  $\Psi_i$  value. Over the entire range of  $\Psi_i$ ,  $g_s$  of field-grown plants at a particular  $\Psi_i$  value was consistently greater than that of growth-chamber plants.<sup>172</sup> For example, a  $\Psi_i$  of  $-1.5$  MPa was associated with almost complete stomatal closure for growth-chamber plants, whereas  $g_s$  of field-grown plants at  $\Psi_i$  of  $-1.5$  MPa was still about 50% of maximum value.<sup>172,176</sup> The differences in  $g_s$  at similar  $\Psi_i$  values for growth chamber and field-grown plants may have been due to larger root systems for field-grown plants.<sup>172,176</sup> Also, in the field, environmental stresses such as high irradiance levels and increased evaporative demand may have influenced osmotic potential, stomatal density, and cuticle thickness, thereby affecting  $\Psi_i$  and  $g_s$ .<sup>172,176</sup>

In a glasshouse study, 'Raritan' and 'Surecrop' strawberry plants were either drought-stressed (soil moisture tensions ranging from  $-0.028$  to  $-0.074$  MPa) or were non-drought stressed (soil moisture tensions ranging from  $-0.002$  to  $-0.010$  MPa).<sup>182</sup> For a given irrigation treatment, 'Surecrop' plants had less negative  $\Psi_i$ , and greater  $A$  and  $E$ , than 'Raritan' plants, possibly as a result of a larger root system and greater utilization of available soil moisture for 'Surecrop' than for 'Raritan' plants.<sup>182</sup> For 'Raritan', drought-stress reduced  $A$  and  $E$  by 24 and 38%, respectively, relative to that of nonstressed plants; for 'Surecrop', drought-stress reduced  $A$  and  $E$  by only 17 and 32%, respectively, again suggesting greater drought tolerance for 'Surecrop' than for 'Raritan'.

Stomatal morphology and density may influence  $g_s$ . In strawberry, stomata occur abaxially on petioles, leaves, and fruit, but not on leaf veins.<sup>180</sup> For several field-grown strawberry cultivars, stomatal density ranged between 200 and 500 stomata  $\text{mm}^{-2}$ , with the greatest density observed near the leaf mid-rib.<sup>180</sup> Stomatal density did not appear to be correlated with drought tolerance, but stomatal density for glasshouse-grown strawberry plants tended to be less than that for field-grown plants,<sup>180</sup> suggesting that light or other environmental factors may influence stomatal density. Cultivar and species differences were observed in regard to stomatal size and position, with stomata of drought-tolerant cultivars being more recessed than drought-sensitive cultivars.<sup>180</sup> However, in another study, no cultivar or species differences were observed in regard to stomatal position.<sup>176</sup>

Under similar glasshouse conditions, stomata of two putatively drought-tolerant *F. chiloensis* clones opened earlier, and remained open longer, than stomata of drought-sensitive cultivars or species.<sup>180</sup> Maintenance of stomatal aperture under drought conditions may be due to osmotic adjustment, which has been observed in *F. virginiana*, *F. chiloensis*, and some *F. x ananassa* cultivars.<sup>116,183-186</sup> With osmotic adjustment, active accumulation of cell solutes results in a more negative cell osmotic potential ( $\Psi_\pi$ ), enabling continued water absorption and the maintenance of cell turgor and physiological and growth processes.<sup>184</sup> In Oregon, turgor potential ( $\Psi_p$ ) (calculated as the difference between  $\Psi_i$  and  $\Psi_\pi$ ) of 'Olympus' strawberry leaves was not affected by irrigation regime despite a more negative  $\Psi_i$  recorded at night and predawn, perhaps as a result of osmotic adjustment in nonirrigated plants.<sup>116</sup> Despite similar  $\Psi_p$  in irrigated and nonirrigated plants, leaf expansion rates were reduced for nonirrigated plants. Osmotic adjustment in *F. virginiana* was dependent on leaf age, with intermediate age leaves exhibiting the greatest capacity for adjustment.<sup>184</sup> Although a single drought cycle reduced  $\Psi_\pi$  by 0.1 to 0.2 MPa, and repeated stress cycles reduced  $\Psi_\pi$  by about 1.0 MPa,  $\Psi_\pi$  reductions were insufficient for maintaining growth rates similar to those of irrigated plants, or for preventing senescence of older leaves.

After 4 drying cycles to near the wilting point lasting 2.25 and 9.75 days for plants of *F. virginiana* and *F. chiloensis*, respectively, osmotic adjustment was observed to occur in *F. chiloensis*, but not in *F. virginiana*.<sup>183</sup> For *F. chiloensis* plants exposed to 3 wilting cycles, total soluble carbohydrate concentration (TSC) was 2.4-fold greater than that of nonstressed plants, while TSC of stressed *F. virginiana* plants was never more than 1.3-fold greater than that of nonstressed plants.<sup>186</sup> Glucose and fructose were the major soluble sugars contributing to the decrease in  $\Psi_\pi$ .<sup>186</sup> Despite the observed reductions in  $\Psi_\pi$  for water-stressed *F. chiloensis*, drought resulted in reduced leaf growth rates and total leaf area.<sup>183</sup>

Although water-stressed *F. virginiana* plants did not osmotically adjust, they exhibited no significant reduction in leaf area.

With rapidly-induced water stress, plants of *F. virginiana* did not osmotically adjust, whereas *F. chiloensis* plants exhibited osmotic adjustment of 0.42 MPa.<sup>185</sup> The observed lack of osmotic adjustment for *F. virginiana* may have been due to the rapid onset of water stress, since osmotic adjustment occurs as a response to a gradually increasing soil moisture stress.<sup>175,187</sup> In one comparative study, plants of *F. virginiana* had 70% greater leaf area and double the root dry weight of the *F. chiloensis* plants,<sup>183</sup> and thus may have had greater E (on a whole plant basis), contributing to a higher rate of soil desiccation. Gradual imposition of water stress resulted in osmotic adjustment in plants of both species, but the magnitude of adjustment was about 0.35 MPa greater in *F. chiloensis* than in *F. virginiana*.<sup>185</sup>

A slower rate of wilting for *F. chiloensis* also may have been related to Darrow and Sherwood's<sup>188</sup> observation that rates of water loss for plants of *F. chiloensis* were consistently lower than those for *F. virginiana*. Similarly, Darrow and Dewey<sup>180</sup> observed that, following a period of drought stress in the field, the number of stomata open at early morning was 4-fold greater for a drought-sensitive strawberry cultivar ('Marshall') than for a drought-tolerant cultivar ('Ettersburg 121'). Thus, drought tolerance in certain strawberry species or cultivars may be due to a greater degree of stomatal control. With such a conservative water-use "strategy," stomata close early in response to water deficits, thereby maintaining  $\Psi_i$  and  $\Psi_p$ , although  $g_s$  and A are reduced. While osmotic adjustment appears to be an important factor in strawberry drought tolerance, other factors, such as control of stomatal aperture in response to water stress may be of equal or greater importance.

Stomatal conductance and  $\Psi_i$  in strawberry appear to be sensitive to increased VPD. An unspecified strawberry cultivar maintained at an ambient temperature of 35°C and a VPD of either -0.5 or -3.5 kPa manifested reductions in  $g_s$  as VPD was increased from -0.5 to -5.0 kPa.<sup>173</sup> Presumably, as evaporative demand increased,  $\Psi_i$  decreased, resulting in reduced guard cell turgor and stomatal closure. Regardless of measurement VPD,  $g_s$  of plants preconditioned at a VPD of -0.5 kPa was consistently greater than that for plants maintained at -3.5 kPa.<sup>173</sup> For strawberry plants maintained at 20°C and an ambient VPD of -1.5 kPa,  $g_s$  was greatest at a measurement VPD of -1.5 kPa, and decreased as VPD decreased or increased.<sup>173</sup> In contrast, for 'Bogota' strawberry plants maintained at 20°C,  $g_s$  remained constant as VPD increased from -1.45 to -2.14 kPa before decreasing slightly at greater VPD.<sup>189</sup> Higgs and Jones<sup>190</sup> observed a strong correlation between seasonal values of  $\Psi_i$  and VPD, and a moderate correlation between seasonal values of  $g_s$  and  $\Psi_i$ , but  $g_s$  was not correlated with VPD. Although VPD was not determined, O'Neill<sup>184</sup> observed that pre-dawn  $\Psi_i$  of *F. virginiana* was most negative at high ambient temperatures, probably as a result of increased VPD. Discrepancies in the stomatal responses to VPD may be due to differences in cultivar, environmental preconditions or experimental conditions.

## B. SOIL MOISTURE, VEGETATIVE AND REPRODUCTIVE GROWTH

Strawberry vegetative growth is sensitive to soil moisture deficits. In general, optimum yield and growth responses of strawberry have been obtained when soil moisture is maintained above 70–80% of field capacity.<sup>176</sup> For strawberry, decreased plastochron interval<sup>191</sup> and increased dry matter production<sup>176,182</sup> were associated with increased soil moisture level and increased water use. Leaf length of irrigated 'Olympus' strawberry plants was greater than that nonirrigated plants 12 days after leaf unfolding.<sup>116</sup> Leaf expansion rates were greatest between 1800 and 2300 hr, apparently being limited by low  $\Psi_i$  or  $\Psi_p$  in the afternoon, and by low temperatures later at night. For 'Olympus' strawberry plants, leaf area of irrigated plants was 205% greater than that of nonirrigated plants after 62 days, due to an effect of irrigation on leaf size and number.<sup>116</sup> Although soil moisture deficit had no effect on leaf growth of 'Tioga' during a drought period, reduced leaf growth rates were observed after drought stress was relieved.<sup>192</sup> For *F. virginiana* plants in containers, short-term water stress resulted in reduced leaf dry weight, leaf area, leaf cell length, and increased specific leaf weight and cell density.<sup>184</sup>

The influence of irrigation may be less noticeable in humid regions. For example, irrigation resulted in increased leaf number, leaf area, and biomass accumulation in a dry year, but there was little effect of irrigation in a wet year.<sup>193</sup> In a year characterized by cool, cloudy growth conditions, leaf area and leaf dry weight were unaffected by irrigation regime, although irrigation resulted in increased crown and leaf number.<sup>194</sup>

Stolon production and early stolon rooting has been reported to increase as a result of irrigation.<sup>195</sup> However, decreased stolon formation with increased soil moisture has also been observed, possibly as

a result of cooler soil and plant temperatures or of excessive soil moisture with irrigation.<sup>196</sup> Rom and Dana<sup>197</sup> found that the initial number of primary roots of developing stolon plants was independent of soil moisture; however, root length and branching increased as soil water potential ( $\Psi_s$ ) increased to field capacity ( $\Psi_s \geq 0.03$  MPa). Petiole length, leaf dry weight, leaf growth rates, and top:root ratio were greater, and secondary root dry weight was reduced for developing stolons attached to mother plants maintained at low soil moisture tensions (0.05 or 0.2 MPa) compared to a high soil moisture tension (1.0 MPa).<sup>198</sup> For developing stolons, leaf area decreased with decreasing soil moisture, yet root development was greatest at intermediate soil moisture, possibly as a result of poor aeration in the wettest treatment.<sup>198</sup>

Irrigation has been shown to increase strawberry fruit yields.<sup>176,182,196,199–206</sup> However, irrigation in years of high rainfall had no effect on fruit yield.<sup>207–209</sup> Although flower and fruit number generally are dependent on adequate soil moisture,<sup>176</sup> irrigation promoted excessive vegetative growth in some studies, resulting in reduced flower bud formation,<sup>210,211</sup> or increased inter-crown competition.<sup>203</sup> Alternatively, soil moisture stress during the period of flower bud initiation in autumn has decreased fruit production the subsequent year.<sup>176</sup> However, soil moisture deficit prior to flower emergence resulted in increased flower numbers, but had no effect on fruit set or fruit weight.<sup>192</sup> Soil moisture deficits after flower emergence reduced flower number, fruit set, fruit weight, leaf number, and leaf size.<sup>192</sup> The observed differences among studies in yield response to irrigation may be due to differences in cultivars, soil moisture levels, timing of the moisture stress in relation to developmental stage, and environmental or preconditioning effects.

Irrigation has resulted in increased fruit size in some studies,<sup>176,192,199,202,204,205</sup> although decreased fruit size in response to irrigation has also been observed, possibly as a result of increased fruit number.<sup>176</sup> Fruit size of strawberry decreased diurnally as a consequence of fruit transpiration,<sup>176</sup> and such shrinkage is reportedly due to fruit transpirational water loss, rather than movement of water from the fruit to leaves or other plant organs.<sup>176,212</sup>

Soil moisture stress can result in an increase in percentage dry weight of strawberry fruit.<sup>213</sup> Similarly, fruit sugar, dry matter and acid content decrease with irrigation, probably due to dilution effects as a result of increased fruit size.<sup>176</sup> Increased fruit size in response to irrigation, and a concomitant dilution of soluble solids and thinning of cell walls, may reduce fruit firmness.<sup>176</sup> Okasha et al.<sup>214</sup> reported increased fruit firmness in light-or intermediate-textured soils compared to heavier-textured soils, probably due to decreased soil moisture availability in lighter soils. Soil moisture deficits have resulted in fruit dehydration and have had an adverse effect on fruit color.<sup>209</sup> Although irrigation promoted early fruit yield in one study,<sup>202</sup> it delayed ripening in another,<sup>176</sup> perhaps due to excessive vegetative growth or reduced temperatures.<sup>176</sup>

The occurrence of guttation from leaf hydathodes of strawberry has been correlated with high pre-dawn  $\Psi_1$  (i.e.,  $\Psi_1 > -0.08$  MPa).<sup>215</sup> Plants exhibiting guttation had greater  $g_s$ , and lower leaf temperatures, suggesting that the presence or absence of leaf guttation could be used as an indicator of plant moisture status.<sup>215</sup>

### C. SALINITY

In areas with low rainfall and marginal water quality, excessive salt accumulation may occur in the soil.<sup>216,217</sup> Strawberry is one of the most sensitive fruit crops to salinity.<sup>163,217–220</sup> High salt concentrations inhibit new root initiation and root growth, resulting in poorly anchored plants, loss of feeder roots, leaf necrosis, and stunted growth or plant death,<sup>163,219</sup> but reductions in fruit yield often occur before visual symptoms of salt damage are apparent.<sup>163,216</sup> Strawberry yield decreases have been observed with a substrate electrical conductivity ( $EC_e$ ) as low as  $1.0 \text{ dS m}^{-1}$ ,<sup>220</sup> and yield reductions of 50% were reported with an  $EC$  of  $2.2 \text{ dS m}^{-2}$ .<sup>219</sup> High concentrations of Cl are especially damaging; Na is less damaging since it is accumulated much less readily in strawberry plants.<sup>217,219</sup> Proper irrigation is important for minimizing salt damage to strawberry. Furrow irrigation resulted in greater salt accumulation at the soil surface than either sprinkler or drip irrigation.<sup>216</sup>

Differential responses to salinity have been observed among strawberry cultivars. 'Shasta' accumulated more Cl and Na, and exhibited leaf necrosis, yield reductions and plant mortality at lower salt concentrations than 'Lassen'.<sup>217,219</sup> As substrate  $EC_e$  increased from  $1.2 \text{ dS m}^{-2}$  to  $2.2 \text{ dS m}^{-2}$ , yields of 'Shasta' decreased by 50%, with a 29% plant mortality after 1 year, but no yield decrease or plant mortality was observed for 'Lassen'.<sup>219</sup> Increased salinity resulted in reduced vegetative growth for both cultivars, but shoot growth for 'Shasta' was reduced more than root growth. Salinity promoted early

flowering for 'Tioga',<sup>221</sup> possibly as a result of a reduction in vegetative growth. Salinity has also decreased fruit size,<sup>214,219</sup> and increased titratable acids and sugars.<sup>219</sup>

Crop sensitivity to salinity can vary depending on environmental conditions. For example, detrimental effects of salinity are often more pronounced under hot, dry conditions than under cool conditions.<sup>219,220</sup> Increased evapotranspiration as a result of high temperature and high VPD increases the concentration of salts in the soil, resulting in a more negative soil  $\Psi_{\pi}$  and a decrease in available soil moisture.<sup>220</sup>

#### D. FLOODING

Strawberry is highly sensitive to excess soil moisture and poor soil aeration.<sup>170,222,223</sup> Moreover, strawberry roots are susceptible to a number of pathogenic fungi and bacteria, including fungi such as *Phytophthora* spp. and *Pythium* spp. that thrive in poorly aerated, waterlogged soils.<sup>223</sup> Although damage to strawberry from poor aeration and pathogen infection under waterlogged soil conditions is widely recognized,<sup>6,163,170,222,223</sup> relatively few studies have been conducted to determine the growth and physiological responses of strawberry to flooding.

The root system of the cultivated strawberry plant is comprised of perennial structural roots, and short-lived feeder roots. Feeder roots are comprised solely of primary tissues and have a maximum lifespan of about two weeks, but under optimal conditions are continually replaced by new roots.<sup>170,222,223</sup> Feeder roots are highly sensitive to poor soil aeration, and die rapidly when exposed to even short periods of flooding.<sup>170,222,223</sup> Strawberry plants may survive short durations of flooding, developing new feeder roots after waterlogging subsides, but long-term survival is dependent on environmental conditions. Environmental conditions conducive to high atmospheric VPD following a period of excessive soil moisture are especially deleterious.<sup>170,223</sup> For containerized strawberry plants, continuous waterlogging of a portion of the root system resulted in root death, reductions in leaf size and petiole length, and rapid leaf senescence.<sup>224</sup>

### V. MISCELLANEOUS STRESSES

#### A. WIND

During a three-year period, growing strawberries outdoors in sheltered plots reduced mean wind velocity from 1.6 to 1.1 m s<sup>-1</sup>, and increased yield by 56% compared to non-sheltered plots (Table 2).<sup>225</sup> Wind protection resulted in increased plant size and crown number, but had no influence on plant survival, number of flower trusses per crown, or fruit size (Table 1). Yield reductions for the non-sheltered plants were attributed to a reduction in vegetative growth due to leaf tissue damage<sup>225</sup>; reductions in yield may also have been due to adverse effects of wind on  $g_s$  and A.<sup>6</sup>

#### B. ACIDIC FOG

Acidic fogs can occur during the winter strawberry production season in southern California, but strawberry plants appear to be relatively tolerant of acid fog. Musselman et al.<sup>226</sup> reported little or no

Table 2 Influence of wind shelter on mean yield, plant diameter, and number of flower trusses per plant during 1967–70 for 'Cambridge Favourite' strawberry plants

|                   | Date | Exposed | Sheltered | Increase due to shelter |
|-------------------|------|---------|-----------|-------------------------|
| Yield tonnes/ha   | 1968 | 9.8     | 16.6      | 69**                    |
|                   | 1969 | 15.8    | 19.1      | 21                      |
|                   | 1970 | 9.8     | 17.3      | 77**                    |
| Canopy width (cm) | 1967 | 39.8    | 46.6      | 17**                    |
|                   | 1968 | 42.1    | 50.8      | 21***                   |
|                   | 1969 | 45.2    | 47.5      | 5                       |
| Trusses/plant     | 1968 | 9.0     | 15.9      | 77**                    |
|                   | 1969 | 17.6    | 22.9      | 30*                     |
|                   | 1970 | 13.5    | 19.6      | 45                      |
| Crowns/plant      |      | 9.6     | 12.9      | 34*                     |

Note: \*, \*\*, \*\*\* indicate significant difference at  $p = 0.05$ , 0.01, and 0.001, respectively.

Adapted from Waister, 1972.

effect of short-term exposure to acid fog at pH of 2.4 or higher on leaf necrosis, vegetative growth, or yield of five strawberry cultivars. Acid fog at pH of 1.6 resulted in plant death after 8 weeks, and marketable yields were reduced due to calyx injury at pH of 2.8 or less.<sup>226</sup> Takemoto et al.<sup>227</sup> observed necrosis of leaves, petioles, flowers and fruit, and reductions in leaf area, and stem and leaf dry wt. for strawberries exposed to acid fog at pH 1.68 relative to control plants, but there was no effect on fruit number or  $g_s$  or A. The differential effects of acid fog between studies may have been due to differences in exposure periods, or to differences in experimental conditions or plant preconditioning.

### C. ELEVATED AMBIENT CO<sub>2</sub>

Exposure to elevated CO<sub>2</sub> concentrations typically enhance A, although concentrations above 1000  $\mu\text{mol mol}^{-1}$  may result in stomatal closure and decreased A.<sup>83</sup> For 'Midway' and 'Raritan' strawberry plants, exposure to 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> for 6 weeks reduced A,  $g_s$ , carboxylation efficiency, and apparent quantum yield relative to plants maintained at ambient (350  $\mu\text{mol mol}^{-1}$ ) CO<sub>2</sub> concentrations.<sup>228</sup> Cultivar differences were observed, in that the Rubisco activation state decreased for 'Midway' and increased for 'Raritan', and soluble Rubisco decreased 10–15% for 'Midway' and decreased 40–45% for 'Raritan'. Sruamsiri and Lenz<sup>229</sup> observed a reduction in  $g_s$  and E as ambient CO<sub>2</sub> concentration increased from 300 to 900  $\mu\text{mol mol}^{-1}$ , although A increased 70%. The influence of elevated ambient CO<sub>2</sub> on physiology and growth of strawberry remains unresolved.

## VI. CONCLUSIONS

*Fragaria x ananassa* is a highly variable and adaptive species that exhibits a greater sensitivity to environmental factors than most other fruit species. With the appropriate photoperiod, temperature, and plant preconditioning, many strawberry cultivars will flower and fruit almost continuously.

There are disparate reports of the influence of environmental factors such as atmospheric VPD, drought, elevated ambient CO<sub>2</sub>, irradiance level, temperature, and chilling on the physiology, growth, and development of the strawberry, indicating the need for additional investigations. The physiological bases for photoperiodic and temperature regulation of strawberry growth and development have not been elucidated. There is little information regarding A, E, and water use efficiency among species and cultivars. Investigations of photoassimilate partitioning and of overall carbon balance of the strawberry plant are needed, particularly in regard to fruit yield and quality in DN cultivars.

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## Temperate Nut Species

Peter C. Andersen

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## I. ALMOND

### A. DISTRIBUTION AND BOTANY

The almond [*Prunus amygdalus* Batsch syn. *P. dulcis* (Mill.) D. A. Webb] (family Rosacea) is closely related to other stone fruits such as peaches (*P. persica* L. Batsch), plums (*P. salicina* Lindl. or *P. domestica* L.), and cherries (*P. avium* L. and *P. cerasus* L.).<sup>1</sup> Genetically, almond is more similar to roses (*Rosa* spp.), and apples (*Malus domestica* Borkh.) than other nut species. However, within *P. amygdalus* there is much more genetic diversity than in closely related species such as peach (*P. persica* (L.) Batsch). Consequently, there is great conspecific variability in phenology, growth, and bearing habit.<sup>2</sup>

Almond originated in southwest Asia. The cultivation of almond has spread to northern Africa, southern Europe, the Mediterranean region, California, and other locations around the world.<sup>3</sup> Climatic and edaphic requirements are exacting and successful culture is limited to select locations.<sup>4</sup>

The almond is a vigorous, medium-sized tree and is generally long-lived compared to other *Prunus* spp. such as peach.<sup>3</sup> Flowers are borne laterally on spurs or shoots. Flowering typically occurs prior to the onset of vegetative growth. The flowers are perfect (i.e., possessing both pistils and stamens); however, the flowers of most cultivars are self-incompatible and cross pollination is required to obtain good yields.<sup>4</sup> The almond fruit consists of the edible seed (kernel), a shell (endocarp), and the hull (mesocarp). Trees typically bear fruit during the third or fourth year.<sup>3,4</sup>

### B. LIGHT

Leaf gas exchange characteristics of container-grown 'Nonpareil' almond trees were unique among five *Prunus* spp. tested.<sup>5</sup> Net CO<sub>2</sub> assimilation (A) of almond leaves did not approach an asymptote at a photosynthetic photon flux (PPF) up to 1600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , whereas maximum A ( $A_{\text{max}}$ ) occurred at a PPF of 400 to 700  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for leaves of peach [*Prunus persica* (L.) Batsch], plum (*P. cerasifera* Ehrh.), and cherry (*P. avium* L.). Significantly higher  $A_{\text{max}}$  values were recorded for almond (up to 18  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) compared to apricot (*P. armeniaca* L.) (7 to 8  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and other *Prunus* spp. (13 to 14  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Leaf nitrogen concentration (on a leaf area basis) was also greater for almond than the other species tested. A positive correlation between A and leaf nitrogen content was expected since a high percentage of leaf nitrogen is in the form of ribulose biphosphate carboxylase/oxygenase

(RUBISCO), the enzyme responsible for the synthesis of CO<sub>2</sub> and ribulose biphosphate to form hexoses. Net CO<sub>2</sub> assimilation, when calculated on a leaf nitrogen basis, was similar for almond, plum, peach, and cherry.<sup>5</sup>

## C. WATER

### 1. Plant Water Deficits

Stomatal conductance to water vapor ( $g_s$ ) and leaf water potential ( $\Psi_L$ ) of almond varied diurnally with maximum  $g_s$  and minimum  $\Psi_L$  recorded during midday.<sup>6,7</sup> Maximum  $g_s$  (up to 375  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and minimum  $\Psi_L$  (as low as -2.1 MPa) have been recorded during midday in Spain.<sup>6</sup> Leaf gas exchange and  $\Psi_L$  of almond was reduced considerably with increases in the leaf to air vapor pressure deficit (VPD).<sup>8,9</sup> Turner et al.<sup>9</sup> established that the A and  $g_s$  of almond and other woody plant species was reduced to a greater extent than that of herbaceous plants in response to increasing VPD. They invoked a lower hydraulic resistance in herbaceous compared to woody species as the factor responsible for the greater  $\Delta g_s / \Delta \Psi_L$ . Torrecillas et al.<sup>8</sup> found a progressive decrease in  $\Psi_L$  in almond as transpiration (E) increased which was also attributed to a substantial internal plant resistance to water flow.

Genotypic variations in plant water relations have been reported within *P. amygdalus*. For example, Sanchez-Blanco et al.<sup>6</sup> observed that the  $g_s$  of cv. Garriques was lower and more dependent on VPD than cv. Ramillete.

The concept of a non-hydraulic signal that is responsible for stomatal closure<sup>10,11</sup> in the absence of a reduction in  $\Psi_L$  has been investigated in almond. Wartinger et al.<sup>7</sup> evaluated the concentration of abscisic acid (ABA) in the xylem fluid and plant water relation of young 'Ne Plus Ultra' almond trees growing in lysimeters in Israel. Diurnally,  $g_s$  was maximum (200 to 400  $\text{mmol m}^{-2} \text{s}^{-1}$ ) at mid-morning and  $\Psi_L$  was minimum at midday (-3.0 MPa), although neither  $g_s$  or  $\Psi_L$  were correlated with the concentration of ABA in xylem fluid. By contrast, maximum  $g_s$  and ABA were inversely correlated when plants experienced gradual soil drying (i.e., predawn  $\Psi_L$  declined from ca. -0.3 MPa during the spring to as low as -2.0 MPa during mid-summer). The authors suggested that a very narrow range of ABA concentrations in xylem fluid may regulate stomatal behavior and proposed that fine roots exposed to soil drying are the source of ABA production and responsible for ABA in xylem fluid. In an adjunct study on 1- to 4-year-old almond trees grown in a lysimeter, FuBeder et al.<sup>12</sup> documented that diurnal or seasonal changes in plant water status (i.e.,  $g_s$ ,  $\Psi_L$ ) were not related to changes in cytokinin concentration in the xylem fluid. Rather the influence of cytokinins appeared to be dependent on ABA concentration, which in turn, was dependent on soil-water status. They concluded that while some cytokinins in xylem fluid may influence stomatal behavior in the short term, the modulation of stomatal aperture is mainly via ABA concentrations.

### 2. Flooding

*Prunus* spp. are less tolerant to waterlogged and/or anaerobic soil conditions than many other genera in the family Rosacea (e.g., *Pyrus* or *Malus*).<sup>13</sup> Interspecific comparisons within *Prunus* have shown that almond and apricot are among the least tolerant to waterlogged soil conditions of all fruit tree species.<sup>13-15</sup> After 2 days of flooding, root growth of 'Chellaston' almonds and 'Nemaguard' peach was severely and moderately inhibited, respectively.<sup>16</sup> The susceptibility of almond rootstocks is exacerbated by a low resistance to fungal infection by *Phytophthora* spp.<sup>15,16</sup> Almonds, regardless of rootstock, should be grown in well-drained soils that are not prone to flooding for even a short period of time.<sup>17</sup> Although Marianna plum rootstock is tolerant to flooded soil conditions and to soil-borne diseases compared to peach, almond, or almond-peach hybrids rootstocks, it has compatibility limitations with almond scions.<sup>18</sup>

The mechanisms responsible for flooding sensitivity among fruit trees is poorly understood.<sup>13</sup> No physiological data are available for almond; however, peach (a closely related species) has been shown to undergo cyanogenesis (i.e., the release of toxic hydrogen cyanide from cyanogenic glycosides) under conditions of anaerobiosis.<sup>17</sup>

## D. TEMPERATURE

The relationship between temperature and flowering of almond has been studied in Australia. Rattigan and Hill<sup>19</sup> used the models developed for peach by Richardson et al.<sup>20</sup> and Ashcroft et al.<sup>21</sup> to predict the date of flowering of 12 almond cvs. over a 7-year period. The model described flowering as a two-stage process. In the first stage, dormant flower buds perceive the cumulative exposure to low temperature

(chilling) until a genotype-dependent level is reached. A chilling requirement of 220 to 320 chilling units was calculated for twelve almond cultivars. In the second stage, flowers began to develop at a rate proportional to temperature. The heat summation requirement ranged from 5300 to 8900 growing-degree-hours above 4.5°C.<sup>20</sup>

High leaf temperatures may have been a contributing factor for a low percentage of successful bud take of almond. Weinbaum et al.,<sup>22</sup> working with young almond trees prone to bud failure during propagation, documented an increased leaf temperature and a reduced  $g_s$  compared to plants not prone to bud failure. Although leaf temperatures of young-grafted trees prone to bud failure were as much as 4°C higher than ambient temperatures (37 versus 33°C) there was no evidence that higher leaf temperatures were lethal.

## E. SALINITY

In many semi-arid regions where almonds are cultivated, quality or quantity of irrigation water are major limitations to production.<sup>23</sup> Olivar<sup>24</sup> reported that one third of the irrigated almond acreage worldwide is adversely affected by salinity. The distribution of salt as a result of irrigation with saline water in a given soil is highly dependent upon the method and rate of irrigation. For example, at low-drip irrigation rates [50% of evapotranspiration (ET)] in an almond orchard with saline irrigation water [electrical conductivity of the saturation soil extract (ECe) = 1.5 dS m<sup>-1</sup>], the greatest ECe (i.e., 5.7 dS m<sup>-1</sup>) was directly below the drip line.<sup>25</sup> Increased rates of irrigation moved the zone of salt accumulation farther from the drip zone.<sup>25</sup>

Symptoms of salt stress (yield reductions, dwarfing, foliar burn, and premature senescence) in *Prunus* spp. may occur at an ECe of 1.5 to 1.7 dS m<sup>-1</sup>,<sup>26</sup> despite the fact that soils are not classified as saline until the ECe reaches 4 dS m<sup>-1</sup>.<sup>27</sup> Maas<sup>28</sup> reported that tree growth of almond was reduced by 19% for every 1 dS m<sup>-1</sup> increase in soil salinity. Salinity damage may be due to an osmotic effect or to the deleterious effect of specific ions (e.g., NaCl, SO<sub>4</sub><sup>-</sup>). In *Prunus* spp. the effects of Cl and Na were greater than the osmoticum effect.<sup>29,30</sup> Sulfate salts were more inhibitory to growth of *Prunus* spp. than isosmotic concentrations of Cl salts.<sup>29,30</sup>

There is sufficient variation in salt tolerance among *Prunus* rootstocks to justify the consideration of salt tolerance as a selection criterion in regions with saline soils. Almond, peach, plum, and almond-peach hybrids have been used as rootstocks for almonds. 'Elberta' peach on 'Lovell' rootstocks accumulated less Cl and were more salt tolerant than trees on 'Shalil' rootstocks.<sup>30</sup> Bernstein et al.<sup>31</sup> also reported that 'Lovell' conferred a greater salinity tolerance to the scion than 'Shalil' rootstocks. Evaluation of the performance of *Prunus* spp. on 'Lovell' rootstocks confirmed that salinity tolerance was determined by both the rootstock and the scion.<sup>31</sup> Genotype-specific rootstock/scion interactions in Cl accumulation and growth also occurred.

Application of a 50:50 mixture of 4000 ppm NaCl and CaCl<sub>2</sub> over a 3-year period to field-grown almond trees near the Rio Grande river resulted in minor changes in cationic composition of leaves.<sup>31</sup> Sodium concentrations were highest in wood, roots, and bark and lowest in shoots and leaves. Leaf Na levels were lower in Texas almond than in peach, plum, prune, apricot, or 'Nonpareil' almond. Based on growth and Cl contents, it was concluded that approximately one half the salinity-induced reduction in growth was due to Cl toxicity and one half was due to an osmotic effect.

Maas and Hoffman<sup>26</sup> ranked salt-tolerance of *Prunus* spp. from high to low as plum, almond, peach, apricot. The salinity tolerance of seedlings of *Prunus* spp. was evaluated in sand-culture experiments in a glasshouse.<sup>23</sup> Trees were irrigated with half-strength Hoagland's solution supplemented with chloride and sulfate salts of Na<sup>+</sup>, Ca<sup>++</sup> and Mg<sup>++</sup> to yield an ECe of 1.5, 4.5, or 6.0 dS m<sup>-1</sup>. Based upon growth (height, dry weight, etc.) and foliar appearance, salinity tolerance from high to low was as follows: 'Titan' almond × 'Nemaguard' and *P. mexicana* Wats., 'Nemaguard' and 'Nemared', 'Myrobolan' plum (*P. cerasifera* J. F. Ehrh.), and bitter almond (*P. amygdalus*).

## F. MISCELLANEOUS STRESSES

Very little information is available concerning effects of other environmental stresses on almond. DeJong<sup>5</sup> found that A of almond leaves increased linearly with increases in intercellular CO<sub>2</sub> concentration (C<sub>i</sub>) when ambient CO<sub>2</sub> concentrations were increased. The slope of the A/C<sub>i</sub> curve was greater for almond than the other four *Prunus* species tested. Unfortunately, there are no data concerning growth and productivity of almond as a function of ambient CO<sub>2</sub> concentrations.

Two additional reports worthy of mention concern frost injury and ozone. Lindow and Connell<sup>32</sup> showed that ice nucleation active (INA) strains of the bacteria *Pseudomonas syringae* accounted for over 99% of the ice nucleation present on almond leaves. Application of antagonistic non-INA strains of bacteria or bactericides reduced both the density of INA bacteria and frost injury at  $-3^{\circ}\text{C}$ .

Ozone sensitivity is another characteristic of almonds. When seedlings were subjected to  $0.25\ \mu\text{l l}^{-1}$  ozone for 4 hrs each day for 4 months per year over a 2-year period, growth was reduced more for almond than for peach or apricot.<sup>33</sup>

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## II. CHESTNUT

### A. DISTRIBUTION AND BOTANY

The genus *Castanea* (family Fagaceae) consists of 12 species of deciduous trees and shrubs native to northern temperate regions; *Castanea* species have separate staminate and pistillate flowers and one to seven nuts enclosed in a prickly, dehiscent involucre.<sup>1</sup> All *Castanea* species have a somatic chromosome number  $2n = 24$ . Chestnuts are monoecious and usually protandrous.<sup>1,2</sup> Flowers are borne on current year's wood. Chestnuts rarely self-pollinate and isolated trees produce few nuts. Pollination is by wind. *Castanea* spp. generally grow fast and have rot-resistant wood.<sup>3</sup> Unlike most other tree nuts, chestnuts are relatively low in protein and fat, yet high in carbohydrates (Table 1, Section IV, A). Essential amino acids represent a fairly high proportion of the amino acid profile.<sup>4</sup> Unlike many temperate zone nut species *Castanea* do not exhibit a strong tendency to bear heavy and light crops in alternate years,<sup>3</sup> which may be a function of the lower lipid/carbohydrate ratio in nuts of *Castanea* species compared to other nut crops. In many regions chestnut trees are still seedling propagated; however, the development of a commercial industry requires the utilization of successful techniques for mass clonal propagation.

The native range of *Castanea dentata* (Marsh) Borkh. (The American chestnut) is characterized by ca. 75 and 120 cm rainfall.<sup>4</sup> The American chestnut was once the dominant hardwood species in eastern North America until the introduction of Chestnut blight, caused by the fungal pathogen *Cryphonectria* (*Endothia*) *parasitica*, which ultimately destroyed ca. 3.5 billion trees.<sup>5</sup> Symptoms of infection by *C. parasitica* include bark cankers, leaf wilting, senescence and eventual tree death. Reductions in hydraulic conductance of stems and  $g_s$ , and transpiration (E) of leaves result from localized canker infection.<sup>6,7</sup> American chestnut trees can be extremely long lived (i.e., over 500 years).<sup>5</sup> There is no cure for Chestnut blight, although American chestnut  $\times$  Chinese chestnut hybrids have been bred with disease resistance.<sup>5</sup>

Chinese chestnut (*C. mollissima* Bl.) is currently the major species of commerce worldwide. The Chinese chestnut has a high degree of blight resistance, sufficient cold hardiness, and acceptable nut quality, but the wood quality is inferior to that of *C. dentata*.<sup>2</sup> Other chestnut species of commercial importance include the Japanese chestnut (*C. crenata* Sieb. and Zucc.) and the European chestnut (*C. sativa* Mill.).<sup>2</sup>

Physiological data on *Castanea* spp. is fragmentary, as is the case for many temperate nut species.

### B. LIGHT

Photosynthetic characteristics of *C. sativa* have been measured via quantifying the assimilation of  $^{14}\text{CO}_2$ .<sup>8</sup> The  $A_{\text{max}}$  was ca. 16 to 17  $\mu\text{mol m}^{-2} \text{s}^{-1}$  when leaves were exposed to 300 ppm  $\text{CO}_2$ . A specific point

of light saturation was not achieved at a PPF up to  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ , although a relatively high  $A$  was recorded at a PPF as low as  $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Apparent quantum yield generally ranged from 0.03 to 0.06 mol  $\text{CO}_2$  mol quanta $^{-1}$ .<sup>8</sup> Stomatal conductance to  $\text{CO}_2$  vapor was ca. 10 times that of total residual conductance to  $\text{CO}_2$  when PPF exceeded  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ , (i.e., residual conductance is the reciprocal of the sum of the resistances for  $\text{CO}_2$  diffusion from intercellular spaces to fixation in the chloroplast).<sup>8</sup> These data underscore the importance of nonstomatal limitations for  $\text{CO}_2$  diffusion and fixation in *Castanea* as reported for citrus.<sup>9</sup>

### C. WATER

Approximately two thirds of the total daily quantity of water used by 6- or 7-year-old *C. sativa* in Germany was transpired between 1000 and 1800 hr.<sup>10</sup> Parenchyma tissue ostensibly contributed water to the transpiration stream between 600 and 1000 hrs since water uptake from the soil was minimal during this period. In China,  $A_{\text{max}}$  of *C. mollissima* occurred during the spring after leaves were fully expanded then declined as leaves aged.<sup>11</sup>

Leaf gas exchange and plant water relations of xeric (*Quercus prinus* and *Q. ilicifolia*) and mesic (*Q. vibra* and *C. dentata*) species were compared seasonal where soil moisture varied from 7 to 13% v/v in a sandy loam soil in the northeastern United States.<sup>12</sup> Net  $\text{CO}_2$  assimilation,  $g_s$ , and  $\Psi_L$  were reduced for all species during peak drought periods (i.e., soil moisture 7% v/v, VPD = 3.5 kPa). Leaf water potential was generally highest for *C. dentata*, yet similar for the other species. Predawn  $\Psi_L$  was typically greater than  $-0.4$  MPa, but fell to  $-0.7$  MPa during a drought period. The  $A_{\text{max}}$  and  $g_s$  were ca.  $6 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $140 \text{ mmol m}^{-2} \text{s}^{-1}$  during early morning, while during drought periods  $A$  and  $g_s$  were near zero. One characteristic contributing to the drought sensitivity of *C. dentata* is an extremely thin leaf (i.e., leaf thickness  $160 \mu\text{M}$ );<sup>13</sup> only *Acer plantanoides* L. and *Alnus incano* (L.) Moench had thinner leaves of 52 forest trees tested.<sup>13</sup> Abrams et al.<sup>12</sup> concluded that stomatal closure was responsible for maintaining a higher midday  $\Psi_L$  in *C. dentata* (i.e.,  $-1.5$  MPa) than in *Quercus* spp.

Osmotic adjustment and changes in tissue elasticity have often been invoked as mechanisms associated with drought tolerance.<sup>12</sup> *C. dentata* manifested a 0.7 MPa reduction in leaf osmotic potential ( $\Psi_\pi$ ) (i.e.,  $-1.6$  to  $-2.3$  MPa) from spring to late summer; during this period relative leaf water content (RWC) declined only 3%.<sup>12</sup> Therefore an active accumulation of solutes and not simply dehydration was responsible for osmotic adjustment. *C. dentata* maintained a lower bulk modulus of elasticity ( $\epsilon$ ), (i.e., greater tissue elasticity) and contributed to a higher leaf turgor pressure ( $\Psi_P$ ) at a lower RWC than would occur during non-drought conditions.<sup>12</sup> Alternatively, it can be argued that tissue with a high  $\epsilon$  will develop low  $\Psi_L$  during episodes of water stress and thereby retain a large gradient which will facilitate continued water uptake with soil drying. Despite osmotic adjustment and increased tissue elasticity, *C. dentata* had lower values of  $A$  and  $g_s$  exchange than the *Quercus* species in dry soil, and as such, should be considered less tolerant to periods of drought, and less competitive under these conditions.

The hydraulic conductance of water flow ( $L_p$ ) through *C. dentata* may be a limiting factor to maintaining high rates of leaf gas exchange. Water flow in xylem vessels of woody spp. is much less than that predicted by Poiseuille's law due to: (1) nonconstant vessel diameter and a finite vessel length; (2) vessel walls are neither smooth nor rigid; and (3) water flow in xylem vessels is often through relatively small pits in axial walls or through perforations in end walls.<sup>14,15</sup> Further difficulty in the assessment of stem  $L_p$  is that only a small percentage of xylem vessels may actually function in water conduction (especially in old trees), and the hydraulic characteristics of the remainder may vary widely. In ring porous species such as *C. sativa* or *Juglans nigra* essentially only the outermost growth ring functions in water transport.

Zimmerman<sup>16</sup> reported that hydraulic constrictions (i.e., more narrow vessels) often exist between the junction of stem/branch, branch/twig, and twig/leaf which cause a reduced pressure drop just apical to the restriction. Salleo<sup>15</sup> determined that a small proportion of vessels ended in nodes for *C. sativa* and *J. nigra* which would minimize the deleterious impact of a gas embolism. The relatively short and narrow vessels formed later in the growing season (i.e., summer) for *C. sativa* and *J. nigra* may substitute as a mechanism to resist embolism formation.<sup>15</sup> Valancogne and Nasr<sup>17,18</sup> estimated the rate of sap flow by a method of heat transference to be within 30% of the actual value of  $E$  (determined by differences in container weight). Estimates of  $E$  by heat transferences tended to be overestimated when sap flow rates were low.<sup>17,18</sup>

## D. TEMPERATURE

*Castena* spp. usually adapt to a wide range of temperatures. *Castena* spp. are generally cold-hardy and generally avoid frost injury to vegetative and reproductive buds because they bloom relatively late in the spring.<sup>2</sup> Sawano<sup>19</sup> reported that cold hardiness of shoots of *C. mollissima* increased from ca. -7 to -12°C from 5 Nov. to 25 Dec.; defoliation of leaves in the fall reduced cold hardiness. A decline in cold hardiness with early defoliation was associated with a high relative water content and a low carbohydrate content in shoots of *C. mollissima*.<sup>19</sup> *C. dentata* and *C. mollissima* have been reported to survive to at least -30°C when properly acclimated to the cold.<sup>2</sup>

## E. RESPONSE TO ELEVATED CO<sub>2</sub>

The response of *C. sativa* seedlings to increases in atmospheric CO<sub>2</sub> was studied in ventilated chambers over a 2-year-period.<sup>20</sup> CO<sub>2</sub> enrichment to 700  $\mu\text{mol m}^{-2} \text{s}^{-1}$  CO<sub>2</sub> resulted in the termination of shoot elongation by mid season compared to those grown in 350  $\mu\text{mol m}^{-2} \text{s}^{-1}$  ambient CO<sub>2</sub>. Early leaf senescence and a reduction in leaf chlorophyll content was associated with the dilution of nutrients due to the increased growth of seedlings in high CO<sub>2</sub>. An increase in root dry weight accounted for nearly all of the carbon gain in CO<sub>2</sub>-enriched seedlings; however, shoot weight and leaf area were reduced in response to elevated CO<sub>2</sub>. These unexpected results indicated that the influence of the increased carbon dioxide concentration occurring globally may be extremely species specific.

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### III. FILBERT

#### A. DISTRIBUTION AND BOTANY

The European filbert (*Corylus avellana* L.), family Betulaceae (birch family) was the dominant tree species in much of northern Europe from 8,000 to 5,500 B.C.<sup>1</sup> Currently, the distribution of filbert is limited to climates moderated by large bodies of water such as the southern coast of the Black Sea and the northern coast of the Mediterranean Sea. Turkey accounts for two thirds of the production worldwide; Spain, Italy, and the west coast of the United States are responsible for most of the remaining production.

All but two *Corylus* spp. are native to southern Europe and/or Asia minor; the remaining two species (*C. americana* and *C. cornuta*) are native to north America.<sup>1,2</sup> Other species of lesser economic importance include the Turkish filbert, *C. colurna* and the Chinese hazel, *C. chinensis* which may grow to over 20 and 35 m in height, respectively.

All nine *Corylus* spp. are deciduous shrubs or trees with a somatic chromosome number of 22, with the possible exception of *C. coburna* ( $n = 18$  or 22).<sup>1,2</sup> All species are monoecious with imperfect (separate male and female) flowers and most species are self sterile. Pollination is by wind and most *C. avellana* cultivars require cross pollination. Thus, two or more cultivars should be planted together. There is conspicuously little physiological data available for filbert.

#### B. ANATOMICAL/MORPHOLOGICAL CHARACTERISTICS OF LEAVES

Valuable baseline data for *C. avellana* have been presented concerning leaf chlorophyll concentration ( $432 \text{ mg m}^{-2}$ ), chlorophyll a/chlorophyll b (3.2), chlorophyll diameter ( $2.8 \mu\text{M}$ ), leaf nitrogen content ( $1.52 \text{ g m}^{-2}$ ), abaxial stomatal density ( $155 \text{ mm}^{-2}$ ) and the ratio of mesophyll cell surface area to leaf area (24.4).<sup>3</sup> Mehlenbacher and Thompson<sup>4</sup> reported that chlorophyll deficiency in filbert was due to a simple recessive gene conferring chlorophyll deficiency. They also found that a gene controlling anthocyanin development was inherited independently. Anthocyanin-deficient plants survived in the field, but chlorophyll deficient seedlings lacking anthocyanin died, presumably in part due to photoinhibition.

#### C. LEAF GAS EXCHANGE AND LEAF WATER RELATIONS

Stomatal aperture increases in response to conditions that enhance rapid A and decreases in response to conditions that enhance rapid transpiration.<sup>5</sup> Cowan and Farquhar<sup>6</sup> suggested that stomatal behavior is "optimal" if a minimum quantity of water is lost per unit of carbon gained. One of the first species for which this theory was tested was *C. avellana*. Farquhar et al.<sup>7</sup> showed that stomata of *C. avellana* respond to humidity, or more specifically, the difference in the water concentration difference between the inside of the leaf and the atmosphere, VPD. When leaves of *C. avellana* were exposed to increasing VPD (at 28°C),  $g_s$  was adjusted (i.e., decreased) to maintain proportionality between E and A. This constant is known as the gain ratio ( $\partial E/\partial A$ ). Maximum E occurred at 2.0 kPa and declined with larger VPD. Thus, the direct response of stomata to humidity was the mechanism responsible for the optimization of carbon gain with respect to water loss. Under severe water stress  $\partial E/\partial A$  appeared to increase implying a greater reduction in A relative to E or  $g_s$  (i.e., there was an increase in the calculated value of  $C_i$ ).<sup>7</sup> However, these data must be viewed with caution without confirmation of stomatal homogeneity.<sup>8,9</sup> (A brief discussion on this topic can be found in the Walnut section (IV) of this chapter; a more detailed discussion appears in the Citrus chapter of Volume II.)

The photosynthetic responses of filbert leaves to light and temperature have not been adequately tested. Harbinson and Woodward<sup>3</sup> evaluated the leaf gas exchange of *C. avellana* and seven other forest tree species growing in the field to simulated sunflecks of low intensity (up to a PPF of  $230 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ). Of the eight tree species, only *C. avellana* and *Ulmus glabra* were not light saturated at a PPF of  $230 \mu\text{mol m}^{-2} \text{ s}^{-1}$ .<sup>3</sup> Maximum A,  $g_s$ , and E for *C. avellana* under the conditions described were  $7.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ,  $300 \text{ m}^{-2} \text{ s}^{-1}$ , and  $3.4 \text{ mmol mol}^{-1}$ , respectively. Under the experimental conditions of

Farquhar et al.<sup>7</sup> (i.e.,  $PPF = 400$  to  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , temperature =  $28^\circ\text{C}$ ) maximum values of  $A$  and  $g_s$  for *C. avellana* were  $9 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $140 \text{mmol m}^{-2} \text{s}^{-1}$ , respectively.

There is a paucity of data concerning the leaf water relations of *C. avellana*. The response of  $A$ ,  $g_s$ , and  $E$  to changes in VPD under well-watered conditions was examined for several herbaceous (i.e., *Helianthus annuus*, *Pisum sativum*, etc.) and woody (i.e., *C. avellana* and *Pistacia vera*) species.<sup>10</sup> A VPD-induced decrease in  $g_s$  and  $\Psi_L$  occurred for all species, but was greatest for woody species. Turner et al.<sup>10</sup> concluded that the VPD around the leaf decreased gas exchange through a direct effect on the leaf epidermis (i.e., guard cells). Turner et al.<sup>11</sup> in a related study found that for the woody species *in situ* psychrometer-derived values of  $\Psi_L$  did not correlate with those measured with a pressure chamber apparatus which they attributed to very low epidermal conductance of water vapor.

## D. TEMPERATURE

Westwood<sup>12</sup> stated that *C. avellana* is cold hardy when dormant. Plants are not usually injured by temperatures that may occur during bloom, although pistillate flowers may be killed at temperatures of  $-10^\circ\text{C}$ .<sup>12</sup> Westwood<sup>12</sup> indicated that vegetative buds require ca. 800–1200 hrs of chilling below  $45^\circ$ , although reproductive buds require considerably less chilling.

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## IV. PECAN

### A. INTRODUCTION

#### 1. Distribution

The pecan [*Carya illinoensis* (Wagenh.) K. Koch] (family Juglandaceae) is a large (i.e.,  $>55$  m height and  $>2$  m diameter) deciduous, monoecious tree native to North America.<sup>1</sup> The pecan tree evolved in deep, fertile, well-drained soils of the Mississippi floodplain. The natural habitat of the pecan in the United States is primarily along rivers from latitude  $26^\circ$  to  $42^\circ$  and longitude  $84^\circ$  to  $103^\circ$  where it may exist as a pure stand.<sup>2</sup> It is not uncommon for pecan trees to be flooded for short periods of time during the dormant season, although flooded soil conditions are less common during the growing season.

The climate of the native range of pecan is characterized by long hot humid summers and moderately

cool winters.<sup>2</sup> Regions having an arid/semi-arid climate and with access to abundant irrigation water are optimum for commercial pecan cultivation. Currently, the cultivated range of pecan extends considerably west and southeast of its native range. The major production areas in the United States are Georgia, Texas, Alabama, Louisiana, Oklahoma, and Arizona. Mexico is also increasing production at a rapid rate. Limited quantities of pecans are produced in Australia, Brazil, Israel, and South Africa.

The acreage of pecans in the southwestern United States has been increasing at a very rapid rate. In the United States the potential for successful pecan production is greater in the Southwest than in the Southeast for three reasons: (1) cloudy/hazy atmospheric conditions prevalent in the Southeast result in much lower light intensities than in the Southwest; (2) high humidity and abundant precipitation during the growing season in the southeast greatly enhances insects and disease pressures; and (3) new cultivars released over the last 30 years are better adapted to the Southwest than the Southeast.

## 2. Botany

Pecan leaves are alternate and odd-pinnate. Flowers are unisexual; male flowers are a drooping catkin; female flowers are a star-shaped terminal raceme.<sup>1</sup> Pistillate flowers are borne terminally in clusters on current years wood and staminate flowers are produced on one-year-old wood. Pistillate flowers arise from the most apical one (or two) primary bud(s) on each shoot, while staminate flowers develop from most primary and secondary buds except for the terminal bud.<sup>3,4</sup> Wood and Payne<sup>5</sup> demonstrated that primary, secondary, and tertiary buds in a given node have the potential to produce staminate and pistillate flowers (and nuts) along the length of the one-year shoot. Staminate flower opening and pistillate flower receptivity is typically asynchronous for a given seedling or cultivar, thus cross pollination is normally essential for maximum productivity. The fruit is a drupe with a stone or nut enclosed in a thick green husk that splits into four parts at maturity.<sup>1</sup>

The period of juvenility (i.e., the phase in the life cycle of a plant that is limited to vegetative growth), is especially prolonged for pecan trees and may last 10 to 12 years. Juvenility in the native habitat of pecan is an adaptive characteristic facilitating rapid vegetative growth and a competitive position in the forest canopy.<sup>6</sup> The desirability for a rapid return on investments after orchard establishment has prompted pecan breeders to choose precocity as an important selection criterion. A high degree of precocity however, has been correlated with a low or variable kernel percentage (i.e., the fraction of nut weight accounted for by the kernel), particularly with older trees.<sup>7</sup>

## 3. Cultivation

Pecans are propagated by budding or grafting the desired cultivar on seedling rootstocks. In the United States 'Curtis', 'Moore' (Southeast), 'Riverside' (West), and 'Giles' (North) are often used as seed for rootstocks, although any "available" seed source has often been used. The reliance on seedling rootstocks (i.e., genotypic variability) and the uncertainty as to the identity of seed source have contributed to the variability in tree performance of a given cultivar.

Pecans have been cultivated for only a very short period of time and are considered 'wild' since plant growth and development resembles a forest tree species rather than a "domesticated" crop.<sup>6</sup> The first pecan cultivar, 'Centennial' was grafted in 1846, and not until the early to mid-1900's were a significant proportion of the pecans named cultivars.<sup>8</sup> Today ca. 500 pecan cultivars have been named and propagated. The pecan industry in many states is still largely based on seedlings and pecan seedlings account for a substantial proportion of total yield in North America.<sup>8</sup>

Lack of tree size control is a major impediment to pecan production.<sup>9</sup> Dwarfing rootstocks are not available and cultivars with a dwarfing growth habit such as 'Cheyenne' have had cultural problems. A low density planting scheme (i.e., plant spacing >15.2 m) is not economically feasible since a prolonged period of time (i.e., ca. 15 years or more) is required for a positive return on investments. In a high density configuration (i.e., plant spacing <12.2 m) trees under intensive management may become overcrowded with a concomitant reduction in productivity after only 10 to 12 years. Since pecan trees do not respond well to pruning, alternate tree removal is often required before a positive return of investments is realized.<sup>9</sup>

Heavy and light crop production in alternate years is a serious limitation to successful pecan production, especially for certain cultivars.<sup>10-16</sup> Native stands of pecans typically bear a good crop once every several years due to competition for limiting resources (i.e., light, water, nutrients) and the extremely high amount of energy contained in oil-rich nuts (Table 1).<sup>6</sup> Only native trees located in an open-environment are capable of producing nuts on a somewhat regular basis, but owing to a large tree

Table 1 Protein, fat, and total carbohydrate content of chestnuts and selected tree nuts

| Tree nuts                               | Protein (%) | Fat (%) | Total carbohydrate (%) |
|---|-------------|---------|------------------------|
| Almonds, dried, unblanched              | 19.95       | 52.21   | 20.40                  |
| Brazilnuts, dried, unblanched           | 14.34       | 66.22   | 12.80                  |
| Cashew nuts, dry roasted                | 15.31       | 46.35   | 32.69                  |
| Chestnuts, raw                          |             |         |                        |
| American                                | 4.83        | 1.32    | 48.58                  |
| Chinese                                 | 4.20        | 1.11    | 49.07                  |
| European                                | 1.98        | 1.63    | 40.28                  |
| Coconut meat, raw                       | 3.33        | 33.49   | 15.23                  |
| Filberts (hazelnuts), dried, unblanched | 13.04       | 62.64   | 15.30                  |
| Macadamia nuts, dried                   | 8.30        | 73.72   | 13.73                  |
| Pecans, dried                           | 7.75        | 67.64   | 18.24                  |
| Pistachio nuts, dried                   | 20.58       | 48.39   | 24.81                  |
| Walnuts, English or Persian, dried      | 14.29       | 61.87   | 18.34                  |

Note: American, Chinese, and European chestnut data.<sup>104</sup> Data for other selected tree nuts.<sup>105</sup>

size, yields per hectare are low. Even under optimum cultural conditions yield of pecans seldom exceeds 2250 kg/ha.<sup>17,18</sup>

Although environmental factors have a profound influence on alternate bearing, little quantitative data are available due to the difficulty in isolating the contribution of each environmental variable. Sparks<sup>19</sup> concluded that no single variable can alleviate alternate bearing in pecan, although a total management program can minimize its' intensity. Factors that tend to enhance the tendency for alternate bearing include: a frost or freeze-damage induced crop loss; insufficient irrigation, fertilization, or irradiance levels; inadequate pest control; and premature defoliation. Alternate bearing has often been correlated with the level of assimilate reserves, particularly the carbohydrate concentration in the root.<sup>12-14,16</sup> Fruiting shoots typically produce fewer flowers the following year compared to vegetative shoots<sup>20</sup> despite containing a similar concentration of carbohydrates.<sup>12</sup> The involvement of plant hormones is suspected, but no quantitative data are available.

The environmental constraints to successful pecan cultivation are location dependent. In the southeastern United States reduced levels of irradiance and high relative humidity during the growing season are important limitations. In the western United States, or in arid regions, the availability of irrigation water can be a major concern. In the northern extremes of the cultivated range the greatest limitation is a growing season of adequate duration to ripen nuts, and to a lesser extent minimum winter temperatures. By contrast, in extreme southern areas a lack of winter chilling can limit productivity.

## B. LIGHT

### 1. Plant Growth and Development

Light is the resource/input that has been least successfully manipulated in pecan production. With the implementation of culture and management practices such as irrigation, fertilization, pest control, etc., the lack of available sunlight may often limit yield and quality in pecan orchards. The total amount of quanta intercepted per hectare of land cannot be manipulated. Unfortunately, for pecan there has been virtually no progress in enhancing the efficiency of light utilization for several reasons.

The inefficiency of light utilization is largely a function of biological constraints associated with growth habit and physiology. Pecan orchards over 60 years old may be overcrowded at a density of 35 trees per hectare. Orchards established at high densities (i.e., >75 trees per ha) and subjected to intensive management may become overcrowded in as little as 15 to 20 years. In overcrowded orchards, the light levels are sufficient for nut production only in the tops of trees since flower initiation and nut development are light dependent. Shading may reduce yield as a result of the light environment of a given year, or the effect may be cumulative.<sup>21</sup> Excessive shading is also associated with a gradual loss of lower limbs, enhanced insect and disease pressures and a reduction in nut quality. For example, Higdon<sup>22</sup> noted that nut size decreased and the number of pops (unfilled nuts) increased with increased

tree density. Andersen<sup>23</sup> also found that trunk cross-sectional area was reduced and limb breakage was increased for 14-year-old pecan trees of 6 cultivars at a high density (112 trees per ha) compared to a lower density (i.e., 43 trees per ha).

A dwarfing rootstock for pecan is not currently available. The growth retardant paclobutrazol has been shown to be an effective growth retardant of pecan,<sup>24,25</sup> but it is not registered for use in many countries including the United States. Thus, improved light distribution can only be accomplished by pruning or by tree removal. However, pruning has either reduced or has had no effect on yield of pecan.<sup>26-31</sup> Crane et al.<sup>27</sup> showed that cumulative yield was essentially zero for the 3 years following severe pruning where scaffold limbs were cut back to stubs. Pruning by the removal of shoot terminals increased kernel quality and shoot length, yet reduced yield.<sup>29,32</sup> Worley<sup>9</sup> found that yield was less than or equal to control trees when 20-year-old 'Elliot', 'Desirable', and 'Farley' (spacing = 14 × 14 m) pruned for 8 years by: (1) removing competing wood from alternate temporary trees as needed; (2) top and side hedging; and (3) selective limb removal. Yields of 4-year-old 'Western Schley' have been increased by 50% after relatively light pruning; however, the significance of these data is unclear as 4-year-old trees do not ordinarily have a high percentage of the canopy heavily shaded.<sup>33</sup>

## 2. Leaf Gas Exchange

The influence of light levels on  $A$  and the associated plant carbohydrate status, has received much attention due to the tendency of pecan to bear heavy and light crops in alternate years.<sup>10-15</sup>

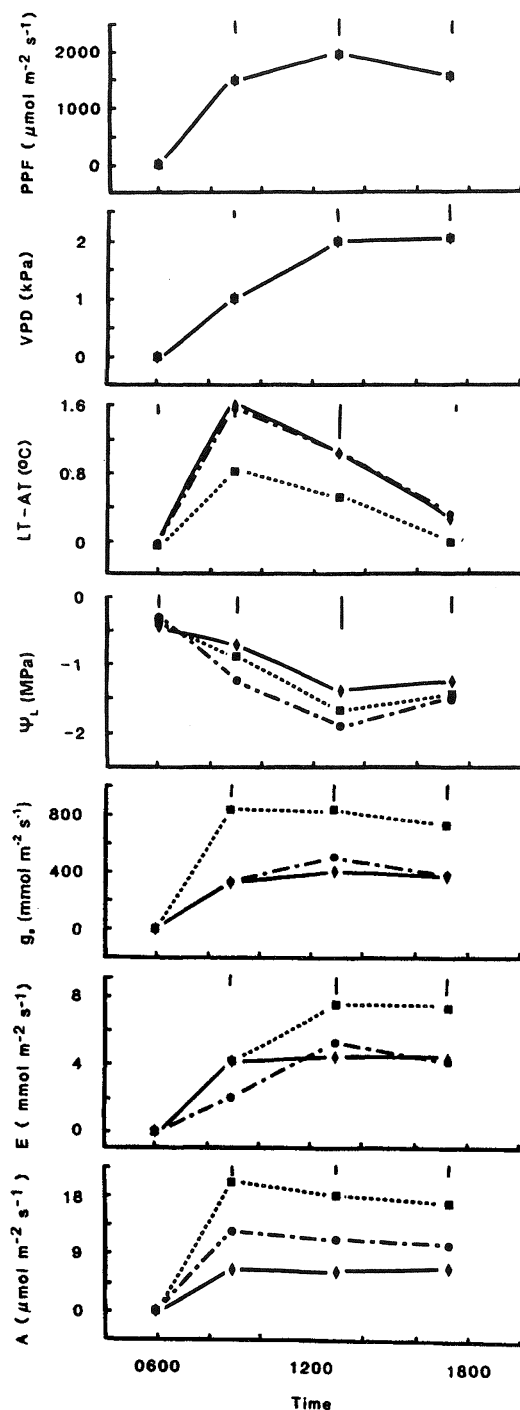
Factors that may influence the effect of light (and other environmental variables) on leaf gas exchange should be noted prior to a detailed discussion on irradiance. First,  $A_{\max}$ ,  $g_s$ , and  $E$  have been recorded for recently expanded leaves; leaf gas exchange was greatly reduced for leaves that were 4-months old compared to recently expanded leaves.<sup>34</sup> A decline in  $A$  and  $g_s$  of pecan was reported during late season compared to mid season; and the presence of a crop resulted in a 10 to 40% increase in  $A$  compared to nonfruiting trees.<sup>35</sup> Evidence that leaf carbohydrate status influences  $A$  of pecan was obtained by Marquard.<sup>36</sup> Girdling fruiting and non-fruiting shoots reduced  $A$  to 30 and 3%, respectively, of the ungirdled control shoots. Leaf gas exchange measured on excised branches or leaves should be avoided since xylem plugging may induce partial stomatal closure in as little as 3 hrs.<sup>34</sup> The above factors plus environmental preconditioning must be considered when interpreting gas exchange data of pecan leaves.

Loustalot and Hamilton<sup>37</sup> first provided evidence that  $A_{\max}$  of pecan leaves was reached at relatively high light levels of (i.e., under clear conditions), although light response curves were not reported. Crews et al.,<sup>38</sup> working with excised shoots of 'Brooks', 'Stuart', and 'Mobile' pecan reported that light saturated- $A$  (i.e., 7  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) occurred at a PPF of ca. 700  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . However, 2- to 3-fold higher  $A_{\max}$  have been subsequently reported for leaves from field-grown trees.<sup>34,39,40</sup>

Recent data have confirmed that light saturation is achieved at relatively high PPF. Diurnal measurements showed that  $A_{\max}$  for leaves of 'Choctaw' and 'Cape Fear' occurred in the morning when PPF approached 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; after late morning,  $A$  remained high (Figure 1) or declined slightly (Figure 2), until early evening. 'Cape Fear' trees that were preconditioned for 15 days to 30% full sunlight by using a neutral filter polyethylene shade cloth, a neutral filter<sup>41</sup> manifested much lower  $A$  during daylight hours (Figure 2).

Light response curves for sun- and shade-preconditioned trees have been established after exposing trees to full sunlight for 1 hr (Figure 3). The light response curves for pecan leaves preconditioned to 100 and 30% full sunlight was similar at low PPF, but diverged at ca. 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Light saturation (i.e., 95%  $A_{\max}$ ) occurred at a PPF of ca. 1500 and 1300  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for leaves preconditioned in 100 and 30% full sunlight, respectively (Figure 3). Apparent quantum yield determined by the slope of  $A/\text{PPF}$  at  $\text{PPF} < 150 \mu\text{mol m}^{-2} \text{s}^{-1}$  was not influenced by light preconditioning, although light compensation points and dark respiration rates were ca. 18 and 35% lower, respectively, for shade- compared to sun-preconditioned leaves.

Net  $\text{CO}_2$  assimilation is greatly reduced in the shaded interior of pecan. For leaves of 'Elliot' naturally shaded in the canopy interior exposed to ca. 15% full sunlight PPF (i.e.,  $\text{PPF} = 312 \mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $A$  was ca. 30% that recorded for leaves in full sunlight (Figure 4). However,  $g_s$  and  $E$  of leaves in the canopy interior were ca. 70% of full sun values, hence water use efficiency (WUE) declined. Steinberg et al.<sup>42</sup> also noted that  $g_s$  was similar for shaded and sun-exposed leaves of 'Wichita'. Evidence for a high light requirement of pecan leaves was obtained by Wood.<sup>39</sup> A moderate level of shading associated with a layer of sooty mold on adaxial leaf surfaces (i.e.,  $\text{PPF} = 1320 \mu\text{mol m}^{-2} \text{s}^{-1}$  compared to 1738

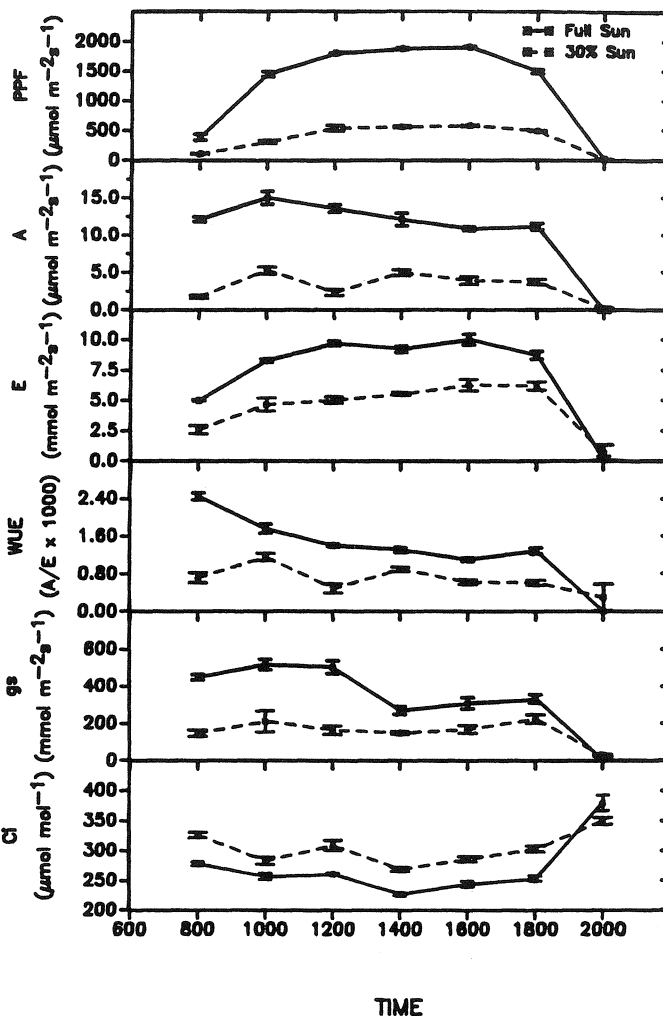


**Figure 1** Diurnal cycle of photosynthetic photon flux (PPF), vapor pressure deficit (VPD), leaf temperature-air temperature (LT-AT), leaf water potential ( $\Psi_L$ ), stomatal conductance to water vapor ( $g_s$ ), transpiration rate ( $E$ ), and net  $\text{CO}_2$  assimilation rate ( $A$ ) of pecan leaves (Andersen and Brodbeck<sup>34</sup>). Spring-flush expanded leaves are represented by ●; summer-flush expanded leaves by ■; and summer-flush expanding leaves by ◆. Vertical bars at the top of the PPF and VPD graphs represent  $\pm 1$  SE; vertical bars represent LSD, 0.05 level.

$\mu\text{mol m}^{-2} \text{s}^{-1}$  in full sunlight) reduced  $A$  by 20%; full sun values of  $A$  occurred after the film of sooty mold was peeled off the leaf.<sup>39</sup>

The above experiments have characterized the response of pecan leaves to relatively constant PPF. However, under natural conditions plants are typically exposed to frequent and sometimes drastic fluctuations in light level.<sup>43-45</sup> Intermittent cloud cover (which can reduce PPF to 10 to 30% of full sunlight), wind-generated leaf movements and mutual leaf shading may result in changes in PPF lasting less than a second to hours.

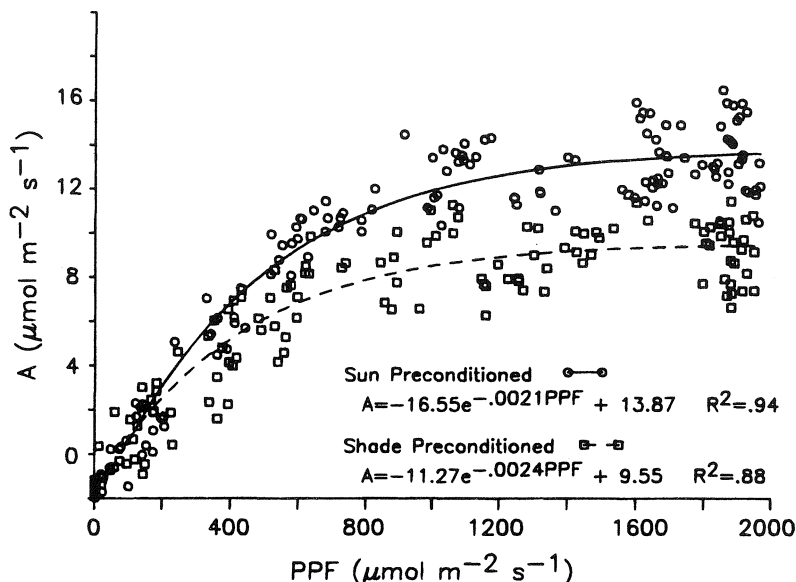
**Figure 2** Diurnal characteristics of leaf gas exchange of 'Cape Fear' pecan leaves preconditioned to 100 or 30% sun for 14 days. Photosynthetic photon flux (PPF), net CO<sub>2</sub> assimilation (A), transpiration (E), water use efficiency (WUE), stomatal conductance to water vapor (g<sub>s</sub>) and intercellular CO<sub>2</sub> concentration (C<sub>i</sub>) from 800 to 2000 hr (Andersen, 1990 unpublished data).<sup>106</sup> Circle and error bars represent mean  $\pm$  SE, n = 4. Leaf temperatures for sun and shade leaves, respectively were as follows: 800 hr, 21.1  $\pm$  0.1 and 22.0  $\pm$  0.3; 1000 hr, 29.2  $\pm$  0.4 and 28.3  $\pm$  0.3; 1200 hr, 31.6  $\pm$  0.2 and 31.4  $\pm$  0.5; 1400 hr, 36.3  $\pm$  0.4 and 34.0  $\pm$  0.2; 1600 hr, 36.6  $\pm$  0.3 and 35.2  $\pm$  0.4; 1800 hr, 33.1  $\pm$  0.1 and 31.4  $\pm$  0.2; 2000 hr, 25.8  $\pm$  0.1 and 26.0  $\pm$  0.2 (mean  $\pm$  SE).



Net CO<sub>2</sub> assimilation of higher plants declines quickly if the PPF declines below light-saturated PPF (with the exception of crassulacean acid metabolism plants) and increases rapidly with a return to full sunlight. The stomatal response to fluctuating irradiance, however, varies widely among species.<sup>43-46</sup> Plants having a stomatal aperture strongly dependent on light level have been classified as "sun tracking" and those having a stomatal aperture essentially independent of short-term changes in irradiance have been designated "non-sun-tracking".<sup>45</sup>

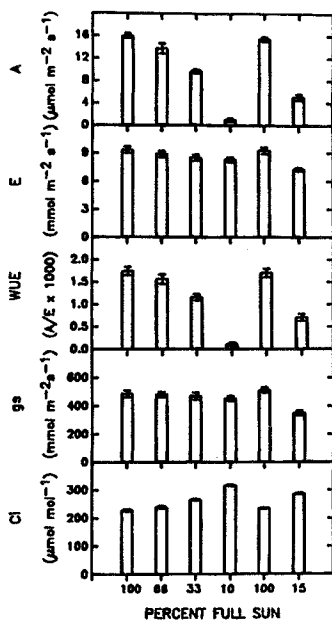
Pecan is a non-sun-tracking species when supplied with non-limiting soil moisture.<sup>47</sup> Pecan leaves were shaded with polyethylene shade cloth in the following sequence to produce 100, 66, 33, 10 and 100% the PPF in full sunlight with each sequence lasting 80 seconds (Figure 4). Net CO<sub>2</sub> assimilation was highest in full sunlight consistent with above data documenting a light saturation of ca. 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . With increasing shade A declined; however, g<sub>s</sub> remained unaffected. Consequently, WUE decreased and C<sub>i</sub> increased with increasing shade. When leaves were reexposed to full sunlight A, g<sub>s</sub>, E, and C<sub>i</sub> were nearly identical to initial values recorded in full sunlight.

When gas exchange of pecan leaves was measured in full sunlight for 18 min then in 30% full sunlight (i.e., PPF = 583  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) for 54 min, an abrupt 50% reduction in A occurred just after shading; however, g<sub>s</sub> declined very slowly such that g<sub>s</sub> was reduced by only 25% after a 54 min period (Figure 5). Consequently, C<sub>i</sub> increased from a steady state 225 to 230  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in full sun to 255 to 265  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in 30% full sunlight. Similarly, Woods and Turner<sup>48</sup> found that g<sub>s</sub> of beech, maple, oak, and yellow poplar reached stable values 12, 18, 20, and 36 min, respectively, after shade was imposed.

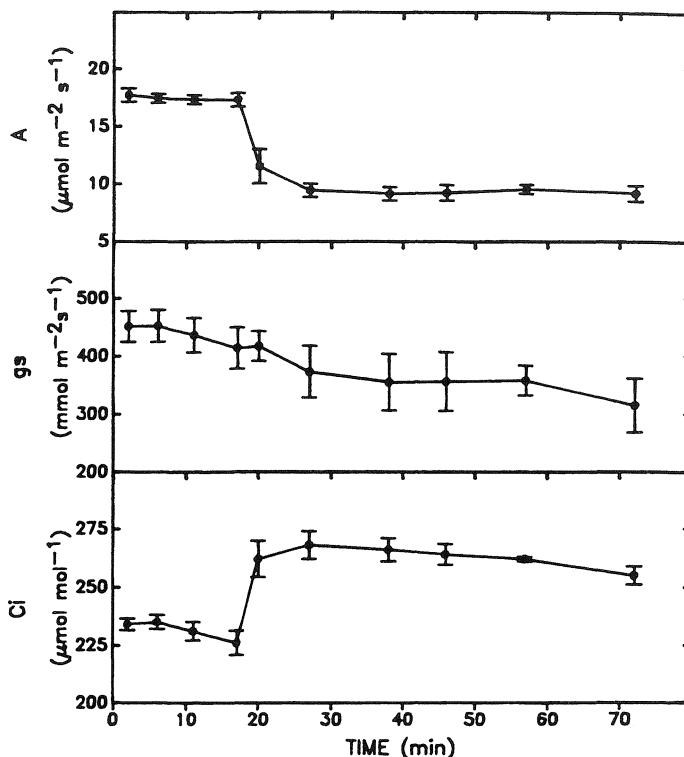


**Figure 3** Net CO<sub>2</sub> assimilation (A) at different levels of photosynthetic photon flux (PPF) for 'Cape Fear' pecan leaves preconditioned to 100 or 30% (shade) of full sunlight PPF for 15 days (Andersen, 1990 unpublished data).<sup>106</sup> Trees of the 30% sun treatment were exposed to 100% sun for 1 to 3 hr prior to measurements. Data were collected from four 100% sun- and 30% shade-preconditioned trees. Vapor pressure deficits and leaf temperatures were  $2.52 \pm 0.04$  and  $2.46 \pm 0.04$  kPa, and  $27.0 \pm 0.2$  and  $26.7 \pm 0.4^\circ\text{C}$ , respectively (mean  $\pm$  SE).

For pecan, A and stomatal aperture were not tightly coupled resulting in great variations in WUE and  $C_i$  with changes in light intensity (Figures 4 and 5). A good correlation between A and  $g_s$  has often been reported in leaves of herbaceous species,<sup>49-51</sup> although nonconstant  $C_i$  has been reported in leaves of peach,<sup>52</sup> grapevine,<sup>53</sup> olive,<sup>54</sup> and blueberry.<sup>55</sup> Knapp and Smith<sup>43-45</sup> have classified most herbaceous species tested as sun-tracking and most woody species tested as non-sun-tracking. In variable sunlight, it appears that for pecan and many woody species carbon gain is maximized at the expense of water loss, whereas for many herbaceous species water loss is minimized at the expense of carbon gain.<sup>45</sup>



**Figure 4** Net CO<sub>2</sub> assimilation (A), transpiration (E), water use efficiency (WUE), stomatal conductance to water vapor ( $g_s$ ), and intercellular CO<sub>2</sub> concentration ( $C_i$ ) of 'Elliot' pecan leaves exposed to 100, 66, 33, 10, and 100% full sun with each sequence lasting ca. 80 sec. (i.e., full sun PPF =  $2083 \pm 43 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) (Andersen 1991).<sup>47</sup> The last column of 15% full sun represents values for naturally shaded leaves located in the canopy interior. Values are means  $\pm$  SE,  $n = 9$ .



**Figure 5** Effect of variable light intensity on net  $\text{CO}_2$  assimilation (A), stomatal conductance to water vapor ( $g_s$ ) and intercellular  $\text{CO}_2$  concentration ( $C_i$ ) of pecan leaves. Leaves were exposed to 20 minutes of full sunlight, (i.e.,  $\text{PPF} = 1924 \pm 24 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), then 50 min of 33% sunlight (i.e.,  $\text{PPF} = 583 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Andersen 1991)).<sup>47</sup> Circles  $\pm$  error bars represent means  $\pm$  SE,  $n = 4$ .

The physiologic response to fluctuating irradiance levels for a given species may be influenced by the level of water stress whether caused by low soil moisture conditions or high VPD.<sup>44</sup> When water conservation becomes more critical than maintaining high levels of A, presumably a plant would tend to behave in a more sun-tracking mode.<sup>43-45</sup> Although whole tree carbon gain has not been adequately quantified for pecan given that light saturation of individual leaves occurred at a PPF of  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 3), Andersen<sup>56</sup> proposed that whole canopies of mature pecan trees are never light saturated under non-limiting conditions of soil moisture and VPD.

## C. WATER

### 1. Water Requirements

Native stands of pecan trees are generally confined to regions with deep alluvial soils (i.e., bottomlands). Upon germination, pecan seedlings repartition the rich energy reserves in the nut to a deep, well-developed taproot. The taproot may extend considerable distances to the water table and allow the tree to survive extended periods of drought; however, a more steady supply of soil moisture in the upper soil horizons is required for optimum tree performance. Irrigation has been shown to be cost-effective in the southeastern United States, the major pecan producing region in the world, which is characterized by a high humidity and abundant but often erratic rainfall.<sup>57</sup>

Irrigation in numerous locations has increased tree growth, yield, nut size, and percentage kernel.<sup>57-61</sup> Drought occurring early in the season have reduced nut size, while deficits during mid- to late-season have reduced percentage kernel, delayed shuck split, and harvest date. Late season water stress has also induced premature defoliation,<sup>58</sup> fruit abortion,<sup>62</sup> and greatly enhanced the percentage of nuts showing vivipary (preharvest germination) or a condition known as sticktight (delayed shuck opening).<sup>60,61</sup>

The water requirements of pecan trees are dependent on tree size/density and climatic and edaphic conditions. Once optimal tree size is achieved for a given tree density per hectare, irrigation requirements should be similar regardless of orchard density. Most (i.e., 95%) of the soil moisture depletion in several high density orchards (60 to 120 trees per ha) in west Texas occurred in the upper 1 m of soil.<sup>63</sup> Soil moisture depletion was independent of distance from the tree.<sup>63</sup> However, Miyamoto<sup>63</sup> cautioned that these data may not apply to pecans grown in deep, well-drained soils. Roots of pecan trees extended

Table 2 Osmotic potential ( $\Psi_{\pi}$ ) at turgor point loss and turgor pressure ( $\Psi_p$ ) and  $\Psi_{\pi}$  at full hydration of spring- and summer-flush leaves

| Leaf age                 | Turgor<br>point loss<br>$\Psi_{\pi}$ (MPa) | Full hydration |                    |
|--------------------------|--|----------------|--------------------|
|                          |  | $\Psi_p$ (MPa) | $\Psi_{\pi}$ (MPa) |
| Spring-Flush (Expanded)  | -2.7                                       | 1.8            | -2.3               |
| Summer-Flush (Expanded)  | -2.4                                       | 1.7            | -2.1               |
| Summer-Flush (Expanding) | -1.6                                       | 0.9            | -1.3               |
| LSD 0.05                 | 0.2  | 0.2            | 0.2                |

Note: Measurements were performed 25–29 August.

far beyond the drip line, and when optimum tree size is achieved for a given density, roots may occupy the upper soil horizons of the entire orchard.

Estimates of water consumption in Texas ranged from 18 cm water per month<sup>64</sup> to 100 cm water per season.<sup>65</sup> (Note: 1 cm per ha is equivalent to 100,000 l ha<sup>-1</sup>). Calculated values of water consumption by Miyamoto<sup>63</sup> were 100 to 130 cm per season; daily water consumption was dependent on tree number  $\times$  tree diameter (and not cross-sectional area). During mid to late summer daily water consumption was up to 1 cm per day.<sup>63</sup> Irrigation is terminated in many regions in September or October to prepare for the orchard floor for harvest; however, Stein et al.<sup>60</sup> advised against terminating irrigation until shuck split under dry conditions.

## 2. Plant Water Deficits

Although relative humidity during the growing season is typically very high in much of the native range of pecan (or in the southeastern United States), pecans have been cultivated successfully in arid regions (i.e., western United States and Israel) when provided with irrigation. Rieger and Daniell<sup>66</sup> reported that three-month-old, container-grown 'Curtis' seedlings were very sensitive to increases in VPD; an increase in VPD from 0 to 2 kPa was associated with a 50% reduction in  $g_s$ . The  $g_s$  of field-grown 'Stuart' trees was reduced slightly less than 50% when VPD was increased from 1 to 3 kPa.<sup>34</sup> By contrast, expanding, recently expanded, and 4-month-old leaves of 'Choctaw' trees in the field manifested consistently high  $A$  and  $g_s$  when exposed to VPD up to 2 kPa (Figure 1). The variable response of  $g_s$  to VPD for pecan is likely related to differences in the extensiveness of rooting, the ratio of leaf area to root absorbing area and tree  $L_p$ .

Pecan seedlings grown in containers maintained an absorptive condition despite a prolonged period of drought. Container-grown pecan seedlings subjected to soil water potentials ( $\Psi_s$ ) of -0.3, -0.6 or -1.1 MPa manifested progressive reductions in  $g_s$ ,  $E$ , and  $\Psi_L$ .<sup>66</sup> At a  $\Psi_s$  of -1.1 MPa  $\Psi_L$  declined to -3.0 MPa. Upon rewetings  $\Psi_L$  recovered within 15 min to pre-treatment values, although leaf gas exchange remained somewhat low for at least a day perhaps due to the residual effects of ABA.<sup>66</sup> Similarly, Taylor and Fenn<sup>67</sup> noted that pecan seedlings regained turgor 1 hr after terminating a 30-day drought period. In a split root experiment on pecan seedlings water was absorbed in wet soil and transferred across the stem or crown tissue and eventually exuded by roots growing in a dry soil.<sup>67</sup> Presumably, the deep taproot of field-grown pecan trees in well-drained soils ameliorates the effects of high VPD or of moisture variations in the upper soil horizons. For example, minimum  $\Psi_L$  reported for field-grown 'Choctaw' occurred during midday and ranged from -1.4 MPa for expanding leaves to -1.9 MPa for leaves that were ca. 4-months-old (Figure 1).

Many physiological changes are associated with the aging of pecan leaves. Leaf gas exchange rates increased for expanding leaves until full expansion then decreased until leaf abscission.<sup>34</sup> The slope of  $g_s/\Psi_L$  also increased and minimum  $\Psi_L$  decreased with increasing leaf age. Stomata of expanded and expanding leaves closed in response to reductions in  $\Psi_L$ ; however, basal leaflets on leaves that were 4-months old did not respond to reductions in  $\Psi_L$  to -4.1 MPa.<sup>34</sup> These data do not provide evidence for a critical threshold for stomatal closure.

The reduction in the  $\Psi_L$  required for stomatal closure with increasing leaf age was mediated, in part, by osmotic adjustment (Table 2). Leaf  $\Psi_{\pi}$  at turgor point loss or at full hydration decreased and  $\Psi_p$  increased with leaf aging.

Andersen and Brodbeck<sup>34</sup> measured the rate of elongation of pecan leaves as a function of  $\Psi_p$  and found that growth rate declined exponentially with a decrease in  $\Psi_p$ ; leaf elongation ceased at a  $\Psi_p =$

0.2 MPa (Figure 6). The biophysical basis for leaf expansion was investigated by relating  $\epsilon$  of different-aged pecan leaves to  $\Psi_p$ .<sup>34</sup> The  $\epsilon$  of all leaf-age categories increased with increases in  $\Psi_p$  (Figure 7). A lower  $\epsilon$  (i.e., higher elasticity) of expanding leaves was recorded only at a  $\Psi_p = 0.1$  MPa, (i.e., well below the minimum  $\Psi_p$  required for leaf elongation). Thus, leaf-averaged values of  $\epsilon$  did not provide a biophysical explanation for expansion growth.

Up to one third of the fruit on some pecan trees may be lost when nut walls split during the water stage of nut filling.<sup>68</sup> Prussia et al.<sup>69</sup> determined the  $\epsilon$  of developing nut wall material of four pecan cultivars. The  $\epsilon$  increased (i.e., tissues became more rigid) with age. 'Wichita' was the cultivar with the highest  $\epsilon$ , yet it was the cultivar most likely to rupture.<sup>69</sup>

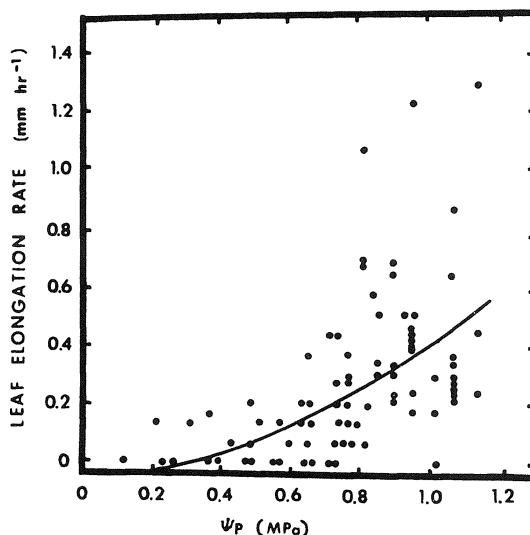
Andersen and Brodbeck<sup>34</sup> stated that the hydraulic system of pecan trees was efficient in maintaining high rates of leaf gas exchange and high  $\Psi_p$  and  $\Psi_L$  under high levels of VPD and leaf temperatures. Steinberg et al.<sup>42</sup> found that the  $L_p$  of pecan trees, as measured by a heat pulse method, was higher than most woody species but similar to values recorded for some herbaceous species. Transpiration and sap flow were closely coupled and  $L_p$  did not vary during the day indicative of a very low level of tree capacitance. Steinberg et al.<sup>42</sup> concluded that the efficient water transport system of pecan facilitates a depression of  $\Psi_L$  down to  $-2.0$  MPa without a reduction in  $E$ .

### 3. Flooding

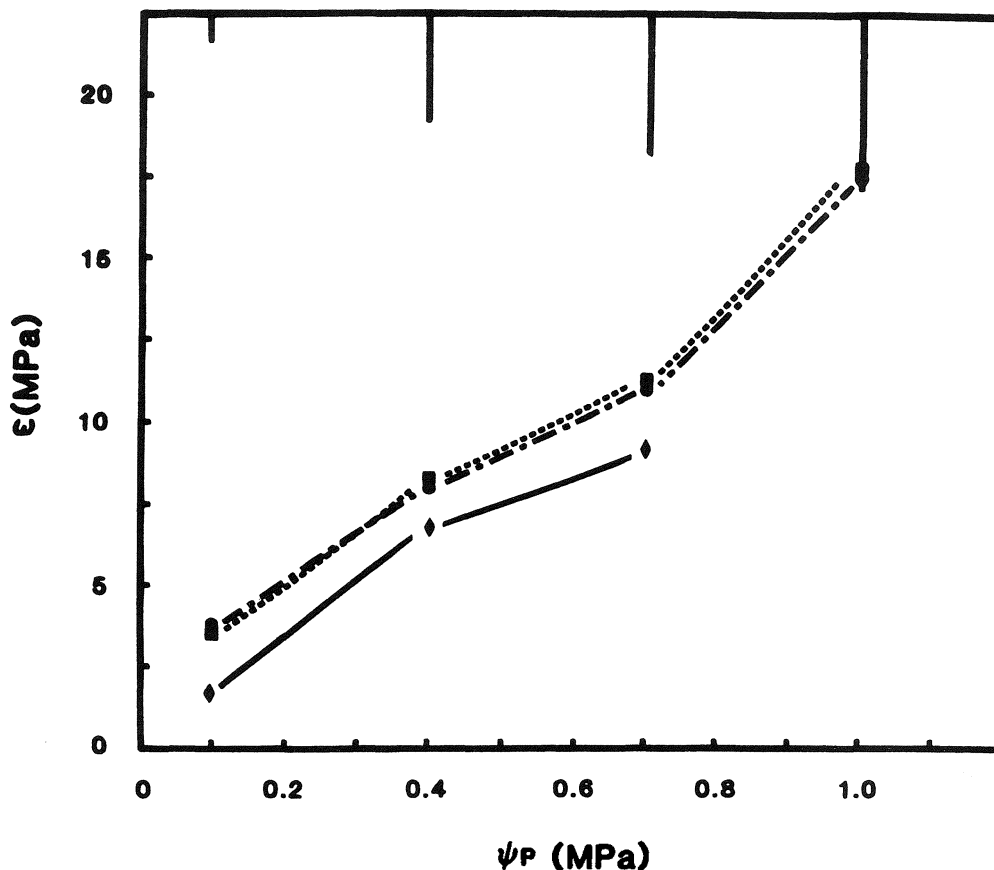
Pecan trees are often exposed to waterlogged soil conditions in their native and cultivated range, particularly during the dormant season. The survival of pecan seedlings after 4 weeks of flooding during the growing season was greater than black walnut, siberian elm, boxelder, and cottonwood but less than bald cypress, green ash, or silver maple.<sup>70</sup> Bitter pecan [*Carya aquatica* (Michaux) Nuttall] has been used as a rootstock for *C. illinoensis* and has had good growth in wet sites.<sup>71</sup> However, there are no quantitative data concerning the intraspecific flood tolerance within *C. illinoensis*. Flood tolerance is determined primarily by the rootstock and not the scion.<sup>72</sup> Since the source of seedlings used for rootstocks is often variable (and sometimes unknown) differential flood tolerance is extremely difficult to quantify on mature trees in the field.

Plant tolerance to waterlogged soil conditions is seasonally dependent.<sup>73</sup> Flooding 'Dodd' pecan seedlings for 28 days while dormant did not affect growth or leaf elemental concentration.<sup>74</sup> Flooding pecan seedlings for 28 days during budbreak reduced root and shoot growth and leaf N and Fe concentrations, while flooding during active growth reduced root and shoot growth and concentrations of most leaf elements. Several months after the termination of flooding, leaf elemental concentrations were similar to the nonflooded controls. Loustalot<sup>75</sup> reported that 35 days of flooding killed as much as 30% of the root system of pecan seedlings. Leaf chlorosis, leaf necrosis, and leaf abscission occurred in response to summer and fall flooding for a 'Stuart' orchard in Louisiana.<sup>76</sup>

Leaf gas exchange declines in response to soil flooding. Net  $\text{CO}_2$  assimilation decreased after 1 day<sup>77</sup> and 5 days<sup>75</sup> of soil flooding. Stomatal conductance (or  $E$ ) and  $A$  were reduced concomitantly in flooded



**Figure 6** The effect of turgor pressure ( $\Psi_p$ ) on leaf elongation rate over a 12-hr period (Andersen and Brodbeck, 1988).<sup>34</sup> Leaves were excised at 1900 hr, transferred to the laboratory and slowly dehydrated to variable degrees under fluorescent lights (PPF =  $256 \pm 87 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). After 12 hr, leaf length and leaf water potential was determined. The relationship between  $\Psi_L$ ,  $\Psi_n$ , and  $\Psi_p$  were determined on seven expanding leaflets by pressure-volume curves, and calibration curve was constructed relating  $\Psi_p$  to  $\Psi_L$ .



**Figure 7** Bulk modulus of elasticity ( $\epsilon$ ) of pecan leaves at leaf turgor pressure ( $\Psi_p$ ) = 0.1 to 1.0 MPa (Andersen and Brodbeck, 1988).<sup>34</sup> Spring-flush expanded leaves are represented by ●; summer-flush expanded leaves by ■; and summer-flush expanding leaves by ◆. Vertical bars at the top of the graph represent LSD, 0.05 level.

plants,<sup>75,77</sup> although  $\Psi_L$  was similar or increased compared to nonflooded controls.<sup>77</sup> Thus, as in many species,<sup>73</sup> flood-induced stomatal closure in pecan was not mediated by a reduction in  $\Psi_L$ .

## D. TEMPERATURE

### 1. Cold Hardiness

#### a. Symptoms of Cold Damage

Freeze damage in pecan is typically most severe in regions of the trunk just above (1 m) the soil line; plant tissue below the soil is usually not directly damaged by low temperatures.<sup>78</sup> Trunks of pecan trees are most susceptible to cold injury since trunks are the last part of the tree to become dormant in the fall, and with very low wind velocities, cold (dense) air tends to settle near the ground. Freeze damage can be identified by discoloration of the region surrounding the vascular cambium. The bark may also split longitudinally or may become separated from the trunk.<sup>78</sup>

When frost or freeze damage occurs on shoots of pecans, buds or leaf scars first become discolored followed by a general discoloration of the inner bark. Pecan buds sustaining damage as a result of an early fall freeze tend to break earlier the following spring than non-damaged buds.<sup>79</sup> However, bud injury sustained during mid-winter or late spring tends to delay bud break.<sup>80</sup>

Symptoms of cold injury or plant mortality can occur at various time intervals after the date of cold injury. Cold injury may result in bud mortality prior to budbreak, shortly after budbreak or by midsummer. Alternatively, tree mortality may be gradual over a several year period or the tree may simply be stunted for a prolonged period of time.<sup>78</sup>

### ***b. Influence of Environmental Factors***

Lang et al.<sup>81</sup> described 3 stages of dormancy as: (1) paradormancy—the initiation of dormancy controlled by environmental factors; (2) endodormancy—the period of deep rest controlled by internal plant factors; and (3) ectodormancy—late winter or early spring dormancy which is controlled by environmental conditions unfavorable for growth.

The extent to which a tree is in endodormancy will have a profound effect on cold tolerance. Pecan trees are particularly vulnerable to cold damage early (paradormancy) or late (ectodormancy) during the dormant period compared to when the tree is in endodormancy.<sup>81</sup> Fluctuating late fall to early spring temperatures will accentuate the damaging effects of a given temperature since fluctuating temperatures do not promote the physiological state of endodormancy. For example, on 19 Nov. 1969 pecan trees in south Georgia sustained cold damage when temperatures dropped to  $-8^{\circ}\text{C}$  because prior fall temperatures were unseasonably mild.<sup>78</sup> By contrast, cold injury does not usually occur in the native range (or most of the cultivated range) of pecan if temperatures are consistently low. Again, during the spring cultivars that tend to come out of dormancy and break bud earlier (e.g., 'Moore', 'Schley') are more likely to incur cold damage than cultivars that come out of dormancy late (e.g., 'Curtis', 'Stuart').<sup>82</sup>

Grauke and Pratt<sup>83</sup> reported that tree damage due to a spring freeze was proportional to the degree of bud development which was influenced by both rootstock and scion. For example, growth was more advanced for 'Elliot' and 'Curtis' seedling rootstocks compared to 'Apache', 'Sioux', 'Riverside' and 'Burkett', and for 'Candy' or 'Cape Fear' scions compared to 'Stuart'. Payne and Sparks<sup>84</sup> noted that cold injury was much more severe for pecan trees on non-juvenile (grafted) compared to juvenile (budded seedling) trunks. They suggested that the greater resistance of juvenile tissue to cold damage may be an adaptation while the tree is young to enhance competitiveness in its native range.

Any stress that weakens a tree going into dormancy such as drought, poor nutrition, premature defoliation, and inadequate insect and disease control will tend to exacerbate the extent of cold sensitivity. Sparks and Payne<sup>78</sup> ascribed the reduced cold tolerance of stressed pecan trees to a failure to enter deep dormancy (i.e., endodormancy) and a tendency toward earlier than normal bud break. A balanced nutritional program minimizes the likelihood of cold injury. Low levels of K or high levels of N fertilization dramatically increased cold injury to young 'Moore' trees.<sup>85</sup> Freeze injury is less likely in bare soil compared to soil with a cover crop.<sup>78</sup> Extreme temperature fluctuations and winter injury (i.e., sunscald damage) to tree trunks have been reduced by painting trunks with white latex paint.<sup>86</sup>

## **2. Chilling and Heat Units in Relation to Dormancy and Harvest Date**

Waite<sup>87</sup> first suggested that pecan buds require an exposure to chilling temperatures in order to break dormancy. Lack of sufficient chilling may delay foliation, cause irregular foliation, result in shorter shoots and smaller leaves, and may result in reduced yields.<sup>88-90</sup> For convenience, chilling hours are often calculated as the cumulative number of hours  $<7.2^{\circ}\text{C}$ , although it is known that temperatures vary in effectiveness in determining the onset and termination of winter dormancy.<sup>90,91</sup> Arnold<sup>92</sup> concluded from a survey of pecan production in locations in Florida, USA with only 100 chilling hours of chilling temperatures below  $7.2^{\circ}\text{C}$  that pecan may have a very low chilling requirement. He suggested that budbreak was mainly regulated by the accumulation of heat units. By contrast, the chilling requirement of stem cuttings of 'Desirable', 'Mahan', and 'Stuart' was 500, 500, and 600 hrs, respectively,<sup>93</sup> while Amling and Amling<sup>94</sup> determined that the chilling requirement of pecan depended on the climatic conditions during the fall (i.e., the phase of paradormancy). It was proposed that the "rest intensity" (i.e., deep dormancy) increases if trees are exposed to fall temperatures  $\geq 1.2^{\circ}\text{C}$ .<sup>94</sup> Amling and Amling<sup>95</sup> later concluded that exposure to low temperature was required for pistillate flower formation. Smith et al.<sup>96</sup> found that  $6^{\circ}\text{C}$  resulted in  $\geq 50\%$  budbreak of Dodd seedlings occurred after 900 hrs at  $6^{\circ}\text{C}$ , although 1000 to 2500 hrs of chilling increased percentage budbreak and reduced the time to budbreak. The duration of chilling required to break dormancy was dependent on bud location and temperature (between  $1$  to  $9^{\circ}\text{C}$ ). Lateral buds had a higher chilling requirement than terminal buds. Lateral budbreak of 'Dodd' seedlings was enhanced more by 1000 hours of chilling at  $5^{\circ}\text{C}$  rather than  $1$  or  $9^{\circ}\text{C}$ ; however, with 2500 hours of chilling at a temperature of  $1^{\circ}\text{C}$  was more effective in promoting budbreak.

The temperature requirements for budbreak of pecan were examined in a comprehensive study incorporating both experimental data and data derived from records obtained from a wide geographic range.<sup>97</sup> Sparks<sup>97</sup> found that budbreak was determined by the interaction of low followed by high temperatures; a meaningful specific chilling or heating requirement could not be established. The heat requirement decreased with increasing chill hour accumulation. Budbreak occurred in the absence of

chilling with sufficient heating; however, this is accompanied by a variability in the timing of budbreak (i.e., consistent budbreak on a tree does have a critical chilling requirement). Heating degree days with minimum temperatures  $<2.2^{\circ}\text{C}$  were inefficient in promoting budbreak;  $3.9^{\circ}\text{C}$  was the most efficient temperature on which to base chill and heat use accumulation.<sup>97</sup>

The regulation of budbreak by the interaction of chilling and heating may be an adaptation that facilitates a broad native and cultivated range of pecan.<sup>97</sup> In the north central United States a high degree of chilling received during the winter is followed by a low heat requirement for budbreak, thus allowing for nut maturation with a minimum of growing degree days. Conversely, pecan trees grown in the southern United States or in regions with little or no chilling (i.e., Brazil or Mexico) manifest delayed budbreak, thus minimizing the likelihood of frost damage during the winter or early spring. In these cases the dormant period is prolonged in the absence of chilling temperature; however, this is not necessarily concomitant with a great degree of cold hardiness.

Sparks<sup>97</sup> found that the fruit development period for pecan cultivars was dependent on geographic origin and varied from 137 to 198 days. Nut weight, and to a lesser degree percentage kernel was proportional to the time required for fruit development. Pecan nut and kernel characteristics were dependent on genotype and environment and genotype/environment interactions.

### 3. High Temperature

Maximum air temperatures in the native range of pecan seldom exceed  $38^{\circ}\text{C}$ , although in arid areas of cultivation air or leaf temperatures can approach  $44^{\circ}\text{C}$ . Leaves appear to tolerate these high temperatures, although  $44^{\circ}\text{C}$  is above the temperature optimum for many processes of growth and development of many temperate zone plant species. For a related species, shagbark hickory [*Carya ovata* (Mill.) K. Koch] damage to the chloroplast membrane was detected by nuclear magnetic resonance at temperature thresholds between  $53$  and  $57^{\circ}\text{C}$ ,<sup>98</sup> ca. 10 degrees higher than is likely to occur for pecan leaves in nature.

Temperature optimums for growth, development, and maximum yield of pecan have not been determined. Lipid reserves in pecan seeds are converted to starch prior to germination.<sup>99</sup> Lipid hydrolysis in germinating seeds is temperature dependent and raising the incubation temperature to  $30^{\circ}\text{C}$  for 3 days substituted for 60 days of stratification at  $4^{\circ}\text{C}$ .

Yates and Sparks<sup>100</sup> quantified the germination of pecan pollen as a function of temperature (i.e.,  $25$ ,  $35$ , or  $45^{\circ}\text{C}$ ) and relative humidity ( $5$ ,  $50$ , and  $97\%$ ). Maximum germination percentage increased as temperature decreased and relative humidity increased. Similarly, Marquard<sup>101</sup> found that germination rate and rate of pollen tube growth was maximum at  $27^{\circ}\text{C}$  and was ca. 0 at  $34^{\circ}\text{C}$ . Pollen can be stored for a prolonged period of time provided that it is oven-dried at  $35^{\circ}\text{C}$  and stored in a moisture-proof bag.<sup>102</sup> Pollen stored at  $-12^{\circ}\text{C}$  for 2 years under these conditions was as viable as fresh pollen.

Crews et al.,<sup>38</sup> working with excised shoots of 'Mobile', 'Stuart', and 'Brooks' pecan, found that  $A_{\text{max}}$  occurred at a leaf temperature of  $27^{\circ}\text{C}$  ( $8 \mu\text{mol m}^{-2} \text{s}^{-1}$ ); at  $40^{\circ}\text{C}$   $A$  declined to  $3 \mu\text{mol m}^{-2} \text{s}^{-1}$ . In that study  $A_{\text{max}}$  was low for a  $\text{C}_3$  mesophyte. Subsequent studies<sup>34,47,103</sup> have shown that  $A_{\text{max}}$  for pecan leaves is ca.  $16$  to  $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The low temperature optimum for  $A$  and the low values of  $A_{\text{max}}$  reported on excised branches<sup>38</sup> may have been a result of xylem plugging.<sup>34</sup> Andersen and Brodbeck<sup>34</sup> found that there was no evidence of a decline in  $A$ ,  $g_s$ , and  $E$  at leaf temperature up to  $41^{\circ}\text{C}$  when trees were supplied with adequate soil moisture; in fact,  $A$  was linearly related to leaf temperatures in the range of  $30.5$  to  $41^{\circ}\text{C}$  leading to the suggestion that maximum temperatures encountered in the field are seldom limiting  $A$  on a leaf area basis. Whole-tree  $A$ , however, may be reduced with increasing temperature above a given threshold since the effect of temperature on respiration of non-photosynthetic tissues is not considered when  $A$  is measured on a single leaf. There is ample justification for more experimentation concerning the effects of both high and low temperature on physiological processes on the whole tree level.

### E. MISCELLANEOUS ENVIRONMENTAL STRESSES

There are little or no quantitative data concerning physiological response of pecan to salt, wind, or atmospheric pollutants (i.e., sulfur dioxide, nitrous oxide, ozone elevated  $\text{CO}_2$  concentrations, etc.). While the limited physiological data has focused on the major environmental stresses existing in the current range of production, there is clearly a need for research on other environmental stresses that may occur presently or in the future.

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## V. PISTACHIO

### A. DISTRIBUTION AND BOTANY

The common pistachio, *Pistacia vera* L., is one of perhaps ten species with edible nuts in the genus *Pistacia*. The pistachio belongs to the family (Anacardiaceae), which also includes the cashew nut, mango, and poison ivy. Most *Pistacia* species are indigenous to the Old World; only two are indigenous to the United States.<sup>1</sup>

Pistachio probably originated in Central Asia, although it has often been referred to throughout recorded history in Western Asia, Asia Minor, and in the Mediterranean countries.<sup>2</sup> Wild pistachio trees remain an important component of the ecosystems in these regions.<sup>2</sup> The native range of pistachio is characterized by long, hot, dry summers and moderately cool or cold winters. Although pistachio will grow in rocky shallow soil, productivity is enhanced in a deep well-drained soil and by proper cultural practices. Turkey, Iran, Afghanistan, Italy, Syria, and the United States (Sacramento and San Joaquin Valleys of California) account for much of the production; lesser quantities are produced in Greece, India, Lebanon, Pakistan, and Tunisia.

The pistachio is a moderate-sized deciduous tree (ca. 7 to 10 m) characterized by imparipinnate leaves.<sup>1</sup> Trees are dioecious and the inflorescences (male and female) are panicles that may consist of several hundred individual flowers. The fruit is borne laterally on the previous season's growth. Pistillate and staminate flowers must bloom concurrently to allow for adequate cross-pollination.<sup>2</sup> Pistachio

inflorescences exhibit strong apical dominance. Terminal flowers of the inflorescence are responsible for most of the crop, although they represent only 8% of the flowers.<sup>3</sup> This, and the tendency to bear heavy and light crops in alternate years<sup>4-6</sup> are two characteristics that limit productivity. The reader is referred to Crane and Maranto<sup>4</sup> or Joley<sup>2</sup> for further general information on pistachio.

Quantitative data concerning the environmental physiology of pistachio has been essentially limited to the most obvious variables that would tend to limit productivity (i.e., drought and salinity) in the cultivated range. Several physiological adaptations have been demonstrated that facilitate growth, yield, and survival of pistachio in regions where few other fruit or nut crops can be successfully grown.

## B. LIGHT

Net CO<sub>2</sub> assimilation characteristics of *P. vera* have not been vigorously evaluated under controlled environment conditions, although the available data indicate that light-saturated values of A occur at relatively high levels of irradiance. Behboudian et al.<sup>7</sup> reported that light-saturated A was ca. 17  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and occurred at a PPF of ca. 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , although detailed data were not presented. Net CO<sub>2</sub> assimilation of *P. vera* and *P. atlantica* Desf. under field conditions in California, USA was maximum (ca. 20  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) during midday when PPF exceeded 1700  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .<sup>8</sup> Both species are indigenous to arid regions of Asia. Rates of leaf gas exchange of a *Pistacia* species indigenous to regions of high summer rainfall (*P. integerrima* Stewart) were much lower, although A<sub>max</sub> also occurred at a PPF > 1700  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .<sup>8</sup> High rates of leaf gas exchange of *P. vera* and *P. atlantica* may be based on a tendency to benefit from relatively short periods of favorable soil moisture.<sup>9</sup>

## C. WATER

### 1. Water Requirements

*P. vera* is drought tolerant, although productivity may be enhanced by maintaining moderate levels of soil moisture. The influence of soil moisture tension on the growth and morphological characteristics of *P. vera* cvs. Fandoghi and Badami has been evaluated in a glasshouse.<sup>10</sup> Leaf, stem and root dry weight, stem length, the number of leaves, and root dry weight were generally not reduced when seedlings were irrigated at a soil moisture tension of -100 kPa compared to -35 kPa, although irrigation at -500 kPa tended to reduce the growth variables.

The performance of *P. vera* cv. Kerman on *P. atlantica* was evaluated under five irrigation regimes [0, 25, 50, 75, and 100% of ET] over a three-year period in a commercial orchard.<sup>11</sup> Although nut weight, nut size, number of nut clusters per tree, nuts per cluster, shoot length, and rachis size were reduced at 0, 25, and 50% ET; tree performance was similar when irrigation was scheduled at 75 or 100% ET. Phene et al.<sup>12</sup> applied drip irrigation to *P. vera* cv. Kerman on *P. atlantica* in the San Joaquin Valley and recorded a reduction in yield at an ET of 25% compared to 50, 70, or 100% ET; however nut quality (as quantified by the number of blank, aborted, non-split and split nuts) was reduced at 25 and 50% ET compared to 75 or 100% ET. Goldhamer et al.<sup>11</sup> concluded that nut abortion and the formation of blank nuts were the physiological processes most sensitive to mild drought stress (75% ET scheduling), while trunk growth, shoot growth, and yield were affected by more severe drought stress.

In the Sacramento Valley of California mature pistachio trees with canopies covering 60% of the orchard floor use about 100 cm of water during an average season.<sup>4</sup> Spiegel-Roy et al.<sup>13</sup> evaluated the growth and yield of *P. vera* Israel 502, 'Kerman' and 'Larsen' on two seedling rootstocks *P. atlantica* and *P. vera* over an 8-year period in the Negev Desert (Israel). During extreme drought (1977), when soil moisture content was below 5% v/v (i.e.,  $\Psi_s$  -1.5 MPa) for a 19-month period, shoot growth was curtailed by May 1, while trunk cross-sectional area (TCA) increased through August. Despite a low yield during a year with extreme drought, flower buds differentiated to allow for a high yield the following year.

Yield of *P. vera* cvs. on 'Kerman' and 'Larsen' rootstocks in the Negev desert were not greatly influenced by the rootstock (*P. vera* vs. *P. atlantica*), although all scion/rootstock combinations exhibited a clear pattern of alternate bearing.<sup>13</sup>

There may be sufficient genetic variation to warrant selection of superior seedling rootstocks for a particular environment. Crane and Iwakiri<sup>3</sup> identified several trees of 'Kerman' on *P. atlantica* seedling rootstocks with superior growth and yield characteristics. Johnson and Weinbaum<sup>15</sup> evaluated 113 of 'Kerman'/*P. atlantica* seedlings and found that TCA, yield, and yield efficiency (yield/TCA) varied among individual trees 4-, 8-, and 3-fold, respectively. Great variations also occurred in the tendency to bear heavy and light crops in alternate years.

## 2. Water Deficits

The evolution of *P. vera* in a semi-arid environment is consistent with the acquisition of various physiological and morphological adaptations to drought. *Pistacia* spp. possess pinnately compound leaves comprised of 1 to 20 pairs of individual leaflets and may be oriented horizontally, vertically or randomly to sunlight.<sup>7</sup> Leaves of *P. vera* are isolateral and randomly oriented (which facilitate maximum light penetration), in contrast to the dorsoventral morphology of most *Pistacia* spp.<sup>8</sup> A xerophytic characteristic of leaves of *Pistacia* spp. is a well-developed palisades tissue.<sup>16</sup> The ratio of abaxial to adaxial stomata varied from 1.3 in (*P. vera*) to 13.3 (*P. integerrima*).<sup>8</sup> (A 3.1 ratio for *P. vera* has also been reported.<sup>7</sup>) In some species (i.e., *P. atlantica*, *P. chinensis*) adaxial stomata are restricted to areas adjacent to leaf veins; some *Pistacia* spp. only possess abaxial stomata (i.e., *P. lentiscus*, *P. mexicana*, *P. weinmannifolia*).

Stomatal conductance to water vapor of most *Pistacia* spp. was generally several times greater for abaxial compared to adaxial leaf surfaces; however, consistent with isolateral leaf morphology abaxial and adaxial  $g_s$  were similar for *P. vera*.<sup>8</sup> Maximum reported values of  $g_s$  of *P. vera* ( $400 \text{ mmol m}^{-2} \text{ s}^{-1}$ )<sup>8,17</sup> are rather high compared to many woody  $C_3$  plants;<sup>18</sup> yet similar to maximum  $g_s$  of many species of temperate fruit or nut trees.<sup>19-23</sup> The maximum  $g_s$  of *P. vera* was greater than or equal to the  $g_s$  of other *Pistacia* spp., in part due to a high adaxial conductance.<sup>8</sup>

Lin et al.<sup>8</sup> noted that *Pistacia* species in California did not manifest a midday depression in  $g_s$  or E, although leaf to air VPD were not given. The relationship of A and  $g_s$  was curvilinear for *P. vera*, *P. atlantica*, and *P. integerrima*. Turner et al.<sup>17</sup> working with container-grown *P. vera* showed that  $g_s$  and  $\Psi_L$  was reduced linearly with increasing VPD from 1.0 to 3.0 kPa, typical of many woody species; A declined from 14 to 11  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  under these conditions.

Turner et al.<sup>17</sup> showed that reductions in  $g_s$  and  $\Psi_L$  with increases in VPD were greater for woody species (including *P. vera*) compared to herbaceous species tested; this is indicative of a relatively low hydraulic conductance of woody species. They also found that the reduction in  $g_s$  with a decline in  $\Psi_L$  ( $\Delta g_s / \Delta \Psi_L$ ) of *P. vera* was greater than other woody species tested which would result in a greater degree of water conservation.<sup>17</sup> Consistent with a high degree of drought tolerance, Behboudian et al.<sup>7</sup> reported a positive A was recorded at a  $\Psi_L$  of  $-5.0 \text{ MPa}$ .

Behboudian et al.<sup>7</sup> monitored changes in the ratio of total resistance to diffusion of  $\text{H}_2\text{O}$  vapor compared to  $\text{CO}_2$  vapor as an index of WUE and found that a reduction in WUE occurred at a  $\Psi_L < -3.0 \text{ MPa}$ . Also, during later stages of drying cycle they reported the occurrence of nonstomatal inhibition of photosynthesis; however, this interpretation should be viewed with caution in the absence of data confirming stomatal homogeneity.<sup>24,25</sup>

Turgor maintenance at low  $\Psi_L$  is a xerophytic characteristic of *P. vera*. Behboudian et al.<sup>7</sup> calculated a  $\Psi_p$  of 0.3 MPa from thermocouple psychrometer-derived values of  $\Psi_L$  ( $-6.0 \text{ MPa}$ ) and  $\Psi_\pi$  ( $-5.7 \text{ MPa}$ ). In another study, *P. vera* had the lowest  $\Psi_\pi$  (i.e.,  $-4.5 \text{ MPa}$ ) of any of over 30 native Asian species tested.<sup>26</sup> Positive turgor at such negative  $\Psi_L$  support the suggestion that *P. vera* is able to tolerate drought conditions better than other fruit or nut crops.<sup>13</sup>

## D. TEMPERATURE

A lack of sufficient chill unit accumulation during the winter, or heat units accumulation during the summer, and the occurrence of spring frosts and minimum winter temperatures are environmental factors that may limit the range of pistachio cultivation. However, few controlled studies concerning the influence of temperature on growth and physiological processes have been conducted.

The amount of winter chilling required for proper growth and development is cultivar dependent. Pistachio trees cv. Kerman require ca. 1000 hrs of chilling below  $5.8^\circ\text{C}$  for satisfactory vegetative and reproductive growth.<sup>27</sup> Thus, pistachio cultivation should be restricted to regions averaging at least 1500 hrs of winter temperatures  $5.8^\circ\text{C}$  or less. Symptoms of insufficient winter chilling on cv. Kerman included delayed and irregular bloom and foliation, the production of leaves with a reduced number of leaflets, stem dieback, reduced yield in the current year and perhaps in subsequent years.<sup>27</sup>

Pistachio trees require long hot summers; however, the critical number of heat units required for nut ripening has not been determined. Based on locations where production has been successful a minimum of 6 or 7 months averaging over  $15.6^\circ\text{C}$  are probably required to complete the fruit development period.<sup>2</sup> With insufficient heat-hour accumulation pistachio will set fruit that will not ripen.<sup>2</sup>

Spring frosts or minimum winter temperatures may not often be a limiting factor for *P. vera* in its native or cultivated range. For example, pistachio trees were not injured by  $-8^{\circ}\text{C}$  in California,  $-18^{\circ}\text{C}$  in Tehran, and as low as  $-30^{\circ}\text{C}$  in Maryland, USA.<sup>2</sup>

The effects of high temperatures on growth and physiological processes of *Pistacia* species has received little attention. In Australia, Behboudian et al.<sup>7</sup> reported that A had an optimum temperature range of 25 to  $28^{\circ}\text{C}$ , although at higher temperatures data concerning VPD were not given. In California, A of three *Pistacia* spp. was maximum during midday at a temperature of  $30^{\circ}\text{C}$ .<sup>8</sup>

## E. SALINITY

### 1. Growth Responses

Pistachio is often cultivated in locations (i.e., Central Asia, Asia Minor, Australia) with high soil salinity. Soil salinity may arise from native soils with a high soluble salt content, irrigation with water possessing a high salt content (i.e., high EC), long-term use of fertilizers with a high salt content, or by salt water intrusion.

Sepaskhah and Maftoun<sup>10</sup> studied the growth of *P. vera* 'Fandoghi' and 'Badami' at three irrigation intervals, i.e., water at a  $\Psi_s$  of ( $-35$ ,  $-100$ , or  $-500$  kPa) and five salinity levels ( $\text{EC} = 0.5, 1.5, 2.5, 3.5$ , or  $4.5 \text{ dS m}^{-1}$ ) in a glasshouse. Salinity reduced leaf dry weight, leaf area, stem length, and plant ET; however there was an interaction between salinity and irrigation. Shoot growth for plants in the two higher irrigation regimes was reduced at an  $\text{EC}_e$  of  $12 \text{ dS m}^{-1}$ ; when plants were irrigated at a  $\Psi_s$  of  $-500$  kPa shoot growth was reduced at an  $\text{EC}_e > 15 \text{ dS m}^{-1}$ .<sup>10</sup> In another glasshouse study, a 50% reduction in shoot and root growth was achieved at an  $\text{EC}_e$  of  $7.9 \text{ dS m}^{-1}$  for 'Fandoghi' and an  $\text{EC}_e$  of 9.3 to  $10 \text{ dS m}^{-1}$  for 'Badami' and 'Kale-ghoochi'; shoot growth ceased at an  $\text{EC}_e$  of 15.5 to  $15.9 \text{ dS m}^{-1}$  for 'Fandoghi' and 18.7 to  $20.6 \text{ dS m}^{-1}$  for 'Badami' and 'Kale-ghoochi'.<sup>28</sup> Sepaskhah et al.<sup>29</sup> suggested that the lower salinity tolerance of 'Fandoghi' compared to 'Badami' may be due to a reduced ability to osmoregulate, and/or the differential uptake, transport, or partitioning of Na and Cl in different tissues.

The remarkably high level of salt tolerance of *Pistacia* spp. was underscored by a study that showed no significant change in dry matter production of *P. atlantica*, *P. vera*, and *P. terebinthus* seedlings when treated with 150 mM Cl and 90 mM Na for a three-week period.<sup>30</sup> *P. atlantica* had higher rates of Na but not Cl uptake and transport compared to *P. vera*; however, in all three species the accumulation of Na and Cl was diluted by growth.<sup>30</sup> Under certain circumstances a critical concentration of Cl may eventually be reached as Ashworth et al.<sup>31</sup> found leaf scorch of pistachio was associated with a Cl concentration of 1.9%.

The accumulation of Na and Cl in *P. vera* was proportional to the level of salinity,<sup>32</sup> but was inversely related to irrigation frequency. Sodium accumulated predominantly in the roots, whereas Cl accumulated predominantly in stems and leaves. Salinity did not influence the tissue concentration of macroelements with the exception of a decline in root K concentration.<sup>32</sup> In another study, Ca but not K or Mg increased in leaves of several *Pistacia* spp. with increased salinity.<sup>33</sup>

Picchioni and Miyamoto<sup>33</sup> evaluated the intraspecific salt tolerance of *Pistacia* spp. in an outdoor lysimeter and found that in all species an  $\text{EC}_e$  of  $8.7 \text{ dS m}^{-1}$  was associated with a reduction of root and stem growth; and leaf growth was more sensitive to salinity than root growth. Although increasing salinity resulted in a higher root to stem ratio, particularly for *P. terebinthus*; clear differences in salinity tolerance among species were not demonstrated. Differences in leaf Na and Cl concentrations occurred between *Pistachia* spp.; however, all partitioned most of the Na to the roots and most of Cl to the leaves.<sup>30,33</sup> Unlike many glycophytes, *P. vera* does not exhibit a positive growth response with increasing salinity,<sup>34</sup> and does not accumulate Cl or Na in leaves to the extent of mangroves *Avicennia marina*,<sup>35</sup> but instead regulates ion distribution more similar to spinach.<sup>36</sup>

### 2. Physiological Responses

Salinity tolerance of *Pistacia* spp. has been quantified based on the quantity of ultraviolet (UV)-absorbing solutes leaking from root apices.<sup>37</sup> In lysimeter experiments solute leakage occurred at a comparable EC, that resulted in an increased leaf Na ( $18.1 \text{ dS m}^{-1}$ ).<sup>37</sup> Cell injury was proportional to salinity and was greatest in a *P. terebinthus* selection with the least Na exclusion ability.<sup>37</sup> No differences in the leakage of UV-absorbing solutes occurred among the other *Pistachia* spp. or selections at a given salinity level. Most importantly, increases in the Na:Ca ratio greatly enhanced the leakage of UV-absorbing

solutes at a given  $\Psi_s$ . Intensification of root damage with low Ca may be related to the stabilizing influence of Ca on cell membranes.<sup>38</sup>

The influence of higher levels of salt applications on the physiology of *P. vera* cv. Kerman have been tested under glasshouse conditions.<sup>7,39</sup> Walker et al.<sup>39</sup> raised the concentration of Cl by 25 mM daily up to 100 or 175 mM Cl (accompanied by Na:Ca:Mg in a 6:1:1 ratio). Although growth was reduced at 100 mM Cl and had ceased at 175 mM Cl; a positive  $\Psi_p$  in leaves was maintained due largely to an increase in the concentration of sucrose and monosaccharides in the short-term (i.e., 2 days). In the long-term (i.e., 40 days), sugars, Na, Cl and to a lesser extent proline and shikimic acid contributed to osmoregulation.<sup>39</sup> Leaf emergence eventually was terminated after treatment with 175 mM Cl and leaf Na and Cl increased to 255 and 142 mM, respectively; however, A and E were unaffected and total plant carbohydrate content increased.<sup>39</sup> They concluded that growth cessation was not due to limitations of photosynthesis, assimilate content, plant water relations, and Na or Cl concentration in expanding leaves.

Net CO<sub>2</sub> assimilation, leaf chlorophyll content and plant water relations (i.e., WUE,  $\Psi_L$ ,  $\Psi_s$ ,  $\Psi_p$ ) of *P. vera* cv. Kerman were not influenced by Cl treatments of 75 mM for 84 days and then 225 mM for 23 days.<sup>7</sup> When the concentration of Cl was increased to 400 mM in daily increments of 25 mM, both A and  $g_s$  were reduced substantially.<sup>7</sup> Behboudian et al.<sup>7</sup> suggested that reduced photosynthesis was not due to effects on the photosynthetic apparatus (i.e., similar reductions in A and  $g_s$ , and slight increase in WUE and no change in chlorophyll content), but rather a result of partial stomatal closure and a lowered  $\Psi_L$  (determined during the morning). In all cases  $\Psi_p$  was greater than 1.0 MPa suggesting that leaf dehydration (or loss of guard cell turgor) may not have been directly responsible for partial stomatal closure, although data concerning midday plant water status were not presented.

All available data indicates that *P. vera* (as well as many of the other *Pistacia* cultivars tested) are most tolerant of all fruit or nut crops to both drought or salinity, with the possible exception of date palm (*Phoenix dactylifera*).<sup>40</sup>

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## VI. WALNUTS

### A. DISTRIBUTION AND BOTANY

The genus *Juglans* (family Juglandaceae) consists of ca. 20 species of deciduous, monoecious trees that are native to North and South America, southeastern Europe, and eastern Asia.<sup>1</sup> *Juglans* spp. possess large aromatic pinnate leaves. Male flowers (catkins) are borne on previous season's wood, while female flowers (racemes) are borne on current year's wood. The fruit is a drupe enclosed within a thick indehiscent husk. The edible seed is 2 to 4 lobed, and is retained within the shell until germination. The somatic chromosome number ( $2n = 32$ ) is similar to that of pecan. *Juglans* spp. contain jugalone, (a naphthoquinone), mainly in leaves, fruit, and bark.<sup>2,3</sup>

The Persian walnut (*Juglans regia* L.) is believed to have originated near the Caspian Sea in Iran and was transported to many regions of Europe and Asia, and more recently to the Americas.<sup>4</sup> Persian walnut trees are medium-sized but tend to have a very spreading growth habit and grow best on fertile, well-drained soils with a pH 6 to 7. Clones of *J. regia* are self-fertile, although asynchronous production of pollen and receptivity of the stigma (dichogamy) can reduce pollination efficiency and yield.<sup>5</sup> Grafted Persian walnut trees are fairly precocious for a nut tree and may bear the first crop in 2 to 5 years. A unique and desirable characteristic of *J. regia* compared to other *Juglans* spp. is that the husk separates from the nut as the nut ripens.

The black walnut (*J. nigra* L.) is a large tree (height > 30 m) native to the eastern United States and southern Canada and is important for its valuable timber and nut crop. *J. nigra* typically occurs on mesic sites with deep well-drained soils.<sup>7</sup> Native stands of *J. nigra* account for a substantial proportion of lumber and nuts harvested. Often plantings are established at relatively close spacings and eventually alternate trees are cut for lumber, while remaining trees are retained for nut production and cut at a later date. Seedling trees are often planted, although many cultivars have been clonally propagated.<sup>6</sup> Like *J. regia*, *J. nigra* is self-fruitful but dichogamy can reduce self-pollination efficiency.

Other *Juglans* spp. of some commercial importance include the Japanese walnut (*J. sieboldiana*), the Manchurian walnut (*J. mandshurica*), the southern California black walnut (*J. californica*), the northern California black walnut (*J. hindsii*), and the butternut (*J. cinerea*); however, there is a paucity of data concerning the environmental physiology of these species. The majority of studies on environmental physiology of *J. regia* and *J. nigra* concern the influence of light exposure and drought; the impact of other environmental stresses have not been adequately investigated.

### B. LIGHT

#### 1. Vegetative and Reproductive Growth

The influence of irradiance level on fruiting, specific leaf weight (SLW), subsequent spur productivity and nitrogen and carbon allocation has been studied for *J. regia* in California. Light distribution in the interior canopy, although not studied, is likely a growth limitation of *J. nigra* given that the amount of light incident on the ground below the canopy is low relative to other species.<sup>9</sup>

Mature Persian walnut orchards have been reported to be among the most shaded of any fruit or nut crop.<sup>8</sup> Ryugo et al.<sup>10</sup> reported that a single walnut leaf transmitted only ca. 50 of 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  incident PPF, and the second leaf transmitted only 10 of 50  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Although no data were given on differences in light quality after passage through a leaf, the ratio of far red to red light is generally enhanced after passage through a leaf. Heavily shaded (PPF = 10 to 30  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) spurs of *J. regia* cv. Hartley had a lower SLW, leaf chlorophyll concentration, number of leaves per spur, leaf area per spur, spur length, spur dry weight, dry weight per unit length of spur, dry weight per nut, number of nuts per spur, and dry weight of nuts per dry weight of spur than sun-exposed (PPF = 600 to 1240  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) spurs.<sup>10</sup> However, dry weight per kernel, oil weight per kernel, percentage oil content in nuts, percentage starch, and soluble carbohydrate concentration in spurs were not greatly influenced by light exposure.<sup>10</sup> In shaded, but not in sun-exposed spurs, the accumulation of starch ceased when nuts began accumulating dry matter; in sun-exposed spurs starch increased up until nut harvest in the fall.

Klein et al.,<sup>11</sup> found that spurs of *J. regia* cvs. Serr and Hartley could be segregated into two categories: (1) sun-exposed for a large portion of the day (i.e., PPF > 700  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), or (2) shaded for most of the day (i.e., total PPF between 100 and 700  $\mu\text{mol m}^{-2} \text{s}^{-1}$  occurring for only 1 hr per day and the remainder of the day PPF < 100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Both leaf nitrogen and SLW were allocated on the basis of light exposure. For example, leaf nitrogen was about 2 and 1  $\mu\text{g mm}^{-2}$  for sun and shade leaves, respectively; SLW was ca. 6 to 9 and 2 to 5  $\text{mg cm}^{-2}$  for sun and shade leaves, respectively.

Spurs of *J. regia* cv. Hartley that were sun-exposed the previous season had a higher return bloom and growth rate.<sup>10</sup> Similarly, spurs of *J. regia* cvs. Serr and Hartley that were shaded the previous season (inferred by a SLW < 4  $\text{mg cm}^{-2}$ ) sustained greater mortality during the winter, which was especially great on shaded spurs that had borne fruit the previous season.<sup>12</sup> Fruit set was enhanced on spurs with the highest SLW and N per unit leaf area (i.e., those that were sun-exposed the previous season), although kernel weight, kernel N, and kernel oil concentration did not vary with SLW in either cultivar. Thus, after fruit set, the level of light exposure the previous season did not generally have an overriding effect on kernel size or quality.<sup>9,11</sup>

The importance of light distribution on bearing of *J. regia* has also been supported by studies on pruning.<sup>13</sup> Flower bud initiation occurred about 4 weeks after they were formed on *J. regia* cv. Chico. Pruning accelerated flower-bud differentiation, and flower-bud differentiation was not reduced by defoliation and/or etiolation. Pruning also increased light penetration and nut distribution through the canopy, nut size and percent edible kernel of *J. regia* cv. Ashley.<sup>13</sup> Yield of biennially pruned trees was similar to that of annually pruned or non-pruned trees in the year following pruning, but was often greater in the alternate year.

## 2. Leaf Gas Exchange

Photosynthetic characteristics of *J. regia* leaves are very similar to those reported for many fruit species. Maximum rates of A of *J. regia* cv. Serr measured on leaves of excised shoots in the laboratory or on mature trees in the field were approximately 13  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .<sup>14</sup> Light-saturated A occurred at a PPF of ca. 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Net  $\text{CO}_2$  assimilation and g, were reported to be linearly related, although the relationship appeared to be curvilinear at high values of A.

## C. WATER

### 1. Vegetative and Reproductive Growth

Based upon native tree distribution *Juglan* spp. are mesophytes. Irrigation is required in many areas of cultivation to achieve maximum productivity.

*J. regia* grown in the arid climate of the central valleys of California are often exposed to atmospheric conditions conducive to high levels of moisture stress (i.e., high light and temperature and low relative humidity), which when coupled with inadequate irrigation may reduce tree growth, yield, and quality.<sup>15</sup> Martin et al.<sup>15</sup> compared  $\Psi_L$ , tree growth, and kernel weight and quality of *J. regia* cv. Ashley after one growing season without irrigation. Reductions in  $\Psi_L$  at sunrise (ca. 0.2 MPa), trunk growth (ca. 50%), kernel weight (ca. 20%), and no difference in kernel quality occurred by the end of the growing season without irrigation, although levels of soil moisture tension were not recorded. Martin et al.<sup>15</sup> reported that the wilting point of container-grown seedlings occurred at a  $\Psi_L$  of -1.9 MPa. The following year, when all trees received irrigation, kernel weights were actually greater for trees not receiving irrigation the previous year; thus the initiation of flower buds was not inhibited by drought. Kernel quality, as determined by the percentage of lightly colored and edible kernels was not affected by drought. However, in a similar trial with cv. Serr, both kernel weight and kernel quality were reduced without irrigation and poor quality nuts occurred in sun-exposed positions of the tree.<sup>16</sup>

In France, yield of *J. regia* cv. Franquette irrigated at 100% ET by sprinkler irrigation or 100, 75, or 50% ET by drip irrigation was increased from 53 to 78% compared to the non-irrigated treatment.<sup>17</sup> Irrigation improved kernel color but had no effect on leaf mineral composition.

Return bloom of field-grown trees,<sup>15,16</sup> and container-grown trees,<sup>18</sup> was unaffected by drought occurring during the previous season. However, phenology and bud dormancy can be influenced by periods of drought. For example, a period of spring drought promoted the growth of normally quiescent buds during the summer.<sup>18</sup>

## 2. Plant Moisture Deficits

The available database for *J. nigra* has been expanded over other *Juglan* spp. largely due to the fact that it is one of the most valuable timber species in North America. In its native range it is often codominant on moist (not wet) sites with species such as sugar maple (*Acer saccharum* Marsh.).

The sensitivity of leaf stomata of *J. nigra* to drought has typically been assessed on: (1) excised leaves or shoots exposed to extremely rapid drying; (2) container-grown plants exposed to fairly rapid drying; and (3) field-grown trees experiencing gradual drying. The more rapid the desiccation, the less likely that physiological and biochemical changes will occur that will influence stomatal behavior. Thus, plant responses to water stress will depend on the rate of imposition as well as the severity of the water deficit.

Davies and Kozlowski<sup>19</sup> evaluated the response of six forest tree species grown in containers to a single drying cycle in a growth chamber, (i.e., 25°C/20°C day/night temperatures and 70–90% relative humidity). Prior to the imposition of drought,  $g_s$  of *J. nigra* (ca. 160 mmol m<sup>-2</sup> s<sup>-1</sup>) was at least twice that of *Fraxinus americana*, *Acer rubrum*, *Cornus amomum*, and *Ulmus americana* and 75% greater than *Acer saccharum*. Stomata of *Acer* spp. were most sensitive to water stress and closed at relative high  $\Psi_L$ , while stomata of *J. nigra* and remained relatively open until a  $\Psi_L$  of < -1.0 MPa. *J. nigra* exhibited the least control over stomatal aperture, and upon rewatering was the only species tested that did not regain turgor. Net CO<sub>2</sub> assimilation for *J. nigra* has been reported to fall to zero at an  $\Psi_L$  = -1.9 to -2.2 MPa.<sup>19</sup> Similarly, nearly complete stomatal closure for container-grown, three-month-old seedlings of *J. nigra* occurred at a  $\Psi_s$  of -0.5 MPa; leaf abscission ensued at a  $\Psi_L$  of -2.2 MPa.<sup>20</sup> Based on the tendency to undergo leaf abscission and the above data the authors concluded that *J. nigra* could only be competitive in sites where water was readily available throughout the growing season.<sup>19</sup>

In contrast, field-grown *J. nigra* in Missouri were unique among 8 forest tree species in that low  $\Psi_L$  (predawn or mid day) was never achieved and  $g_s$  remained relatively high as drought increased.<sup>21</sup> Drought avoidance by deep rooting and by a gradual abscission of older leaves (starting in late July) was invoked as drought avoidance mechanisms for *J. nigra*.<sup>21,22</sup> An acropetal progression of leaf abscission has been considered to be an adaptive response to drought since basal leaves with a lower photosynthetic potential are shed first while the root to shoot ratio is enhanced.<sup>23,24</sup>

The anatomy of xylem vessels is largely based on a compromise between a high efficiency of water conduction (favoring long and wide vessels) and resistance to the formation and passage of gaseous emboli (favoring short and narrow vessels often with bordered pits conferring high resistance).<sup>25</sup> The greater resistance to water flow between soil and leaves (R) and water potential gradients between the root and crown of mature *J. nigra* compared to a gymnosperm, *Juniperus virginiana* has been attributed to a high resistance to water flow through the bordered pits of tracheids of *J. virginiana*.<sup>22</sup> In diffuse porous wood such as in *Vitis vinifera* L. with long wide vessels, zones of protection against cavitation reside largely in the nodes, whereas in ring porous trees (i.e., *J. nigra*) short narrow vessels accompany the larger vessels along the whole shoot.

Ni and Pallardy<sup>26</sup> compared the R of glasshouse-grown seedlings of *J. nigra* to R of *Quercus alba*, *Q. stellata* Wangenh. and *Acer saccharum* under high ( $\Psi_s \geq -0.3$  MPa) and low ( $\Psi_s < -1.5$  MPa) soil moisture conditions. *J. nigra* had greater R at high soil moisture conditions and a greater rate of increase in R with soil drying than the other spp., despite drastic reductions in E. There was no evidence of the formation of a substantial number of emboli in xylem vessels of these species; a great portion of the increased resistance to water flow was attributed to increasingly prevalent air gaps formed across the soil/root interface.<sup>26</sup> The contradictory results discussed for container-grown seedlings<sup>26</sup> compared to mature trees<sup>22</sup> was likely due to: (1) the rate of soil drying; (2) the probability that the young seedlings had not yet adequately explored the soil; and (3) differences in the root to shoot ratio and carbon partitioning between seedlings and mature trees.

The potential to resist damage during dehydration is thought to be associated with maintenance of membrane integrity during dehydration.<sup>27</sup> A stress-induced loss of membrane integrity results in an efflux of solute from cells.<sup>28</sup> Dehydration tolerance of *J. nigra* and other forest tree species have been evaluated by quantifying electrolyte leakage from leaf discs.<sup>23</sup> Drought-tolerant *Quercus* spp. manifested less electrolyte leakage than drought-susceptible *J. nigra* or *A. saccharum*.<sup>23</sup> As drought intensified, seedlings of *J. nigra* and *A. saccharum* showed no and little tendency for drought hardening, respectively.

*J. nigra* seedlings obtained from seven geographic origins were subjected to six different levels of drought stress.<sup>29</sup> The survival of stem cambial tissue of *J. nigra* to a predawn  $\Psi_L$  ( $\Psi_{LPD}$ ) as low as -4.0 MPa was facilitated by leaf abscission in an acropetal direction. More than 80% of leaves abscised

from nearly all plants from each geographic region at a  $\Psi_{\text{LPD}}$  of  $-3.5$  MPa or less. No differences in mortality (near 0%) or leaf abscission patterns occurred between genotypes. The capacity for both osmotic adjustment and increased tissue elasticity in eight seedling sources of *J. nigra* varied from absent to substantial, depending upon seed source. Osmotic potential at turgor point loss was reduced by 0.7 to 0.8 MPa which would facilitate growth by cell expansion and permit physiological processes such as continued leaf gas exchange at a lower  $\Psi_L$  than would be possible in the absence of changes in solute concentration. The relative contribution of increased solute accumulation and tissue elasticity to dehydration tolerance was also genotype-specific.

### 3. Water Use Efficiency

Ni and Pallardy<sup>20</sup> tested the hypothesis that higher rates of  $A$ ,  $g_s$ , and WUE (defined as  $A/g_s$ ) under conditions of low soil moisture occur for xeric (i.e., *Quercus alba* and *Q. stellata*) compared to mesic (*J. nigra* and *A. saccharum*) species. They found that seedlings of *Quercus* spp. had higher gas exchange rates at both high and low  $\Psi_s$ ; however, there was no trend for increasing WUE in the more xeric species. Rates of leaf gas exchange were relatively low and WUE relatively high for *J. nigra* seedlings. They suggested that a high WUE under dry conditions may actually serve as a disadvantage since water may ultimately be used by competing plant species.<sup>20</sup>

Parker and Pallardy<sup>30</sup> measured a decrease in WUE with drought progression for four seedling sources of *J. nigra*, which they attributed to nonstomatal inhibition of  $A$ . This conclusion must be viewed with caution without data confirming stomatal homogeneity and data characterizing chlorophyll fluorescence.<sup>31–35</sup> Stomatal conductance,  $E$ , or  $A$  measured by infrared gas analyzers is a volume-averaged value. If leaves are not homogeneous (or relatively homogeneous) in respect to stomatal aperture calculated values of WUE and intercellular  $\text{CO}_2$  concentrations are erroneous as a result of the curvilinear relationship between  $A$  and  $g_s$ . The consequence of “stomatal patchiness” is to underestimate WUE and overestimate  $C_i$  if measurements/calculations are made with conventional gas exchange instrumentation. Since  $A$  and  $g_s$  were more closely related to  $\Psi_s$  than to  $\Psi_L$  Parker and Pallardy<sup>30</sup> invoked the possibility of a nonhydraulic sensing mechanism or signal occurring from the root to the shoot as has been previously reported for root synthesized abscisic acid in corn.<sup>36</sup>

### 4. Root Growth

*J. nigra* grows best in deep, well-drained soils with a high moisture holding capacity. Although deep rooted, the majority of the root system of *J. nigra* is located in the upper 60 cm of the soil.<sup>37</sup> The growth of roots of deciduous trees may occur all year which may be particularly important for *J. nigra* given the high minimum  $\Psi_L$ , the tendency for leaves to abscise under conditions of drought and the importance of depth of rooting for this species.<sup>22</sup> Indeed, Frossard et al.<sup>38</sup> found that the taproot of *J. regia* cv. Franquette seedlings was a major storage organ (particularly the central parenchyma) for both water and carbon.

Increases in root length, number of growing roots, and suberization were evaluated in a rhizotron in relation to  $\Psi_s$  and soil temperature of mature *J. nigra*.<sup>39</sup> Root growth, the number of growing roots, and the rate of suberization decreased markedly as  $\Psi_s$  decreased from 0 to  $-0.5$  MPa, and reached zero at a  $\Psi_s$  of  $-0.5$  to  $-1.0$  MPa. Root growth began at a soil temperature of  $4^\circ\text{C}$  and maximum root growth and the number of growing roots were recorded at 17 to 19 and  $21^\circ\text{C}$ , respectively.<sup>39</sup>

For *J. nigra* the  $\Psi_\pi$  at full hydration of leaf tissue was much greater than that of root tissue, indicating that the root system is capable of releasing a larger quantity of water than leaves in response to decreasing  $\Psi_L$ .<sup>24</sup> This “capacitance” of root tissue, would serve as a substantial reservoir of water available to shoot tissue, and should be viewed as both a seasonal and a diurnal adaptation to plant moisture stress. In addition, the reduction in root  $\Psi_\pi$  reported in genotypes of *J. nigra* would favor turgor maintenance and permit the absorption of soil moisture at a lower  $\Psi_s$ .<sup>29</sup> The authors concluded that there was sufficient variation in tissue water relations of genotypes of *J. nigra* to justify selection of specific genotypes to specific regions.

Soil amelioration via soil mixing, subsoiling, or the addition of soil amendments have not resulted in a cost effective increase in tree growth.<sup>37</sup> Dey et al.<sup>41</sup> found that decreases in plant growth of *J. nigra* were associated with reduced  $\Psi_s$  and  $\Psi_L$  when multicropped with either tall fescue (*Festuca arundinaceae* Schreb.), orchard grass (*Dactyles glomerata* L.), or lespedeza (*Lespedeza striata* Thunb. cv. Kobe).

Several studies have documented the importance of mycorrhizae on growth of *J. nigra*.<sup>42,43</sup> The inoculation of *J. nigra* with vesicular-arbuscular mycorrhizal fungi (VAM) improved growth and

increased leaf retention at low levels of available soil phosphorous (i.e.,  $\leq 50$  ppm), but not at high levels of available phosphorous (i.e., 75 ppm).<sup>42</sup> Ponder<sup>44</sup> suggested that the frequency of irrigation altered the ratio of introduced and indigenous mycorrhizal fungi on *J. nigra*.

## 5. Flooding

The tolerance of *Juglans* spp. to flooded soil conditions is dependent on various biotic (e.g., tree age, nutritional status, and phenological stage of developments) and abiotic factors (e.g., temperature, VPD, soil porosity, and chemistry).<sup>45</sup> Flooding tolerance is often assessed on a relative basis. For example, plant survival after 4 weeks of soil flooding was greater for pecan [*Carya illinoensis* (Wagenh.) K. Koch] than for *J. nigra*.<sup>46</sup> Survival and growth of *J. siebaldiana*, *J. cinerea*, and *J. mandshurica* has been reported to be good in a floodplain habitat with 20 days or less of flooding annually.<sup>47</sup> Observational data collected in France has indicated that *J. nigra* may be more tolerant to waterlogging than *J. regia*.<sup>48</sup> By contrast, survival of container-grown *J. nigra* and *J. hindsii* was about equal with 50% of the trees surviving after 12 to 16 days of flooding at a root-zone temperature of 23°C.<sup>49</sup> Catlin et al.<sup>50</sup> reported that seedlings of *J. hindsii* and *J. regia* were much more sensitive to flooded soil conditions than *Pterocarya stenoptera* DC; Paradox seedlings (hybrids between *J. hindsii* and *J. regia*) were more flood tolerant than either parent but more flood sensitive than *P. stenoptera*. After 4 to 5 days of flooding at a root-zone temperature of 33°C, one half of the *J. regia* or *J. hindsii* survived while all *P. stenoptera* survived 26 days of flooding. *P. stenoptera* was also the most resistant of the walnut rootstocks to infection by six *Phytophthora* spp.<sup>51-53</sup>

Abscisic acid has often been invoked as a possible signal emanating from the root that may account for plant symptoms associated with soil flooding (i.e., reduced growth stomatal closure, leaf chlorosis, leaf abscission).<sup>45</sup> Although ABA may be a component of symptom expression, it increased only in leaves of *J. hindsii* but not in *J. regia* with soil flooding.<sup>50</sup> In *P. stenoptera*, ABA concentration was the same in leaves from flooded or control treatments.<sup>50</sup> It was concluded that ABA could not be used to screen genotypes for sensitivity to flooding. A leakage of phenolic substances from the flooded root systems of *Juglans* spp. has been demonstrated; however, the leakage of vacuolar phenolic compounds was viewed as a phenomenon secondary to an anaerobiosis induced decline in energy content (i.e., ATP) and membrane integrity.<sup>50</sup>

## D. TEMPERATURE

### 1. Carbon Assimilation

Tombesi et al.<sup>14</sup> reported that the optimum temperature for  $A_{\max}$  of leaves of *J. regia* cv. Serr was about 20 to 24°C (at PPF = 900  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , VPD = 1.5 kPa); a sharp decline in A was noted above 30°C. Sun-exposed leaves of *J. regia* in California manifested reductions in A as ambient temperatures (and presumably VPD) increased above ambient levels.<sup>14</sup> Leaf gas exchange of *J. nigra* has not been rigorously evaluated as a function of temperature.

### 2. Cold Hardiness

Minimum winter temperature is an important environmental limitation to the successful culture of *Juglans* spp. For example, the successful culture of *J. regia* in north and mid-Western United States, Canada, northern Europe, and northern Asia is precluded by minimum winter temperatures. In Russia, *J. nigra* and *J. mandshurica* were reported to have a lower shoot water content during the dormant season than *J. regia*.<sup>54</sup> *J. nigra* and *J. mandshurica* withstood -30 to -36°C and *J. regia* withstood -18 to -30°C without appreciable damage. Similarly, a minimum temperature of -24°C resulted in ca. 25 to 50% survival of pistillate and staminate flowers of cold-hardy clones of *J. regia*.<sup>55</sup> In Pennsylvania, *J. regia* sustained cold injury (i.e., stem dieback) during 1983-1984 (minimum temperatures of -26 to 29°C).<sup>56</sup> Among the 12 most cold hardy selections identified in Iowa there was no relationship between the timing of fall defoliation and cold hardiness.<sup>57</sup>

### 3. Dormancy

There is a paucity of quantitative data concerning the requirement of chilling temperatures for releasing dormancy of *Juglans* spp. From September to January, Mauget<sup>58</sup> transferred 3- to 4-year-old *J. regia* cv. Franquette from the orchard during dormancy to a greenhouse maintained at 15 to 20°C. All trees transferred from the orchard before January manifested delayed foliation indicating that the total chilling units accumulated before January were insufficient to permit normal budbreak and foliation. In any

event, in most of the cultivated range the inadequate winter chilling is not as great a limitation to production as minimum winter temperatures.

### E. WIND

Wind is a selection criterion that may direct leaf morphology one way when winds velocity is predominantly low, and another way when wind velocity is high.<sup>59</sup> Instability of leaves at low wind velocities may result in the loss of an optimal skyward orientation for  $A_{\max}$ ; at high wind velocities leaves may tear, or if they have a high drag coefficient may result in limb breakage or tree uprooting. The compound leaves of *J. nigra* formed an elongated cylinder which decreased in diameter with increasing velocity.<sup>54</sup> Vogel<sup>59</sup> studied the drag coefficient of 8 forest tree species and found that species with pinnately compound leaves (i.e., *J. nigra* and *Robinia pseudoacacia* L.) had the lowest drag coefficient; however, the threshold wind velocities for physical damage to leaves were not generally greatly different among species.

### F. ELEVATED CARBON DIOXIDE CONCENTRATIONS

The influence of elevated CO<sub>2</sub> concentrations on plant performance is a relevant topic considering the global increases in CO<sub>2</sub> occurring over the last 50 years. Tombesi et al.<sup>14</sup> reported that A of *J. regia* cv. Serr increased linearly with increasing C<sub>i</sub> (i.e., in response to elevated ambient CO<sub>2</sub> concentrations), typical for a C<sub>3</sub> plant. Wood and Hanover<sup>60</sup> found that 700 to 2100  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> increased dry weight and plant height of *J. nigra*; 1400 to 2100  $\mu\text{mol mol}^{-1}$  increased leaf area and leaf number; 2100  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> increased the root/shoot ratio more than the other treatments.

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## VII. CONCLUSIONS: TEMPERATE NUT SPECIES

The database concerning the environmental physiology of temperate nut crops is limited compared to many fruit crops, due to a number of factors. First, temperate nut crops are of limited economic importance on a worldwide scale, and current production is usually limited to specific geographic locations. Second, the cultivation of many nut crops is a very recent phenomenon and many species have not been genetically manipulated or domesticated to the extent of other food crops. Third, the very large size and long life span of many nut species increases the difficulty of experimentation (i.e., due to physical constraints, and the influence of environmental preconditions on plant physiology and plant assimilate/hormonal status). Fourth, most species are subjected to non-intensive cultivation, and often traditional/sustainable cultural practices are often employed.

Many nut crop species evolved as a climax forest tree species. To establish dominance in a forest canopy assimilates/nutrients are preferentially diverted into vegetative growth processes. Reproductive growth occurs when the assimilate/hormonal status of the tree is appropriate and when resources such as light, water, and nutrients are above a given threshold. Temperate nut species have often not been successfully manipulated from a horticultural standpoint. One example is the lack of progress concerning the efficiency of light utilization by pecan. Moreover, most nut species that are clonally propagated are still grown on seedling rootstocks. Quite often the seed source of seedling trees is not known and very few studies have been directed at quantifying the growth characteristics of seedlings from different seed sources.

The temperate nut crop species are very diverse genetically. The one commonality is the production of an energy-rich organ, typically high in protein and oil. The energy costs required to produce an organ so high in calories is much greater than most other reproductive (or vegetative) structures in the plant kingdom. Consequently, yields (i.e., kg/ha) are extremely low even under intensive management conditions compared to other fruit crops. For many nut species, compounding yield limitations are a relatively prolonged period of juvenility and a tendency to bear heavy and light crops in alternate years. These characteristics are also indicative of the amount of energy reserves that must be invested in reproductive structures. Several temperate nut species [i.e., almond (*Prunus amygdalus*), chestnut (*Castanea* spp.), pecan (*C. illinoensis*), and pistachio (*Pistacia vera*)] have high rates of A compared to other  $C_3$  forest tree or fruit crop species which would help meet the energy demands of a developing nut.

Agricultural sustainability has been increasing in importance. Although nut species produce a limited yield per hectare, in optimum habitats they require a minimum of inputs compared to most other fruit or vegetable crops. In the United States for example, seedling trees or native stands of pecans or black walnut (*J. nigra*) account for a substantial proportion of total nut production. In parts of Asia nuts of pistachio, filbert (*Corylus avellana*), and chestnut spp. (*Castanea* spp.) are often collected from native stands and/or plantings that are not under intensive management. Irrigation, fertilization, or regimented pest control programs are often not regularly employed.

Few generalities can be applied to the environmental physiology of temperate nut species. Nut crops have colonized a wide range of habitats. For example, *Pistacia* spp. grow in arid regions and are among the most drought tolerant food crop species. By contrast, black walnut is a strict mesophyte, requiring a steady supply of moisture. It utilizes leaf abscission as a drought avoidance mechanism at a  $\Psi_L$  of ca.  $-2.0$  to  $-2.5$  MPa.

For many species (i.e., almond, chestnut, pecan, pistachio) net  $CO_2$  assimilation is light saturated at relatively high PPF ( $\geq 1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). In addition, a relatively thick tree canopy may result in excessive shading for many species [almond, pecan, black walnut, Persian walnut (*J. regia*)] and limit productivity.

As has been emphasized throughout this volume that it is extremely difficult to interpret the influence of a given environmental stress under field conditions independent of other environmental factors. For example, high temperatures have often been cited as deleterious to physiological processes; however, the influence of increased VPD may be an overriding factor. There is no evidence to suggest that high temperatures occurring in the field approach lethal levels for species of nut crops. The extent to which physiological and growth processes are limited by high temperatures have not been adequately delineated.

Temperate nut species require a period of cool/cold winter temperatures followed by warm temperatures for normal budbreak, growth and development. The chilling requirement may vary from 200 to 300 hours for almond to more than 1000 hours of cumulative chilling for cultivars of pistachio. Pecan trees show elasticity in terms of a chilling requirement and may be grown in many geographic locations. Pecan trees will eventually bloom without a chilling period when sufficient heat units accumulate, although bloom period may be abnormally prolonged.

Salinity tolerance has been studied for those species frequently exposed to high salinity as a result of cultivation in inherently saline soil, irrigation with saline water, long-term use of fertilizers with a high salt content, wind blown salt spray, or salt water intrusion. Almond and pistachio are moderately and extremely tolerant of saline soils, respectively; an adequate database does not exist for the other temperate nut crops. Similarly, environmental stresses such as wind, atmospheric pollutants or elevated ambient  $CO_2$  concentrations have received very little attention.

In summary, with the exception of pecan, the current database concerning the environmental physiology of temperate nut crops is not very comprehensive. Even for pecan the physiological database is an order of magnitude less than for other fruit crops such as apple, grape, or peach. Physiological data are critically needed to refine culture and management practices, to fully identify geographic locations of adaptability and to model tree growth and productivity.

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