Timothy D. Paine
Editor

Invasive For

Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems

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Ecological Pest Management in Global Forests of a Changing World

Edited by

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Cover photo acknowledgement: The Greater St Lucia Wetland Park (GSLWP) in South Africa is a recently proclaimed World Heritage Site, 14200 ha of SiyaQhubeka land, 12000 ha commercial plantations and 2200 ha of natural vegetation, and has been incorporated into the GSLWP and game including elephant, rhino, buffalo, have unrestricted access into this area. The photograph is part of the original herd of 17 elephants that were introduced into the park in 2002.

The photograph was taken on SiyaQhubeka Forests land by Norman Neave for the Nyalazi Conservancy.

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Preface

Movement of plant and animal species around the world has been characteristic of human activity for millennia. People have moved agricultural plants and domestic animals with them as populations have expanded and new areas are colonized. Polynesians moved food plants and animals in voyaging canoes across the Pacific. Europeans brought many domesticated animals and plants with them when they colonized the New World. They also took plants from the conquered lands back to Europe.

In addition to the intentional transport and introduction of new species, unintentional introduction of animals, plants, and diseases also occurred. The black rat and the house fly developed cosmopolitan distributions as a result of unintentional anthropogenic transport. The bacteria causing plague was unintentionally transported from Asia into North America where it is now resident in rodent populations and is occasionally transmitted to humans. Despite the regular accidental movement of species across geographic barriers, the pace of introductions was relatively slow for before the age of steam because the number of individuals moving between continents was relatively low and the speed of movement was relatively slow.

The development steam powered transport, both rail and ships, enabled more individuals and goods to move greater distances and at lower costs than had occurred previously. The movement of people and goods stimulated economic growth, development, and world trade. It also created greater stimulus for intentional movement of crops plants, livestock, domestic companion animals, game animals, and ornamental plants. Increased movement and increased trade also presented opportunities for unintentional introductions. The pace of movement accelerated once again with flight and the widespread movement of goods and people by air. Air transport shortened the travel time allowing more fragile organisms to survive transit times that would have prevented their movement under steam.

The global economy has facilitated a global flora and fauna. In particular, the global requirements for cellulose in the form of raw logs, dimension lumber, manufactured timber products, paper, paper products, and cellulose fiber have escalated dramatically in the last three decades. Many nations continue to harvest timber in their native forests, but many others have adopted plantation forest management to provide timber for their domestic and international markets. Native trees may be used in their plantations. Alternatively, timber companies may import tree species from different parts of the world to meet demand for timber with particular economic value. For example, *Eucalyptus* spp. are among the most widely planted trees in the world and form the basis for the timber industries in parts of South America, South Africa, countries around the Mediterranean, and parts of Asia. In addition, species of *Eucalyptus* are being used in plantations in Australia but well outside their native ranges on that continent. Monterey pine, *Pinus radiata*, is native to a narrow geographic range in coastal central California, but is now widely planted as a valuable plantation species in Chile, New Zealand, and South Africa.

Current plantation forestry creates environments that are very different from native forests. The trees are growing in different densities, in different age structures, in different levels of genetic variation, in different community mixes, on different soils, in different physical environments, and often on different continents that they would in natural stands. Consequently, the trees often exhibit different patterns of growth, different physical form, and different levels of stress and resistance to herbivores or diseases. The plantation forests have different arthropod communities, including herbivores, predators and parasitoids, and saprophytes, and different microbial communities, including mycorrhizae and pathogens, than would be found in natural stands. These differences can include both reduced numbers of species as well as mixes of native and introduced species. As a result of different community compositions, the interactions among species, the communities with environmental conditions, and the ecological processes that occur in these forests may be very different and affect the trees in the stands in unpredictable ways.

The objective of this volume is to examine the ecological processes that are occurring in new forest environments. I am not referring to newly planted forests. Rather the authors of the chapters have been asked to address issues of new changes and the responses of communities to those changes. The global environment is changing, community compositions of herbivores, pathogens, or natural enemies are shifting as new species are introduced, populations of existing species are reduced in size, or host shifts occur in native species, the growing conditions are changing, all trees are being planted in new places. All of these factors have ecological, economic, and social implications that can be important for the future of new and existing forests.

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Timothy D. Paine

M. K. KAY

CHAPTER ONE

ARE ISLAND FORESTS VULNERABLE TO INVASIVE DEFOLIATORS?

Strength in Simplicity

1. INTRODUCTION

Islands are profoundly interesting ecosystems in which to examine evolutionary patterns and processes. Their isolation and simplicity provide natural ‘Ecotrons’ in which to seek an understanding of the role of biological diversity in the functioning of ecosystems. Insular biotas are typically relictual, depauperate and disharmonic (Paulay 1994) and hold significantly less biodiversity than equivalent mainland habitats (Whittaker 1998). The MacArthur and Wilson (1967) theory of island biogeography also suggests that the continuous immigration and extinction of species on islands results in a dynamic equilibrium of constant species turnover. Not surprisingly it has become axiomatic to represent island ecosystems as simple, vulnerable, and particularly susceptible to the loss of endemic biodiversity following invasion by continental biota (MacArthur & Wilson 1967, Paulay 1994, Whittaker 1998, Primack 2002). Although empirically not well supported (Wilson 2001), the appealing logic of the equilibrium theory persists and has even been applied to insect: plant interactions (Janzen 1968, Opler 1974, Feeny 1976). However, the spectacular divergence of island biota has been recognized since Wallace (1858) and Darwin (1859). Collectively, islands hold greater biodiversity than the continents and the disproportionate endemicity of island flora, and co-evolved associate invertebrate fauna, suggests evolutionary time-scales of stability or predictability.

Coevolution and predictability are at the basis of our current understanding of insect: plant interaction (Cornell & Hawkins 2003). In explanations of secondary plant compounds and insect host-specificity, Dethier (1954) and Erlich and Raven (1964) argue for a dynamic coevolution where, in reciprocal adaptations, plants are selected to produce novel compounds as a defense against herbivores, while herbivores develop defense-catabolizing mechanisms in response. Feeny’s (1975, 1976) concept of host apparency attempted to classify these plant secondary compounds and to explain their floristic distribution with regard to the community

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status of the plant. Southwood (1961) had already demonstrated a positive correlation between the geographic range, or the predictability of host plant occurrence, and the diversity of associated herbivores for the trees of Britain. Feeny contended that plants that are more ‘apparent’, through abundance or longevity, have to adapt to this greater diversity of herbivores. He reasoned that woody climax species, which often occur as virtually monospecific communities, should employ ‘quantitative defenses’, such as tannins and leaf toughness, to provide protection against a wide range of herbivores. These non-specific deterrents provide a non-negotiable defense, which reduce foliage digestibility in proportion to their consumption. In contrast, he considered that less apparent plants may escape herbivory in space and time, or be ‘qualitatively defended’ by relatively low concentrations of unique toxins, which may only be countered by specialist herbivores. The melding of the coevolution and apparency hypotheses was taken a step further by Levin (1975), who predicted that plant resistance to invertebrate herbivores would best be sought at the center, the area of greatest apparency, of a plant’s geographic range. However, the geographic variation in plant defenses against herbivores has not been well addressed empirically.

Janzen (1975), Levin (1976) and later Moody (1978) argued that a negative correlation in the latitudinal distribution of alkaloids and other secondary plant compounds was a response to grazing pressure. The gypsy moth (*Lymantria dispar*) bioassays of Miller and Hanson (1989) produced evidence that tropical trees are better defended than temperate counterparts and literature reviews (Coley & Barone 1996, Dyer & Coley 2002) support that conclusion. Carlquist (1974) described the Hawaiian Islands as being exceptionally poor in poisonous plants and suggested that a relaxation of herbivore pressure on islands led to the loss of defensive chemicals in island flora. The loss of cyanogenesis in plants of the Galapagos Islands has also been interpreted in terms of reduced herbivore pressure (Adersen et al., 1988), and a general loss of defenses against vertebrate herbivores in insular plants is reported by Bowen and van Vuren (1997).

The collective wisdom from biogeography, coevolution, apparency and biodiversity hypotheses would predict that simple, temperate, insular flora should exhibit an inherent vulnerability to invading continental, *r*-selected generalists. Why is it then that the temperate, insular, New Zealand forest flora is apparently resistant to invasive, polyphagous, continental Macrolepidoptera?

2. THE NEW ZEALAND EXPERIENCE WITH DEFOLIATORS

Some would consider New Zealand to be more than an island. However, 65MY of isolation and periods of glaciation and marine transgression, which at times restricted the endemics to tenuous refugia, have limited the present day endemic biota to a state considered depauperate even by island standards (Lawton 2000, Rosenzweig *pers. comm.*). Watson (2002) would argue that the difference in character between a biota built through vicariance, and one built by long-distance dispersal, would be lost over such a period. However, the oceanic debate may be of little consequence, for the thesis offered here appears to apply equally to mainland islands, or any plant population that is isolated, even when surrounded by congenerics.

2.1. Bioassays with invasive Lepidoptera

Lymantriids are not present in the New Zealand endemic invertebrate fauna and a rash of establishments and interceptions of lymantriids (*Orgyia thyellina*, *Teia anartoides*, *Lymantria dispar*) and the invasive arctiid, *Hyphantria cunea*, over the last decade should have resulted in the easy naturalization of those forest defoliators. Considerable eradication programs were put in place to prevent this (Hosking et al., 2003) and were supported by coincidental bioassays of the invaders to assess the risk they posed to the naturalized and endemic flora. All of the bioassays followed the methods of Matsuki et al. (2001). In no-choice randomized block trials, parameters of larval mortality and development of neonates were recorded till death or pupation.

2.1.1. Differences between continental and island plants

The bioassays (Kay 2002, 2003, 2004; Kay et al., 2000; Matsuki et al., 2001; Hosking et al., 2003) showed a surprising degree of resistance to these defoliators within the endemic flora. Furthermore, the New Zealand representatives of the Southern Hemisphere climax forest genus, *Nothofagus* (Fagales: Nothofagaceae), were largely unpalatable to these exotic defoliators.

Nothofagus species are the long-lived, climax dominants of the endemic temperate forests of the Southern Hemisphere and typically occur as 'predictable' monospecific forests. The greatest species diversity and geographic range of the genus occurs in South America. In an apparent paradox, the bioassays revealed that the continental South American species of *Nothofagus*, which are subject to a far greater diversity of invertebrates than the New Zealand representatives (McQuillan 1993; Ogden et al., 1996; Veblen et al., 1996), were generally more palatable than those of New Zealand. Some South American *Nothofagus* were more palatable to the assaying Lepidoptera than their primary Northern Hemisphere host plants!

2.1.2. Latitude and Nothofagus *defense*

If plant defenses are negatively correlated with latitude, one would expect lower latitude *Nothofagus* to be better defended than higher latitude species. This is not borne out for the *Nothofagus* of South America. The most northern species *N. obliqua* (33°-41°S) is demonstrably the most palatable in all bioassays. However, *N. alessandri* (35-36°S), a tiny (350 ha) relictual population at the same latitude is the least palatable species (Russell et al., 2000; Kay 2002; Matsuki et al., 2001). Furthermore, *N. obliqua* has the greatest number of associated invertebrates and *N. alessandri* the least (McQuillan 1993). The Australian *N. moorei* (28-32°S) is the most northern of the temperate *Nothofagus*, but is also of very limited distribution. It is the least palatable of the Australian species (Kay 2002). *Nothofagus alessandri* and *N. moorei* could be considered to be mainland islands of *Nothofagus*, and it would appear that the limited geographic range of a species is just as important for plant defense on mainlands as it is on islands. It would also appear that area is more important than latitude in determining plant defense.

A compounding effect of latitude may be demonstrated in bioassays of provenances of *N. truncata*, New Zealand's least palatable beech species. *Nothofagus truncata* is the least common of the New Zealand beeches and has a small (ca 40ha) southern population at Haast (44°S), isolated by some 260 km to the south of the nearest substantial population of the species (Mark & Lee 1985). In a bioassay with *T. anartoides* and two provenances of *N. truncata*, the southernmost, Haast provenance proved totally resistant (100% larval mortality) whereas larvae on some replicates of the Mangorewa (38°S) provenance, close to the center of the geographic range of *N. truncata*, survived to produce male pupae (Fig. 1).

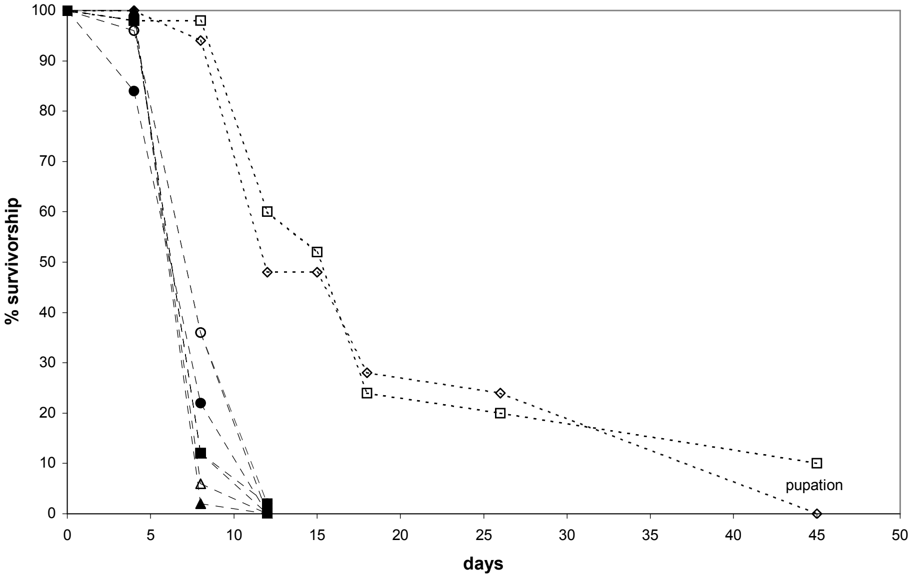

Figure 1. The survivorship of Teia anartoides *fed on Haast (solid) and Mangorewa (hollow) provenances of* Nothofagus truncata.

2.1.3. A reciprocal test

Pinus radiata is the main plantation species in New Zealand. *Pinus* is almost exclusively confined to the Northern Hemisphere and the geographic range of

P.radiata is limited to three discrete mainland and two island populations, along the coast of California.

In a bioassay, foliage from the natural populations of *P. radiata*, grown in a common garden in New Zealand, was fed to the New Zealand indigenous geometrid, *Pseudocoremia suavis*. Larval growth rate was poorest on the two island provenances of *P. radiata* and there was a positive correlation between the growth rate and the geographic range of the individual Californian provenances (Fig. 2). The island provenances were the least palatable, but also the provenances of lowest latitude. The provenance with the smallest geographic range (Cedros Island) was the least palatable. Interestingly the New Zealand landrace, the first generation commercially selected for growth, was the most palatable.

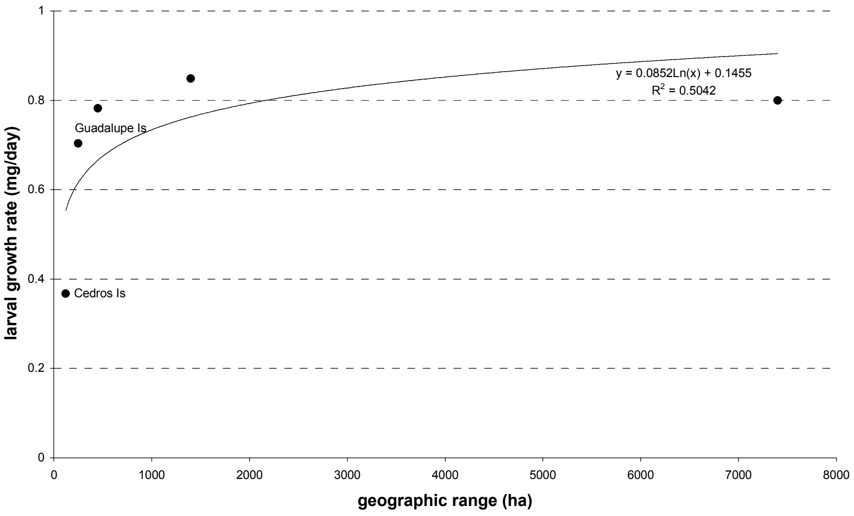

Figure 2. The growth rate of Pseudocoremia suavis *fed on* Pinus radiata *from geographically distinct natural populations.*

3. AN EXPLANATION OF THE NEW ZEALAND EXPERIENCE

The Island Resource Allocation (*IRA*) hypothesis (Kay & Wratten 2004) was developed as an explanation of the apparent resistance of the New Zealand flora to novel defoliators. The basis for the *IRA* hypothesis is a redefinition of the fundamental ecological principle of the species: area relationship. Species diversity increases with area, but the relationship is more pronounced at higher trophic levels (Holt 1996). Habitat fragmentation studies (Schoener 1989, Kreuss & Tscharntke 1994, Lawton 2000, Komonen et al., 2000) and trophic level patterns in spatially discrete ecosystems (Schoenly et al., 1991; Holt 1996) show that the trophic components of invertebrate communities do not change uniformly with area. Rather, during habitat fragmentation, the higher trophic levels are lost prematurely or disproportionately, or cannot be maintained in small habitats. In redefining the species: area concept, the *IRA* hypothesis contends that islands, or similarly geographically constrained ecosystems, support lower biodiversity, have fewer trophic levels, and consequently have a lesser top-down regulation of herbivores by natural enemies. The hypothesis posits that if plant fitness is influenced by herbivores, then, when top-down regulation of herbivores is weak because of a lack of trophic complexity, plants that cannot escape in space or time will be selected to allocate resources to bottom-up defenses. If trophic diversity drives resource allocation for plant defense, the lower biodiversity typical of higher latitudes may compound the species: area effect.

The breakup of the Gondwanan continent represents a fragmentation of the *Nothofagus* ecosystem on a macroecological scale, over evolutionary time. The remnants of that temperate ecosystem exist in Australia, New Zealand and South America. The isolation and inundation of the New Zealand landmass has resulted in an island-like depauperate biota lacking trophic complexity. On the continents similar climatic events have marginalized some species so that they resemble mainland islands. Bioassays show that these geographically constrained species are well defended against defoliators.

4. DISCUSSION

4.1. The IRA hypothesis

It is generally accepted that, in response to herbivore selection pressure, plants have evolved a multitude of physical, chemical, phenological and symbiotic strategies which provide a bottom-up limitation on the plant material available to defoliators (Edwards & Wratten 1980). These strategies may be complemented by the actions of natural enemies, which effect a top-down regulation of herbivores (Hairston et al., 1960). This regulatory plurality is now considered to exist in most systems (Hunter & Price 1992), but it is empirically difficult to demonstrate the relative roles of each (Walker & Jones 2001).

With the trend to reductionist studies there seems to have been few empirical attempts to put plant defense strategies into a community or ecological context. The majority of literature on the interaction between insects and plants neglects the concomitant interaction with other trophic levels. The task may be impossible empirically. Even the modelling of such interaction is seen as daunting in its complexity (Holt & Loreau 2001) and yet unrealistic if simplified (Polis 1991). The ‘Green World’ hypothesis (Hairston et al., 1960) argues that the necessity for plant defenses is minimal because of the top-down regulation of herbivores that is effected by natural enemies. Conversely, not all plant material is available to herbivores. Plant defenses may provide a bottom-up limitation of herbivore populations (White 1978). It would appear logical that, if insect herbivory does influence plant fitness, then, when a robust top-down regulation of herbivore populations by natural enemies is reduced or absent over evolutionary time, plants that cannot escape in space or time should be selected to allocate resources to a 'bottom-up' defense. The role of biodiversity in ecosystem stability is a hotly debated issue (Kinzig et al., 2001), but the *IRA* hypothesis contends that ecosystem stability may be achieved through a reconciliation of top-down and bottom-up processes mediated primarily by biodiversity *via* habitat area. This appears counter-intuitive only because of long established, but poorly supported, hypotheses of biogeography and plant apparency.

Feeny's classification of defensive plant compounds has become blurred. Feeny (1975) himself argued for both quantitative and qualitative strategies in climax plant species and the comparative palatability of British trees has not been convincingly demonstrated (Edwards et al., 1986). More recently qualitative defenses have been shown to act in a dose-dependent quantitative manner (Lindroth & Hemming 1990) and the role of tannins in plants has been the subject of numerous studies which show a great and varied array of responses. Needless to say, bioassays vary, tannins are an extremely variable group of compounds and the apparency hypothesis persists (Coley 1983; Forkner et al., 2004). The *IRA* hypothesis would conclude that the polarity of the apparency hypothesis should be reversed. Widely dispersed plants are protected from the excesses of herbivores by an accompanying complex trophic web. Geographically constrained plants need inherent defenses against herbivores and the need increases as habitat area decreases *i.e.* an 'unapparency' hypothesis of plant defense might be more appropriate.

Corollaries of the apparency (Feeny 1976) and coevolution hypotheses posit that isolated plants with non-evolving defensive compounds would be easily overcome through herbivore selection pressure, and that related plants should have similar secondary chemistries. The ecography of secondary plant chemicals has not been well addressed however, Bohm's (1998) limited review of insular secondary plant chemistry shows that island plant chemical profiles are somewhat ambivalent. They may be similar, simpler or enriched, when compared to the profiles of equivalent continental species. The New Zealand flora has a high (80%) degree of endemism (Allan 1982) which may provide a novelty that would deter the most catholic of feeders. However, in numerous well-documented instances New Zealand plants have richer arrays of compounds than their continental counterparts. Plant phylogeny does play a part in chemical profiles, but for *Nothofagus* the resistance to defoliators occurs within and between the three temperate subspecies and landmasses, which suggests that factors other than phylogeny influence chemical expression.

Levin's (1975) claim that resistance to herbivores should be found at the center of a plant's geographic range because of the greater diversity of herbivores, neglects the influence of natural enemies which would be expected to accompany the herbivores. The *IRA* hypothesis, which includes community trophic complexity, indicates that resistance should be sought in isolated populations or at the edges of populations. The expansion and contraction of plant ranges due to climate or competition will produce 'marginal populations' *sensu* Stern and Roche (1974), which act as 'mainland' islands. These isolated populations are subject to the selection extremes of climate and competition for the species. It appears, as has been demonstrated for *Nothofagus* and *Pinus radiata*, that these marginal populations are also selected for defense against herbivores. A similar demonstration of resistance at the edge of populations has been seen in the interaction between the white pine weevil and spruce in Canada (Alfaro et al., 1999).

Biologically active compounds in plant leaves may well permeate through the food web, unless catabolized by the plant at leaf senescence. Interestingly, Wardle et al. (1997) found that the accumulation of secondary plant compounds in litter increased with the inverse area of islands of high latitude Scandinavian lakes. Area is debatably the best predictor of biodiversity (Rosenzweig 1995, 1997). If biodiversity is the mediator in the deployment of plant defenses, high latitude and high altitude populations of a species may also reveal resistant plants.

4.2. Latitude: are the temperate and tropical forests so different?

Latitudinal gradients in biodiversity are some of the oldest observations in published ecology (Wallace 1878). The evidence from the *Nothofagus* forests shows a marked divergence from the commonly advocated ideas of latitude and the deployment of herbivore defense. For the lower latitude species, *N. obliqua, N. alessandri* and *N. moorei*, area, or the extent of a plant's geographic range, appeared to have a much greater influence than latitude. For *N. truncata* and *P. radiata* the influence of latitude may be compounding the low area: biodiversity effect.

Tropical forests differ markedly from those of the boreal or temperate regions in that they consist of a vast array of plant species rather than the more mono-specific forests of the higher latitudes. Is it that in such a diverse tropical environment individual plants are 'islands' in their own right, *sensu* Janzen (1968) and Opler (1974), and have to defend themselves despite the great overall diversity of natural enemies? The spatial complexity of the tropical forest may make regulation of herbivores by natural enemies more difficult. Could the bottom-up limitation of herbivores that appears to operate on oceanic and mainland islands be extrapolated to individual trees in the tropics?

Host specialization is generally construed as a result of coevolution with qualitative chemical defenses. Dobzhansky (1950), Pianka (1966) and MacArthur and Wilson (1967) speculated that the greater diversity of herbivores in the tropics resulted from a greater degree of host specialization, which allowed greater species packing. Specialization has been quoted as a feature of tropical invertebrate herbivores (Dyer & Coley 2002), but it is also a feature of New Zealand invertebrates (Dugdale 1975). Is the concentration of secondary plant compounds in the tropics apparent only because previous authors have not considered the influence of area? It is always easier to assay a common representative of a temperate genus or family, than a rare one and bioassay results of temperate species are often extrapolated to include congenerics (Barbosa & Krischik 1987). The results from the study by Miller and Hanson (1989) using *L. dispar* bioassays and tropical plants are no better than temperate New Zealand examples using the same assay.

4.3. Growth-rate and plant defense

Several authors have postulated that resource allocation to defense is greatest in slow-growing plant species in resource-poor environments (Janzen 1974; Coley et al., 1985; Coley 1988; Price 1991; Herms & Mattson 1992). In New Zealand the contrast between the slow growth rate of endemic forest trees and the spectacular growth rate of exotics was recognized by early foresters. Although New Zealand was almost totally covered by forest at the time of European settlement, the slow growth of endemic timber species necessitated a switch to exotic forest species within 100 years to create a sustainable forest industry. That exotics grow better in New Zealand than in their homelands suggests that New Zealand endemics are not constrained by resources. Is their slow growth rate a result of allocation of resources to defense rather than a need for a defense because they grow so slowly? There is little in the way of comparative growth data for *Nothofagus*. However, New Zealand species failed to thrive in the experimental plantings of the genus in UK, whereas the South American species *N. obliqua* (the most palatable species) has potential for plantation forestry there (Tuley 1980). It is also interesting to note that New Zealand commercial selections of *Pinus radiata* grow more rapidly than the original Californian populations, but are considerably more palatable to invertebrate defoliators. The artificial selection for growth appears to have been at the expense of resource allocation to defense.

5. CONCLUSION

The complexity of food web dynamics has restricted the empirical synthesis of the ecological forces that shape species evolution within component communities. The truth of the matter is, that very few insect: plant studies have included tritrophic interactions, other than the effect of plant defense chemistry on the fitness of natural enemies. A plethora of hypotheses has been developed for specific interactions but no over-arching hypothesis, that is empirically testable, suits all. The *IRA* hypothesis is testable and offers a ‘red-shift’ proof that biodiversity determines ecosystem function, without reverting to speciously simplified models or expensive anthropogenic ecotrons. Contrary to accepted wisdom, island forests appear resistant to invading continental defoliators. A marked difference in the deployment of defense against invertebrate herbivores has been demonstrated between congeneric and conspecific plants in essentially identical habitats of differing area. For insular forests there appears to be an inherent strength in the simplicity of island communities. Area is the primary determinant of biodiversity and trophic complexity. The *IRA* interpretation of the interaction between climax forest and defoliators refutes established hypotheses. Instead it posits that for any forest the interaction with defoliators is determined by the relative strengths of top-down and bottom-up forces system, which are mediated by habitat area, and that the habitat area may be oceanic or continental, and of temperate or tropical species.

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F. LIEUTIER

CHAPTER TWO

CHANGING FOREST COMMUNITIES: ROLE OF TREE RESISTANCE TO INSECTS IN INSECT INVASIONS AND TREE INTRODUCTIONS

1. INTRODUCTION

Changes in forest communities are the consequences of two main phenomena: the plantations of exotic tree species in new environments, the commercial and tourist exchanges bringing exotic living organisms, especially insects, in new ecosystems. An important general consequence is the modification of the functioning of the forest ecosystems, and in particular a modification of the tree-insect relationships at the ecosystem level. Tree-insect relationships are changing through insect access to new resources (novel hosts), changes (often indirectly) in quality and quantity of the existing resources (native hosts), and change of the biotic environment (other than host plant) of the insect (new competitors, parasites and predators). The results are modifications of existing tree-herbivore relations (without host shifting), as well as building of new associations (host shifting). In these conditions, the questions are: What are the risks for both native forests and exotic plantations? How can pest management adapt to protect forest resources?

It is well known that tree resistance plays a crucial role in the ecology of forest insects (Larsson, 2002). One can thus expect tree resistance to be highly concerned by the changes in tree-insect relationships, through guiding them or being modified by them and, regarding possible phytosanitary problems resulting from the changes, tree resistance must be taken into account in the adaptation of pest management programs. It is thus essential to appreciate the role that it can play on both the nature of the concerned tree-insect relationships and the extent of their modifications in time and space.

Barbosa and Schaefer (1997) hypothesized that “host plant availability and quality (as a consequence of either inter- or intra-plant species variation) is a major driving force determining the spread and abundance of invading species, subsequent to their invasion”. Although not explicitly formulated, the role of plant resistance (in a broad sense) in colonization and spread of invasive herbivorous species is included in this statement. The authors used the examples of three invasive and one native species of Lymantriidae to justify their hypothesis. The objective of this

T. D. Paine (ed.), Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems, 15–51.

chapter is to illustrate the reality of the above hypothesis with a series of examples representing various aspects of tree resistance to insects. I will however enlarge its field by considering not only the situation of indigenous trees facing insect invasions, but also that of introduced trees (mainly plantations) facing indigenous insects during their establishment (including perpetuation) process in the novel ecosystem, either naturally [naturalization with the meaning of Richardson et al., (2000)] or artificially by man. All this refers to the idea that tree resistance can guide the changes in tree-insect relationships. In fact, another idea is that tree resistance can be modified by the changes in tree-insect relationships or, in other terms, that insect invasions or tree introductions can affect the resistance of indigenous trees to indigenous insects. This could occur through modifications of the environment (biodiversity, competition, microclimate ...) of the indigenous trees after introduction of an exotic tree species, or through damage caused to them by an invasive insect species. I will however not consider this aspect and will thus focus only on the role of tree resistance to insects in the colonization and spread of invasive insects and in the establishment of introduced trees.

In its broad sense, tree resistance can be defined as situations where insect attack or establishment is disfavored because of certain characteristics of the trees. Resistance mechanisms can be passive or active. Active mechanisms of resistance refer to defense. According to Karban and Baldwin (1997), resistance must be distinguished from defense. Resistance is considered from the insect's perspective and refers to the difficulty in establishing in the host. Defense refers to the host facing the insect. With Mattson et al. (1988), it is possible to distinguish the following main mechanisms (or levels) of tree resistance to insects, from approximately the simplest to the most complicated.

- Escape, which can be temporal (in relation to tree phenology), or spatial (in relation to the distribution of trees and different levels of resistance).
- Preformed resistance mechanisms, corresponding to resources investment by the tree in various chemical or physical defensive structures, before insect attack.
- Induced resistance mechanisms, corresponding to resources investment in defense by the tree, only in response to attacks. They can be immediate and localized (often called hypersensitivity) or delayed and systemic.

Environmental factors such as temperature, drought, soil fertility, carbon dioxide concentration, pollution, fires, etc. have been reported to affect tree-insect relationships, through effects on insects, on tree resistance or on both (Mattson & Haack, 1987; Jones & Coleman, 1991; Herms & Mattson, 1992; Larsson, 1989; Tuomi et al., 1991; Koricheva et al., 1998; Lieutier, 2004; among others). These factors are thus important when considering tree resistance in relation to insect invasions or tree introductions, especially in the present context of global change. Nevertheless, they will not be taken into account and the role of global change will not be discussed. Indeed, these aspects could constitute by themselves the matter of a complete chapter and considering them here would be out of the scope of the present chapter.

The chance for a species or population (here an invasive insect or an introduced tree species or population) to get established and to extent in a novel ecosystem always depends on two kinds of factors that interfere simultaneously: the invasiveness of the introduced / exotic / invasive species, and the invasibility of the ecosystem in which the exotic species is introduced. Invasiveness relates to all parameters depending on the newcomers and which contribute to their establishment and spread in their novel environment. Invasibility relates to factors depending on the ecosystem and which contribute to decrease its "resistance" to invasions or introductions and consequently facilitate the establishment and spread of the newcomers. In this chapter, the different types of tree resistance will be presented as factors of both invasiveness and invasibility, by considering the possibilities of insect shifting from its natal to its novel host. The capacity of trees to resist insect attacks can be considered as a negative factor of ecosystem invasibility in the case of insect introductions, and a positive factor of population invasiveness in a situation of tree introduction. The capacity of insects to adapt to tree resistance can be considered as a positive factor of population invasiveness in the first case, and as a negative factor of ecosystem invasibility in the second situation. It must be mentioned also that, in case of insect introduction, generally only one insect species is concerned by a possible shift, whereas in case of tree introduction, several insect species are concerned, especially when the native closely related tree species are numerous.

I will present and illustrate successively the temporal aspect with the role of host phenology, the role of chemical or physical resemblance (including most preformed and induced resistance mechanisms) between the novel and the natal host, and the spatial aspect with the role of the diversity and spatial distribution of tree resistance levels. Then, the capacity of trees to adapt to new insect species, and the capacity of insects to adapt to the resistance of novel host species will be discussed. All these factors can determine the nature of the species (trees or insects) able to succeed in a novel environment, as well as their spreading modalities.

2. PHENOLOGICAL COINCIDENCE

Host phenological synchrony, that is initiating and concluding feeding at the right time, is an important condition for establishment on a new host (Du Merle et al., 1992). This is true for the invading insects that face the local trees, as well as for indigenous insects in their attempts to shift to exotic hosts. At the opposite, escaping grazing by the indigenous insect species may be a condition of success for exotic trees. Several other papers have also underlined the importance of this condition for host shifting or simply for insect surviving on their usual host (Du Merle, 1983, 1988; Barbosa & Schultz, 1987; Tuomi et al., 1989; Quiring, 1992, 1994; Fraser & Lawton, 1994; Niemelä & Mattson, 1996; Carroll & Quiring, 2003; Tikkanen & Julkunnen-Tiito, 2003; Dixon, 2003; among others). For example, for the winter moth *Operophtera brumata* on *Quercus robur* (the preferred host), a small mismatch of 30 degree days between bud burst and hatching of larvae is sufficient to cause 50% decrease of the fitness of the insect, mainly due to increase of condensed tannins in foliage after bud burst (Tikkanen & Julkunnen-Tiito, 2003).

2.1. Role of phenology in the success of shifting

This concerns the establishment of indigenous insects on exotic trees as well as that of introduced insects on local hosts.

Following the introduction of Sitka spruce *Picea sitchensis* in UK, several phyllophagous indigenous species, among which *O. brumata*, have been able to shift from angiosperms to Sitka spruce (Fraser & Lawton, 1994). A comparison between shifting and not shifting species (all from angiosperms and representing taxonomically comparable samples) showed that a large proportion of shifting species overwinter in the egg stage and hatch in spring (Fig. 1). On the contrary, the not-shifting species or even the originally conifer-feeding species overwinter mainly as larvae and thus hatch in summer or autumn. This early emergence certainly helped the corresponding species to shift to spruce. Emerging early is indeed an advantage because it assures a good synchrony with the bud burst, thus allowing the young larvae to feed on a soft host and young foliage free of aromatic compounds, much more edible than the old one.

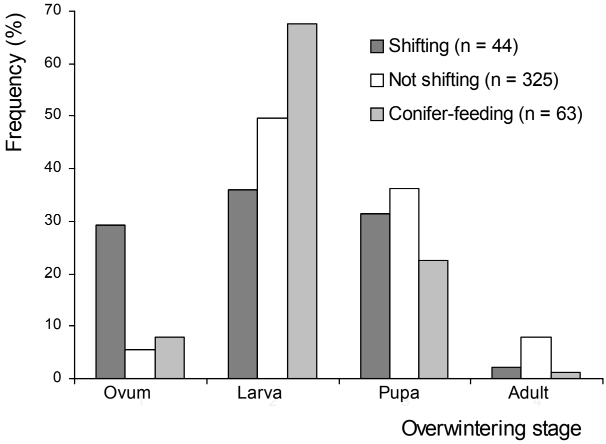

Figure 1. Shift of Lepidoptera from Angiosperms to Sitka spruce: frequency of shifting, not-shifting and originally conifer-feeding species that overwinter at various developmental stages (from Fraser and Lawton, 1994, modified)

In northeastern American forests, the damage on *Tilia americana* by *Thrips calcaratus* introduced from Europe and their extension can be largely explained by the close synchrony between adult emergence from soil and *Tilia* bud opening

(Raffa et al., 1992), especially because this synchrony is better than that of the indigenous and other introduced exotic *Thrips* species (Fig. 2).

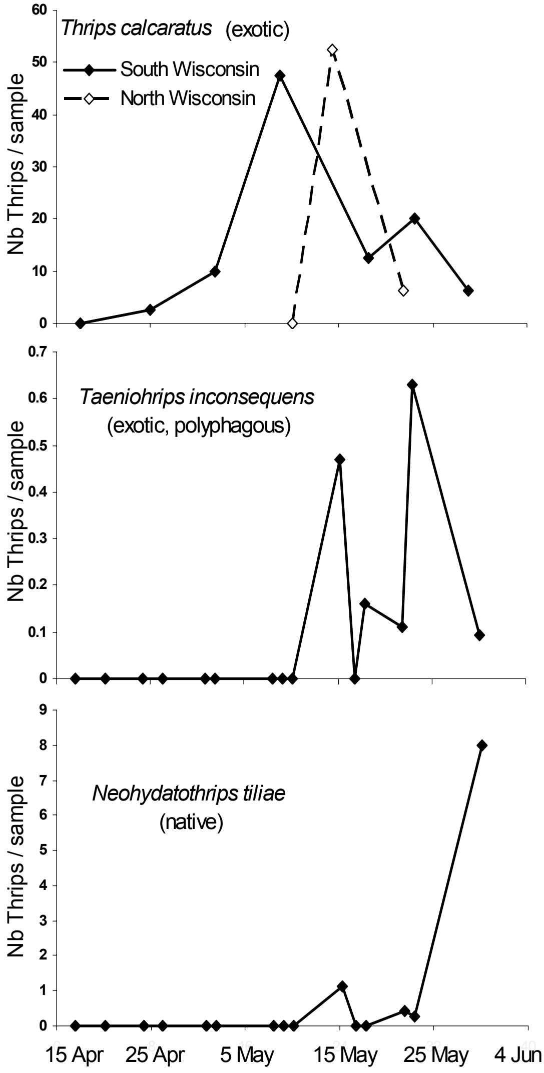

Figure 2. Periods of emergence of different Thrips *species in northeastern American forests (from Raffa et al., 1992, modified*)

Thrips calcaratus in North America emerges even ahead of its synchrony with its host plants in Europe. The fir leaf roller *Choristoneura murinana*, originating from eastern Europe where it develops on *Abies alba*, first developed on the same host species when extending westward and especially in France. Recently however, it adapted to the Atlantic Cedar *Cedrus atlantica* where it causes important damage, while evidencing capacities to adapt to other species of *Abies* and even other conifer genera such as the Douglas fir *Pseudotsuga menziesii* (Du Merle *et al.*, 1992). The reason seems to be large inter-population variations, allowing the insect to cope with various phenologies. The decisive role of the phenological coincidence with its novel host for an insect introduced in a new area has been experimentally demonstrated by Du Merle (1988) in the case of the oak green leafroller, *Tortrix viridana*, in an experiment which can be considered as mimicking the situation of an introduced insect species. The larvae of this insect can feed on any species of oak, and the eggs of the different populations generally hatch in coincidence with bud burst, even for sympatric populations, suggesting an adaptation of these populations to the date of flushing of their host (Du Merle, 1983). This hypothesis has been tested by transferring in autumn females from stands of holly oak (*Quercus ilex*), a lately flushing species, located at an elevation of 700m, to a 40km distant stand of pubescent oak (*Q. pubescens*), an early flushing species, at various elevations from 400m to 1,350m (Du Merle, 1988). The following spring, the survival of young larvae was very low at lower elevations but very high at higher elevations (Fig. 3), in parallel to a later flushing date at high than at low elevation, demonstrating that adaptation to the host corresponds to its flushing date rather to other host characteristics such as food quality.

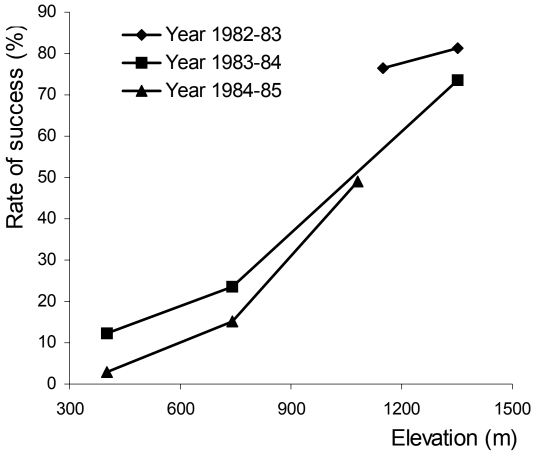

Figure 3. Rate of success of a population of Tortrix. viridana *after transfer from* Quercus ilex *at 700m to* Quercus pubescens *at various elevations (from Du Merle, 1988, modified).*

2.2. Role of phenology in escaping by exotic / native host trees from grazing by indigenous / introduced insects

In the continuation of the above examples, one may wonder if phenological discordance can be a long term strategy that trees can use to escape to damage by a novel insect species.

The possibilities for insects to adapt to asynchronies are generally high and these adaptations are rapid (Dixon, 2003). Moreover, the modifications of the date of bud burst, initially described as tree delayed induced responses to defoliations can be, in several cases, interpreted as tree manipulations by the insects to increase the phenological coincidence at the population level (Tuomi et al., 1989; Quiring & McKinnon, 1999; Carroll & Quiring, 2003). The strategy of changing its phenology for a tree to escape insect attacks is thus very questionable. In fact the most efficient way to avoid large defoliation through using phenology is, for a tree, to have bud-flushing dates ranging on a large continuum and, for a stand, to be composed of trees among which the mean flushing date is as diversified as possible, thus making difficult an adaptation of the defoliating insect. In seed orchards of Siberian larch, *Larix sibirica*, the date of bud-flushing can vary by up to one month on a same twig, hence causing high mortality among young larvae of the larch gall midge, *Dasyneura laricis*, hatching all simultaneously from the eggs deposited on the buds of this twig (Isaev et al., 1988). In southeastern France, the mean date of bud-flushing of *Q. ilex* can vary by more than two months between trees of the same stand in the same season, causing a very varied larval survival rate in the oak green leafroller populations (Du Merle, 1988). Similar observations have been reported for *Q. robur* and *O. brumata*, by Tikkanen & Julkunnen-Tiito in (2003) who mentioned that a large phenological variation within a stand can limit the colonization by dispersing larvae.

All these examples relate to indigenous trees and insects. Possibly, similar situations could occur for introduced trees regarding indigenous insects or for native trees regarding exotic insects. However, in the first situation, the genetic variability of the trees is generally very limited (cf. 5.1). The second situation is more favorable to the trees although insects can adapt rapidly (cf. 6.2).

3. RESEMBLANCE / DISSEMBLANCE BETWEEN CHEMICAL OR PHYSICAL CHARACTERISTICS OF THE STRUCTURES INVOLVED IN RESISTANCE MECHANISMS OF THE NATAL AND THE NOVEL HOSTS

This paragraph gathers preformed and induced resistance, with all their chemical and physical mechanisms. Tree resistance to shift can be related to one or the other phenomenon, depending on the mechanisms interfering in tree-phytophage interactions.

Resemblance / dissemblance have often been cited as important factors in the adaptation of insects to new hosts, while referring to them as taxonomic proximity / relatedness or taxonomic isolation (Strong et al., 1984; Haack & Mattson, 1993; Niemelä & Mattson, 1996; Degomez & Wagner, 2001). However, although the resemblance is most often due to the taxonomic proximity between the original and the new hosts, it is not always the case. Plants can indeed share similar secondary compounds meaningful for insects, without being taxonomically close (Rosenthal & Berenbaum, 1991; Strong et al., 1984). The chemical or physical resemblance between the original and the novel hosts indeed plays a very important role for indigenous insects to shift from local to exotic trees or for exotic insects to adapt to potential hosts in a novel environment. But this must be considered in relation to the insect host range (generalist or specialist).

The general idea, that can be called the “rule of resemblance / dissemblance” is: For a specialist insect, the more similar its natal and its novel hosts are, the less resistant the novel host is to the adaptation of the phytophage. In other words, the differences between the natal and the novel hosts are the resistance to shift. For a generalist insect, differences between natal and novel hosts are not so essential, the resistance to shift is thus weak, but preferences still exist. The effects of insect host range could however be modulated by the degree of intimacy of association (with the meaning given by Mattson et al., 1988) that the insect has with its host tree during its life cycle, a very intimate association (an internal feeder during its entire life cycle) being theoretically able to generate more violent defense reactions than a loose association (an external feeder during only part of its life cycle).

This rule has two corollaries:

- For an introduced tree species facing local insects, and referring to the level of insect damage as a decisive factor for establishment in and colonization of the new environment, resembling the local tree species is not a favorable situation. A large dissemblance from the local trees is, at the opposite, favorable to the establishment of the introduced tree and may even lead it becoming an invasive species.
- For an introduced insect species facing local trees on the contrary, its resemblance with the local insect species (in the sense of having natal hosts similar to the local tree species) favors its establishment and invasion in its novel environment, although it may suffer from inter-specific competition. A large dissemblance (having natal hosts very different from those of the local insects) makes it very difficult for the adaptation of the introduced insect species to the novel environment, except if it can exploit a host under-exploited by the local insect species and resembling its natal host (particular situation of an exotic insect following an exotic tree).

Several exceptions to the above rule exist, as it will be seen below. Nevertheless, it is interesting to note that, as a consequence of these two corollaries, considering the mechanisms of invasions by focusing on tree resistance to insects, leads to conclusions in agreement with the statement by Sakai et al., (2001) that “A species” (here an insect or a tree) “may be invasive either because it shares traits with the resident native species or, alternatively, because it possesses traits different from those of native species and thus can occupy empty niches”.

To examine and discuss the above rule and its corollaries with some details, I will develop firstly some considerations on the effect of insect host range and the role of generalist species in tree colonization. Then, I will present and comment on examples of shifting and not-shifting insect species, in relation to the degree of taxonomic proximity or physical and chemical resemblance between the natal and the novel hosts, while referring to resistance mechanisms. This will allow seeing to what extent the above ideas can explain the success or failure of insect invasions or tree introductions, and how these results can be modulated by the insect host range and the intimacy of the insect-tree association.

3.1. Effect of insect host range and role of generalist species in tree colonization

Although they can eat on a large array of plant genera and families, even the generalists have preferences, which are most often visible at the plant genus level. For example, oaks are the preferred hosts of *Lymantria dispar* whereas apple and pear trees are those of *Euproctis chrysorrhea* (Barbosa, 1997) and poplars seem to be those of the Asian longhorn beetle *Anoplophora glabripennis* (Lingafelter & Hoebeke, 2002), although these species can develop on a large range of tree species. A wide host range is always a considerable advantage to adapt to a novel host, and all examples regarding the role of insect host range lead to the same conclusion that polyphagous insects are favored when shifting.

Generalists are the first colonizers of newly introduced exotic plants (Andow & Imura, 1994; Fraser & Lawton, 1994; among others). They can then evolve slowly towards a specialization to adapt on their novel host. However, if the exotic plant has closely related plant species in its area of introduction, native specialists can also slightly extend their host range to adapt rapidly to the new host (cf. below). Similarly, the polyphagy of generalist insects contributes largely to their rapid extension after they have been introduced in new areas, as for *L. dispar* and *A. glabripennis*.

Exceptions to the "rule of resemblance / dissemblance" are most often due to generalist insect species. In UK, several species of Lepidoptera have shifted from local angiosperms to the introduced conifers, especially *Picea sitchensis*. A comparison between shifting and control species (all from angiosperms and representing taxonomically comparable samples) revealed that most of the shifting species were generalists (Fraser & Lawton, 1994) (Fig. 4). In Texas and Louisiana, the indigenous polyphagous bug *Leptoglossus zonatus* has adapted at high densities to the fruits of the introduced Chinese tallow tree *Sapium sabiferum*, although no close relative was present (Johnson & Allain, 1998). Among all European insect species introduced to North America, only those that are oligophagous or polyphagous have been able to colonize tree genera that are not naturally

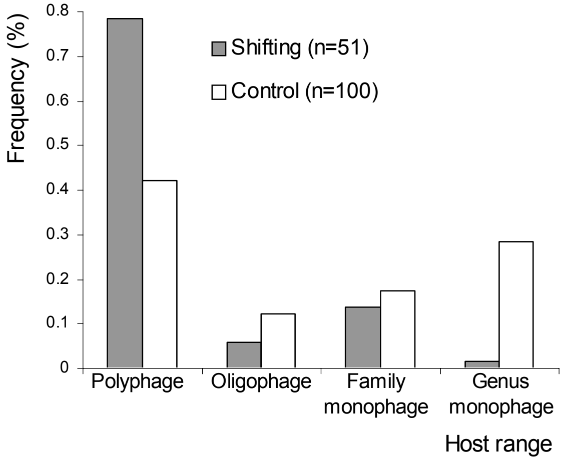

Figure 4. Shift of Lepidoptera from angiosperms to Sitka spruce: Frequency of species with various diet breadths in shifting and control (random sample) species (from Fraser & Lawton, 1994, modified).

represented in Europe, such as *Carya*, *Chamecyparis*, *Pseudotsuga* and *Tsuga* (Niemelä & Mattson, 1996). It has also been demonstrated that the gypsy moth *L. dispar* is able to complete its development on at least 26 Australasian native species, and that at least five of them are as good as the preferred hosts (oaks) for larval performance, although the insect has never been naturally in contact with them (Matsuki et al., 2001). These observations make the gypsy moth a serious threat for Australia. In Papua New Guinea where the species *Piper aduncum* and *P. umbellatum* were probably introduced between 100 and 150 years ago, the probability for an alien *Piper* to be colonized by an indigenous caterpillar increases from 3% for a caterpillar species feeding on a single plant family to 92% when the host range exceeds 10 plant families, although the number of colonizing species decreases (Novotny et al., 2003) (Fig. 5). Consequently, the chance to shift is proportional to the diet breadth and most colonizing caterpillar species are polyphagous.

It may be also significant that all insect species in these examples but *Anoplophora* are external feeders which have only loose associations with their hosts.

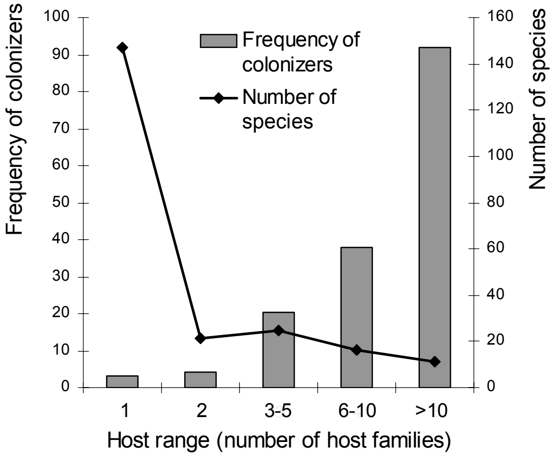

Figure 5. Frequency and number of colonizing Lepidoptera species on alien Piper *species, in relation to the caterpillar host range (from Novotny et al., 2003, modified).*

3.2. Shifts between taxonomically and chemically / physically closely related tree species

There is a multitude of examples of shifts involving closely related tree species. To realize this, it is enough to remind that, when introduced to North America from Europe, monophagous and many oligophagous insect species have been able to colonize only the same genera as those they use in Europe, mainly *Pinus*, *Picea*, *Betula*, *Quercus*, *Ulmus*, *Acer*, and *Populus* (Niemelä & Mattson, 1996).

In such cases (congeneric tree species generally), the novel and the natal hosts most often have very similar food quality and only slight differences in the mechanisms of resistance, making a shift very easy, which is in agreement with the rule of resemblance / dissemblance. However, because of a long coevolutionary history, host trees have often been able to develop very efficient resistance mechanisms against their usual insects, especially those with a narrow host range, while the novel hosts have not. They have also developed more efficient resistance mechanisms against the local than the exotic insects. One can thus expect that, when considering specialized insects shifting between closely related hosts, the slight differences in host mechanisms of resistance favor the shifting insects. Consequently, in case of tree introductions, the performances of specialized indigenous insects should be higher on the alien than on the local hosts. Similarly, in case of insect introductions, the performances of the specialized invaders should be higher on their novel than on their natal hosts. As we shall see in the below examples, such situations are by far the most frequent ones. In some situations, favoring the performances of the shifting insect could even lead it to better succeed in its novel host than the usual insects of this host do, and finally to displace them. All these considerations suggest that the rule of resemblance / dissemblance should be modulated.

The above suppositions are based on the existence of a free choice by the insect, a situation not always realized, especially in the case of an insect introduction or when an introduced tree species is planted over large areas. The exotic insect in the first situation and the local insect in the second are submitted to high selection pressures for adaptation to the resistance of the novel hosts [encountered-frequency hypothesis (Strong et al., 1984)]. The result is certainly a strengthening of the above tendencies. A lack of natural enemies on the novel host has also been demonstrated in some cases to be able to explain better insect performances on this host, and can thus also complete the above mechanisms involving tree resistance.

It must be also noticed that, in case of insect introduction as well as in case of tree introduction, it cannot be concluded from the above considerations that an insect shifting to a novel host will cause damage to it. Indeed, although increasing damage means better performance, a better performance does not necessarily mean damage. It is true that the literature reports mainly on situations with damage, but it does not mean that damage is the rule. The only rule is that, in a situation of close taxonomic proximity between the two hosts, the shifting insects are favored and their performances are improved in the novel host, when compared to those in their natal host. In the examples below, I present cases where the performances of insects with narrow host range have been compared on both their novel and their natal trees.

Several examples relate to insects introduced in new areas. The green spruce aphid, *Elatobium abietinum*, is indigenous from Northern and Central Europe. It has followed Norway spruce when this tree has been planted in Western Europe, and has then shifted to the introduced Sitka spruce on which it causes severe damage (Speight & Wainhouse, 1989). In tests of preferences carried out on different species of spruce in UK, Sitka spruce belongs to the preferred species (Nichols, 1987). After its introduction in southwestern USA, the green spruce aphid has also become an invasive pest which causes considerable damage on *Picea engelmanni* and *Picea pungens* (Lynch, 2004). Similarly, the bark beetle *Dendroctonus micans*, certainly originating from the spruce forests of Siberia, has colonized all spruce stands during its extension westward through Eurasia and Western Europe (Grégoire, 1988) and has been particularly damaging for the introduced Sitka spruce (D. Piou, personal communication). The aphid *Pineus boerneri* and the scale *Matsuccocus resinosae*, both introduced from Japan to North America, have better survival and higher fecundity on their adoptive (*Pinus resinosa*) than on their natal (*Pinus thunbergiana*) hosts, although both hosts belong to the same botanical subsection of the genus *Pinus* (McClure, 1990) (Fig. 6). The involved mechanisms are suspected to be between-host differences in bark structure and chemistry (McClure, 1985, 1990), both of them relevant to the constitutive resistance.

Many examples also concern introduced trees. In Northern Europe, the native willow species *Salix cinerea* responds to defoliations by the native leaf beetle *Phratora vulgatissima*, by producing new leaves with an increased density of trichomes (Dalin & Björkman, 2003) (Fig. 7). As a result of this induced reaction, the new larval generation has a more dispersed feeding behavior (as attested by the higher number of feeding holes) and consumes a lower quantity of foliage. Finally, damage is much lower, although there is no effect on larval growth (Fig. 7). The introduced *Salix viminalis* responds the same way as the native *Salix* but the trichomes are longer and thinner and can be removed by the larvae when eating at their base (Dalin et al., 2004). There is consequently no decrease in leaf consumption by the new generation and thus no decrease of damage (Fig. 7). It is therefore a difference in the efficiency of the induced response which makes the

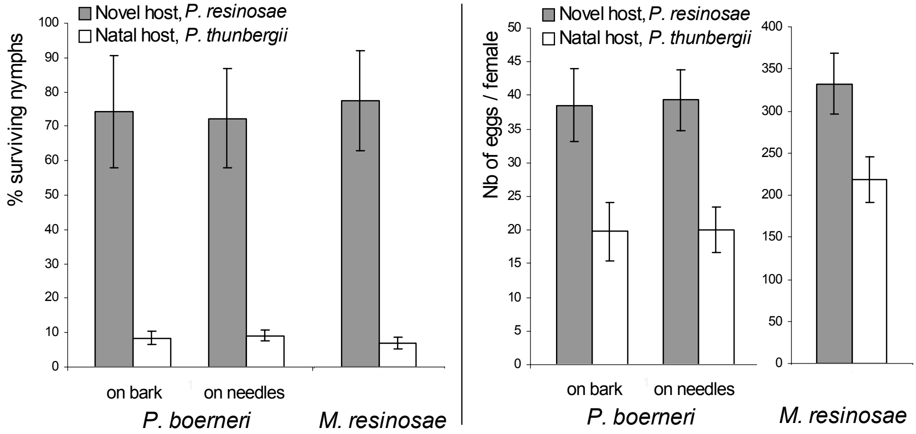

Figure 6. Survivorship and fecundity of Pineus boerneri *and* Matsucoccus resinosae *on their adoptive and natal hosts in North America (adapted from McClure, 1990).*

performances of the insect higher on its novel than on its natal hosts. The fact that *P. contorta*, after its introduction to Europe, exhibited a higher susceptibility than local pines to many indigenous insects, such as bark beetles (Langström et al., 1995), *Rhyacionia buoliana* (Esbjerg & Feilberg, 1971), cone and seed insects (Roques et al., 2002a, 2002b) and others, may also be interpreted by less efficient resistance mechanisms. The high number of such cases for this pine can probably be explained by the presence of several pine species in the area of introduction. A similar case concerns the higher susceptibility of the exotic *Larix leptolepis* than the indigenous *Larix europaea* to the larch case-bearer *Coleophora laricella* (Sindelar & Hochmut, 1972). In Florida, the survivorship of leaf-mining insects is better on the introduced Fagaceae *Castanea crenata* and *Quercus acutissima* than on the native one *Q. nigra* (Auerbach & Simberloff, 1988). There is a lower parasitism rate on *C. crenata* than on *Q. nigra*, but the foliage of the former has also a better food quality for the miners. Moreover, *Q. acutissima*, with more local native congeners than *C. crenata*, supports also a higher number of mining species. In Turkey, the indigenous scale *Matsucoccus josephi* does not cause damage to its natural host *Pinus brutia*, while it does to *P. halepensis*, a taxonomically closely related species, suggesting that the later is not a relict there but was introduced by man (Mendel, 1992).

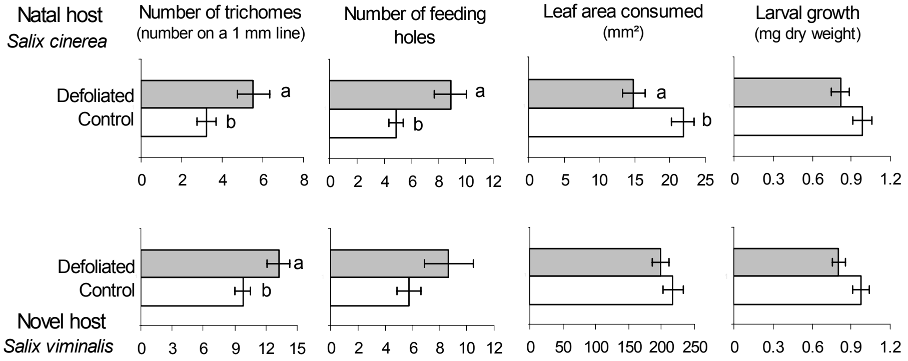

Figure 7. Compared performances of Phratora vulgatissima *on its novel introduced host* (Salix viminalis) *and its local natal host* (Salix cinerea), *in relation to tree response to defoliations. Different letters indicate significant differences. (From Dalin & Björkman, 2003; Dalin et al., 2004; modified).*

Favoring the shifting insect is thus very frequent when considering shifts between tree species belonging to the same genus. However, similar differences between the susceptibility of the novel and that of the natal tree might also exist at the intra-specific level. The scale *Matsucoccus feytaudi* introduced from Spain to southeastern France found there another population of its usual host (*Pinus pinaster*). This led to a rapid spreading of the insect and to considerable damage to pine stands (Schvester, 1971). In Finland, *Betula tortuosa* trees, originating from a locality distant from 100km, were planted together with local birches. The fecundity of *Epirrita autumnata* was twice higher on the introduced trees than on the native ones (Haukioja et al., 1988). However, although the inability of the novel host to produce efficient defensive mechanisms may be involved, in both situations an alternative explanation has been proposed: lack of competitors for *M. feytaudi* (Schvester, 1971), and unnatural growing conditions for the introduced birches (Haukioja et al., 1988). An interesting example involving tree defense concerns the performances of the indigenous polyphagous grasshopper *Melanoplus angustipennis* on *Sapium sebiferum* introduced from Asia to North America in the late 1700s (Siemann & Rogers, 2003). The growth rate of the grasshopper is higher and its foliage consumption lower on seedlings recently coming from China than on seedlings coming from the introduction area and playing there the role of indigenous host. A physiological explanation has been proposed in that case. A modification of the strategy of allocation of the photosynthates by the plant, abandoning a pioneer behavior and favoring defense over growth and reproduction, seem to have occurred after its introduction (Siemann & Rogers, 2003) (cf. also 5.3).

All the above examples, mostly involving specialist insects, thus confirm that the performances of the shifting insect are always better on the novel than on the natal host, when these hosts are closely related.

In addition, in such situations of closely related hosts, the shifting insect has co-evolved with a host physically and chemically close to its novel host and has thus acquired adaptations close to that of the insects already present on this host. It could thus much better compete with them than in the case of an important host shift. A probability even exists that its adaptation to the resistance of the target hosts be better than that of the insects feeding on those hosts. As a result, there are cases where a native insect has been displaced by an invader. Similarly, cases are conceivable where a local insect could displace an exotic insect introduced together with its native host. Following *Cupressus sempervirens* during its extension westwards in the Mediterranean basin, the cone bug *Orsillus maculatus* has displaced from its usual hosts the western indigenous species *O. depressus* initially adapted to the small cones of Cupressaceae, because of its longer rostrum better adapted to the large cones of *C. sempervirens* (Rouault, 2002). The seed chalcid *Megastigmus rafni*, initially living on various species of *Abies* in North America, has adapted to *A. alba* in Europe where it seems to displace the native species *Megastigmus suspectus*, at least in southern and eastern France (Fabre et al., 2004). The reason for this displacement is not known but the longer ovipositor of *M. rafni*, allowing it to better cope with cone thickness than *M. suspectus*, might play a role (Auger, personal communication).

3.3. Shifts between taxonomically and chemically / physically distant tree species

It is generally the case of shifts between different plant families or much bigger taxonomic distances, thus constituting exceptions to the rule of resemblance / dissemblance. It is in fact a very common situation for generalist insect species, which has been presented above (cf. 3.1), but in some cases, it exists with specialist insects. In the below examples, generalists will be cited when helping in underlying aspects that have not been discussed previously or in showing interactions between host resemblance and other factors.

Before extending to Western Europe and causing damage to *Cedrus atlantica*, *Choristoneura murinana* has always been considered as a monophagous species on *Abies alba*. The recent extension of its host range (cf. 2.1) demonstrates polyphagous tendencies (Du Merle et al., 1992). Large possibilities of adaptation to host phenologies have been observed, but the food quality of the hosts also interferes. However, all three genera *Abies*, *Cedrus* and *Pseudotsuga* belong to the same botanical family (Abietaceae). In Papua New Guinea, most caterpillar species colonizing the two introduced species of *Piper* are polyphagous (cf. 3.1) but, in addition, about 70% of them come from another plant family than that to which the genus *Piper* belongs (Fig. 8), although several indigenous *Piper* species and especially *Piper macropiper* exist in the area of introduction (Novotny et al., 2003). To resist attacks by the indigenous caterpillar species, the native *Piper* species may have developed mechanisms that the exotic species could not develop in the absence of selective pressure. Considering this, it is interesting to note that the number of caterpillar species developing on the local *Piper macropiper* is two to three times lower than on the introduced *Piper* species (Novotny et al., 2003).

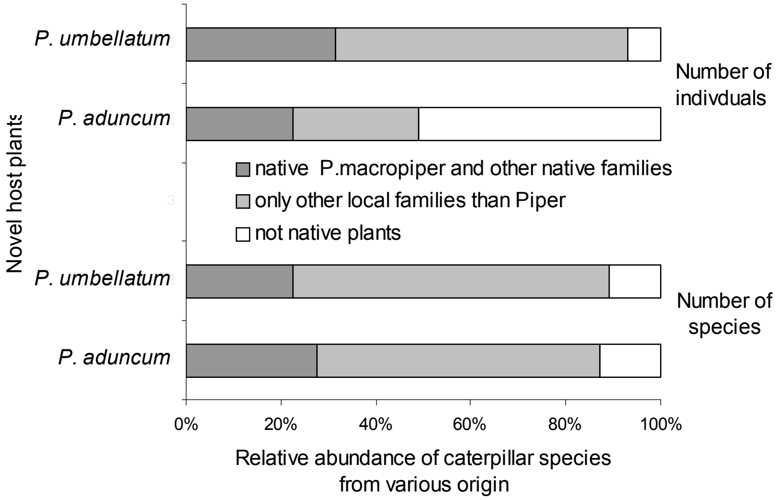

Figure 8. Abundance of caterpillars from various origins that have shifted to two introduced species of Piper *(from Novotny et al., 2003, modified).*

In UK, *O. brumata* is one of the lepidopteran species that have shifted from angiosperms to Sitka spruce, and different populations of this insect can now be distinguished in relation to the food quality of their host plant. The individuals of the oak (native host) population have a bigger adult size and their larval survival is much affected negatively when they are reared on spruce (Vanbergen et al., 2003). However, each of these populations can cause outbreaks by using its own host only

(Day & Leather, 1997). In these conditions, one can question why such an adaptation was possible with so distant plant species and so bad survival after artificial transfer. The answer involves three types of resistance mechanisms. The first step refers to the high selective pressure due to the high frequency and abundance of spruce, in agreement with the encounter-frequency hypothesis (Strong et al., 1984) (low spatial discordance, cf. 4). Then, the variations in host chemistry in relation to phenology interfere (Vanbergen et al., 2003). In oak leaves, there is a rapid decrease of nitrogen concentration after bud opening, simultaneous to an increase in phenol concentration (Fig. 9), thus decreasing rapidly the food quality. This creates, in the insect populations of oak, a high selective pressure for a synchrony between egg hatching and bud opening. In spruce, the decrease in nitrogen is less rapid and phenol concentration decreases instead of increasing (Fig. 9), making the selective pressure for synchrony much lower and thus facilitating the shift. *Operophtera brumata* is a generalist but several Lepidoptera species, specialists at the plant genus or family level, have also shifted from angiosperms to conifers (Fig. 4). It is conceivable that the abundance of spruce has triggered mechanisms comparable to those described above for the generalist species.

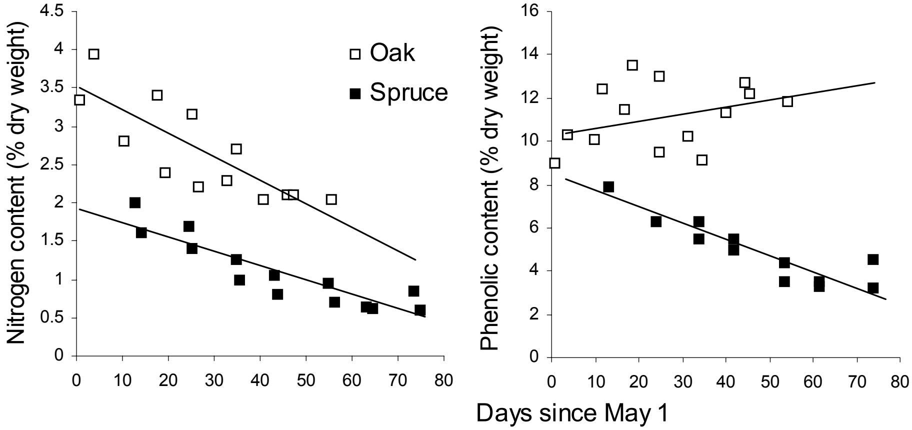

Figure 9. Concentration of nitrogen and phenolic compounds in the leaves of oak and Sitka spruce over time (from Venbergen et al., 2003, modified).

It is worth mentioning that, apparently in opposition to the case of two closely related tree species (cf. above 3.2), a shift between two distant tree species (involving mainly generalist species) does not seem to always exhibit better performances on the novel than on the natal host. The longhorn beetle *A. glabripennis*, after its introduction into North America and in agreement with the general behavior of specialists on closely related host trees, develops better on novel hosts (*Betula nigra* and *Platanus* x *acerifolia*) which do not exist in its native area, than on natal hosts (*Koelreuteria paniculata* and *Prunus calleryana*) existing in that area (Morewood et al., 2004). The mechanisms involved could be related to the abundance of sap flow and the tree chemical composition. However, the better performances of *O. brumata* on oak than on spruce (cf. above) relate to the opposite tendency.

3.4. Limited shifts between taxonomically and chemically / physically distant tree species

There are many examples of this situation in agreement with the "rule of resemblance / dissemblance", for both introduced trees and invasive insects.

The introduction of the Douglas fir *P. menziesii* from northwestern US to Europe where no native *Pseudotsuga* exists was not followed by significant damage due to indigenous insects even in the regions where the plantations cover large areas. The only problems are caused by *Megastigmus spermotrophus*, an exotic seed chalcid introduced from the native area of Douglas fir within the seeds of its host (Roques & Skrzypczynska, 2003). A similar example is given with *Cedrus atlantica* introduced from Morocco to France where no native *Cedrus* exists. Significant damage is not caused by indigenous insects, but mainly by exotic insects originating from the area of origin of the tree or from regions where the genus *Cedrus* is natural. These are the cases for the sap-suckers *Cinara cedri* and *Cedrobium laportei*, the defoliator *Epinotia cedricida* and the seed chalcid *M. pinsapinis*, all from North Africa (Fabre, 1989; Fabre et al., 1999), and more recently that of the seed chalcid *M. schimitscheki*, initially on *C. libani* and introduced from Lebanon, which have even supplanted *M. pinsapinis* (Fabre et al., 2004). Inversely, none of the exotic pests introduced together with *Pseudotsuga* or *Cedrus* have been able to shift to the local conifers species, except *M. schimitscheki* on fir but to a very limited extent (Fabre et al., 1999; 2004). *Eucalyptus* species have been introduced from Australia in many different places in the world. Their particular taxonomic situation and chemical composition certainly explain why they have almost never been attacked by indigenous insects in their area of introduction, but always by species such as *Gonipterus scutellatus* or *Phoracantha* spp. which have followed them from Australia. Inversely, these latter pests have never adapted to the local trees species.

Following the introduction of *Pinus pinaster*, *P. pinea* and *P. halepensis* from Mediterranean Europe to South Africa, where no close relative conifer existed (the taxonomically closest conifer was a Cupressaceae from the genus *Widdingtonia*), these species and especially *P. pinaster* succeeded so well and spread so fast that this latter became rapidly invasive. It is thought that the lack of indigenous insect species able to shift to the introduced pines has certainly played a role in the success of *P. pinaster*, leaving its multiplication potentialities without efficient regulation factors (Roques et al., 2002a, 2002b). Experiments are presently developed aiming at introducing insects affecting seed production in the area of origin, such as the cone weevil *Pissodes validirostris*, in order to limit the extent of this pine.

More generally, according to Ridley et al. (2000), the important floristic divergence between the continents of the Southern hemisphere and those of the Northern hemisphere is the reason why major pest invasions occur only according to east-west movements and never from one hemisphere to another.

In the above examples, since few local insect species adapted to the introduced tree species, it is clear that such limited shifts between distant tree species are very frequent, not only for monophagous but also for polyphagous insect species. This can be explained by various hypotheses. Certainly in such situations with large taxonomic between-host distances, the chemical or physical structures of the potential novel hosts, as proposed in the above examples, can be efficient barriers to shifting because they present novel defenses to which the potential aggressors are not adapted (Lankau et al., 2004). Moreover, considering insect introductions, the local insects that already exploit the native hosts are certainly better physiologically and biochemically adapted to its resistance mechanisms than invaders coming from a taxonomically distant host, and are thus advantaged competitively. As a consequence, some time is needed for the candidates to shift, be they local insects facing introduced tree species or invaders facing local hosts, to develop new adaptations (cf. 6.1). However, phenomena other than novel defenses can interfere. The barrier can be behavioral rather than physical or biochemical. In such a situation, the novel host fits in with the nutritional requirement of the insect and has no dissuasive structure, but the insect lacks the adaptations necessary to recognize the plant as a suitable host. The plant is simply nonapparent for the insect (behavioral constraint), as demonstrated by Lankau et al. (2004) in the case of *Sapium sebiferum* regarding its resistance to Acrididae in southern US. Another limiting mechanism to shift could be the spatial discordance, even on a local and small scale, between the novel and the natal host.

3.5. Limited shifts between taxonomically and chemically / physically closely related tree species

This situation occurs at the congeneric level and is in some way the complement to the situation in 3.2. I consider here only species that do not shift to the novel hosts, apparently in disagreement with the rule of resemblance / dissemblance. Although less frequently reported in the literature than for taxonomically distant host species and polyphagous herbivores (cf. above), such cases are very frequent. Indeed, even in case of host species belonging to the same genus, a number of introduced insect species do not shift to a potential novel host, and not all indigenous insect species feeding on a host shift onto an introduced tree species. The reasons for these lacks of shift are often not very clear. *A priori*, the same hypotheses as for taxonomically distant plant species can be considered and, regarding resistance phenomena, there is the possibility that the resistance of the novel host to the local insect be higher than that of the natal host (novel defense hypothesis). I only mention below two examples illustrating different possibilities and suggesting or not an interference of host resistance.

About 100 years ago, *Robinia pseudoacacia* was introduced from eastern US to Arizona where *R. neomexicana* is native, and the two species are presently growing within the same range. The study of the arthropod diversity revealed 251 arthropod species on the native plant, among which only 12 were also present on the exotic plant although this later had been colonized by 174 arthropod species (Degomez & Wagner, 2001) (Fig. 10).

It means that more than 95% did not adapt to the conspecific host, in spite of the elapsed time. The number of occasional species (found only one to three times) was about 90 to 140 in the indigenous species (60 to 90 in the exotic). Removing them from the total thus does not change the conclusion. This low level of shift from the native to the exotic species may be partly explained by the 9.7 times larger area occupied by the native species (Degomez & Wagner, 2001), thus fitting with the encounter-frequency hypothesis (Strong et al., 1984). Host resistance could thus interfere as spatial discordance, but the novel defense hypothesis may also be concerned.

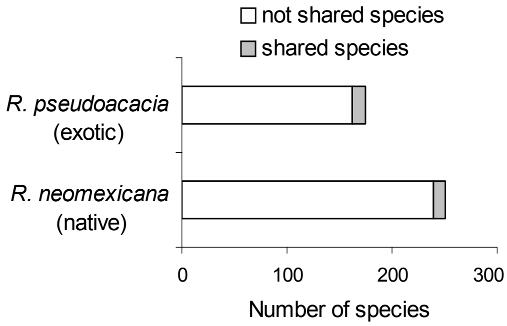

Figure 10. Number of insect species in Robinia pseudoacacia *and* Robinia neomexicana *in Arizona (from Degomez and Wagner, 2001, modified*

Piper aduncum and *P. umbellatum*, exotic species introduced to Papua New Guinea have been presented above (3.1 and 3.3). They are eaten by respectively 9 and 10 caterpillar species (total load 32 and 45 respectively) also present on the native species *P. macropiper* (Fig. 8) of which the total load is 12 species (Novotny *et al.*, 2003). This may seem quite a high proportion of species shifting from the indigenous plants to the introduced ones, compared to the previous example, but all of these shifting species are polyphagous and develop also on several other native families. No native caterpillar species feeding on *P. macropiper* but not on other native host families colonized the exotic *Piper*. It is possible that the resistance of the alien *Piper* to the caterpillars specialized on *P. macropiper* is higher than that of their original host (novel defenses). Unfortunately, no information is available on the chemistry of these three plants. However, the observation may also be explained by both a behavioral constraint and a spatial discordance. Indeed, *P. macropiper* is a climber growing in secondary and primary forests, whereas *P. aduncum* is a small tree of early stages of rainforest succession, and *P. umbellatum* is a sub-shrub of open secondary vegetation (Novotny et al., 2003).

3.6. Conclusions about the "rule of resemblance / dissemblance"

The rule is often verified but it also suffers from many exceptions, making all situations possible, in interference with the insect host range. Moreover, even in the case of specialized insects and hypothesizing that the phenological coincidence is always realized, the rule of resemblance / dissemblance must be modulated to take into account possible coevolutionary processes. Otherwise, it is not the only possible explanation of a shift from one host tree to another. Factors such as behavioral constraints, novel defenses, abundance and frequency of encounters with the novel host, and relative distribution of the two hosts have been mentioned. The two latter factors also relate to the trees' resistance mechanisms (coincidence / discordance on the spatial level) and are presented in the next section.

4. DIVERSITY AND SPATIAL DISTRIBUTION OF TREE RESISTANCE LEVELS

It can be the case of an exotic insect coping with the distribution of potential novel host trees, or the type of distribution of an exotic tree species regarding possible shifts of indigenous insects. Examples have already been discussed above to explain exceptions to the rule of resemblance / dissemblance. Such discordances can affect the nature of the species (trees or insects) accepted by the ecosystem, but mainly rather the modalities of colonization and spread of insects on their novel hosts, these factors varying also depend on the variations of the distribution of long term resistances.

4.1. General considerations

Host tree diversity and its spatial distribution must be considered at two levels:

- interspecific (botanical) diversity and host plant distribution, linked to the problem of insect specificity (generalist or specialist insects). In this case, the role of the botanical diversity concerns only the insect introductions, but the role of spatial distribution of host trees applies to both insect and tree introductions.
- intraspecific diversity and structure of tree populations. This relates to insect as well as tree introductions, although the introduced trees have frequently a low genetic diversity (selected provenances).

In each level, the effects on insects take place on two time scales:

- Short term effects, mainly on insect moving. Variations of tree chemistry at the regional level are often natural barriers to monophagous insects, while monospecific plantations of the right species play an opposite role. Indeed, although there is a higher probability that a suitable host be present in a diversified than in a monospecific stand, there are also higher difficulties to localize it, slowing down the colonization and spread of the insect. Inversely, polyphagous insects are *a priori* not affected by stand diversity or monospecificity, be the establishment or the colonization concerned. Their broad host range can even facilitate colonization (Simberloff, 1989; Andow & Imura, 1994). In some cases however, heterogeneity can have indirect nonfavorable effects even for generalists. Fragmentation is however disastrous for all.

- Long term effects, related to possible genetic adaptations. Both specialist and generalist insects are concerned, and effects depend on how the diversity of the resistance is spatially organized. If the different resistance levels are well separated on the regional scale (frequent case when their diversity is related to tree interspecific differences), an individualization of insect populations each adapted to a given level of resistance is conceivable. If the different resistance levels are mixed and much diversified with many intermediate levels (frequent case of tree intraspecific variations, except for plantations of selected provenances), insect adaptations to resistance are more difficult.

I present below examples illustrating these different situations and their consequences for the colonization and spread of introduced insects in a novel ecosystem or establishment of indigenous insects on exotic trees.

4.2. Interspecific diversity and species distribution

The geographical range and abundance of tree species are the first characteristics of their distribution considered as parameters of insect adaptation. In general, the insect species load of a plant species is positively related to the size of the plant geographical range and its abundance within that range (Southwood, 1960; Strong, 1974; Opler, 1974; Strong et al., 1977; Neuvonen & Niemelä, 1981; Kennedy & Southwood, 1984, Leather, 1986). This relation also applies for forest insect species adapted to exotic tree species. In UK, the number of non-conifer feeding Lepidoptera that have shifted to exotic conifer species is directly related to the area planted with the latter (Fraser, 1997) (Fig. 11). Several examples have been presented in section 3, regarding the role of tree abundance in the frequency of contacts with insects and thus, at least partly, the possibility of shift of native insects or the adaptation of introduced insects.

Botanical diversity and spatial distribution of the host is, of course, particularly important for the specialist insects. The monophagy of *Leucomia salicis* associated with the large distribution and abundance of poplars greatly favored its spread immediately after its introduction in North America (Barbosa & Schaefer, 1997). The fragmented distribution of the Douglas fir in Europe interferes greatly with the dispersal ability of the specific seed chalcid *M. spermotrophus*, and only plantations located at a distance smaller than 5km from each other can contribute significantly to the dispersion (Jarry et al., 1997). On the contrary, fragmentation of the forest may favor the establishment of species, such as aphids, that have a life cycle alternating a woody and an herbaceous plant. In case of insects such as cynipids, which need two host trees for complete development, the relative distribution and abundance of these two hosts, in addition to the area occupied by each of them, can affect the rapidity of spread. In Britain, the oak gall wasps *Andricus corruptrix*, *A. kollari* and *A. lignicola* are exotic and their life cycle alternates between a secondary host, *Quercus petreae* or *Q. robur* (both native), supporting agamic generations, and a main host *Q. cerris* (introduced) supporting sexual generations.

Their invasion is thus expected to spread more rapidly through regions where the introduced oak species are as abundant as the native ones (Walker et al., 2002). The well separated phenology of different oak species leading to the differentiation of different populations of *T. viridana* has already been mentioned (2.1) (Du Merle, 1983, 1988).

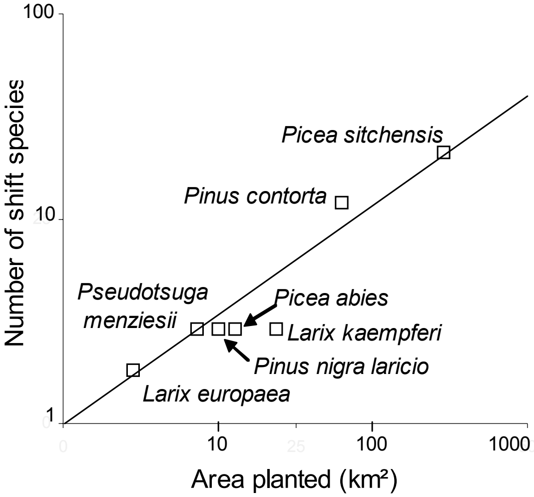

Figure 11. Number of Lepidoptera species that have shifted to various exotic conifers in UK, in relation to the area planted (from Fraser,1997, modified).

However, generalist insects can also be concerned in certain situations and the effect of the botanical heterogeneity can then be more subtle. In Finland, different populations of *O. brumata* have adapted each to a particular host tree species (*Prunus padus*, *Quercus robur*, *Populus tremula* and *Salix phylicifolia*) but, when reared on *P. padus* and *Q. robur*, growth and development of the larvae are better on the former than on the latter, whatever the original host of the tested populations (Tikkanen and Niemelä, 2000). Nevertheless, the protandry of hatching of adults was much disturbed on an alternative host, either by increasing or decreasing it, while it was normal when larvae were grown on their original hosts (Fig. 12). It has consequently been suggested that, in a heterogeneous environment, this disturbing effect of alternative hosts may decrease the population density and growth rate compared to a homogeneous environment (Tikkanen & Niemelä, 2000). On another scale, the lower diversity in both plant and age composition in the European than in the North American forests, together with a higher fragmentation and a smaller cover, have been suggested to be partly responsible for the fact that much less forest insect species (specialists and generalists as well) have been successfully introduced from North America to Europe (34) than in the opposite direction (about 300) (Niemelä & Mattson, 1996).

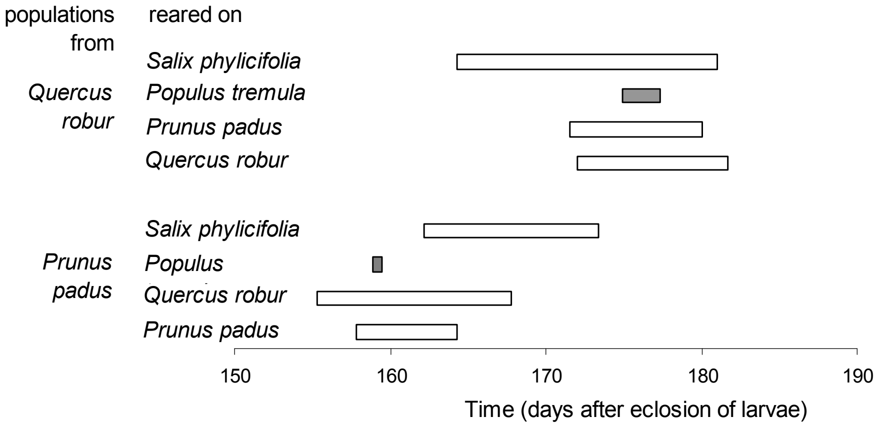

Figure 12. Delays between hatching dates of males and females of Operophtera brumata *populations originating from* Quercus robur *and* Prunus padus *and reared on various hosts. White rectangles indicate protandry, black rectangles indicate progeny. (from Tikkanen & Niemelä, 2000, modified).*

4.3. Intraspecific diversity and structuration of tree populations

Examples of intraspecific diversity regarding the resistance of forest trees to insects and examples of variability in the response of insects facing different individual trees / clones of a same tree species / provenance are numerous. However, many concern between-provenance or between-clone comparisons in nurseries, but not comparisons between trees growing in forests. Nevertheless, there are in forests several examples of intraspecific variability in tree resistance to insects, for which it has been observed that this diversity can determine the spatial distribution of insects, the modalities of their dispersion and / or the dynamics of their populations. These examples do not relate to invasive insect species or tree introductions but they demonstrate that natural intraspecific variations in the distribution of tree quality can have consequences on the spatial ecology of forest insects. It is reasonable to think that similar mechanisms can occur in the spread of invasive insect species or in the colonization of an introduced tree species by indigenous insect species. Several examples of spatial variations have been given in 2.2 for the phenology of bud flushing. I thus present below examples not related to tree phenology.

In Pennsylvania, the concentrations of various foliar phenolics vary considerably among individual trees in a same stand composed of various natural hybrids between *Quercus rubra* and *Q. velutina* (Hunter, 1997). Counting insect densities on leaves of different trees revealed that gall densities and leaf-miner densities increase with increasing astringency and proanthocyanidin concentrations, while leaf-chewer densities decrease with increasing gallotannin concentrations. In southwestern France, the distribution of the scale *Matsucoccus feytaudi* in stands of *Pinus pinaster* is inversely related to bark thickness, whereas that of *Dioryctria sylvestrella* depends on the terpene content of the sapwood (Kleinhentz et al. 1999; Jactel et al., 2002) Similarly, variations in the susceptibility of *P. menziesii* to attacks by *Choristoneura occidentalis* and larval performances of the insect could depend on differences in terpene content in the foliage within and among tree populations, thus generating spatial variations in insect densities (Cates & Zou, 1990). In the Tatras mountains, six plots of Norway spruce located around an *Ips typographus* outbreak area differed by their resistance level to bark beetle attacks as appreciated by their phenol content (Lieutier et al., 2003). Trees killed by *I. typographus* during the three following years were located in the two plots which had the lowest resistance level. The spatial distribution of attacks and the spread of the outbreak were thus in agreement with the spatial distribution of the trees' resistance levels. More generally, considering all natural systems, Hunter (1997) has underlined that "plant chemistry is one mechanism determining the distribution and abundance of insect herbivores".

It must also be reminded, although it would be out of the focus of this chapter to present them, that there are numerous examples of effects of age and physiological status on the level of trees' resistance to insects. The distribution of age classes in a forest and that of the factors affecting tree physiology (soil, climate, pollution…) thus influence the diversity and the distribution of resistance to insects, and consequently the spreading modalities of insect invasions.

4.4. Effect of rapid temporal variations in spatial diversity and distribution of host tree resistance

All parameters considered above in the present section, even the species composition, can vary with time, which can thus modify the spatial distribution of the resistance levels. I focus here on natural temporal variations that are able to interfere rapidly (few years) in the modalities of invasion. It is especially the case of insect attacks (native or invasive), which modify the level of trees' resistance to the same or other insect species. Although the tree species composition stays the same, there can be considerable resulting changes in the spatial distribution of tree resistance levels, with further consequences on the spatial development of invasions. In several deciduous tree species, it has been reported that repeated defoliation, over several seasons, induces considerable chemical modifications in the new foliage (delayed induced response), especially accumulation of defensive secondary metabolites and decrease of the nutritional quality of the foliage, often causing a decrease of insect performances on such trees (Benz, 1974; Tuomi et al., 1984; Mattson et al., 1988; Neuvonen & Haukioja, 1991; Ruohomäki et al., 1992; Haukioja & Honkanen, 1997). The often irregular distribution of outbreaks at the regional level would consequently modify the distribution of the resistance levels.

Such modifications in the foliage of mountain birch (*Betula tortuosa*) defoliated by the autumnal moth *Epirrita autumnata* in Finland cause similar effects (Haukioja et al., 1988) and would be a reason why a new outbreak would not occur at the same place immediately after the previous one (Haukioja 1980). This example deals with native insect and tree species but, since the toxicity of the involved compounds is generally not very specific, the described phenomena could determine the spreading modalities of an invasive species that would be introduced in a forest where such outbreaks occur frequently. An example involving invasive species could be the hypothesized spatial relations between *L. dispar* and *Euproctis chrysorrhoea* in eastern North America. The former has been supposed to restrict the area available to the second, through modifications of the foliage quality of their common host trees (Barbosa & Schaefer, 1997). In the case of *L. dispar* invading a new area, Barbosa and Schaefer (1997) have proposed that chemical modifications induced on an invasive front of *L. dispar*, could make the heavily defoliated hosts (located behind the front) much more resistant than the not or slightly defoliated hosts located ahead of the front. Larval survival and development and adult fecundity would be consequently higher in front of the leading edge than behind, thus resulting in more rapid growth of populations in the former areas. It has been hypothesized that this mechanism explains the pattern of spread of the gypsy moth (Barbosa & Schaefer, 1997).

In conifers, defoliations do not seem to often trigger delayed induced responses (Haukioja & Honkanen, 1997) but are especially known to weaken trees and to make them more susceptible to bark beetle attacks (numerous references in Lieutier, 2004). Defoliations can thus modify the spatial distribution of conifer resistance to bark beetles with consequences for the spreading modalities of those insects. Bark beetle attacks themselves could have opposite effects on tree resistance but could lead to similar conclusions regarding modifications of the distribution of tree resistance. Indeed, it has already been proposed that failed mass attacks of conifers by bark beetles make the victorious trees more resistant to further attacks (Krokene et al., 1999). As tree defenses against bark beetles do not seem specific to the aggressor species (Lieutier, 2002, 2004), this could have consequences for the spreading mechanisms of a possible invasive bark beetle species.

5. CAPACITY OF TREES TO ADAPT TO NOVEL INSECT SPECIES

The capacity of trees to adapt to novel insect species must be considered in relation to the genetic characteristics of the tree populations and to the environment in which they live. I shall thus discuss successively the extent of the genetic diversity, the selective pressures previously encountered by the trees, and the role of environment.

5.1. Role of the extent of the genetic diversity

The extent of their genetic diversity is an important factor that conditions the possibility for the trees to genetically adapt to insects. In case of an insect introduction, the tree population has a generally high genetic diversity (except in plantations of selected trees) and faces an insect population with a rather limited genetic diversity. Trees are thus in a favorable situation to develop genetic adaptations against insects. By contrast, in the case of tree introduction, the genetic diversity of the tree population is often very limited, especially in the modern forestry where introductions often concern seeds of a few number of selected provenances. On the contrary, the genetic diversity of the indigenous insect populations is always very high (cf. 6.1). The result is that the possibilities of adaptation of an introduced tree species to indigenous insects are very limited. Moreover, even if many tree genotypes / phenotypes are selected before introduction, the selection most often concerns characters related to tree productivity and very rarely to insect resistance. In addition, in all situations, the adaptive phenomena are very slow and have thus a low chance to interfere in the spread of an insect invasion. In some situations, resistance mechanisms against local insects have been reported to have developed rapidly in exotic trees after their introduction in a new area, as for *Sapium sebiferum* in southern USA. In this case however, the improvement of tree resistance corresponds rather to an adaptation to the novel environment than to a selective pressure exerted by insects (cf. 3.2 and 5.3).

5.2. Importance of selective pressures previously supported

The selective pressures previously supported by the tree population play a very important role which relates to pre-adaptation phenomena. In this context, the resemblance between the damage caused by the previous aggressors and that caused by the novel aggressors is important, since the nature of the resistance mechanisms that interfere is determined by the type of damage, be these mechanisms preformed or induced. For example, defense mechanisms involved against leaf chewing insects may not depend on the species of leaf chewer, but are certainly different from defense mechanisms involved against leaf miners of leaf sap-suckers. The taxonomic proximity between the natal and the novel aggressors certainly also plays a role because the intensity of the tree responses depends on the nature of the aggressors, even if the kind of tree response can be the same for a given category of aggressors.

During their evolutionary history, trees have developed efficient responses to resist attacks by their usual insect species. It means that a tree species that has experienced, for a very long time, repeated attacks by a same insect species is presently pre-adapted to cope with and resist attacks by this species. This idea has been used in section 3 to explain the success or failure and the performances of various insects on their novel host, in relation to the taxonomic proximity between that latter and the natal host. It can be used again to predict the capacity of trees to resist attacks by novel aggressors. In other words and first considering specialist insects, between closely taxonomically and chemically / physically related host trees, the one that should resist the best to a novel insect should be the host (exotic or indigenous) which has experienced the insect species the closest to the novel aggressor. It does not seem that there are exceptions to that “rule” (cf. 3.2). On the contrary, if the hosts are taxonomically far from each other, the one adapted to an insect species close to the novel specialist aggressor is disadvantaged because it will be chosen preferably to the other host. With generalist insects, the host that has experienced the insect species the closest to the novel aggressor should always be favored, within the limits of the host range of the generalist insect, but exceptions exist (cf. above 3.3). Examples of all these tendencies have been presented in section 3.

This pre-adaptation of trees is conceivable with any kind of resistance mechanism, preformed or induced. However, the phenological discordance is a valuable pre-adaptation only if the phenology of a population is as diversified as possible among the different trees (cf. 2.2).

5.3. Role of the environment

The environment determines the modalities of the resistance expression. It is a crucial factor, for acclimatizing an exotic tree species facing local insects as well as for the resistance of indigenous trees to insect invaders. The problem is very complex and meets the study of the role of climatic and environmental factors on resistance expression in general. I only remind that the effect of the environmental factors on tree resistance to insects, in direction and intensity, seems to depend essentially on the available resources, the intensity of the stress supported by the tree, and the nature of the insect guilds (Mattson & Haack, 1987; Jones & Coleman, 1991; Herms & Mattson, 1992; Larsson, 1989; Tuomi et al., 1991; Koricheva et al., 1998; Lieutier, 2004; among others). Moreover, the various types of resistance mechanisms (especially preformed vs. induced) could be affected differently (Lombardero et al., 2000).

In all situations, the physiological status of the trees plays an essential role. It is essential for an introduced tree to be physiologically well adapted to the physical environment of its novel ecosystem in order to resist attacks by indigenous insects. The physiological status of the indigenous trees is also essential to determine how they will cope with the arrival of a novel insect. It must be reminded also that, depending on the environmental conditions of their novel ecosystem, certain introduced plants could change their demographic strategy, abandoning a pioneer behavior to develop a strategy where investment in defense is increased at the expense of growth and reproduction. This seems to be the case of the Chinese tallow tree *Sapium sebiferum* in Texas, where varieties from the introduced range are more resistant to herbivory than varieties from the native range (Siemann & Rogers, 2003) (cf. 3.2). The intraspecific competition between tree species or the presence of a local aggressor facilitating or impeding the attacks of an introduced species (cf. 4.4) are also elements of the environment that must be taken into account in the variations of resistance of indigenous trees to invasive insects. Similar factors can also interfere in the variations of the resistance of introduced trees to local insects.

6. CAPACITY OF INSECTS TO ADAPT TO THE RESISTANCE OF NOVEL HOST TREE SPECIES

6.1. General considerations

The capacities of insects to adapt to the resistance of novel hosts in general are high. They are sometimes even so complete that the exotic hosts have become the only hosts, as for many species of Lepidoptera in the gardens of the urban-suburban environments (Shapiro, 2002). Regarding tree resistance, insect adaptations exist to all kinds of tree defenses and situations: indigenous insects to exotic hosts, exotic insects to local hosts; host range extension of indigenous insects to indigenous hosts (cf. references above in section 3). Adaptations to host resistance are especially easy for phenological resistance (Dixon, 2003). Examples have already been given in section 2 about the possibilities for insects to easily adapt the phenology of hosts in a new area (Du Merle, 1983, 1988; Raffa et al., 1992). The genetic variability of the hosts may be a problem if it represents a continuum, but insects have often increased their own variability in these cases. In addition, particular relationships with their host plant or particularities of their life cycle may facilitate the adaptation of some insect species to the host phenology (cf. 6.4)). Adaptations to other forms of resistance (preformed or induced, physical or chemical) are also possible since such adaptations exist in the area of origins (Mattson et al., 1988; Wagner & Raffa, 1993; Lieutier et al., 1999; Wagner et al., 2002). However, they take more or less time, depending on the host range of the insects, the genetic diversity of the host population, and if the insects have been previously submitted to similar defense mechanisms. In both cases of tree and insect introductions, even polyphagous insects sometimes face chemical or physical defenses that are completely unknown to them (novel defense). In such cases, the introduced insects generally disappear, whereas the local insect facing a new host will be obliged to invent new physiological and biochemical adaptations, thus making a long time lag to take place before their establishment on the host occurs (Lankau et al., 2004).

6.2. Role of the genetic characteristics of insect populations

Insect genetic diversity is very high in case of indigenous insects facing exotic trees. The selection of the genotypes adapted to the novel host, of which the genetic diversity is often very low (cf. 5.1), can thus be rapid, especially when this host is introduced over large areas; thereby, creating an intense selective pressure for the local insects to adapt to a rather uniform population of trees. Examples of such cases have been given in section 3. On the contrary, the genetic diversity of the introduced insect populations is not especially high, and depends on the size of these populations. An invasive population composed of a small number of individuals has a smaller genetic diversity than the original population, and it has been demonstrated that the size of the "inoculum" in the new area has positive effects on the success of colonization (Berggren, 2001). However, an insect species is submitted to high selective pressures from different origins when introduced in a novel environment and this, combined with a generally short generation time, accelerates the process.

Consequently, the genetic diversification is generally very rapid in novel environments, as observed for the green spruce aphid *E. abietinum* on Sitka spruce in UK (Nicol et al., 1998) and Iceland (Sigurdsson et al., 1999) and for the cynipid *Andricus quercuscalicis* extending westwards throughout Europe while following the human introduction of its host *Quercus cerris* (Stone & Sunnucks, 1993). *Lymantria dispar* also adapts rapidly to the variability of the bud burst dates of its hosts, by a two to three week - long period of egg hatching on a same site (Stoyenoff et al., 1994). This high genotypic and phenotypic plasticity greatly facilitate insect invasions (Liebhold et al., 1995).

Parthenogenesis has been reported to facilitate the success of the invaders (Simberloff, 1989; Niemelä and Mattson, 1996 and references therein) but this does not seem to account for adaptation to tree resistance. On the other hand, polyploidy and heterozygosity, which also favor invasions because of conferring broader ecological amplitude to the invader (Bullini & Nascetti, 1990; Niemelä & Mattson, 1996), can be important for a quick adaptation to tree resistance.

6.3. Importance of selective pressures previously encountered by the insect population

As for tree adaptation (5.2), the characteristics of the original environment of the insects have defined selective pressures that have shaped their populations so that they have become more or less pre-adapted to new hosts. With regards to host shifting, the essential factors that have been conditioned by these selective pressures are certainly the host range (monophagy / polyphagy) of the insects and their ability to find a host.

6.3.1. Insect host range and taxonomic proximity of hosts

A wide host preference is an important trait related to establishment of invasive insects (Liebhold et al., 1995). It is also an important trait for indigenous insects to adapt to the introduced trees. The initial host range by itself is important. Polyphagous insects adapt more easily to novel hosts than monophagous or oligophagous insects (cf. Fig. 4 and 5, and several other examples in 3.1). Few monophagous insects could slowly shift to a host species distant from their natal one, colonizing only the few empty niches left by the other species (Turnipseed & Kogan, 1976). Moreover, generalists can adapt to tree species that do not belong to their original host range, as demonstrated for indigenous Lepidoptera shifting from angiosperms to Sitka spruce in UK (Fraser, 1997) and for the exotic *L. dispar* able to shift to several indigenous potential hosts in Australia (Matsuki et al., 2001) (cf. 3.1).

The taxonomic proximity between the original and the novel hosts often interferes in relation to the host range of the insect and defines the ability of this insect to adapt to new hosts. Numerous and various examples have been given in section 3 on the joint role of these two parameters in the success of host shifting. These examples are, in fact, possible or demonstrated situations of pre-adaptation of insects to the resistance of new hosts. Rules have also been proposed regarding the facility of shifting while taking into account these parameters (cf. beginning of section 3 and 3.2). They can be used to appreciate the degree of pre-adaptation.

6.3.2. Capacity to find the host

Mobility is most often necessary for an invasive insect species and can be considered as an insect adaptation to the spatial discordance of the trees. Insect mobility can be ascertained by the insects themselves either actively by the adults and the old larvae, or passively by the young larvae transported by the wind. For example, wind dispersion has a large part of responsibility in the extension of *L. dispar* populations, the old larvae completing the dispersion by wandering from defoliated trees (Barbosa & Schaefer, 1997). Sometimes however, due to behavioral-constraint, there is no possibility, even for a mobile insect to find certain hosts (cf. 3.4).

The structure of the environment in their original area can also interfere with the ability of the insects to adapt to and find their hosts in the introduction area. Niemelä and Mattson (1996) have suggested that the higher fragmentation of the European comparable to North American forests, have selected European insects with a high behavioral, morphological and physiological plasticity, making them more adapted to invasions than their North American counterparts, explaining partly why insect introductions have been much less numerous from North America to Europe than in the opposite direction.

6.4. Role of environment and insect biology

An invasive insect can adapt more easily to local hosts, even those not taxonomically close to its original host, if it is introduced with its native or a closely related host. Indeed, that allows it to "wait" until the genotypes adapted to another host appear. This can explain that the shift of certain exotic insects to local hosts has occurred only several years after they had been introduced. *Choristoneura murinana*, originating from Eastern Europe and initially attached to *A. alba* in France, has then adapted to *Cedrus* where it causes important damage (Du Merle et al., 1992). Similarly in Hawaii, the presence of the exotic tree *Myrica faya* (native to Madeira and the Azores) increases by 2 to 19 times the abundance of the exotic Cicadellidae *Sophonia rufofascia* (originating from Asia) on the native Hawaiian plants (Lenz & Taylor, 2001).

The host abundance and dispersion are important factors for insect adaptation to exotic trees. When the novel host becomes very abundant, occupying numerous and extended areas, contacts with the insects are so frequent that it can appear to them as the only food source. In these conditions, the exotic host can force the adaptation of insects, even specialists, over the requirement of taxonomic proximity with the original hosts. This situation is especially true for insects introduced in a novel environment, but it happens also quite often in case of extensive monospecific plantations of exotic trees. Several examples demonstrating or suggesting such mechanisms have been presented in section 3.

Biological particularities interfering with environment can also facilitate the adaptation to new hosts. For example, Niemelä and Mattson (1996) have mentioned that the characteristics of the photoperiod in the area of insect origin, because they have selected insect populations for a given period of diapause (Tauber et al., 1986), could greatly facilitate the adaptation of the invaders to the phenology of their novel hosts, especially in case of a transfer of insects from higher to lower latitudes. A remarkable example of adaptation to several different host plants mediated by environment is that of the treehopper *Enchenopa binotata* (Membracidae) in eastern North America (Wood et al., 1990). Host plant species and the insect are all indigenous, but the example gives an idea of how high the capacity of adaptation on different trees, including possible exotic ones, could be in some cases. In the same location, eggs hatch in spring in perfect accordance to the phenology of the host species on which they have been laid in autumn, although the host phenology greatly differs from one tree species to another. It has been demonstrated that egg hatching depends on breaking of their dormancy by hydration due to the ascent of sap when tree activity begins and does not seem to be under genetic determinism. These particularities allow the insect to develop on six different genera representing five different families of deciduous trees.

7. CONCLUSIONS

No doubt in a large array of situations, the hypothesis by Barbosa and Schaefer (1997) that "host plant availability and quality (as a consequence of either inter- or intra-plant species variation) is a major driving force determining the spread and abundance of invading species, subsequent to their invasion" applies to tree resistance to insects when considering either insect or tree introductions. Tree resistance to insects often plays a decisive role in the processes of colonization and spread of insect species introduced in forests and in the success of establishment of exotic trees. When focusing only on tree resistance to shifting insects, these situations vary from polyphagous insects adapting to tree species taxonomically very distant from their natal host, to specialized insects which do not shift to a novel host very close to their natal host. The mechanisms that determine the resistance to shift refer to novel defenses in the novel host, behavioral constraints that make the novel host inaccessible for the insect, and frequency of encounter with the novel host. On another scale, any kind of resistance mechanisms can interfere, representing a large diversity of phenomena: phenological discordance between the susceptible stage of the tree and the aggressive stage of the insect, constitutive resistance, active immediate or delayed defense, spatial discordance between trees and insects at the levels of both inter- and intra-specific variations of host trees.

It appears that the taxonomic proximity of the natal and the novel host can play a decisive role in insect shifting, but most often in combination with the insect host range and the intimacy of the tree-insect contact. Theoretically, a polyphagous insect species having loose contacts with its natal host tree adapts more easily to a novel host tree than a monophagous insect species having narrow contact with its host, and a close taxonomic proximity between the natal and the novel host facilitates the insect shift. However, it appears also that this classical general "rule of resemblance-dissemblance" between the natal and the novel hosts must be largely modulated, mainly as a result of trees' adaptations to their usual aggressors, especially in the case of close proximity between the two hosts. The insect performances being generally better on the novel host, particularly with specialist insects.

The capacities of the trees to adapt to novel insect species and those of the insects to adapt to a novel host tree depend first on the genetic characteristics of the two populations, especially their genetic variability. They also depend on the selective pressures previously encountered, the environment of the populations, and the particularities of the insect biology. Insects generally have good potentialities to rapidly adapt to tree resistance of a novel host, mainly due to their short generation time, the abundance of their populations even in case of introductions, and their rapid genetic diversification in novel environments.

However, although tree resistance frequently plays a role in the invasion processes of insects and establishment of exotic trees, its importance can vary depending on the species and circumstances. Other factors can indeed interfere in complement. Especially, the presence or absence of natural enemies could have been a valuable alternative explanation in several examples presented in this chapter. It is impossible to define general rules regarding the respective role of host resistance and natural enemies in explaining the existence or the lack of insect shift. Each situation is a particular case and must be carefully studied before concluding in one direction or another. By reasoning with a theoretical model, Hunter (1997) has demonstrated that, even in situations where natural enemies dominate the herbivore population dynamics, "the equilibrium density of the population depends on both natural enemies and host plant quality simultaneously". In each case, it is thus essential to clarify the respective role of these factors and their interrelations, in order evaluate the risk of damage in changing forest communities.

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CHAPTER THREE

SOUTHERN HEMISPHERE EXOTIC PINE PLANTATIONS THREATENED BY INSECT PESTS AND THEIR ASSOCIATED FUNGAL PATHOGENS

1. INTRODUCTION

Plantation forestry based on non-native tree species in the southern hemisphere expanded rapidly during the latter part of the 20th Century. These plantations now cover many millions of hectares, mainly of *Pinus* and *Eucalyptus* and to a lesser extent *Acacia* species in countries of South America, Africa and Australasia. They represent a major industrial resource, in many cases contributing substantially to local economies through trade in solid timber and pulp products. In addition, non-native plantation forestry has provided local sources of timber products, in some cases alleviating the need to utilize native forest resources.

The success of plantation forestry based on non-native trees in the southern hemisphere has clearly been associated with remarkably rapid growth of trees, often exceeding that associated with the same trees in their native environment. Recent technological advances making it possible to propagate plantation trees vegetatively have also contributed to the success of plantation forestry in the southern hemisphere. This capacity has for example made it possible to capitalize on hybridization between species with highly desirable characteristics and thus to develop specialized products and niche markets.

It is widely believed that the exceptional growth and productivity of plantations in the southern hemisphere is closely linked to the separation of the propagated trees from their natural enemies. The so-called enemy escape hypothesis, although open to debate has relatively wide support (Jeffries & Lawton, 1984; Keane & Crawley, 2002) and we believe that it represents a major factor associated with the success of plantation forestry in the Southern Hemisphere. Thus trees have been able to grow in the absence of damage caused by insect pests and diseases that can severely impede their potential productivity.

T. D. Paine (ed.), Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems, 53–61.

While separation of plantation trees from their natural enemies has clearly conferred a major advantage on southern hemisphere forestry operations, this is a situation that must logically change. Indeed, there is clear evidence of an increasing number of pests and diseases appearing in southern hemisphere plantations. In the case of insects and fungal pathogens, there are many examples of native pests and pathogens that have adapted the capacity to feed on exotic plantation trees. In addition, increasing numbers of new insect pests specific to these trees in their native environments have also been introduced (Tribe, 1995; Gebeyehu and Wingfield, 2003). Where serious pests or pathogens have become adapted to new hosts, they have become potentially important threats to the natural flora of the countries where these trees are native (Coutinho et al., 1998). In some respects, exotic plantation forestry might thus have given rise to new pests and pathogens that could significantly complicate forestry in the future.

An area of forest protection that has not received particularly focused attention is where insect pests and pathogens interact to damage trees. The specific mutualistic relationship between, for example bark beetles (Coleoptera: Scolytidae) and fungi, including some that are well-known pathogens, has long been recognized (Whitney, 1982; Beaver, 1989; Paine et al., 1997), but remains poorly understood (Paine et al., 1997). Thus, the question of whether bark beetles require fungi to kill trees continues to evoke considerable debate (Wingfield et al., 1995; Six, 2003). Likewise, the relationship between siricid wood wasps (Hymenoptera: Siricidae) such as *Sirex noctilio*, its fungal symbiont, *Amylostereum areolatum*, is peripherally well understood, but deserves deeper investigation. For example, recent studies focused on the fungal symbiont have substantially increased our understanding of the population biology of the wasp (Slippers et al., 2001; Slippers et al., 2002).

While strongly evolved relationships between pests and pathogens, such as those between bark beetles or siricid wood wasps and fungi are well recognized, there are other relationships between these two groups of organisms that appear to have been overlooked. These relate to the interaction of wounds made by insects and the subsequent infection of these wounds by pathogens that would otherwise not be able to damage trees. An outstanding example of this type of interaction is found in the case of the pitch canker pathogen that has become one of the most serious threats to pine plantation forestry in the southern hemisphere. This review considers the potential importance of insects that might ultimately raise the pitch canker pathogen to a level that could threaten the sustainability of non-native pine plantation forestry in the southern hemisphere. It particularly serves as an example of the importance of interactions between insect pests and pathogens, beyond the well-recognized mutualistic relationships between these agents that damage trees.

2. PITCH CANKER DISEASE

2.1. An emerging pine disease

The disease known as pitch canker of pine trees (*Pinus* spp.) is caused by the ascomycetous fungus *Fusarium circinatum* (sexual state *Gibberella circinata*). The fungus causes resin soaked cankers on the trunks and lateral branches of trees such as *Pinus elliottii* in the southeastern United States. In the case of highly susceptible species such as *Pinus radiata*, mature trees can be killed in large numbers.

Pitch canker was first discovered in the southeastern United States in the 1940's (Hepting &Roth, 1946) where it caused serious damage, particularly to *Pinus elliottii* (slash pine). The disease has remained endemic in that area and has caused sporadic outbreaks of severe damage, usually under conditions of abiotic stress. Around the time of the first discovery of pitch canker in the United States, it was speculated that the pathogen was exotic and might have originated in Haiti (Hepting & Roth, 1953).

Although the pitch canker pathogen occasionally caused serious damage to pines in the southeastern United States, in a global sense it was somewhat of a curiosity and relatively unimportant. This situation changed irrevocably in the late 1980's, when it was first recorded on *Pinus radiata* in California (McCain et al., 1987). In the early stages of its first appearance in California, damage was largely to street and ornamental trees. But this situation soon changed, and by 1992 pitch canker had spread to native stands of *P. radiata* in the Monterey Peninsula. It subsequently spread throughout the coastal regions of California, from San Diego in the south to Mendocino County, north of San Francisco (Gordon et al., 2001). In only ten years, the disease came to represent one of the most serious tree disease epidemics that has been recorded in the last 100 years.

One of the greatest concerns pertaining to the pitch canker epidemic in California has been that *P. radiata* is so highly susceptible (Hodge & Dvorak, 2000; Gordon et al., 1998). This tree, native to a relatively small part of the western United States, has become one of the most widely used plantation trees in the world. It has thus been planted in various parts of South America, Africa, Australia and New Zealand. In some countries (notably Chile and New Zealand) this pine species forms the primary resource of huge forestry industries and any serious threat to it, would seriously threaten their economies. Another species, widely planted as a non-native in the southern hemisphere that is highly susceptible to pitch canker is *Pinus patula*. Thus, two of the most important species of pines grown in the southern hemisphere plantations, are highly susceptible to infection by *F. circinatum* and thus seriously threatened by it.

The extent of the pitch canker epidemic in California is typical of that associated with an introduced pathogen. Relatively recent population genetic research has confirmed this view and also indicates that the pathogen was probably introduced into California from the southeastern United States (Wikler et al., 2000). It is also most likely that *F. circinatum* is native to Central America including Mexico, where it is known to exist in natural forest stands (Wikler et al., 2000; Britz et al., 2001).

It is of considerable concern that *Fusarium circinatum* has been introduced into exotic plantation forestry programs in the southern hemisphere. The pathogen was first discovered causing significant damage to seedlings in South African pine nursery in 1990 (Viljoen et al., 1994). It has subsequently been shown to be highly pathogenic to *P. patula* and has caused substantial damage to this species in nurseries throughout the country (Wingfield et al., 1999). More recently, the pitch canker pathogen was discovered for the first time in Chile (Wingfield et al., 2002).

In this country, *F. circinatum* has also remained restricted to nurseries where it has resulted in substantial losses, especially to hedge plants used to produce cuttings for commercial propagation. *Fusarium circinatum* appears to have been introduced into South Africa on pine seed from Central America (Britz et al. 2001), which has been an important source of seed for the country.

2.2. Association with insects

The pitch canker pathogen requires wounds to infect trees. These wounds can emerge from mechanical damage such as that caused by wind or by harvesting machinery. Studies in the southeastern United States where pitch canker has been known for the longest period of time have provided good evidence to show that various insects can provide infection sites for *F. circinatum*. These include diverse groups of insects such as the weevil *Pissodes nemorensis* (Coleoptera: Curculionidae) (Blakeslee et al., 1978) and moths such as *Ryacionia buoliana* (Lepidoptera: Olethreutidae) (Matthews, 1962).

In the more recent pitch canker epidemic in California, insects have been shown to be closely associated with infections. Some of the closest associates of the pathogen that appear to provide wounds for infection are *Ips paraconfusus* (Coleoptera: Scolytidae) (Fox et al., 1991; Storer et al., 1994, 2002a), *Pityophtorus setosus* (Coleoptera: Scolytidae) (Dallara, 1997), *Conophthorus radiatae* (Coleoptera: Scolytidae) and *Ernobius punctulatus* (Coleoptera: Anobiidae) (Hoover et al., 1996). Individuals of these species carry *F. circinatum* propagules and transmission of the pathogen has been demonstrated both in field trials and in controlled studies. Hence all of these species are regarded as vectors of *F. circinatum* in California (Storer et al., 1999).

3. FACTORS ASSOCIATED WITH THE ABSENCE OF PITCH CANKER ON MATURE TREEES IN SOUTHERN HEMISPHERE PLANTATIONS

Currently, the pitch canker pathogen is known to be present in only two southern hemisphere countries. All available information suggests that in both South Africa and Chile, the fungus is restricted to nurseries or to field situations where infected nursery stock appears to have been planted. A prevailing question amongst forestry managers in both these countries is whether the mature tree manifestation of pitch canker will emerge in the future. This question is not only important in South Africa and Chile, but is also of great concern to forestry companies in southern hemisphere countries where the pathogen has not yet been detected.

Interrogating the question of whether the pitch canker pathogen will move from nurseries to large trees in South Africa and Chile is complex. Both countries propagate very large areas of highly susceptible pine species and wounds on trees are common. Thus opportunities for infection appear to abound. One view amongst researchers is that the fungus is relatively new in these countries and that the inoculum load in the environment is currently insufficient to drive a process of natural infection. If this is true, it is probably only a matter of time before full blown pitch canker is observed on mature pine trees in plantations. This view is also supported by the fact that new biological invasions often take up to 30 years before they become established (Bright, 1988).

One of the possible constraints to the development of pitch canker on mature *P. radiata* or *P. patula* in South African or Chilean plantations could be a lack of interaction between the pathogen and insects in these countries. Certainly, various insects such as the cone and shoot feeding beetles and weevils present in California, do not occur in Chile or South Africa. These sorts of insects might be important in allowing infections to become established on mature trees.

A counter argument to the view that the absence of insects might account for the lack of pitch canker infections in Chile and South Africa is that insects known to be associated with pitch canker in the southeastern United States are present in both countries. The deodar weevil, *Pissodes nemorensis* is a relatively important pine pest in South Africa where it can be found to damage both *P. patula* and *P. radiata* (Gebeyehu & Wingfield, 2003). Repeated isolations from damage caused by this insect in South Africa have failed to yield cultures of the pitch canker fungus (Wingfield, unpublished). However, in preliminary greenhouse trials (Gebeyehu & Wingfield, 2004) *F. circinatum* has been shown to easily infect feeding wounds made by this insect and its presence has also been shown to exacerbate infections. Likewise, one of the most important insect pests of pine, the pine shoot moth *Ryacionia buoliana*, is present in Chile and produces feeding wounds on shoots of *P. radiata* that would appear to be ideal infection sites for the pitch canker fungus. Inoculations on wounds very similar to those made by the pine shoot moth provide ideal infection sites for *F. circinatum*.

In both Chile and South Africa, it would appear that insects might not represent the major factor restraining the appearance of pitch canker on established trees in plantations. If this is indeed true, the absence of the disease from plantations represents an enigma. There are various possible explanations for the absence of an association between the pitch canker fungus and *R. buoliana* in Chile or *P. nemorensis* in South Africa. These include the following:

- It is possible that the spore load of the pathogen is insufficient to have allowed natural infections to occur.

- Insect damage may not occur at the time of the year when optimum spore production occurs and thus a disjuncture between inoculum and infection sites.

- Assuming that spores are available, the climate at the time of insect damage may not be optimal for infection.

- Infections may be occurring on mature trees, but these are at a level that is currently not sufficient to be detected.

4. LONG TERM PROSPECTS

Pitch canker of pines has clearly become one of the most serious threats to exotic pine forestry in the southern Hemisphere. In this regard, its importance is closely linked to the high degree of susceptibility of some of the most important pine species growing in this area. Like other canker diseases, pitch canker can girdle stems and thus kill entire trees or at least damage them sufficiently to substantially reduce their commercial value.

Whether the pitch canker fungus will spread from nurseries to established trees in the field in Chile and South Africa is very difficult to predict. Certainly isolates of the fungus in those countries are highly virulent. Inoculations of plantlets in greenhouse trials result in rapid death of susceptible plants and inoculations of mature trees in field trials (Wingfield, unpublished) result in typical pitch canker symptoms. The worst-case scenario is that the disease will eventually appear on established trees. This will certainly be a very serious impediment to forestry and it will most likely also increase the threat of the disease moving to other countries where it is currently not present. The latter view is based on the fact that most pests and diseases that have become established in new environments appear then to have moved rapidly to adjacent countries and areas. This is for example well illustrated by the movement of the *Sirex* wood wasp in the southern hemisphere.

The role of insects as a potential driving force that will cause the pitch canker fungus to move from nurseries and plantations in Chile and South Africa deserves serious consideration. There are clearly arguments for and against the view that the lack of insect pests has prevented the outbreak of pitch canker on mature trees in these countries. Questions relating to the availability of susceptible wounds at a time when spores are also available need to be considered. Furthermore, the role of climate on potential infection in areas such as Chile and South Africa deserves careful consideration.

The pitch canker pathogen is already a very serious problem in pine nurseries in both Chile and in South Africa. In these areas, it has resulted in severe constraints to the production of plants for plantation establishment. It has also seriously retarded tree-breeding research where high value breeding stock has been killed by *F. circinatum*. There is a real possibility that it will emerge on established trees in the future and great effort will need to be made to reduce its impact. In this regard, the best possible option is to establish plantations of trees that are known to be highly tolerant to infection. Opportunities here include planting species of *Pinus* that are highly resistant to infection or to select clones of pure species or hybrids that are tolerant to infection by *F. circinatum*. Because of the highly desirable properties of *P. radiata* and *P. patula*, the latter option will be the most likely choice. Forestry companies and organizations supporting them are already actively participating in disease screening programs aimed at identifying disease resistant breeding and planting stock (Gordon et al., 1998 ; Hodge & Dvorak, 2000).

The pitch canker fungus has the capacity to spread rapidly and easily across long distances. A unique feature of *F. circinatum* is that, unlike many other *Fusarium* spp., it possesses an airborne spore state (Storer et al., 2002b). This certainly accounts for its rapid spread in nurseries. Furthermore, it can sporulate profusely on infected tissue and could easily be moved between countries on pine timber. It is also known to be seed-borne (Storer et al., 1999) and this certainly appears to have been the manner in which it has moved to South Africa and Chile. Based on the threat of pitch canker, countries such as Australia and New Zealand have banned the importation of pine seed. While this is perhaps a wise decision, it seriously hampers opportunities to establish large new areas with new *Pinus* spp. and it can also impede opportunities to increase the genetic variability in pine planting stock. Ironically, it is exactly this variability, which will provide the best possible protection against debilitating damage by the pitch canker fungus.

5. CONCLUSIONS

During the course of the last decade and a half, pitch canker has emerged as one of the most serious constraints to pine plantation forestry in the southern hemisphere. In recent years, *Fusarium circinatum* and the disease associated with it, have been the subject of a relatively large number of studies. While our knowledge of pitch canker and its causal agent has increased substantially, many fundamental questions remain to be answered. Some of these are crucially important to the long term sustainability of pine forestry in the southern hemisphere.

While the pitch canker fungus does not have an established mutualistic relationship with insects, these agents clearly interact closely in many disease situations. Introduction of new pine shoot- and cone- feeding insects into areas such as South Africa and Chile could seriously exacerbate losses currently associated with the pitch canker fungus. Southern hemisphere countries that propagate *Pinus* spp. susceptible to *F. circinatum* should make every effort to exclude both the fungus and insects that might become associated with it.

The establishment of foci of pitch canker in new areas significantly increases the threat of this disease further moving to additional environments. Thus the implementation of quarantine measures, both for the pitch canker fungus as well as for insects that might be associated with it, should be considered as an international rather than solely a national issue. In this regard, collaboration between forestry groups particularly in high-risk areas should be strongly encouraged. While the presence of the pitch canker fungus in a country might represent a perceived or real constraint to trade, declaration of new outbreaks, is essential. Failure to declare the presence of the pitch canker fungus in new areas is irresponsible and substantially increases its global threat. Ironically, this approach is also likely to retard research that might reduce the impact of the disease in the countries in which pitch canker occurs.

The association of the pitch canker fungus with pine-infesting insects is intriguing and relatively poorly understood. Clearly, this association differs substantially between groups of insects and these different forms of association deserve further study. The possible interactions between *F. circinatum* and *R. buoliana* in Chile and *P. nemorensis* in South Africa should also be closely studied. Knowledge emerging from such studies should contribute to a greatly improved understanding of the threat of pitch canker developing on established trees in the latter countries.

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CHAPTER FOUR

NATIVE INSECTS COLONIZING INTRODUCED TREE SPECIES—PATTERNS AND POTENTIAL RISKS

1. INTRODUCTION

Biological invasions are today considered to be among the greatest threat to biodiversity on earth (Gurevitch & Padilla 2004). The many examples of introduced plant species that have spread and appear to out-compete native plants illustrate the severity of this problem (Crawley 1997, Vitousek et al. 1997, Richardson & Higgins 1998). One commonly accepted mechanism behind plant invasions is that the plants experience decreased regulation by herbivorous insects and other enemies in the new environment. This is often referred to as the enemy-release hypothesis (Keane & Crawley 2002) or the escape-from-enemy hypothesis (Wolfe 2002). However, not all introduced plant populations have spread and become invasive (Grotkopp et al. 2002, Louda & Rand 2003). For example, some plants might be rapidly colonized by herbivorous insects (Strong 1974, Strong et al. 1977, Auerbach & Simberloff 1988), which may in turn limit the spread of the species (Maron & Vilà 2001, Louda & Rand 2003). The control of exotic plant species by the native biota is often referred to as the biotic resistance hypothesis (Elton 1958, Maron & Vilà 2001) which, similar to the enemy-release hypothesis, assumes that herbivorous insects can be participants in the regulation of plant populations. This suggests that the ability and the rate at which native insects can shift to feed on introduced plants might determine the plants' success in the new environment.

Plants usually establish in new environments through natural dispersal in response to environmental change. However, some plants establish in new environments by the influence of humans, either by accident or by purpose. For example, trees are moved between continents and planted in new environments to be used as new sources of economic development and to reduce the harvest of native forests. Ecologists are concerned that these plant introductions may affect forest biodiversity and ecosystem processes in the recipient communities (see e.g. Vitousek et al. 1997). Among foresters, there are also concerns that introduced tree species may be more subject to insect pests and diseases than native tree species (Zobel et al. 1987). Several examples from the literature show that native insect pests can reach outbreak levels on introduced tree species (Zobel et al. 1987, Watt &

T. D. Paine (ed.), Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems, 63–77.

Leather 1988). To be able to assess the risks of native insects becoming pests on introduced tree species; we first need to understand how native insects are recruited onto the plants. Also, to better understand the mechanisms behind plant invasions, such information can be used for testing some of the assumptions behind the enemy-release and the biotic resistance hypotheses. For example, the enemy-release hypothesis predicts that host plant shifts by specialist insects should be rare onto introduced plants (Keane & Crawley 2002). In this paper we present results showing that the recruitment of generalist and specialist insects can vary considerably among plants of the same species when the species is introduced into environments with different occurrence of taxonomically closely related native plants.

1.1. Patterns of insect recruitment

The rate at which native insect species are recruited onto introduced plants is often rapid at first but then decreases over time (Strong et al. 1977, Strong et al. 1984). For a successful colonization, it is important that the insects recognize the tissue of the plant as food and are capable of digesting the tissue and dealing with its secondary chemistry. It is believed that the group of insects that has the highest probability of being recruited is the generalists (Strong et al. 1984). Generalist insects are less specific in their preference for oviposition and their larvae are adapted to feed on a wider range of host plants than specialist insects. Generalist insects may, therefore, be more likely to shift to feed or oviposit on a new host plant species than specialist insects. Several examples in the literature show a faster recruitment of generalist insect species onto introduced plants than for specialist insect species (Turnipseed & Kogan 1976, Fraser & Lawton 1994, Novotny et al. 2003).

However, there is growing evidence that the recruitment of specialist insects can be influenced by the taxonomic relationship between the introduced plant and the native flora (Connor et al. 1980, da Ros et al. 1993, Jobin et al. 1996). Closely related plant species are often similar in terms of biochemistry, morphology and phenology, which seem to facilitate host plant shifts among herbivorous insects (da Ros et al. 1993). It has, therefore, been hypothesized that also specialist insect species that, in some way, are pre-adapted to feed on the introduced plant should have a high probability of being recruited (Lawton & Strong 1981). Native specialist insects feeding on plants that are taxonomically different from the introduced plant should, on the other hand, have a low probability of being recruited. As a consequence, plants introduced into environments where they become taxonomically isolated may recruit few insect species, whereas the same plant species introduced into environments where congeneric native plants are present may be rapidly colonized by both generalist and specialist insect species.

1.2. Approaches for studying the recruitment of insects

Different types of approaches have been used in studies trying to reveal what factors determine the recruitment of insects. One approach has been to compare the faunas of insects recruited among different plant species introduced into the same environment (da Ros et al. 1993). Such comparisons can reveal information about host plant characteristics that are important for host plant shifts by insects (Fraser 1997). Another approach is to study the insects themselves by comparing life-history characteristics of shifting and non-shifting species (Fraser & Lawton 1994, Fraser 1997). A third way is to compare the fauna of insects recruited with those found on related native plants (Jobin et al. 1996, DeGomez & Wagner 2001, Novotny et al. 2003). These studies tells us from where (i.e. which types of native host plants) the insects are likely to be recruited. Many studies indicate that the taxonomic affinity between the introduced plant and the native flora influence the recruitment of insects. However, few studies have compared the recruitment of insects onto the same plant species when the species is introduced into environments with different occurrence of taxonomically closely related native plants (Connor et al. 1980, Roques et al., in press).

To attempt such a comparison, we have used the published data on insects that have colonized the introduced conifer lodgepole pine (*Pinus contorta*) in Sweden and in England. Specifically we asked the following questions: (*i*) What types of native insects have colonized the introduced conifer, in terms of feeding guilds and host-plant specificity? (*ii*) Where do the insects come from; i.e. what type of native host plants do they normally feed upon? (iii) Do the patterns of insect recruitment differ for lodgepole pine between England and Sweden?

2. LODGEPOLE PINE

2.1. Lodgepole pine in England and Sweden - predictions

Lodgepole pine is a coniferous (Pinaceae) tree species that was introduced to Europe from North America mainly to produce timber. In England and Sweden, the first large-scale introductions of lodgepole pine took place in the late 1950's and 1960's. The total areas covered by lodgepole pine are approximately 102,000 ha in England and 600,000 ha in Sweden (Fraser 1997, Lindelöw & Björkman 2001). In England, lodgepole pine has mainly been planted on moorlands with the dominating plants in the surroundings belonging to the plant families Ericaceae and Myricaceae; e.g., heather (*Calluna vulgaris*) and bog myrtle (*Myrica gale*). The abundance of taxonomically related native conifers, such as the Scots pine (*P. sylvestris*), is relatively low in England compared with in Sweden. In Sweden, the native Scots pine grows more or less throughout the country and lodgepole pine has mainly been planted on previously forested areas where both Scots pine and Norway spruce (*Picea abies*) grow in close proximity. Thus, the presence of closely related native conifers, both at local and regional scales, is higher for lodgepole pine in Sweden than in England.

Winter (1974) and Hatcher and Winter (1990) have summarized the knowledge on lepidopteran species known to feed on the lodgepole pine (and also on other introduced conifer species) in England. Winter (1974) summarized the information of the species of Lepidoptera that had, thus far, been recorded on introduced conifers in England, whereas Hatcher and Winter published an updated list of the macrolepidopterans in 1990. To compare the recruitment of insects between England and Sweden, we first combined the data on macrolepidopterans from Hatcher and Winter (1990) with the species of microlepidopterans from Winter (1974), before comparing with the data from Sweden published in Lindelöw and Björkman (2001). Lindelöw and Björkman (2001) summarized all types of insect species, both herbivorous (including macro- and micro-lepidopterans) and saproxylic insects, known to occur on lodgepole pine in Sweden. When comparing the recruitment of insects between England and Sweden, we focused on the Lepidoptera, because information about this group of insects is available from both countries. We refer to polyphagous insects as those that feed on plants from more than one plant family, oligophagous as those that feed on plants from one family (Pinaceae), and monophagous as those which are restricted to feed on plants within one genus (*Pinus*).

Because lodgepole pine in Sweden is more common close to congenial native conifers than in England, we expected lodgepole pine to recruit both more insect species and a greater proportion of specialist insects in Sweden than in England. The climate and the insect fauna are similar enough between England and Sweden for us to believe that the comparison is appropriate.

2.2. Insect recruitment in England and Sweden - patterns

The data from Winter (1974) and Hatcher and Winter (1990) show that, in total, 23 species of Lepidoptera have, thus far, been found feeding on lodgepole pine in England. In Sweden, the number of Lepidoptera is somewhat smaller; a total of 19 species have been found on lodgepole pine (Lindelöw and Björkman 2001). There is little reason to speculate about whether the number of species recruited in the two countries differs, because the number of species found is probably, to a large extent, influenced by the activity of entomologists. For example, plantations of lodgepole pine probably do not attract many amateur entomologists, who are important information sources for studies such as the ones in England and Sweden. We conclude that the number of lepidopteran species recruited by lodgepole pine seems to be similar in England and Sweden, or, at least, that there is no striking difference between the two countries. However, among those species recruited, the proportions of specialist and generalist insects differ between England and Sweden. In England, lodgepole pine has mainly been colonized by generalist (polyphagous) insect species whereas in Sweden, lodgepole pine has mainly been colonized by specialist (oligo- and monophagous) species (Fig. 1). The proportions of specialists and generalists recruited differ significantly between England and Sweden ($\chi^2 = 15.9$, $p < 0.01$, d.f. = 1; Chi-square test[1]).

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[1] In the statistical test we compared the proportion of specialists (mono- & oligophagous species added together) with the proportion of generalists (polyphagous species) recruited onto Lodgepole pine between England and Sweden. The numbers of mono- and oligophagous species were added in order to get high enough expected numbers to test for significant differences with a Chi-square test.

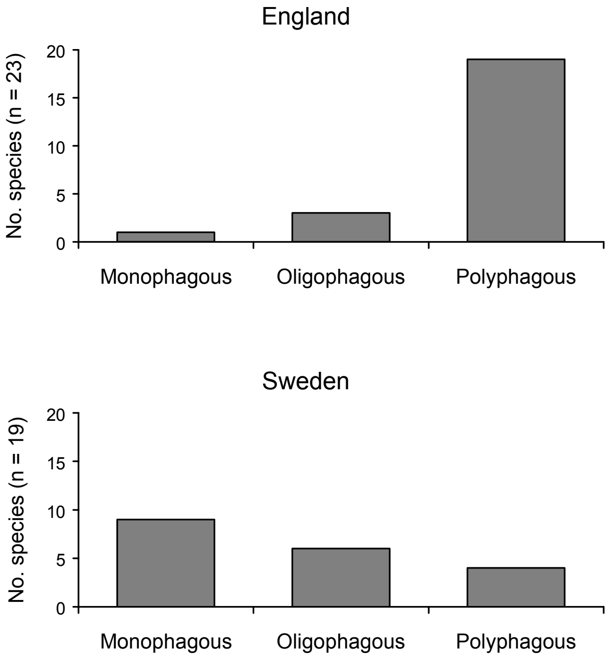

Figure 1. The numbers of lepidopteran species that have colonized the introduced conifer lodgepole pine (Pinus contorta) *in England and Sweden. By monophagous we refer to those insect species that are restricted to feed on plants within the genus* Pinus*, oligophagous as those that feed on plants within the family Pinaceae, and polyphagous as those that feed on plants from several families.*

The pattern, i.e. that lodgepole pine has recruited different types of insects in Sweden and England, is also illustrated by the fact that only 3 out of the total 39 species have been recruited in both countries. The species of lepidopterans found on lodgepole pine in both countries are *Rhyacionia duplana* (Tortricidae), *Panolis flammea* (Noctuidae) and *Bupalus piniaria* (Geometridae). The result of the comparison between England and Sweden suggest that the recruitment of insects were based on the local pool of species available in the areas of introduction. The composition of insect species might therefore vary considerably for the same plant species when the species is introduced into different environments. The data from Winter (1974) and Hatcher and Winter (1990) show that most of the insects that have colonized lodgepole pine in England are generalist insects feeding on plants in the moorland habitat (e.g. generalist species feeding on Ericaceae and Myricaceae plants). In Sweden, lodgepole pine has mainly recruited specialist insects from the native conifers in the surroundings (Lindelöw & Björkman 2001).

Lindelöw and Björkman (2001) compared the numbers of mono-, oligo- and polyphagous species found on the native Scots pine with those recruited onto lodgepole pine in Sweden. The results showed that almost every monophagous lepidopteran (9 out of 10) that feeds on Scots pine in Sweden had colonized lodgepole pine. The proportions of the more generalist lepidopterans were much smaller, about 25-30% of the oligo- and polyphagous species had colonized lodgepole pine (Lindelöw & Björkman 2001). A similar pattern was found for the sawflies, even though all of them are monophagous (Björkman & Larsson 1991), i.e. a high proportion (11 out of 13) of those feeding on Scots pine has colonized lodgepole pine.

This indicates that, in Sweden, specialist insects have colonized lodgepole pine both more rapidly and to a larger extent compared with generalist insects. As suggested by Lindelöw and Björkman (2001), the rapid colonization by specialist insects is probably related to similarities in chemistry and morphology between lodgepole- and Scots pine. The specialist insects that usually feed on the native Scots pine are probably pre-adapted to also feed on lodgepole pine, which seems to facilitate host-plant shifts among such insects (Lawton & Strong 1981).

Based on these observations we propose a conceptual model for why the recruitment of insects onto introduced plants may differ among specialist and generalist herbivorous insects. The model considers similarities among host plant species and the number of potential colonization events. The group of insects that will be recruited first will be those specialist insects that are pre-adapted to feed on the introduced plant. By pre-adapted we refer to those insects that are physiologically capable of feeding and surviving on the introduced plant, which can apply for both specialist and generalist insects. The main difference between the specialist and the generalist insects is that the specialists are more sensitive to plant cues, such as volatile compounds, than generalist insects (Bernays 2001). The specialists therefore discriminate more efficiently among potential host plant species than generalists. Consequently, if the introduced plants share important characteristics used by insects for host plant identification and acceptance with native host plants, the probability of recruitment will be higher for the specialist insects than for the generalist insects. Experiments have shown that specialist insects locate and accept their host plants faster than generalist insects (Bernays & Funk 1999, Bernays 2001). However, the recruitment will be slow or non-existent for those specialist insects that are adapted to feed on native plants that are taxonomically, biochemically and morphologically different from the introduced plant. This is because of the specialists' strong sensitivity, which makes them less likely to colonize and accept a non-suitable host plant than generalist insects. We therefore suggest that the group of native insects that should have the highest probability of being recruited from the local pool of species should be the pre-adapted specialists, whereas the generalist insects should have a somewhat lower probability. The group of insects that should have the lowest probability of recruitment should be the specialist insects that feeds on native plants that are taxonomically different from the introduced plant species; i.e. non-adapted specialist insects.

Another aspect that needs to be considered when building a model for the recruitment of insects is the number of potential colonizing events. By colonizing events we refer to occasions where an insect moves over to feed or oviposit on the introduced plant. The probability of a certain insect species to move over to an introduced plant species is, partly, influenced by the likelihood that the insect encounters the plant. The more abundant the insect and the plant are, the more likely the two species are to encounter each other, and the higher probability of recruitment. Considering lodgepole pine in Europe, the trees have recruited more specialist insect species in Sweden than in England. This difference is probably due to lodgepole pine growing together with native conifers to a larger extent in Sweden than in England. Lodgepole pine should therefore have encountered pre-adapted specialist insects more often in Sweden. Thus, the number of potential colonizing events by specialist insects should have been higher for lodgepole pine in Sweden than in England. Because native conifers are scarce in the moorland habitats where lodgepole pine has been planted in England, the trees have mainly recruited generalist insects from common plants in the moorland habitats (i.e. from Ericaecae and Myricaceae plants). Thus, whether an introduced plant species will recruit specialist insects or not depends on the availability of pre-adapted specialist insects in the recipient community.

How well can this model predict patterns in other systems? Connor et al. (1980) studied the numbers of specialist leaf-mining insects that have colonized introduced oak species (*Quercus* spp.) in North America and in Australia. In North America, where native oak species are present, the introduced *Quercus suber* has recruited several species of native specialist leaf-mining insects. However, for *Q. suber* introduced into Australia, where no native oaks grow, the introduced oak has not recruited any native leaf-mining insects at all so far (Connor et al. 1980). This shows that when plants are introduced into areas where taxonomically related plants are present, as is the case for *Q. suber* in North America, specialist insects are recruited. However, when the exotic plant is taxonomically isolated, as is the case for *Q. suber* in Australia, the recruitment of specialist insects will be slow or even non-exist, at least until some of the insects adapt to the new host-plant. Thus, this example does not contradict our model.

A second example from the literature illustrates the role of native relatives in close proximity to introduced plants. It comes from Switzerland where two species of exotic Asteraceae have been introduced (Jobin et al. 1996). The introduced *Solidago altissima* has been colonized by only a few specialist insect species, whereas the other Asteraceae, *Heracleum mantegazzianum*, has been colonized by several species of specialist insects (Jobin et al. 1996). Native relatives of both *Solidago* and *Heracleum* are present in Switzerland. However, *H. mantegazzium*, which has recruited the greatest number of specialists, often grows together with the native relative *H. sphondylium*, whereas *S. altissima* mainly grows in other regions than its native relatives (e.g. *S. virgaurea*) (Jobin et al. 1996). This example shows a similar pattern as for lodgepole pine in Europe, suggesting that the recruitment of specialist insects is greater if the introduced plant grows together with taxonomically closely related native plants.

Another example that illustrates the significance of native relatives in the proximity comes from the system of thistles (genus: *Circium*) studied in the prairie grassland of North America (Louda & Rand 2003). The introduced bull thistle, *Cirsium vulgare*, has become an invasive weed in some areas of North America. However, it has remained scarce in regions where it grows together with native thistles, such as the tall thistle, *C. altissimum*. It is suggested that the control of bull thistle in areas with native thistles could be due to specialist insects that have shifted to feed on the introduced thistle (Louda & Rand 2003). Native specialist insects feeding on the developing buds and flowering heads reduced seed production of the bull thistle by >70% in areas where the plants were growing together with native thistles. This example not only illustrates that specialist insects are recruited in areas where congeneric native plants are present, but also that these insects may prevent introduced plants from becoming invasive.

2.3. Patterns among feeding guilds

In a review by Strong et al. (1984) it was shown that externally chewing and sucking insects were more likely to colonize new host plant species than endophagous leaf miners and gall-formers. However, for lodgepole pine introduced into Sweden, the opposite relation was found (Lindelöw & Björkman 2001). The proportion of species recruited from Scots pine onto lodgepole pine was highest for the shoot- and bud-boring insects and lowest for the externally feeding species. Another interesting pattern was that, for lodgepole pine in Sweden, the herbivorous insects mainly come from Scots pine whereas the saproxylic species (i.e. those insects that feed on the phloem or xylem of dead or dying trees) come from Norway spruce. As suggested by Lindelöw and Björkman (2001), these patterns are probably due to the specific chemical and morphological properties of the different plant tissues in the three conifer species. Unfortunately, no data, to our knowledge, are available on saproxylic insects feeding on lodgepole pine in England, which prevents a comparison with the data from Sweden.

2.4. Summarizing thoughts about the patterns

The introduction of trees for silvicultural practices has mainly occurred during the last centuries and the trees will probably continue to recruit insect species over time. It is therefore not unlikely that the proportions of specialist and generalist insects also may change over the time. For example, lodgepole pine has mainly recruited monophagous species in Sweden, whereas the fauna of insects feeding on the native Scots pine is dominated by oligophagous and polyphagous species (Björkman & Larsson 1991). It could be expected that, in the future, many of the generalist species that have not yet been recruited also start to feed on the lodgepole pine. The proportions of generalist and specialist insects may thereby become more similar to those for Scots pine. However, there are several potential reasons why the communities of insects may remain different between logdepole- and Scots pine. First, some of the native insect species feeding on Scots may not be able to colonize lodgepole pine successfully. For example, the two conifer species may differ in important plant characteristics (e.g. biochemistry, morphology or phenology) which may prevent some of the insects on Scots pine from colonizing lodgepole pine. Second, inter-specific interactions among early and later colonizing insect species could be influenced by the host-plant use by the early colonizers. Early colonizing species will also get a longer time period to adapt to the new host plant species, which may influence the outcome of such interactions. Third, as herbivorous insects are recruited, so are also their natural enemies, which could affect the development of insect communities on the plants (Lawton & Strong 1981). Further studies are, therefore, needed to better understand how insect faunas on introduced plants may change over time and how early colonizing species and natural enemies may affect the process of insect colonization.

2.5. Insect abundance and damage – potential risks

As is the case for most introduced plant species, we have little information about insect abundance on lodgepole pine in England and Sweden. Although lodgepole pine seems to have recruited many species of insects, the total number of species is not necessarily correlated with the levels of damage (Keane & Crawley 2002). For example, some of the insects may only occur sporadically on the plants and inflict minor damage. A few studies have explicitly compared insect abundance on introduced and native plants (Yela & Lawton 1997, Memmott et al. 2000, Novotny et al. 2003). These studies have revealed a great variation in the patterns; in some cases introduced plants support more herbivores than native plants, in other cases the opposite relation is true. It should be remembered that insect abundance often varies greatly, in both time and space and among individual plants within the same plant species, which may affect the conclusions of such studies. Studies on what factors determine the population levels of insects on introduced plants are, however, needed because insect abundance is more likely to correlate with damage-levels than number of species (Keane & Crawley 2002). There is also growing awareness that exotic plants can negatively and indirectly affect the native flora if the introduced plants support large herbivore populations that “spill-over” onto native plants (Rand & Louda 2004).

The abundance of insects on introduced plants can be low because colonizing insects are ill-adapted to their new environment. For example, the life history traits of native insects can be expected to be adapted in synchrony with the native flora, but may then be out of synchrony with the introduced plant. It was shown that, for 28 spruce (*Picea* spp.) species introduced into France, those spruce species that had the most similar flowering phenology to the native spruce (*P. abies*) recruited the most cone-feeding insects and received the most damage (da Ros et al. 1993). Introduced spruce species that were out of synchrony phenologically with the native spruce received fewer insect species and less damage. Other plant quality traits that may affect the preference and performance of insects include nutrition and plant secondary metabolites (Schoonhoven et al. 1998). The abundance of insects is also likely to be influenced by natural enemies, which are important sources of herbivore mortality (Cornell & Hawkins 1995). For factors that are likely to influence the abundance of herbivorous insects, it may be difficult to predict whether the introduced or the native plants will be superior for the insects. When comparing introduced and native plants, it is therefore necessary to keep an open mind about how herbivore abundance may differ between the two groups (Yela & Lawton 1997).

Many of the insect species found on lodgepole pine in Europe have only occasionally been observed to feed on the plants and may therefore inflict minor damage. However, some of the insects seem to perform well on lodgepole pine and may cause more severe damage. Local outbreaks of, for example, the pine beauty moth (*Panolis flammea*) have been observed in stands of lodgepole pine in England (Watt and Leather 1988) as have outbreaks of the European pine sawfly (*Neodiprion sertifer*) in Sweden (Olofsson 1989). Lindelöw and Björkman (2001) proposed that the outbreaks of *N. sertifer* could be influenced by the relatively low concentrations of resin acids (diterpenoids) in lodgepole pine. Larvae of *N. sertifer* feeding on Scots pine needles low in resin acids perform better and the adults lay more eggs than those feeding on needles rich in resin acids (Larsson et al. 1986, Larsson et al. 1993). Plant secondary metabolites, such as resin acids and other diterpenoids, seem to play an important role in many plants' defense systems against insects (Rosenthal & Berenbaum 1992). It is therefore possible that some of the insects that normally feed on Scots pine may benefit from feeding on lodgepole pine because of its relatively low levels of resin acids. However, more studies are needed on the relationship between resin acids and insect performance on lodgepole and Scots pine to determine whether the insects may benefit from feeding on the introduced lodgepole pine.

Another insect, the pine flower beetle (*Anthonomus phyllocola*) is one of the most common insect species in lodgepole pine stands in Sweden (Lindelöw & Björkman 2001). Larvae of *A. phyllocola* develop in the male flowers and it seems that the relatively large male flowers and the earlier flowering of lodgepole- compared with Scots pine enhances the beetles' performance and population growth (Lindelöw 1990, Lindelöw & Björkman 2001). Apparently, lodgepole pine differs from Scots pine in important characteristics, which may either be good or bad for the insects that colonize lodgepole pine. One example where lodgepole pine is a bad host is the bark beetle *Pityogenes chalcographus*, which frequently colonizes newly felled trees but has a poor reproduction in the stems (Lindelöw & Björkman 2001).

The performance of insects and the risks of outbreaks are not only influenced by biotic factors, such as plant quality and natural enemies, but also by abiotic factors such as the climate. For example, the risk of severe insect damage over large areas on lodgepole pine is considered low in Sweden because the conifer has mainly been planted in the northern parts of Sweden (Lindelöw & Björkman 2001). The pine weevil (*Hylobius abietis*), which is the most important forest insect pest in Sweden, can attack and kill lodgepole pine plants but its abundance decreases towards the north of Sweden where most of the stands have been planted. Also, many of the forest insects known to cause damage in central Europe, such as the pine looper moth (*Bupalus piniaria*) and the pine beauty moth (*Panolis flammea*) seldom cause any damage in Sweden, especially in the north. Thus, from an applied point of view, insect pest damage on trees introduced for silvicultural practices could be reduced if the trees are planted in areas where known forest pests are rare or even absent. However, for lodgepole pine in Sweden, it is likely that the ongoing climate change will lead to increases in the abundance of potential insect pest species.

In summary, it may be difficult to predict whether introduced plants will be more prone to insect outbreaks and damage compared with native plants. Some insect species recruited may be ill-adapted to use the new host plant species whereas other native insects may perform well on the new plant. As herbivorous insects are recruited, they will in turn accumulate natural enemies that will influence herbivore population dynamics (Memmott et al. 2000). To be able to assess the risk of native insects becoming pests on introduced tree species; it is therefore necessary to also understand how natural enemies are recruited and how tri-trophic level interactions are affected by introduced plants. The high abundance of herbivorous insects sometimes observed on exotic trees may, for example, be due to a reduced control efficiency of native parasitoids on introduced plants (Roques et al. in press).

3. CONCLUSIONS

For lodgepole pine introduced into Europe, our comparison between England and Sweden suggests that the taxonomic affinity between the introduced plant and the native flora influence the recruitment of insects. For plants (e.g. lodgepole pine) introduced into areas where native relatives (e.g. Scots pine) are common and grow in close proximity, specialist insects may be the dominating insects recruited. For the same tree species introduced into areas where native relatives are rare and mainly grow in other regions (as for lodgepole pine in England), generalist insects may be the dominating insects recruited.

The rapid colonization of lodgepole pine by specialist insects in Sweden suggests that the native insects feeding on Scots pine are pre-adapted to also feed and survive on the introduced lodgepole pine. In this paper, we proposed a conceptual model for the recruitment of generalist and specialist insects onto introduced plants. We suggest that specialist insects pre-adapted to feed on the introduced plant should have the highest probability for recruitment, whereas generalist insects should have a somewhat lower probability. Specialist insects that are adapted to feed on other types of plants should have a low probability for recruitment. By comparing other systems we found some support for the idea that the model could be a good predictor for the recruitment of specialist insects. However, we are unable to explain why so few generalist insects have so far colonized lodgepole pine in Sweden. Possibly, the high number of generalist insect species recruited in England can be due to the life-history characteristics of these species (Fraser 1997). Lodgepole pine has mainly been planted on moorlands in England and many of the generalist species recruited seem to feed on a wide range of trees and shrubs in this habitat. Thus, the moorland habitat may harbor many extreme generalists that can feed on many types of plants and, thereby, also colonize lodgepole pine. In Sweden, lodgepole pine has mainly been planted in areas where many of the insects known to be feeding on lodgepole pine in England are scarce or absent.

Although lodgepole pine has recruited different types of insects in England and Sweden, the total number of lepidopteran species recruited seems to be similar in the two countries. Factors that determine the numbers of insect species on a particular plant species include plant abundance (Neuvonen & Niemelä 1981), geographical distribution (Strong 1974), time present in an area (Kenney & Southwood 1984), plant size and structural complexity (Lawton and Schroeder 1977) and defense mechanisms (Lawton 1976). Most of these factors can be expected to be similar for lodgepole pine in England and Sweden. For example, lodgepole pine has been present for a similar time period and the area planted does not vary considerably between England and Sweden. Thus, although taxonomic affinity appears to influence the composition of generalist and specialist insects, other factors may be of greater importance in determining the total number of species.

Foresters are concerned that exotic tree species may face a higher risk of encountering insect outbreaks and therefore become severely damaged more often than native tree species. However, several studies indicate no major difference in insect abundance between native and introduced tree species. Some insects seem to perform well on introduced plants, which may lead to population outbreaks, whereas other native insects seem to be ill-adapted to use the introduced plants. It could therefore be difficult to predict whether an introduced tree species will suffer from insect outbreaks more often than native tree species. As herbivorous insects are recruited, so are also their natural enemies. So far, few studies have looked at the recruitment of natural enemies onto introduced plants (Memmott et al. 2000). To be able to assess the risk of native insects becoming pests on introduced tree species, we suggest that future studies should consider the preference and performance of known insect pests and how their natural enemies are recruited onto the plants.

Another major threat to forest ecosystems of today is invasions by exotic plant species. In this paper we mainly focused on trees introduced for silvicultural practices and the risk of insect outbreaks. However, some introduced pine species have spread and out-competed native flora, especially in the Southern hemisphere (Richardson and Higgins 1998). One commonly accepted mechanism behind plant invasions is that introduced plants receive a reduced regulation by herbivores in the new environment. The enemy-release hypothesis predicts a reduced influence by specialist herbivores when plants are introduced into new environments (Keane & Crawley 2002). It is argued that a reduced influence by specialist herbivores may explain why some plant populations have spread and become invasive after being introduced into new environments (Wolfe 2002, Louda & Rand 2003, Blair & Wolfe 2004). The variation in the recruitment of generalist and specialist insects displayed in this paper could serve as a basis for studying the role of herbivorous insects in the regulation of plant populations. It is likely that similar variations in the recruitment of insects can be found for other plant species introduced into other environments.

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R. G. VAN DRIESCHE

CHAPTER FIVE

BIOLOGICAL PEST CONTROL IN MIX AND MATCH FORESTS

1. INTRODUCTION

Forestry takes places at many nodes along two spectra. One spectrum is that of simplification, ranging from lightly exploited natural forests, to modified forests, to intensively managed, cropping of trees in plantations. The other spectrum is that of native vs. exotic species composition of the organisms (tree, herbivores, natural enemies) present. Forests are often considered perennial, stable, lightly modified systems in which the forces of biological control are free to operate. Yet, this only corresponds to conditions present at some nodes on these axes. Here, after discussing the ways in which simplification and invasion affect the composition of forest systems, I have identified a series of cases that represent major positions defining these axes. For each of these cases, I present examples of the potential applications of biological control and the kinds of risks, if any, that each type of biological control entails.

1.1. The Simplification Spectrum

The least simplified end of this spectrum is anchored by the native forest, in a lightly exploited or virgin state. In this condition, logging is followed by natural regeneration of local native trees. There is no use of fertilizers or herbicides to suppress competing vegetation. Present management of the mixed hardwood/conifer forests in southern New England (USA) illustrates this kind of forest. Harvest is done on a small scale, without replanting, in a landscape that is predominantly natural forest. Pest problems in such forests may be caused by native insects such as forest tent caterpillar (*Malacosoma disstria* Hübner) or invasive species such as the gypsy moth (*Lymantria dispar* [L.]).

Modified native forests are artificially replanted after logging, treated with herbicides for release of young trees from competing vegetation, and thinned. Fertilizers are not generally used, nor are soil preparations done. Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests on the national forest lands of western Oregon (USA) that are managed for saw logs fall into this category. Sites

T. D. Paine (ed.), Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems, 79–99.

are often remote and rugged, and cutting cycles are long (60 years or more in temperate climates). These forests tend not to be pure monocultures, despite being replanted to predominately one species, in part because managed stands are intermixed with unmanaged, more diverse stands in riparian zones or other protected areas.

The most simplified conditions occur when trees are grown like agricultural crops in plantations. In plantations, trees (which may be native or exotic) are planted into prepared ground, usually in rows that allow for cultivation and mechanical harvesting. Fertilizers and herbicides are used one or several times in the crop cycle, together with thinning. Insecticides may be applied. Stands are near monocultures, with minimal understory or herbaceous plant layers. The pine plantations in the southeastern United States managed for pulp, the cottonwood farms in Oregon, and the eucalyptus stands in Brazil, and Portugal (among others) planted for fiber or pole production are some examples of such systems, among many.

1.2. The Native-Exotic Species Spectrum

Each of the trophic levels in the forest – the trees, the herbivorous insects, and their natural enemies – may be local natives or exotic imports. At one end of this spectrum is the all native system; at the other is a forest in which all levels are species brought in from other biogeographic regions. In between are various combinations such as native trees attacked by exotic insects, exotic trees attacked by local native or invasive exotic pests, or exotic natural enemies brought in to control a native or invasive exotic pests. In the following section we examine several such combinations and discuss what role biological control may play in controlling pests and what risks the use of biological control may entail in each of its various forms.

2. PESTS IN NATURAL OR MODIFIED NATIVE FORESTS

2.1. Case I: Native Herbivores in Native Forests (I-n, T-n, F-n). Type Example: White Pine Weevil and Spruce Budworm in Eastern North America

2.1.1. Description and Opportunities to Use Biological Control for Case I

Natural control and consequence of its disruption. Most native insects that feed on native trees in natural forests occur at naturally low levels due to some combinations of restraints from natural enemies, tree resistance, and the effects of the climate and site. These species are not considered pests under these conditions, but do represent an enormous pool of insects from which pests can be created by human actions. Such native herbivores can become pests by several mechanisms. This might occur, for example, when a new tree species, favorable as a host for the insect, is introduced into the herbivore's geographic range. Since the exotic tree is likely to be grown in plantations, this new favorable host is likely to occur in large monocultures of impoverished plant diversity, with associated reduced natural enemy diversity. These factors then allow for the formerly innocuous native insect to increase to pest densities. Outbreaks of the geometrid moth *Oxydia trychiata* (Guenée) in Colombia on planted exotic pines is an excellent example (see Case V). Another route by which harmless native herbivores can become damaging pests is planting of local native trees in plantations. Pest status is reached because of the influences of high tree density, low floral diversity, and reduced natural enemy abundance (see mahogany borer, Case VI).

2.1.2. Native species for which natural control is inadequate.

Separate from the above groups of potential pests, some native forest insects are pests in their native ecosystems (from man's perspective) because they periodically erupt to high densities, defoliating or killing trees. Such is the case, for example of spruce budworm, *Choristoneura fumiferana* (Clemens), and various bark beetles. Native natural enemies are often abundant in such systems, but under some circumstances fail to keep pest population growth rates low. A large body of literature on the role of natural enemies in such systems exists and it is not our purpose to review it here. But it is important to bear in mind that these eruptive species are not representative of native herbivores in general, but rather are specifically those species for which biological control periodically fails. Because pest outbreaks in such systems are often driven by large scale abiotic factors such as drought or weather-mediated changes in the degree of insect-plant synchrony, there are few opportunities for use of classical biological control to suppress these outbreaks. The most widely used approach to dealing with such outbreaks is to treat infested areas with pesticides, or if available, with biopesticides, such as *Bacillus thuringiensis* Berliner. For Lepidoptera and sawflies, host-specific baculoviruses have been extensively evaluated, but rarely used because of high production costs. While not useful as commercial pest control products, these viral pesticides can be employed effectively in government-supported programs. Such support is justified because of the high selectivity and environmental safety of such biopesticides.

Other native herbivores for which natural control is inadequate from an economic point of view are species that cause economic losses at low densities. White pine weevil (*Pissodes strobi* [Peck]), for example is a native insect in North America, where it kills leaders of regenerating white pines (*Pinus strobus* L.), greatly reducing their value as saw logs. This species is a chronic pest, able to cause damage in all years at its normal, low densities because a single insect can ruin the value of a whole tree.

To enhance the impact of natural enemies on such native eruptive or chronic pests, it has been suggested that parasitoids be collected from related insect species (same genus) or ecologically similar species found in separate biogeographic areas with similar climates and released for permanent establishment. For example, parasitoids of European species have been considered for release in Canada against spruce budworm and spruce budmoth (*Zeiraphera canadensis* Mutuura and Freeman) (Mills, 1983, 1993). Similar suggestions have been made for the chronic pest *P. strobi* (Mills & Fischer, 1986; Kenis & Mills, 1994).

This practice of taking parasitoids from taxonomically related or ecologically equivalent species in other regions has in recent decades been termed "new association" biological control (Hokkanen & Pimentel, 1984, 1989), but the process is older than the name, dating back to the earliest days of classical biological control.

Tothill et al.'s (1930) successful suppression of the coconut moth (*Levuana irridescens* B-B.) in Fiji in the 1920s, for example, was based on the use of a tachinid (*Bessa remota* [Aldrich]) collected from a different species of moth in the same family as the target pest, since the pest's native home (apart from Fiji) was never located. Currently a project is being implemented in North America to control mirid bugs in the genus *Lygus* that are agricultural pests by introducing parasitoids from species of European *Lygus*. One introduced parasitoid has already reduced density of the tarnished plant bug (*Lygus lineolaris* [Palisot de Beauvois]) by over 60% in alfalfa (the pest's principal habitat) in the northeastern United States (Day, 1996). Similarly, the successful control of the sugarcane borer *Diatraea saccharalis* (F.), in Barbados with *Cotesia flavipes* (Cameron) is based on use of a parasitoid from another host species from Asia (Alam et al., 1971). These and other cases clearly set the precedent that control using natural enemies collected from species similar to but not the same as the target pest can work. However, in many such new combinations, the target host may be physiologically unsuitable or unattractive to parasitoids taken from related species, as was the case, for example, for parasitoids reared from conifer-feeding geometrids in Europe for possible use against the eastern hemlock looper in *Lambdina fiscellaria fiscellaria* (Guenée) in Newfoundland (West & Kenis, 1997). Careful study of the taxonomy, biology, and ecology of species involved is required to discern situations with reasonable prospects of successful control.

2.1.3. Risks Associated with Biological Control for Case I

Since the native insects and native trees are in some sort of ecological, historical balance, there is no ecological rationale for new association introductions. Rather, pest reduction is sought for purely economic reasons. Thus these economic benefits alone would have to be judged against any potential ecological harm to decide if, on balance, a proposed natural enemy introduction would be beneficial or not. Thus for example, if European parasitoids of white pine weevil were to be introduced one would have to conduct host range estimations for each candidate, compare that information to the native fauna, identify native insects that might be parasitized, and decide if attack on those species was okay or not, given the magnitude of the losses to the timber industry from the pest and the likelihood of reducing those losses through the parasitoid introductions. Methods for estimating the likely host ranges of introduced entomophagous insects are rapidly developing and are reviewed in Van Driesche et al. (*in press*). Making risk/benefit decisions for new association introductions against native pests requires that the potential ecological risks to native nontarget insects be compared to an estimate of the potential magnitude of the economic benefits from pest reduction. This is inherently difficult because ecological and economic values are qualitatively different, lack a common "currency" for comparisons, and accrue to different groups. Also, while the magnitude of the potential gain (i.e., the size of the pest problem) can be estimated fairly accurately, the likelihood that the biological control project will be successful can only be estimated in a very qualitative and statistical sense, judging the "power" of the agent in cage trials. This means in practical political terms that regulatory agencies must agree that ecological risks are small, that potential economic gains would be large, and that it is at least plausible that these gains might be achieved. At extremes (low perceived ecological risk and enormous potential economic gain), such qualitative estimates are sufficient, but as the contrast diminishes (medium or very uncertain ecological risks coupled with lower potential economic gain), the imprecision in the quantities being compared leads to rejection of actions that change the status quo (i.e., new risks are not accepted and the project is not approved).

2.2. Case II: Native Herbivores as Newly Important Pests in Modified Native Forests (I-n, T-n, F-modified). Type Example: Red Oak Borer in the Ozark Mountains (USA)

2.2.1. Description and Opportunities to Use Biological Control for Case II

Red oak borer, *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae), is a native insect whose hosts are various native oaks in the United States. An unusual epidemic of this insect is currently killing large numbers of oaks in the Ozark Mountains of Arkansas (Stephen et al., 2003). This outbreak is unprecedented and contrasts with the low density, sporadic populations of this borer that were typical in the past. The roots of this outbreak are still unclear but the working hypothesis (Stephen et al., 2003; Stephen, *pers. comm.*) of entomologists studying the problem is that it stems from silvicultural practices used in the region since the last clear cutting cycle in the 1920's. Following that cycle of forest removal, oaks regenerated profusely by stump sprouting. This regrowth, coupled with implementation of a USDA Forest Service fire suppression policy, increased oak as a component of the forest such that the forest is now ca 75% oak, most of which are older trees (72% are 40-90 years old and 20% are over 90 years old). The working hypothesis suggests that increased oak abundance and older age, in combination with the generally droughty soils in these mountains and a recent drought cycle, combined to provide the red oak borer with an abundance of susceptible hosts. Exact mechanisms that might be increasing red oak borer population growth rates, such as possible better survival in older oaks, are still under investigation. Assuming that the basic causes of this outbreak are silvicultural, the role for biological control would be limited. If as suspected, advance tree age and lack of fire are to blame, change of these factors will be the basis for reducing the level of the outbreak.

In other modified forests, silviculture practices may have acted to reduce or exclude key natural enemies. If specific deficiencies (nectar, alternative hosts, etc.) have caused key parasitoids or predators to drop out of modified forests, then restoring those missing elements might be a means to regain control of the insect outbreaks.

2.2.2. Risks Associated with Biological Control for Case II

In cases such as the red oak borer, causes of the outbreak are likely to be linked to the silvicultural factors that have reshaped the forest in ways that either favor the insect directly or do so indirectly by excluding or reducing important natural enemies. As such, parasitoid introductions are not the appropriate response. Rather, the silvicultural practices used in the forest need to be changed in ways that make the forest less favorable for the herbivore or more favorable for a key, but missing, native natural enemy. Neither of these courses of action poses ecological risks and therefore both the risks and costs of potential management practices can be directly compared in economic terms.

2.3. Case III: Exotic Pests in Native Forests (I-e, T-n, F-natural). Type Example: Winter moth or larch casebearer in Canada

2.3.1. Description and Opportunities to Use Biological Control for Case III

Exotic pests on native trees in natural forests present a clear ecological justification for implementation of classical biological control through importation of any specialized natural enemies associated with the pest in its native range. A complicating factor in such cases is that these invasions by definition involve colonization of a new tree species (often in the same genus) by the invading insect. Since that itself can influence the severity of the pest problem (due to the new tree species being a better host or being more sensitive to feeding by the pest), one cannot be certain that the problem is rooted solely in release from specialized natural enemies. Also, since the climates of the native and invaded regions are likely to vary, such differences may also play a role in causing the invader to become a more serious pest. Separating tree-species vs. natural enemy effects is possible using transplantation experiments done in both the pest's native and invaded ranges. In deciding if natural enemy importation is merited, several cases need to be distinguished:

2.3.2. Species that are pests in their native range.

If the invading insect is a well known pest in its native range, it is much less likely that searching for natural enemies there will reveal species able to solve the problem in the invaded area. However, this is sometimes done. Thus, for example, it is doubtful if the fall webworm (*Hyphantria cunea* [Drury]) – a North American insect that is invasive in Eurasia (e.g., in China: Ji Rong et al., 2003) – could be controlled with North American parasitoids since it is a common and somewhat eruptive pest in its native range in eastern North America (*pers. obs*., RVD).

2.3.3. Species damaging due to new tree associations.

Clearly the acquisition of new hosts that accompany some pest invasions can be the root cause of the pest status of the invader. While it is clear that this can happen, proving that it is the case in a particular instance is difficult, since the effects of separation from specialized natural enemies in the native range and influences of the new host plant co-occur and confound each other. To separately characterize the importance of natural enemies vs. new tree host, one must conduct paired experiments in both locations with both host trees. For example, if the pest were a North American insect that had invaded Europe, the required experiment would be to plant the European and North American host trees side by side in both Europe and North America and observe the level of damage from the pest. If tree species is the primary cause of the pest damage in the invaded area (Europe), then damage would be predicted to be low on the North American tree species planted in Europe, but high on the presumably more favorable European tree species. And by extension, we would predict that the pest would reach pest status in North America on planted specimens of the European tree species, even though the insect would be exposed to its native natural enemies.

One further caveat with these sorts of experiments is that isolated plantings of trees of any species often suffer higher pest levels because they occur outside the web of biological control agents and influences found in the natural forest. McClure (1986), for example, found that in Japan densities of the diaspidid scale *Fiorinia externa* Ferris were 20 to 30-fold higher on cultivated specimens of the two native Japanese hemlocks (*Tsuga diversifolia* Masters and *T. sieboldi* Carriere) than on the same trees in natural stands. Thus, in running such experiments, it may be better to plant the non-native tree in stands of the native species to minimize the effect of changing from a forest to a landscape setting.

Possible examples in which greater sensitivity of the new tree host may be the cause of problems from invasive insects include the destruction of Bermuda cedar (*Juniperus bermudiana* L.) by two invasive scales (*Carulaspis minima* [Targ.] and *Insulaspis newsteadi* [Sulc]) in the 1940's (Cock, 1985) and the widespread debilitation of European plane trees (*Platanus orientalis* L.) in southern France and Italy by the American insect, *Corythuca ciliata* (Say) (sycamore lacebug), which feeds in its native range on *Platanus occidentalis* L. Similarly, the destruction of American beech (*Fagus grandifolia* Ehrhardt) by beech scale (*Cryptococcus fagisuga* Lindinger) and *Nectria* blight pathogens (*Nectria coccinea* var. *faginata* Lohmman, Watson and Ayers and *Nectria galligena* Bres.), contrasts with the much lower level of damage by the same insect in Europe on European beeches (*Fagus sylvatica*) (Wainhouse, 1983).

2.3.4. *Invasive species separated from their natural enemies.*

It is difficult to be sure in advance that any given invasive species falls in this group. However, if an invasive pest is successfully suppressed by importing and establishing specialized natural enemies from its native range, this proves that missing natural enemies were the critical factor leading to its pest status. Invasive insect pests that have been suppressed by means of natural enemy importations into North America following their invasions include winter moth (*Operophtera brumata* [L.]), larch casebearer (*Coleophora laricella* [Hübner]), European spruce sawfly (*Gilpinia hercynia* [Hartig]), and, partially, larch sawfly (*Pristiphora erichsonii* [Hartig]) (Van Driesche et al., 1996 and references therein).

2.3.5. *Risks Associated with Biological Control for Case III*

Since a native tree is threatened, there are clear ecological values being defended. While natural enemy introductions might also have economic benefits, the risk/benefit assessment can be done initially in terms of the ecological risks to the forest of doing nothing versus the risks of having the introduced parasitoid or predator attack some native insects. For example, to evaluate the wisdom of the classical biological control program against hemlock woolly adelgid (*Adelges tsugae* Annand) preventing damage from loss of hemlocks would be balanced against a low risk to a few native adelgids (Zilahi-Balogh et al., 2002). The most likely non-target prey would be the eggs of other bark-feeding or twig gall adelgids, which are themselves pests.

The key to managing any risks inherent in such importations is to (1) estimate the likely host range of the natural enemy to be introduced; (2) use that information in conjunction with an analysis of the relevant native fauna to form an estimate of the value of the species potentially affected; and (3) place that estimate of value at potential risk in the context of a risk/benefit analysis by comparing the potential harm from leaving the pest unchecked. A synthesis of means to estimate the host ranges of parasitoids and predators used against pest arthropods is found in Van Driesche et al. (*in press*)

3. PESTS IN TREE PLANTATIONS

3.1. Case IV: Exotic Pests in Exotic Tree Plantations (I-e, T-e, F-plantation). Type Example: Eucalyptus *borer on eucalypts in California (USA).*

3.1.1. Description and Opportunities to Use Biological Control for Case IV

This case is extremely common and of great concern to industrial forestry and to the arboriculture and nursery industries, which often plant exotic tree species in urban locations. Plantations of exotic trees are common means of producing fiber or lumber in areas lacking suitable native trees. While such plantations often start out pest free, with time insects native to the tree's homeland find these isolated plantings and become established. *Eucalyptus* species in California are a clear example, having enjoyed over a century of near pest-free status, California eucalyptus stands have within the last 15 years acquired a series of borers, defoliators, and sap suckers, including the cerambycid borers *Phoracantha semipunctata* (F.) and *Phoracantha recurva* Newman, the defoliating beetles *Gonipterus scutellatus* Gyllenhal (Curculionidae) and *Trachymela sloanei* Blackburn (Chrysomelidae), and at least six psyllids, especially *Ctenarytaina eucalypti* Maskell (blue gum pysllid), and two lerp psyllids, *Glycaspsis brimblecombei* Moore and *Eucalyptolyma maideni* Froggatt (all pysllids in the Spondyliaspidae) (Paine & Millar, 2002). Three of these invaders have since been brought under effective biological control through importation of specialized parasitoids attacking them in Australia: *C. eucalypti* (Dahlsten et al., 1998ab), *P. semipunctata* (Hanks et al., 1995, 1996), and *G. scutellatus* (Hanks et al., 2000).

Other examples of effective biological control of exotic insects attacking tree species planted outside their native range include eucalyptus snout beetle (*G. scutellatus*) on introduced *Eucalyptus* species in South Africa (Greathead, 1971), oak leafminer (*Phyllonorycter messaniella* [Zeller]) on introduced European *Quercus* spp. in New Zealand (Swan, 1973), Eurasian pine adelgid *(Pineus pini* [Macquart]on introduced *Pinus* species in Hawaii (USA) (Culliney et al., 1999), and ash whitefly (*Siphoninus phillyreae* (Haliday) on introduced ornamental pears (*Pyrus* spp.) in California (USA) (Picket & Pitcairn, 1999).

An interesting point concerning the re-association of such exotic species with their original tree hosts is that the system in the new region is still not a duplicate of that in the native home of the pest because the climate is likely to be different. For example, *Eucalyptus* species such as the Tasmanian blue gum (*Eucalyptus globulus*) were planted in California and were later attacked by two cerambycid borers (*P. semipunctata* and *P. recurva*) from their native Australia. But the climates of California and the part of Australia that these trees came from differ in regard to summer rain. In the native range, there is significant summer rain, but in the Mediterranean climate of southern California, there is summer drought. In the absence of these borers, these eucalypts were able to survive this summer drought and thrive (T. Paine, *pers. comm.*). But summer drought has apparently deprived the trees of an important defense. Under drought conditions, the inner bark's water content is significantly lower, too low to kill young borer larvae. Thus borer survival goes up, populations rise, and trees are killed. Apparently, the magnitude of this influence is such that the addition of an egg parasitoid, *Avetianella longoi* Siscaro, reduces borer survival just enough to prevent this population increase and avoid tree mortality (Hanks et al., 1995, 1996).

Also, biological control of exotic pests in plantations of exotic trees functions in a much simplified system relative to natural control of the same herbivore in its native habitat. This may well increase the efficacy of the introduced biological control agents by reducing the damping effects of intraguild predation.

3.1.2. Risks Associated with Biological Control for Case IV

The potential risks of biological control of these pests can be low if the introduced agents are tested for their host ranges relative to native insects in the region of introduction. One should not assume that the parasitoids will be limited in their habitat to the exotic tree plantations. Rather, it should be assumed that they will spread well beyond those sites and attack other native species within their host range. The incentive to make these introductions is not ecological, but rather economic, being the protection of the values of the exotic trees as sources of wood, fiber, or for use as ornamental plants.

Safety of introductions against pests attacking exotic trees may be increased relative to Case III if the chemistry of the exotic tree is very different from that of the local native trees and if the introduced parasitoid or predator finds its hosts by first responding to volatiles specific to the exotic tree species. This is the case, for example, with the egg parasitoid *A. longoi,* which first orients to *Eucalyptus* odors. In California, this confers great safety to native insects as no native trees have chemistry similar to those of *Eucalyptus* (Paine et al., *in press*).

3.2. Case V: Native Pests in Exotic Tree Plantations (I-n, T-e, F-plantation). Type Example: The native geometrid Oxydia trychiata *on exotic pines in Colombia.*

3.2.1. Description and Opportunities to Use Biological Control for Case V

When exotic crop plants or tree plantations are established in new regions, they become concentrated patches of potential resources for local herbivores. Some of the species that move onto such exotic plants may have been pests on similar native economic plants, but others may previously have been non-pests. In South Africa, 68% of 188 arthropod pests of 14 introduced crops are native species that were not previously in contact with crops they now attack (Dennill & Moran, 1989).

In Colombia, a native geometrid, *O. trychiata,* became an eruptive defoliator on plantations of exotic pines (*Pinus patula* Schiede & Deppe) and cypress (*Cupressus lustianica* Miller) were planted (Bustillo & Drooz, 1977). Unexpectedly, control was achieved by a new host: parasitoid association created by importing the egg parasitoid *Telonomus alsophilae* Viereck from North America, a species that was a parasitoid of other geometrids (Fedde et al., 1976).

In Arizona, a comparative study of herbivores associated with two specie of locust trees, the exotic *Robinia pseudoacacia* (L.) and the native *Robinia neomexicana* Gray, found that some but not all of the herbivores of the native species had, over a hundred year period, colonized the new host tree species (De Gomez & Wagner, *in press*).

Similarly, the Old World mahogany borer *Hypsiplya robusta* (Moore) readily attacks plantations of New World mahoganies (such as *Swietenia macrophylla* King) planted in plantations in Asia (Floyd & Hauxwell, 2001). This borer is, however, a well-known pest in plantations of some local species as well.

3.2.2. Risks Associated with Biological Control for Case V

How to resolve this sort of pest problem is not obvious. One approach might be to try to determine what local native natural enemies are associated with the native species on its natural host in natural forests and then attempt to learn what prevents those agents from exerting control in the exotic tree plantations. Possible mechanisms of pest creation include: (1) the switch in tree species, (2) resource concentration from the high tree density in plantations, or (3) loss of natural enemy biodiversity from vegetation simplification. If it is the tree species itself that is causing the outbreak by being an intrinsically more favorable host, one solution would be to replace that species with an alternate, more resistant tree species (if an economically acceptable equivalent crop tree were available). One could learn if the crop tree were the problem by out-planting small clumps of the tree in the natural forest in the native herbivore's habitat. If tree identity is the critical factor, then one predicts that high populations would develop on such out-planted trees. The importance of resource concentration (vs. tree species identity) can be assessed by comparing pest levels on large vs. small patches of the tree species planted in the native forest. If pest populations do not develop on the exotic trees planted into the natural forest, it would suggest that the critical change was in the simplification inherent in plantation plantings. Exactly what is different about plantations may be difficult to establish, but an approach to finding out would be to construct comparative life tables for the pest in the plantations vs. natural forest.

3.3. Case VI: Native Herbivores in Native Tree Plantations (I-n, T-n, F-plantation). Type Example: The Latin American mahogany borer Hypsipyla grandella *on native mahogany.*

3.3.1. Description and Opportunities to Use Biological Control for Case VI

Plantation production of high value tropical hardwoods in the Meliaceae in genera such as *Kyaya, Toona, Cedrela,* and *Swietenia* (including several species such as big leaf mahogany, *S. macrophylla*) is associated with significant damage from shoot borers, in the genus *Hypsipyla* especially *Hypsipyla grandella* (Zeller) in the Americas, and *H. robusta* in parts of Africa, south Asia, southeast Asia, Indonesia, and Australasia (Griffiths, 2001). While some information is available about the natural enemies of these borers (see Sands & Murphy, 2001 and Blanco-Metzler et al., 2001), almost nothing is known about the population consequences of such natural enemies, in either natural forests or plantations. Blanco-Metzler et al. (2001) may well be the only study to even attempt to collect such data (for plantations in Central America). Since the pest seems to prefer to oviposit in full sun on young trees, resource concentration in sunny sites (not under shade of older trees) may be the root of the problem, in a manner similar to that causing increased damage from a different shoot borer, *Rhyacionia frustrana* (Comstock) (Nantucket pine tip moth), in pine plantations (especially *Pinus taeda*[L.]) in the southeastern United States. In that system, life table studies provide a much clearer understanding of the role of natural enemies under plantation conditions (Gargiullo & Berisford, 1983). However, even in this much better studied system, corresponding information about the role of natural enemies in natural pine stands is not available. Asaro et al. (2003) synthesized information on the population dynamics of this pest. Pine plantations are rapidly colonized by the pest, but damage decreases as trees age because tree leader flushing becomes increasingly out of synchrony with flights of adult moths, thereby reducing rates of successful oviposition. Parasitoids are initially rare in a newly planted block and can only colonize stands after a host population develops. This process is influenced by associated vegetation, which provides resources to parasitoids. Herbicide suppression of non-pine herbaceous vegetation initially causes tip moth intensity to increase, but trees grow more rapidly with no plant competition, leading to earlier crown closure, such that the net effect of herbicide use is positive (Ross et al., 1990). In this system, pesticide use (herbicides regularly, insecticides as needed) offsets the loss of floral resources that promotes increased tip moth density.

In theory, if basic studies of population dynamics showed that a significant drop in key natural enemies occurred when mahoganies were produced in plantations (versus natural forests); this might provide an avenue for control, if reasons for the change could be identified. Commonly advanced reasons for such changes are lack of floral resources for adult parasitoid nutrition or lack of important alternate host species needed to maintain parasitoid populations (see Barbosa, 1998; Pickett &

Bugg, 1998 for background information on these ideas). However, little or nothing has been done along these lines for mahogany plantations, in part perhaps because the fundamental population dynamics work in the forest is lacking.

An alternate means for the use of biological control in mahogany plantations was advocated by Bennett (1973) and others (see Cock, 1985 for a review), based on the new association concept. The intent of the project was to establish in the Americas, parasitoids associated in Asia with *H. robusta* and related species. Four main parasitoids were released (the chalcidid *Antrocephalus renalis* Wtstn., the braconid *Phanerotoma* sp., the eulophid *Tetrastichus spriabilis* Wtstn., and the trichogrammatid *Trichogrammatoidea robusta* Nagaraja), mainly in Belize and Trinidad-Tobago. The only recoveries made were of *T. robusta* in Trinidad (Cock, 1985). The authors of the work considered that only a small part of the available species had been tried.

A final suggested, but not implemented, approach is mass release of egg parasitoids (trichogrammatids) in mahogany plantations to kill moth eggs (Blanco-Metzler et al., 2001). But this has not been followed up on, being viewed as too expensive considering the long period over which the tree crop would have to be protected.

3.3.2. Risks Associated with Biological Control for Case VI

If the approach taken is to change plantation conditions to favor local natural enemies there is no ecological risk. If the approach taken is to make new association introductions from congeners in other biogeographic regions, risk to native species needs to be estimated and judged acceptable before making introductions. Given the limited understanding of the insect fauna of tropical areas and the relative scarcity of entomologists in developing countries, such risk assessments would be difficult to conduct. The new association approach might have fewer problems caused by such lack of information in temperate areas and countries with better known insect faunas.

3.4. Case VII: Exotic Pests in Native Tree Plantations (I-e, T-n, F-plantation). Type Example: Nantucket pine tip moth on Monterrey pine in California (USA).

3.4.1. Description and Opportunities to Use Biological Control for Case VII

Attack of a native tree by an exotic insect, when the tree is grown under plantation conditions, is much the same as the case of an exotic insect attacking a native tree under natural forest conditions (Case III). The root issue in both cases is likely to be the exotic nature of the pest (and corresponding lack in the local area of effective natural enemies). While effects of plantation production *per se* might exist and thus be additional factors promoting pest populations, this is likely to be secondary in importance. Examples of this scenario would include: (1) Nantucket pine tip moth (*R. frustrana*) as a pest of Monterrey pine (*Pinus radiata* D. Don) grown in California (where it is native) in Christmas tree plantations and (2) hemlock woolly adelgid (*A. tsugae*) in the northeastern United States on eastern hemlock (*Tsuga canadensis* Carriere) grown in nurseries for use in landscapes as hedges. In such limited acreage contexts (at least for nurseries), chemical control would be the method of choice. In the case of Christmas tree production, enough acreage may be involved to justify importation of natural enemies from the pest's native range. In fact, for Nantucket pine tip moth, the principal parasitoid (*Campoplex frustranae* Cushman, Ichneumonidae) from the pest's native range (the eastern United States) was introduced and became established in California, and a decrease in pest damage followed (Scriven & Luck, 1978). For hemlock woolly adelgid, classical biological control is being attempted in the eastern United States through the introduction of Asian ladybird beetles and derodontid beetles from western North America (Cheah & McClure, 1998; Zilahi-Balogh et al., 2002). If successful in the forest, these same ladybird beetles may also suppress the pest in nurseries.

3.4.2. Risks Associated with Biological Control for Case VII

The ecological risks of the use of biological control in this case are identical with those of Case III.

4. PESTS IN FORESTS MADE UP OF NATURALIZED EXOTIC TREES

4.1. Case VIII: Pests in Forests of Naturalized Invasive Trees (I-n or e, T-e, F-natural). Type Example: Pines in South Africa

4.1.1. Case Description and Opportunities to Use Biological Control for Case VIII

In New Zealand, Australia, and South Africa, introduced exotic pine trees have escaped from plantations and become invasive in native grasslands and forests. Some societies view the forests formed by such invaders as a weed problem (as is the case in South Africa because of impacts on water flow in afforested river basins [Moran et al., 2000]), but in other cases, these invasive but valuable trees may come to be seen as a valuable resource (Australia, *P. radiata*). In that case, it is not inconceivable to imagine the day when considerable tracts of land are covered with exotic trees growing without human effort as exotic but natural forests. Such forests, like their plantation counterparts (of the same tree species) would be subject to insect invasions. When and if such invasions occur, the pests could, if deemed in society's interests, be subject to classical biological control. Society would have to decide if the exotic tree was a friend or a foe, weighing its economic value against the ecological harm from its invasion. This would be a one time decision because once classical biological control was achieved against the pest insects, their potential value as biological weed control against the tree would be lost.

4.1.2. Risks Associated with Biological Control for Case VIII

The risks of this type of introduction are the same in Case III, but with the added requirement that a social decision on the nature of the invasive tree's status be made.

5. LESSONS FOR USE OF BIOLOGICAL CONTROL IN A WORLD OF MIX AND MATCH ECOLOGY

Lesson 1: Native pests can be targets for natural enemy introductions

Introductions of natural enemies from congeners of native pests in other biogeographic regions with similar climates are a possible route to solve some native pest problems. Difficulties in doing so, however, are greater than in classical biological control and the need to anticipate potential harmful impacts of such introductions is also greater.

Lesson 2: Pests can be created through silviculture

Modification of native forests can create new pests from formerly harmless herbivores if the modified forest is a better resource for the herbivore or it natural enemies fauna is impoverished. Such effects arise from practices applied consistently over long periods of time and are not quickly reversed. Efforts to anticipate problems should be made.

Lesson 3: Trade brings us new pests

International trade in plants and other products facilitates the introduction of species that are able to attack local native trees in natural forests. Some such introductions can be mitigated through classical biological control, but not all. Extensive damage may occur first. Every effort should be made to avoid importing forest products from forest areas in separate biogeographical regions with a similar climate. Those will be the sources of damaging invaders.

Lesson 4: If you plant it, they will come

Movement of tree species and their cultivation in plantations, while economically valuable, inherently sets the stage for subsequent pest problems. These should be anticipated and should not come as a surprise. For trees grown outside their native ranges, the eventually invasion of species from their original ecosystems should be assumed to occur eventually. Likely invaders are readily suggested by species associated with a given tree species that have already invaded other regions with plantings of the same tree. Preparations to engage in classical biological control against such pests should be made at the outset of starting large scale plantings of exotic trees in new regions.

Lesson 5: Monocultures favor pest build up

Plantations by their nature enhance the environment for local native pests able to utilize the crop tree by reducing losses caused by dispersal to find hosts (unnecessary) and mortality from natural enemies (scarcer in plantations due to reduction in vegetative diversity and alternate hosts). It should be assumed that such problems will develop and outplanting experiments should be conducted to anticipate which species of native insects are likely to become damaging in plantations and why. An appreciation of the mechanism of pest creation is needed to choose the right tools for resolving these problems.

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Table 1. Summary of biological control options for various cases of species mixing (I-VIII as discussed in body of chapter), with notes on potential benefits, economic costs, and ecological risks.

Case	*Biological control options*[a]	*Benefits*	*Economic Costs*	*Ecological Risks*
Case I.- White pine weevil in North America (I-n, T-n, F-n)	New association BC	Potentially large if successful, because control is permanent and infested area is large	Same as CBC, high at beginning due to exploration and host range testing; costs per unit fall for large infested areas	Potentially somewhat higher than CBC because species are not co-evolved and thus average host range is likely to be broader
Case II. Red oak borer in Ozarks-USA (I-n, T-n, F-modified)	Conservation BC	Low to moderate, depending on degree of efficacy	Over long periods, costs are high because they are incurred annually without end	Low to none because no new species are introduced
Case III.-Winter moth in Canada (I-e, T-n, F-n)	CBC	Potentially large if successful, because control is permanent and infested area is large	High at beginning due to exploration and host range testing; costs per unit fall for large infested areas	Moderate if host range testing reveals natural enemies with narrow host ranges

Case	*Biological control options*[a]	*Benefits*	*Economic Costs*	*Ecological Risks*
Case IV. Eucalyptus borer in CA, USA (I-e, T-e, F-plantation)	CBC	Low to moderate, since infested areas are not large	Ibid	Ibid
Case V. *O. trychiata* on pine in Colombia (I-n, T-e, F-plantation)	New association CBC	Low to moderate, since infested areas are not large	Same as CBC, high at beginning due to exploration and host range testing; costs per unit fall for large infested areas	Potentially somewhat higher than CBC because species are not co-evolved and thus average host range is likely to be broader
Case VI. *H. grandella* on mahogany in Central America (I-n, T-n, F-plantation)	New association CBC	Moderate, infested areas are not large, but product is high value	Same as CBC, high at beginning due to exploration and host range testing; costs per unit fall for large infested areas	Potentially somewhat higher than CBC because species are not co-evolved and thus average host range is likely to be broader
	Conservation BC	Low to moderate, depending on degree of efficacy	Over long periods, costs are high because they are incurred annually without end	Low to none because no new species are introduced

Table 1. (Continued)

Case	*Biological control options*[a]	*Benefits*	*Economic Costs*	*Ecological Risks*
Case VI (cont.)	Parasitoid mass release	Moderate to high, depending on level of efficacy	Typically high if effective	Moderate to low, assuming agents do not survive long or establish
Case VII. Nantucket pine tip moth on Monterey pine in CA, USA (I-e, T-n, F-plantation)	CBC	Low to moderate, since infested areas are not large	High at beginning due to exploration and host range testing; costs per unit fall for large infested areas	Moderate if host range testing reveals natural enemies with narrow host ranges
Case VIII. no known example (I-e or n, T-e, F-n but exotic)	CBC if I-e; new assoc. if I-n	Potentially large if successful, because control is permanent. Provided infested area is large	High at beginning due to exploration and host range testing; costs per unit fall for large infested areas	Moderate if host range testing reveals natural enemies with narrow host ranges

[a] Types of biological control: cbc-classical biological control via introduction of co-evolved natural enemy from native range of pest; new association-introduction of natural enemy from different species, usually one with some taxonomic or ecological similarity to the pest; conservation biological control- modification of silvicultural practices to improve conditions for key natural enemy in plantations; parasitoid mass release- release in plantations of insectary-reared natural enemies for control of pest.

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CHAPTER SIX

IMPACTS OF INSECTS IN FOREST LANDSCAPES: IMPLICATIONS FOR FOREST HEALTH MANAGEMENT

1. INTRODUCTION

The devastating forest fires and catastrophic outbreaks of both native and introduced forest insect and disease pests, witnessed in recent times throughout North America, are in part a consequence of forest management practices of the last century. The frequency and intensity of these fires and pest outbreaks exceed all historical records and many view a deteriorated state of the forest environment as a primary cause for those problems. To address this issue President George W. Bush in 2002 launched the Healthy Forest Initiative (HFI). Subsequently the Healthy Forests Restoration Act of 2003 (HFRA) became law and thereby provided a new emphasis to forest management in the US.

Forest protection deals with the agents that cause undesirable change in the conditions and resources of the forest environment. It is an applied component of forest management that traditionally includes research, development, and applications activities associated with impacts of insects, diseases and fire. Frequently issues associated with impacts of insects and diseases are considered together while fire is addressed separately. Specific direct activities of forest protection include assessing the impact of agents causing change in the forest environment; suppressing and preventing negative effects of destructive agents; monitoring forest resources and conditions; and management-planning, problem-solving, and decision-making.

The HFI and HFRA will profoundly influence the forest protection agenda of the future. Defining the specific elements of that agenda will require examining insects and diseases within the spatial dimensions of the forest landscape and in the temporal context of the process of ecological succession. Accordingly, the goal of this chapter is to consider impacts of insects in forest landscapes within the framework of forest health management. Our specific objectives are (1) to consider the evolution of forest management models in relation to forest health, (2) to consider forest health in an ecological context, (3) to consider how insects serve as

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agents for change in forests and (4) to examine two forest insect case histories of current relevance: the southern pine beetle and the red oak borer.

2. FOREST MANAGEMENT IN RELATION TO FOREST HEALTH

The structure and composition of forest landscapes in the US today are the legacies remaining from the application of a series of management models employed in forestry over a period of ca. 150 yrs. Our concepts of forest health and the current federal mandate to manage for healthy forests evolved from those different models. Below, we consider the contrast in philosophy and approach among the models. This contrast is noteworthy as it illustrates both an evolving technical knowledge base for forest management and a changing land-use management ethic. Following, we briefly review each model's basic tenets and identify where the notion of *health* entered the lexicon of forest management.

2.1. Background –the Models of Forest Management

The history of formal forest management in the US traces from the 1870s and includes five different models (Yaffee 1999): (i) dominant-use management, (ii) multiple-use management, (iii) environmentally sensitive, multiple-use management, (iv) ecosystem management, and (v) landscape management.

2.1.1. Dominant-use Management

Dominant-use was the initial model used for forest management in the US. It persisted from the 1870s through the 1950s. It is an anthropocentric (human-centered) concept that focused on a single objective or purpose and emphasized economically valuable species, e.g., pine wood or fiber production. Typically the goal was to maximize production. Protecting the means of production was also a goal and this was accomplished, in part, by manipulating ecological processes such as disturbance regimes, e.g., controlling forest fires or suppressing insect outbreaks. It is noteworthy that the dominant-use approach is still employed in special-use forests (e.g. seed orchards, nurseries, Christmas tree plantations) and on many nonfederal forests (e.g., industrial forests and forest properties owned by individuals).

2.1.2. Multiple-use Management

In multiple-use management emphasis was placed on the fact that forests could provide a variety of goods and services that were valued by humans. Clearly this model is also anthropocentric. Initially, managed forest resources included timber production, fish and wildlife, hydrology, recreation, and grazing (the list of values has been expanded today). Traditional multiple-use management sought to maximize different resource values and do so on a sustainable basis. The term *sustainability*, in this context, means continuous production of desired outputs, e.g., non-declining and even flow in the case of wood fiber (Yaffee 1999). The concept of sustainability, when applied to aesthetic values such as scenic beauty (an element of recreation), included preservation of natural vistas. The Multiple-Use Sustained Yield Act (1960) defined the model and provided the legal basis for management of National Forests in the US.

2.1.3. Environmentally Sensitive, Multiple-Use Management

Environmentally Sensitive, Multiple-Use Management also focused on the production of goods and services for human consumption. However, forests were viewed as ecological systems with biotic and abiotic components. Production was subject to ecological and environmental constraints. Key management principles included sustained yield, minimizing negative environmental impacts, and protecting species diversity. This approach recognized that alternative management regimes were possible and it added, in the case of public lands, input from stakeholder groups (citizens, corporations, organizations, governmental agencies) (Yaffee 1999). Again, this is an anthropocentric concept. The tenets of the Environmentally Sensitive, Multiple-Use Management concept were formalized in the National Forest Management Act (NFMA) of 1976. This act established a planning process for land-use management on public forests in the US. This act also provided for the creation of a Committee of Scientists to help the Secretary of Agriculture formulate the regulations needed to implement the Act. This Committee of Scientists was later commissioned to consider issues of ecosystem management (discussed below) as well. The ineffectiveness of the Environmentally Sensitive, Multiple-Use Management approach triggered public outrage that served as the genesis of the ecosystem management concept.

2.1.4. Ecosystem Management

Even though many scientists and practitioners advocated a holistic approach, there was no broad-based support for the use of ecosystem concepts in land-use management until 1993. At that time President William J. Clinton convened the Pacific Northwest Forest Conference in a response to controversy over forest management on public lands in the Pacific Northwest, US. The event was significant in that it provided authorization to enact the use of a new paradigm for federal land-use management in the US, i.e., ecosystem management. One tangible product from this activity was the Northwest Forest Plan.

Ecosystem management represents a significant departure from the production-driven models described above that emphasize forest resources. Ecosystem management is a biocentric (biologically centered) concept. The goal is to maximize ecological integrity or *health,* subject to the need to allow for sustainable human uses. Ecosystem protection is the first priority and the wants and needs of people the second (Yaffee 1999). In contrast, the previous approaches focused on maximizing human use of forest resources, subject to environmental constraints. The ecosystem concept has an ecological, science-based foundation, but the term is also used as a metaphor for holism.

Sustainability, integrity, and health are prominent elements of the concept of ecosystem management. Sustainability is defined as a function of organization, activity, and resilience of an ecosystem (Haskell et al.1992, NRC 1998). Therefore a sustainable ecosystem is one that, through a period of time and in the face of management practices, (i) retains the basic elements of its structure, (ii) has processes (which define how the system functions) that operate within normal or expected ranges (Landers et al. 1999), and (iii) the system can withstand disturbance and return to the normal condition. Sustainability also has a temporal component, which is generally defined by a number (usually three) of human generations (Forman 1995). This time frame is a practical boundary that attempts to set a realistic planning horizon. Integrity is defined simply to mean the state of being whole, entire, or undiminished. The term can refer to elements of structure or the processes associated with ecosystem function or change (Pimentel et al. 2000, Woodley et al. 1993). *Ecosystem health* is a term (and metaphor) taken from medical practice to describe conditional states of ecosystems. By definition, "an ecosystem is healthy...if it is active and maintains its organization and autonomy over time and is resilient to disturbance" (Haskell et al. 1992, Constanza 1992). The terms ecosystem health, forest ecosystem health (Bartuska 1999) and forest health are used synonymously.

Although a great deal has been written about ecosystem management and many in the forestry community embraced the basic tenets, the concept has proved difficult to implement.

2.1.5. Landscape Management

Last in the progression of the models is landscape management. Yaffee (1999) refers to this approach as ecoregional (Bailey 1998) management. This concept builds from the platform of ecosystem management discussed above. However, there are important differences. In this model, managing the forest environment is considered to be a "place-based" activity involving discrete human activities enacted on a spatially explicit land area. The management unit in this model is the landscape which is defined as "a mosaic where a cluster of local ecosystems is repeated in similar form over a kilometers-wide area" (Forman 1995). This integrative perspective of the forest environment leads to an ecocentric management ethic (combining anthropocentric and biocentric views) where emphasis is on interconnections among all landscape components. Specific elements of the biota are not emphasized, but considered as parts of the larger whole, and human activities are explicitly included.

3. THE HEALTHY FOREST INITIATIVE (HFI) AND THE HEALTHY FOREST RESTORATION ACT (HFRA)

In 2002 President George W. Bush launched the HFI as a response to widespread and destructive fires that were consuming forest lands, damaging communities, and degrading environmental quality of the Western US. The intent was to reduce hazardous fuel loads and restore healthy ecological conditions on Federal and, by implication, private forests in the US. In 2003 (10 years after the Pacific Northwest Conference) the HFRA became law and thereby provided the statutory means to implement the HFI. See < http://www.healthyforests.gov/> for details regarding the HFI and HFRA.

The HFRA does not call for a new forest management model. Rather, it is a set of guidelines for directed actions that are intended to adjust (and perhaps regulate) the conditions of the forest environment and thereby alter the frequency and amplitude of natural disturbances (fire and insect and disease outbreaks in particular). The guidelines fit within the context of the landscape management model discussed above. The state of the forest environment frequently leads to predictable responses from the agents of change, e.g., intense fires follow the accumulation of large fuel loads, extensive bark beetle outbreaks are associated with overstocked old-growth pine and spruce forests. Consequently, one means of addressing the depredations of the agents of change involves a restoration strategy that returns the forest environment to states where natural disturbances operate within normal or expected ranges. The HFRA is intended to guide the restoration processes.

The HFRA has six sections, referred to as Titles, which include the following:

Title I - Hazardous Fuel Reduction on Federal Land

Title II - Biomass

Title III - Watershed Forestry Assistance

Title IV - Insect Infestations and Related Diseases

Title V - Healthy Forests Reserve Program

Title VI - Inventory and Monitoring Programs.

Title I (Hazardous Fuel Reduction on Federal Land) directly addresses the issue wildfire on Federal lands. The principal rationale for this title is that excessive fuel loads on public lands are the immediate cause of the devastating fires and expedience in addressing the problem is needed. This title and the means proposed for implementing it have been criticized on several fronts: e.g., ambiguity associated with language describing the scope and placement of logging operations intended to reduce fuel loads; concessions regarding enforcement of a suite of existing environmental laws (such as the National Environmental Policy Act and the Endangered Species Act) and limitation of citizen involvement in management of public lands.

Our interest in this chapter centers on Title IV (Insect Infestations and Related Diseases). The purposes of this title are (1) to develop an accelerated basis and applied assessment program to combat infestations by forest-damaging insects and associated diseases, (2) to engage the stakeholders (including universities, state agencies, and private landowners) to carry out the program, and (3) to implement applied silvicultural assessments. Silviculture deals with the theory and practice of controlling forest establishment, composition, and growth. Several species of forest-damaging insects were identified to be of immediate concern: the southern pine beetle (*Dendroctonus frontalis*), mountain pine beetle (*D. ponderosae*), gypsy moth (*Lymantria dispar*), hemlock woolly adelgid (*Adelges tsugae*) emerald ash borer (*Agrilus planipennis*), and red oak borer (*Enaphalodes rufulus*). Title VI (Inventory and Monitoring Programs) also deals with forest damaging insects and diseases. That title has several foci that include the North American exotic forest information system, forest health protection, rapid pest detection program, pest suppression, forest health monitoring, and forest inventory and analysis.

4. HEALTHY FOREST RESTORATION IN AN ECOLOGICAL CONTEXT

Principles of ecology provide guidelines for directed restoration of forest landscapes. But, what from ecology is relevant? The substance of ecology has been summarized for several purposes, including characterization of the basic principles, use of ecological principles for land-use and landscape management, and use of ecological principles in planning and design.

An overview of the subject matter of ecology was provided by Cherrett (1988) who developed a rank-ordered list of the 50 most important concepts, based on input from the membership of the British Ecological Society. The listing summarizes ecology as a scientific discipline and does not emphasize land-use management; nevertheless 'ecosystem' and 'succession' were identified to be 1st and 2nd in importance in Cherrett's classification. Odum (1992) provides an additional view by identifying "twenty great ideas in ecology." The intent was to address issues in ecology in a broader context, but some of the ideas relate directly to land-use management.

The applicability of ecology to land-use management has been evaluated on several fronts with perspectives from Dale et al. (2000) and Forman (1995) being particularly relevant to healthy forest restoration. Following is a summary of those ecological principles important for managing land-use as identified in Dale et al. (2000):

> *Time*: Ecological processes function at many time scales…; and ecosystems change through time.
>
> *Species*: The particular species and networks of interacting species have key, broad-scale ecosystem-level effects.
>
> *Place*: Local climatic, hydrologic, edaphic, and geomorphological factors as well as biotic interactions strongly affect ecological processes and the abundance and distribution of species at any one place.
>
> *Disturbance*: The type, intensity, and duration of disturbance shape the characteristics of populations, communities, and ecosystems.
>
> *Landscape*: The size, shape, and spatial relationships of land-cover types influence dynamics of populations, communities, and ecosystems.

Forman (1995) defined 12 principles of landscape and regional ecology, all of which are relevant to land-use management. We selected four examples to illustrate this broad scale perspective.

> *Patch-corridor-matrix*: The arrangement of patches and corridors within a matrix is a major determinant of flows of energy, materials, and species through a landscape.
>
> *Interactions among ecosystems*: All ecosystems in a landscape are interrelated, but ecosystems in close proximity exchange energy, materials, and species more freely.
>
> *Metapopulation dynamics*: For subpopulations in a landscape, the local extinction rate decreases as patch size increases, and recolonization increases as a function of the presence of corridors, stepping stones, or short inter-patch distance.
>
> *Landscape change*: Land transformation results in perforation, fragmentation, and attrition of landscape elements which contributes to habitat loss and isolation.

Also relevant to the discussion are the principles of ecology with respect to landscape design and planning (Karr 2002). This perspective was presented in the context of a broader discussion on ecology and design in which ecologists and landscape architects collaborated (Johnson and Hill 2002). Rather than provide specific principles, Karr (2002) identified and defined key words for ecological thinking. The words, which abstract broad ecological issues, include the following:

Integrity and Health
System and Scale
Landscape and Context
Parts and Processes
Natural History and Life Cycle
Resilience and Resistance
Disturbance and Equilibrium
Change and Change
Trajectory and Cycles
Connections, Limits, and Collapse
Root Causes and Patterns
Effect, Consequence, Aftermath
Simplification, Complexity, and Diversity
Uncertainty and Surprise

At the beginning of this section we asked the question "what from ecology is relevant to forest restoration." The principles and concepts identified and summarized by Cherrett (1988), Odum (1992), Forman (1995), Dale et al. (2000), and Karr (2002) illustrate the utility and fundamental importance of ecological science in guiding forest restoration in particular and land-use management in general. However, the difficult question is "how can we use principles of ecological science, in combination with knowledge from other subject domains, to modify and manipulate landscape structure, function, and rate of change in predictable ways"?

This challenging question is the central issue of landscape management and a fundamental element of the HFRA.

5. HOW INSECTS SERVE AS AGENTS FOR CHANGE IN FORESTS

Forest landscapes change as a result of four basic processes: activities of organisms living in the environment, activities of humans (cultural disturbances), occurrence of natural disturbances, and through operation of geomorphic processes. Our focus centers on impact of insects as components of living organisms present in the forest environment. We define the term impact broadly to mean any effect on the forest environment resulting from activities of insects and other arthropods. The effects are seen as qualitative or quantitative change in forest conditions (the state of the forest environment) and/or resources (all things consumed within the forest environment) and those effects can be positive or negative (Fig. 1). Following, we briefly describe how insects impact forest conditions and resources, and conclude by placing impact assessment in the context of ecological succession.

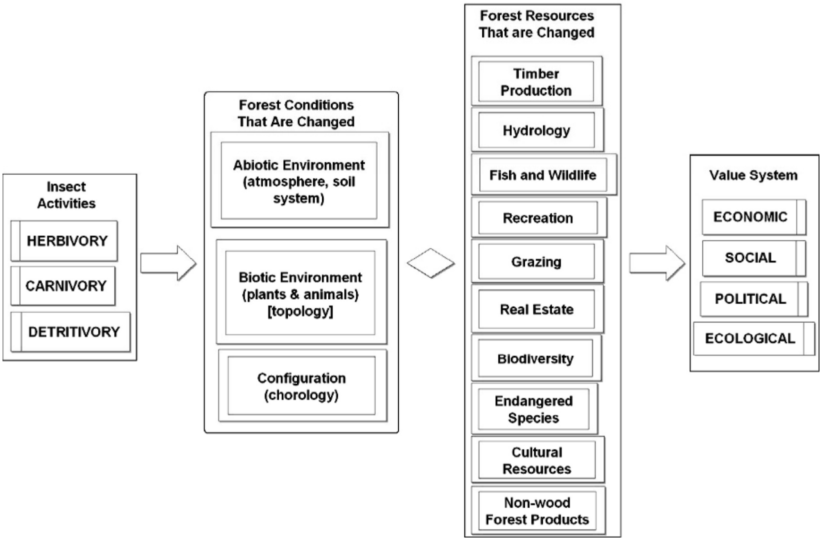

Figure 1. Activities of insects affect the conditions and resources of forest landscapes. Assessment of impact requires an evaluation through a value system. (Knowledge Engineering Laboratory, Texas A&M University).

5.1. Changes in Forest Conditions Caused by Insects

Insects, as herbivores, carnivores and detritivores, bring about change in forest conditions. In particular insects influence the state of the abiotic environment, the biotic environment and forest configuration (Fig. 1).

5.1.1. The Abiotic Environment

Insects influence the abiotic environment principally by accelerating rates of decomposition and nutrient cycling. Nutrients become locked up in living biomass, which reduces their availability to the community. If plants and their consumers were not decomposed, the supply of nutrients would eventually be exhausted. Insects and other arthropods maintain forest productivity through decomposition of plant debris, animal carcasses, and excreta. Many of the species, as well as microorganisms, are associated with the leaf litter and soil (Coleman and Crossley 1996). The interaction of decomposition and mineralization processes provides nutrients to the soil that are used by green plants for growth, development, and reproduction.

5.1.2. The Biotic Environment

Insects influence the biotic environment in a myriad of ways. Forest entomologists tend to focus on activities of herbivorous insects. In some instances plant parts (leaves, stems, branches, cones, etc.) are the targets of herbivory and in other instances entire individuals are actually killed (Harper 1977 and Harper et al. 1986). Herbivory impacts the forest in different ways: killing selected species of trees, altering plant community species composition and age structure, weakening trees and increasing their vulnerability to plant pathogens and natural disturbances, modifying the growth form and appearance of trees, reducing food supplies used by other herbivores, reducing or enhancing regeneration, and fertilizing the forest floor (Coulson and Wunneburger 2000). In addition, reproduction of many flowering plants in the forest is dependent on insect pollinators (Coulson et al. 2005). The interest in activities of carnivorous insects in forests has traditionally centered on the impact of insect parasitoids and predators as regulators of populations of pest herbivore species, i.e., as biological control agents. In their role as disease vectors insects also can have a dramatic impact on population dynamics of wildlife species.

5.1.3. Forest Configuration

Forest configuration can also be influenced by insect activity. Forest configuration deals with the kinds of ecosystems that form the landscape and their size, shape, number, and arrangement. Selective herbivory that results in tree mortality creates both structural and age class diversity within forest landscapes, i.e., more and different kinds of patches. In some instances configuration is directly influenced by insect herbivory. For example, bark beetles in the genus *Dendroctonus* (Coleoptera: Scolytidae) often select and kill tree in older age classes of their preferred host species. Herbivory, which results in host tree death, creates disturbance patches in the forest matrix. These patches can range in size from less than 1.0 to several hundred ha. Defoliating insects (e.g., the Gypsy moth (*Lymantria* dispar), Douglas-fir tussock moth (*Orgyia pseudotsugata*), spruce budworms *(Choristoneura* spp., etc.) can also alter forest landscape structure by selectively removing tree species or creating disturbance patches. Furthermore, insects acting as vectors of plant pathogens can effect change in the configuration of forest landscapes. There are several noteworthy examples. The chestnut blight, caused by *Cryphonectria parasitica* eliminated American chestnut, *Castanea dentata*, from the deciduous forest of the eastern US. The epidemiology of this disease was linked to both insect and bird vectors. Likewise, Dutch elm disease, *Ophiostoma ulmi*, markedly changed the urban landscape of the northeastern and midwestern US by selectively eliminating American elm, *Ulmus americana*. This disease is vectored by the smaller European elm bark beetle (*Scolytus multistriatus*) and by the native elm bark beetle (*Hylurgopinus rufipes*). Effects of insect herbivory are often amplified by natural disturbances. Openings in the forest matrix caused by herbivory can be expanded by events such as wind and ice storms.

5.2. Changes in Forest Resources Caused by Insects

In this section we examine how insects as herbivores, carnivores and detritivores bring about change in forest resources. Although the landscape model of forest management is ecocentric, the concept also emphasizes the importance of forest resources for human consumption. Given this reality, impact assessment often centers on situations where insects compete with humans for valued goods and services. In particular insect herbivory and carnivory often disrupt management plans and schedules, deplete the quantity or degrade the quality of resources, and interfere with human uses of the forest environment.

Our focus here centers on insects as pests and we examine some of the major types of insect impacts on forest resources. It is important to recognize that each of the feeding groups (Coulson and Witter 1984) affects forests in different ways. The exact nature and extent of the impact is determined by (1) the resource of concern, (2) the type of insect activity, (3) the size and distribution of the insect population, and (4) the metrics used for evaluation.

5.2.1. Timber Production

In intensively and extensively managed production forests, insect herbivory is often the issue of greatest concern to forest managers. Herbivory can directly affect the economics of timber and fiber production, which is a principal management goal.

5.2.2. Hydrology

Hydrologic impacts of insects on forests are measured in terms of water quantity (yield), timing and duration of high and low flows (regimen), and water quality. In general, outbreaks in forests increase water yield and decrease water retention time on watersheds. These circumstances occur because reduced vegetation levels, resulting from insect herbivory, decrease the rate of evapotranspiration and increase the rate of runoff. A striking example where water retention is increased may be seen in interior British Columbia where mountain pine beetle has killed millions of lodgepole pine, *Pinus contorta*, and eliminated the primary means for evapotranspiration, transforming some forest lands into virtual swamps. Water quality is influenced in several ways: increased nutrient content of streams (primarily nitrogen and phosphorous) and organic debris, increased turbidity, and slightly increased temperature. Nutrient loading of streams and increased turbidity occur as a result of increased levels of insect frass production. Increases in stream temperature occur because of reduced shading resulting from tree mortality or defoliation.

5.2.3. Fish and Wildlife

Insects have profound impacts on fish and wildlife populations. Outbreaks of phytophagous insects are of particular importance to wildlife in forests, as stand parameters such as vegetation density, species composition, and age structure are modified. Changing vegetation patterns also influence fish populations by modifying water quality and quantity. Of course insects serve as primary or secondary food sources for insectivorous birds, mammals, and fish. During outbreaks, these insectivores exploit high insect population densities. In some instances insects are parasites of wildlife species and as such may serve as vectors of disease organisms, as they may also do in humans.

5.2.4. Recreation

Forests are used for many types of recreation. The most popular include walking, non-consumptive wildlife activities, biking, sightseeing, non-pool swimming, fishing, family gathering, and picnicking. There are five distinctly different phases of outdoor recreation: anticipation, travel, on-site experience, travel back, and recollection. Insects can have an impact on recreation by intervening in one or more of these phases. Negative or positive impacts influence not only the individual(s) involved directly in the recreation activity, but the service industries that provide the facilities and means for recreation.

5.2.5. Grazing

Phytophagous insects can affect domesticated and wild herbivores by increasing grazing capacity of the forest. This circumstance occurs when the activities of insects (e.g., defoliation, tree mortality) create conditions that support greater forage production. In general, although grazing capacity of the forest may be increased as a result of insect outbreaks, the value of the benefits, in terms of cash receipts for livestock, is negligible. Furthermore, other values such as timber and fiber production are affected to a greater degree by insect outbreaks.

5.2.6. Real Estate

We define real estate to be “land, including the buildings or improvements on it and its natural assets, as minerals, water, trees, etc”. The issues associated with insect impacts on real estate vary with type of forest environment. In urban/suburban forests and special use settings, such as city parks, human enterprise often modifies the environment in ways that amplify insect impacts. Insect outbreaks are often triggered by disturbances associated with road construction, modification of drainage patterns, soil compaction, application of fertilizer and herbicides, and introduction of exotic plant species. Aggregation of human activities in urban/suburban forests increases concentrations of atmospheric pollutants, such as photochemical oxidants, which further stress vegetation. Under these stress conditions, outbreaks of phytophagous insects often occur and tree mortality follows. Insects also impact real estate in production forests. Natural cycles in abundance of noxious pests influence human use of the forest environment.

5.2.7. Biodiversity

Insects influence forest biodiversity both through their own taxonomic composition and as a consequence of their activities in those forests. In contrast to other taxa, insects are distinctive in their variety of trophic interactions, environmental adaptations, ecological services provided, niche exploitations, etc. (Coulson and Crossley 1987). Insects serve as essential links in both grazing and detritus food chains. Insect biodiversity contributes to the stability (resistance and resilience) of forest ecosystems. Insects, acting as disturbance agents, serve to trigger ecosystem succession and invasive exotic insect species may reduce forest biodiversity by killing particular plant species. Native insects that are noteworthy disturbance agents include bark beetles in the genus *Dendroctonus*, the Douglas-fir tussock moth (*Orgyia pseudotsugata*) and the spruce budworms (*Choristoneura fumiferana* and *C. occidentalis*). Examples of exotic insects changing forest biodiversity include the gypsy moth (*Lymantria dispar*), hemlock wooly adelgid (*Adelges tsugae*) and more recently emerald ash borer (*Agrilus planipennis*).

5.2.8. Endangered Species

Loss and isolation of critical habitat needed for survival, growth, and reproduction are central issues in endangered species protection. Outbreaks of phytophagous forest insects, as well as actions taken by humans to suppress populations and/or to prevent damage can affect endangered species. The ability of southern pine beetle to kill pines in which Red-cockaded woodpeckers nest illustrates a dramatic interaction between forest insect herbivory and an endangered species.

5.2.9. Cultural Resources

Cultural resources associated with forests encompass both present and past human uses and include ethnological, anthropological, and archaeological components. Insects impact each component (Coulson & Schneider 1992).

5.2.10. Non-wood Forest Products

Most non-wood forest products are commodities extracted and used by humans. Included are food products, spices and condiments, industrial plant oils, plant gums, natural pigments, oleoresins, fibers, vegetable tanning materials, latex, insect products, incense woods, plant insecticides, medicinal plants and animal products. When insects have an impact on these commodities, it is in their role as consumers and hence competitors with humans. Insects are also the source of several valued non-wood forest commodities such as honey and wax from honey bees, *Apis mellifera*.

5.3. Placing Value on Insect Impacts

In the previous sections we examined how insects as herbivores, carnivores, and decomposers affect forest conditions and resources. Whether their impacts are perceived as good, bad, or inconsequential requires a value system. Impact can be viewed categorically from ecological, economic, social, and political perspectives (Fig. 1).

Ecological impact refers to the functional roles that insects play in forests. By functional roles, we mean the activities of insects that affect the forest environment. Our focus can be directed to insect effects on individual trees, plant (and litter/soil and aquatic) communities, forest ecosystems, and forested landscapes.

Economic impact is simply defined as the effect of insects (and other injurious agencies) on the monetary receipts from the production of goods and services on forest lands. Specifically, an economic impact occurs when there is any change in (i) a socially useful forest product, (ii) socially useful items needed to produce a fixed level of forest products, or (iii) the distribution of forest products, the income derived from them, or the cost of production. Therefore, economic impact has three elements: production level, inputs for production, and the distribution of production and costs.

Social (axiological) impact refers to the effects of insects on aesthetic, moral, and metaphysical values associated with forests. Social impacts are difficult to express in quantitative terms but, nevertheless, represent a category of impact important to a large segment of forest users. In general, aesthetic values stem from recreational uses of forest; that is, aesthetic values usually occur in conjunction with other primary activities such as hunting, fishing, and camping.

Political impact refers to the effects of insects on the forest environment that result in actions, practices, and policies of local, state, or federal governmental agencies. The mechanism of political impact is the corpus of laws and regulations that have evolved to provide for protection, conservation, and use of public and private forests (Smardon and Karp 1993). From a forest protection perspective, we are particularly concerned with (i) laws that charter and enable governmental agencies (e.g., the USDA Forest Service), (ii) laws that govern forest management practice and policy (e.g., the Wilderness Act, the Healthy Forest Restoration Act), and (iii) laws that regulate inter- and intra-movement of plant and animal materials (e.g., the Plant Pest Act).

6. IMPACT ASSESSMENT IN THE CONTEXT OF ECOLOGICAL SUCCESSION

Implementation of the HFRA will involve the modification and manipulation of forest landscape structure (linkage and configuration of constituent ecosystems), function (flux of energy, materials, and species), and rate of change. One goal of this activity will be to adjust (and perhaps regulate) conditions of the forest environment and thereby alter frequency and amplitude of natural disturbances (fire, insect, and disease outbreaks in particular).

Implicit in the concept of restoration is that there is a fundamental understanding of the normal (nominal) conditional states through which a forest landscape passes as it ages. Information about change in ecological systems (ecosystems or landscapes) is summarized in literature dealing with the concept of ecological succession. Ecological succession is an active process that involves change in both the organisms and physical environment (Odum 1997).

Ecological succession is envisioned to be a cyclic process consisting of four principal stages: exploitation, conservation, release, and reorganization (Holling 1986, 1991, 1992, 1995). These stages roughly correspond to birth, growth, death, and renewal (Fig. 2). In the exploitation stage, rapid colonization by plants and animals of recently disturbed areas occurs. In the conservation stage there is slow

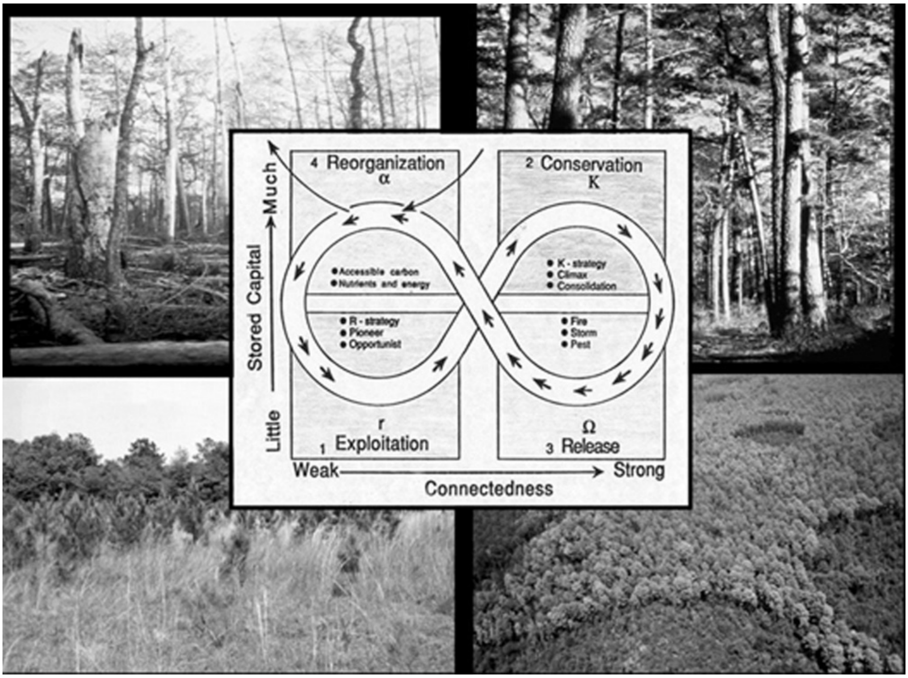

Figure 2. The general model of ecological succession (Modified from Holling 1992).

accumulation and storage of energy and materials (referred to collectively as "capital"). In the release stage (which is also referred to as the "creative destruction" stage), the accumulated and tightly bound biomass and nutrients are suddenly liberated by agents such as insect outbreaks, intense episodes of grazing, windstorms, forest fires, etc. The organization ("connectedness") of the landscape is diminished. In the reorganization phase, the operation of soil processes minimizes leaching and assembles nutrients so that they become available for the next phase of exploitation (Holling 1995). Fig. 2 illustrates an instance of each of these stages in the succession of a loblolly pine forest ecosystem in the Southern US.

There are several noteworthy features in Holling's model of ecological succession: (i) During the cycle, biological time flows unevenly. (ii) The release → reorganization sequence is rapid. Resilience and recovery of the constituent ecosystems are determined in this sequence. (iii) The exploitation → conservation sequence is slow. Stability and productivity of the ecosystems are determined in this sequence. (iv) In some instances the impact of disturbance events (in the release phase) leads to a new type of ecosystem with different attributes. In this model, insect and disease outbreaks are considered to be normal and expected occurrences.

Although the details of ecological succession in different forest landscapes vary, the processes are the same. Ecological succession provides a model for evaluating the probable consequences of specific forest restoration activities. It also provides a means for diagnosing why certain forest management practices have led to dysfunctional conditional states.

7. CASE HISTORIES: THE SOUTHERN PINE BEETLE AND THE RED OAK BORER

7.1.1. Southern Pine Beetle Impact on Forest Landscape Structure

The southern pine beetle (Fig. 3) is a cryptic insect that spends most of its life history in the inner bark of host trees. Southern pine beetles attack their host trees in mass and if successful they kill the tree, reproduce within the host and their brood development is completed there. The host tree provides a protected habitat as well as food resources. Upon completion of a life cycle, the brood adults disperse to attack and colonize a new host.

There are three types of habitat targets required by the insect in a forest landscape mosaic: acceptable host species, susceptible habitat patches, and lightning-struck hosts. Acceptable host species include all pine species within the native range of southern pine beetle, but primarily the commercially important species of southern yellow pines: loblolly (*Pinus taeda*) and shortleaf (*P. echinata*). Susceptible habitat patches include stands containing mature loblolly or shortleaf pine with high basal area and stagnate radial growth. Such stands are considered to be high hazard. When southern pine beetle is present in high hazard stands the forest landscape is at risk (Paine et al. 1984). These stands are important in southern pine beetle epizootiology as they represent habitat patches and they are suitable for growth (enlargement) of infestations. In some instances the infestations can occupy several ha. A pine forest landscape mosaic generally consists of a collection of patches (stands) that range from low to high hazard. Lightning-struck hosts represent a special instance of an acceptable host species. The insect can locate these hosts and easily colonize them. Presumably southern pine beetle identifies the hosts from resin volatiles produced as a consequence of lightning striking the tree. The strike also diminishes the effectiveness of the resin system as a defense mechanism. Lightning-struck hosts function as epicenters for the initiation of multiple-tree infestations, refuges for dispersing beetles, and stepping stones that link southern pine beetle populations in habitat patches (Coulson et al. 1999).

Schowalter et al. (1981) considered the role of the southern pine beetle and fire in maintenance of structure and function of the southeastern coniferous forest. They suggested that herbivory by the insect served to truncate ecosystem development at a time when the forest had become stagnant or "overconnected." In the Holling (1992) scheme of ecosystem succession, the southern pine beetle serves as the agent of creative destruction and its actions result in the release of tightly bound biomass and nutrients associated with the large trees of old-growth forests.

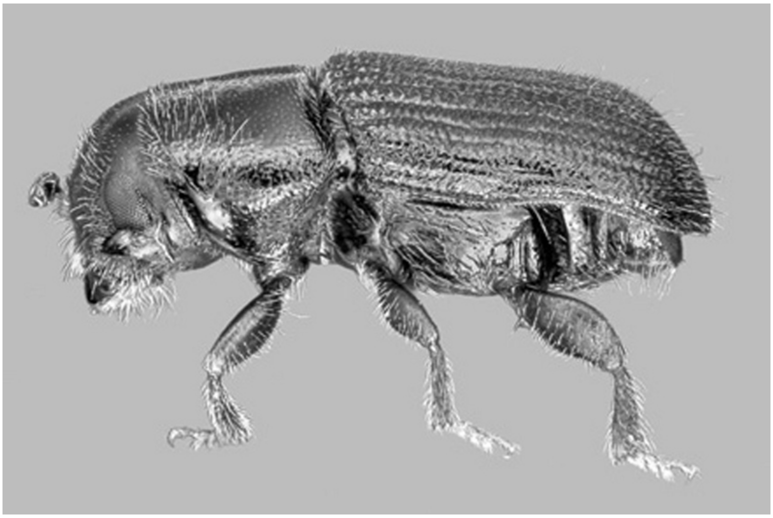

Figure 3. An adult southern pine beetle (2003 University of Florida, D. T. Almquist, photographer).

How this scenario plays out in an actual pine forest is very much a function of the structure of the landscape. Fig. 4 represents a specific instance of herbivory that occurred over several years in the Little Lake Creek Wilderness Area on the Sam Houston National Forest in southeast Texas (US). This 1,495 ha landscape was vegetated primarily with uniform old-growth loblolly pine (Fig. 5). Several infestations of the southern pine beetle occurred in the forest and created isolated patches (Fig. 6). Regeneration of pines within the patches followed and this circumstance introduced a new age structure to the forest landscape. Later, a

Figure 4. Change in landscape structure brought about by herbivory of the southern pine beetle on Little Lake Wilderness Area, Sam Houston National Forest, Southeast, TX (Knowledge Engineering Laboratory, Texas A&M University).

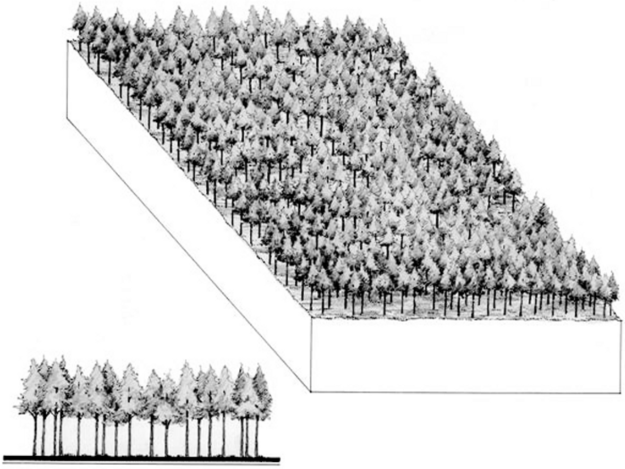

Figure 5. Pine forest landscape consisting of contiguous old-growth (60 years +) yellow pine, which provides suitable habitat and food for the southern pine beetle.

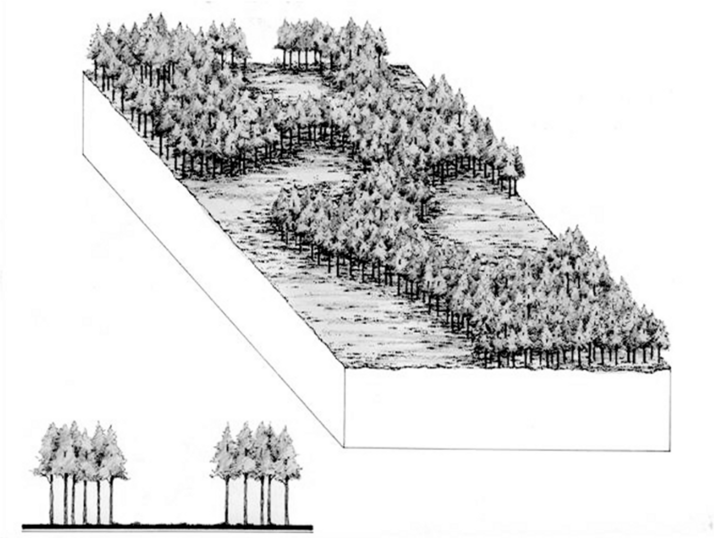

Figure 6. Several infestations of the southern pine occurring during the same season created isolated patches. Rates of decomposition of infested host trees proceeds rapidly in the Southern US. Regeneration of pines within the patches commonly occurs.

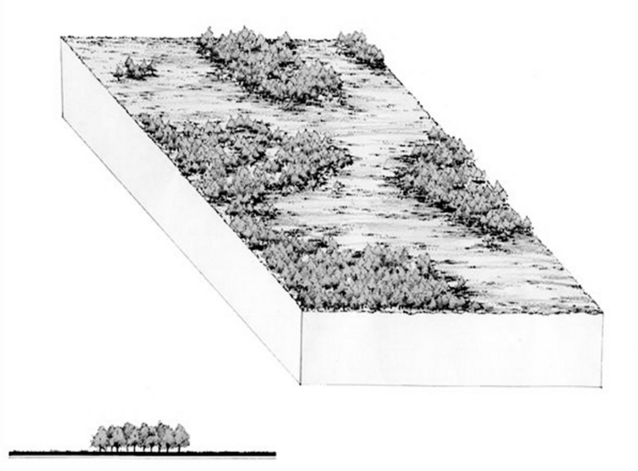

Figure 7. A large infestation of the southern pine followed and the remaining old-growth pines were killed. Again, regeneration of pines occurred.

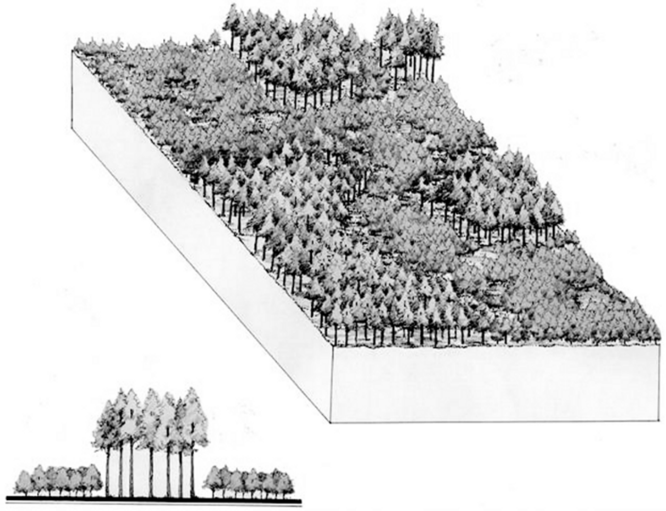

Figure 8. The structure of the forest landscape was fundamentally altered by the sequence of herbivory. Herbivory by the southern pine beetle introduced a new age structure and resulted in fragmentation of the forest landscape.

massive infestation of the southern pine beetle resulted in mortality to the remaining old-growth pines (Fig. 7). Again, regeneration of pines followed. However, the structure of the pine forest landscape was fundamentally altered by the sequence of herbivory (Fig. 8). Growth of pines in the initial infestations had progressed and these patches now contained the oldest age class present in the landscape. Herbivory by the southern pine beetle introduced a new age structure and resulted in fragmentation of the forest landscape. Infestations of the southern pine beetle will occur again as the forest matures, but the impact will be ameliorated by the fact that large contiguous areas of old-growth pine no longer exist.

This example illustrates how southern pine beetle herbivory impacts forest landscape structure (i.e., components of the landscape and their linkages and configurations). As wilderness areas within National Forests are not managed for commercial purposes, the forest uses affected are primarily fish and wildlife, recreation, hydrology, biodiversity, endangered species, and cultural resources. The impacts are mainly ecological and social (Coulson & Wunneburger 2000).

7.1.2. Red Oak Borer Impact on Ozark Forests

In 1999 and 2000, the oak-hickory forests of the Ozark Mountains in Arkansas, Missouri and Oklahoma began to show evidence of extensive mortality to red oaks. The USDA Forest Service estimated that in excess of 180,000 ha. has been impacted (Heitzman et al. 2004). Examination of these forests (Fig. 9) revealed tens of thousands of oak trees with poor crowns, die-back of small branches, and holes in the basal stems resulting from emerging beetles. When pest management specialists searched for causes of this oak mortality they concluded that these forests were suffering from oak decline, but the primary contributor to oak mortality was a native cerambycid beetle, the red oak borer (*Enaphalodes rufulus* (Haldeman). Although red oak borer is native to North America, it had never been considered an important mortality factor previously, nor had it ever been reported as contributing to tree mortality during an oak decline episode.

Figure 9. Impact of the red oak borer on oak forests of the Ozark Mountains in Arkansas, Missouri and Oklahoma.

The red oak borer is a cryptic species that spends most of its life cycle in the phloem and xylem tissue of living oaks, primarily those in the red oak subgenus, *Erythrobalanus*. It has an unusual life history with synchronous adult emergence occurring only in summers of odd numbered years. The adults are large brownish beetles that are active primarily at night (Fig. 10), do not feed as adults, lay their eggs singly under bark and lichens on the trunks of their host oak trees, and live only for a few weeks. Eggs hatch shortly after oviposition, larvae chew through the hard outer bark, and begin to feed in phloem tissue, where they overwinter and resume feeding activity in the following spring. By early summer their feeding behavior has changed and they begin constructing feeding galleries into the xylem tissue. They remain and feed in these galleries during the summer and fall, overwinter a second time, then feed for a short time in the subsequent spring. The insect pupates and emerges in the summer of their second year. Research by Hay (1974), Donley and Acciatvati (1980) and others outlined this life history, and confirmed that red oak borer population densities in trees rarely reached more than one or two individual large larvae or adults --- not enough to kill or severely damage most trees. The

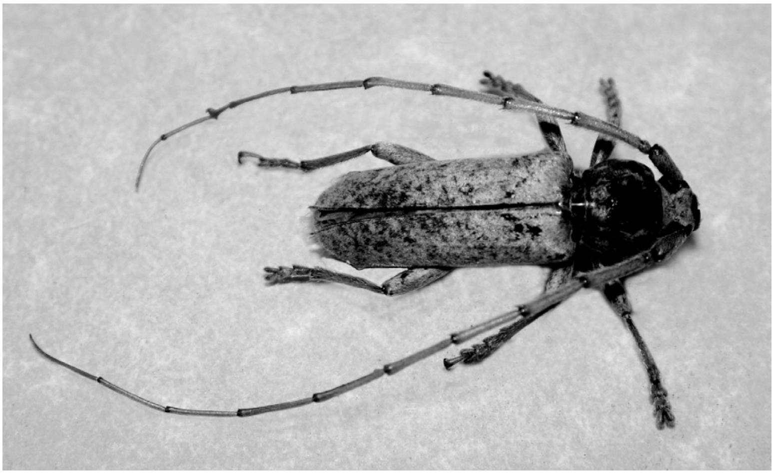

Figure 10. Adult red oak borer, Enaphalodes rufulus.

current outbreak in the Ozarks is unique in the fact that red oak borer populations are orders of magnitude higher than ever previously reported (Stephen et al. 2001) (Fig. 11). In 1984, Donley and Rast reported an average attack density of 2.0 per entire tree bole from 144 oaks in Pennsylvania. In the same study they found an average of 3.6 attacks per tree from 277 trees in Indiana. Hay (1974) studied red oak borer for three generations, over a seven-year period and reported similar results in Ohio. In the Ozarks, Fierke et al. (2005) found an average attack density of 600

Figure 11. Larvae of the red oak borer. The outbreak in the Ozarks is unique in the fact that red oak borer populations are orders of magnitude higher than ever previously reported.

per tree from 38 trees. The underlying mechanism for this remarkable population increase is not yet known.

The Ozark Mountains are prehistorically old (Paleozoic) and were formed by uplift and subsequent erosion. They are comprised in large part by sandstone and limestone formations and the forests that grow on them are those that are associated with xeric conditions and dry sandy soils. When European settlers began to arrive in the early 1800's they found large expanses of forests that had been subject to frequent burning by Native Americans. These forests were dominated by oaks (*Quercus* species) and in some areas shortleaf pine (*Pinus echinata*). The first settlers cut timber to clear land for agriculture, but later the valuable oak lumber was extensively harvested (to move the railroads west), resulting in nearly complete deforestation of much of the Ozarks by the early 1900's. Formation of the Ozark National Forest in the early 1900's resulted in protection and management of forests in a manner that promoted oaks. Oaks were favored both through advance regeneration and because cut oak stumps vigorously sprout. Subsequent enthusiastic fire suppression policies resulted in forests that today are often overstocked and with two-thirds of the total basal area in oak and of this often fifty percent are red oaks, many of which now are overmature to senescent.

Forest decline, a gradual failure of health, has been a subject of interest and controversy since the early 20th century (Millers et al. 1989). It is clear that forests in decline are not healthy in the traditional sense. Numerous authors have addressed the concepts associated with decline events and speculated as to their causes. Sinclair (1965) suggested that decline events develop from non-linear interactions of multiple factors; what he termed 'predisposing', 'inciting' and 'contributing' factors. The long-term slowly changing factors, such as soil, site and climate predispose trees' ability to withstand injury-inducing agents. Inciting factors such as short-term drought or insect defoliation then often become responsible for the first visible features of decline, i.e., reduction in carbohydrate reserves, small branch dieback, and reduction in growth (Sinclair 1965). Building on Sinclair's conceptual framework, Manion (1991), expanded these ideas into a definition of what he termed 'decline disease' that included an ordered progression of interchangeable abiotic and biotic factors that results in gradual deterioration of tree health and often ends in tree death. Many of the biotic agents considered as inciting or contributing factors are pathogens such as *Armillaria* root rot or insects. Severe defoliation by gypsy moth, canker worms, leaf rollers and others have been repeatedly identified as inciting factors, while two-lined chestnut borer (*Agrilis bilineatus*) and other stem and twig borers are common contributing factors. These factors are often normal and appropriate progression in forest succession. Manion terms this the 'decline disease spiral.'

Mueller-Dombois (1986, 1992) emphasized the importance of tree genetics and normal aging in developing the idea of cohort senescence. Within this context, forest stands may form as a result of disturbance events such as hurricanes, fire or clearcuts and become mature and over-mature at different rates and in a spatially differentiated manner. The stands may then be subject to a disturbance event, often abiotic, such as drought, which triggers the process of synchronous stand-level mortality. Mueller-Dombois (1983) puts forth an interesting perspective on 'decline diseases' in suggesting that these tree diebacks, or plant population diebacks should be considered in the context of plant population dynamics, community ecology and succession. His view can well be extended to more complete studies of forest health. 'Healthy' or 'unhealthy' forests should be diagnosed and considered not as a snapshot in time, but rather in the context of ecological succession, where dynamic forest conditions that now appear unhealthy may be moving normally along successional trends to healthy conditions (Fig. 2). Forest stands in the Ozark Mountains are now providing an abundance of senescent and weakened trees for the red oak borer. Under this scenario, this normally endemic insect is perhaps simply the fortunate recipient of this abundant food resource and acting as the unexpected agent of change in this process of ecological succession.

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ANDREA BATTISTI

CHAPTER SEVEN

INSECT POPULATIONS IN RELATION TO ENVIRONMENTAL CHANGE IN FORESTS OF TEMPERATE EUROPE

1. FORESTRY IN EUROPE

Main focus of this paper is the forests of Europe included in the vegetation zones (Fig. 1).

1.1. Mediterranean zone

Forest trees are an important component of Mediterranean flora; the number of tree species is larger compared to Central Europe (100 vs. 30, respectively), with the genus *Quercus* alone having more than 20 species in the region (Scarascia-Mugnozza et al., 2000). The distribution of forests around the Mediterranean basin is rather uneven, as 65% of the forest area is found on the Northern rim, whereas the remaining area is almost equally divided between Northern Africa and the Near-East. The proportion of forest cover in relation to the total land area is also quite different among Mediterranean sub-regions: it varies from 20 to 30% in the Northern countries to 1–8 and 5–10% in Southern and Eastern countries (Scarascia-Mugnozza et al., 2000).

Nevertheless it must be stressed that Mediterranean forests - around 81 million hectares - are rather unique ecosystems accounting for about 1.5% of the planet forests (Fabbio et al., 2003). In addition, some 80–90% of these unique types of forests are concentrated in the Mediterranean Region, the rest being split amongst small areas of Australia, South Africa, California and Chile.

The area is characterized by harsh and unpredictable Mediterranean-type climate, associated with recurrent disturbance related to fire and an intense use of livestock farming, major determinant of forest transformation into open woodland. The climate change is the recent, further large-scale disturbance increasing climatic extremes occurrence as prolonged summer drought, high temperatures and associate rainfall decrease.

T. D. Paine (ed.), Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems, 127–140.

Figure 1. Distribution of forest area in Europe, indicate by gray shading (from FAO 2000, Forest Resources Assessment: http://www.fao.org/forestry/fo/country/index). The continuous and dotted lines show the approximate upper boundary of the temperate and Mediterranean zones, respectively.

1.2. Temperate zone

As the term ‘temperate’ is often vague and ambiguous (Spiecker, 2003), because of it covers a too wide area, where insects may show dramatic differences in life cycle and phenology, we prefer to follow here the terminology used by Flora Nordica (Jonsell, 2004), with the addition of the alpine type of forests. The ‘nemoral zone’ represents the main part of central Europe, with forests of deciduous trees such as European beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*) and a limited presence of coniferous trees, mainly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). All of the nemoral zone has been deeply modified by man’s activities during thousands of years. The original ratio between broadleaved tree forests and coniferous forests of 7:3 changed to its opposite, followed by a great increase in both stand productivity and pest outbreaks (Schwerdtfeger, 1981; Baltensweiler, 1985; Ellenberg, 1986). Main result is that today the area covered by coniferous species expands far beyond the limits of their natural range. The area of beech, oaks (*Quercus* sp.), and other broadleaved species has been reduced while the area of Scots pine and Norway spruce has been increased substantially (Spiecker, 2003).

There is a substantial variation in the climate of nemoral zone, as the Atlantic climate in the western part turns to a continental climate with decreasing humidity and higher temperature variation in the eastern part of Europe. This fact has consequences on both forest composition and herbivore's biology.

The 'alpine zone' includes the main mountain chains of central Europe, i.e. the Alps, the Carpathians and parts of the Balkans, where the low temperature related to the high altitude is the main limiting factor for tree growth. There is a strong similarity with the boreal zone of the North, however the rugged topography and the consequent rapid change of elevation and aspect creates conditions which deserve to be considered separately, especially for the consequences they may have on herbivore's populations. Native coniferous trees are predominant here, even if the human activity has deeply modified the landscape in centuries of logging and livestock breeding (Ellenberg, 1986). The present use of the territory, especially for tourism, and the climate change are serious threats for these ecosystems, which are at the same time very important spots for the protection of the biodiversity.

At upper latitudes, a transition between nemoral and boreal conditions (boreo-nemoral zone according to Jonsell, 2004) is observed in a large belt of southern Fennoscandia and Eastern Europe. Coniferous forests, mainly pine and spruce, prevail excepted in the most western part, whereas a few broadleaved trees find here the northern limit of their ranges, as for beech and pedunculate oak (*Quercus robur*). More northern the boreal zone is characterized by conifer forests and mountain birch (*Betula pubescens*).

2. ENVIRONMENTAL CHANGE AND FORESTRY

2.1. Effects of climate change

Climate change information has been used for modeling the future of the forests in Europe. In the Netherlands, a gap model predicts a reduction of Scots pine and an increase of broadleaved species (van der Meer et al., 2002). A mechanistic model for central Europe predicts more broadleaved species in spruce stands and claims benefits for carbon sink, soil quality, water balance, but does not take into consideration any likely effect on herbivores and pathogens (Pietsch & Hasenauer, 2002). A regional gap model predicts more broadleaved species entering the Scots pine stands in the Brandeburg area, but overall diversity decreases (Lasch et al., 2002). Lindner et al. (2002) developed the method of Integrated Assessment to understand the effects of climate change on the forests at all levels. The high complexity of the model makes predictions uncertain.

These predictions and the new demands of the society for a multipurpose function of forests, with primary attention paid to water-related issues and relevant importance of non-wood forest products (European Commission, 2002; Fabbio et al., 2003), have been taken as the premise for planning long-term projects of conversion of the pure coniferous stands to stands mixed with broadleaved species

(Spiecker et al., 2004). The assumptions are that mixed stands improve sustainability, resilience, and biodiversity. Evidence for this is given mainly on observational data, often extended over several years, whereas experimental testing is scarce due to the obvious difficulties related to the forest size and distribution. The biodiversity-stability theory has been often invoked for justifying decisions in forest management, however much debate is going on about this (Price, 1984; McCann, 2000) and there is a growing need for assessing how much mixed stands can improve the ecosystem stability and resilience.

Different types of consequences can be envisaged for the vegetation zones. In the Mediterranean there will be a loss of tree species, because the warmer conditions may cause the local extinction of taxa, associated with the simplification of the forest ecosystems. The higher frequency of drought may depress the growth and modify the tree physiology. In the temperate zone the warming will progressively contribute to the elimination of the artificial coniferous stands and to the increase of broadleaved tree proportion, leading to higher heterogeneity in forest composition, whereas in the alpine zone the climate change will involve a shift of the vegetation belts at higher altitude, as it has been described for the climatic oscillations of the past.

2.2. Effects of forest sustainability

Forest sustainability becomes a concern when a growing human population begins to deplete resources beyond expected rates of renewal. As used today in forest management, the term means maintaining the forest for a long time, showing concern for the well-being of future generations, making reasonable estimates of future needs, knowing current rates of resource use and regeneration, and reaching consensus on appropriate levels of resource use (Floyd et al., 2001).

The long term sustainability of forests in Europe is achieved from one side by silvicultural measures addressed to obtain stands more resistant to environmental perturbations (Spiecker, 2003), from another side by favoring the renewal of the forest in marginal areas (Fabbio et al., 2003). A new perspective in estimating benefits of these processes is given by the possibility to assess the carbon sink function of the ecosystem, which is now quantified in term of market price (van Kooten et al., 2004).

Monitoring programs are essential to understand the ongoing changes and to adapt the management to the most urgent needs. These monitoring systems utilize a broad suite of indicators of key ecosystem components and processes that are responsive to many biotic and abiotic stressors, including those anticipated from climate change. A good example comes from mountain forests of Central Europe, where several years of intense damage by insect outbreaks, drought and pollution have dramatically jeopardized the forest area (Fleischer, 2001).

Another issue related to the sustainability is the preservation of biodiversity. The need to protect endangered species of organisms living in forest habitats is emphasized in several national and international acts, among which the European network of protected areas called ‘Natura 2000’ is the most prominent. Management options suitable to preserve endangered species in the protected areas should be identified and assessed for each group of target species. Generally, it seems that old-growth stands with a considerable amount of dead wood are important for various groups such as birds and insects. However, according to Er and Innes (2003) the application of this criterion alone will not meet the goal of maintaining biodiversity in terms of species richness, nor will it maintain the structural and functional diversity of ecosystems.

Management has to keep into account in each case the extension of the forest area, the nature of the protected species, and the multi-functionality of the forest ecosystems, as well as the frequency and intensity of natural disturbances (e.g. pest damage, drought, fire). Predicted changes for the Mediterranean zone are the increase of forest area and the conversion of management from coppice to high forest. In the temperate zone the forest exploitation will be reduced, and the new management techniques should increase the resistance to the extreme events such as drought and heat (Charnet et al., 2004).

3. ENVIRONMENTAL CHANGE AND FOREST INSECT RESPONSES

3.1. Responses linked to the tree composition: insect herbivory in pure and mixed stands

The hypothesis that mixed stands are characterized by lower insect herbivory than pure stands has received recently some support (meta-analysis of Jactel et al., 2004; Zhang & Schlyter, 2004), whereas previous papers did not bring evidence for such a difference, based on both mathematical models (May, 1973; Pimm & Lawton, 1978; Michalski & Arditi, 1999) and bibliographic reviews (Watt, 1992; Barthod, 1994; Landmann, 1998; Gadgil & Bain, 1999), which indicated the need of an experimental testing.

The problem has to be considered under a larger perspective, because it could be risky to draw general conclusions from small data sets. It could result in fact that tree species composition may have a role in determining susceptibility to herbivores, but the effect can be confounded with many other variables involved. The limitation of the area heavily attacked by forest insects is a major constraint for obtaining good data set for testing hypotheses related to this issue. This does not mean that tree species composition is not important for affecting herbivory, but that it has to be considered for its precise, mechanistic importance in each situation, any generalization being of little relevance for providing advice to the forest managers.

The hypothesis that plant diversity is associated with a reduction of the impact of herbivores on the primary production has been tested through experimental manipulation of herbaceous communities, by exposing to herbivores plots with a different number of species. The hypothesis has been rejected because plant biomass and herbivore damage increased with species richness in both individual studies (Mulder et al., 1999; Koricheva et al., 2000) and meta-analysis (Coupe & Cahill, 2003). This is in contrast with previous observations done on agricultural crops

(Andow, 1991), but the comparison is difficult because only crop plants were used for yield assessment.

Even if it seems difficult to extrapolate data from herbaceous to tree communities, we have to take into account that an acceptable experimental testing is possible only with herbaceous plants. On the other hand, herbaceous plants share the same guilds and specialization level (mono-, oligo-, polyphagous) of herbivores living on trees (Speight et al., 1999). It seems interesting to note that monophagous species may have a greater impact on the host plant when hosts were growing in habitats with lower tree diversity or isolation (Jactel et al., 2004) (Fig. 2). Thus monophagous herbivores seem to fit the Root's (1973) hypotheses that in more diverse agricultural communities, population density of specialist insect herbivores is limited by decreased foraging efficiency (the resource concentration hypothesis), or greater abundance and effectiveness of natural enemies (the natural enemies hypothesis). According to Jactel et al. (2004), polyphagous herbivores may have a different response to a diverse tree community, called 'diversion' and 'contagion' effects. The diversion effect is explained by the association with a more palatable secondary tree species which would be infested first, reducing the damage on the most represented tree species. As shown previously for herbaceous communities (Coupe and Cahill, 2003), the benefit from growing mixed stands will depend whether the total ecosystem or the single species production are considered. If the diversion effect is present, one should argue that the preservation of production of the main host will be compensated by a loss for the secondary host. The contagion effect occurs when an association of several host species leads to an increase of forest pest damage in tree mixtures, and it is also called associational susceptibility (White & Whitham, 2000). Typical example here is given by both gypsy and nun moth (*Lymantria dispar* and *L. monacha*), when the neonate larvae develop on high quality food (young leaves of broadleaved trees and conifer male cones, respectively) and mature larvae feed on poor quality conifer needles (Gottschalk & Twery, 1989; Jensen, 1991).

3.2. Responses linked to the variation of tree quality due to the increase of CO_2

As an indirect mechanism related to global change, an elevated concentration of CO_2 may affect the performance of phytophagous insects through the modification of the nutritional properties of the host plant (Jones et al., 1998; Hunter, 2001). As CO_2 is the main carbon source for photosynthesis, its increase could alter the carbon/nutrient balance of plants, increasing the C/N ratio and thus diluting the nitrogen content of the tissues. However, the response of plants to increased CO_2 varies among species. A high concentration causes an increase of tannins in the leaves of birch, poplar and maple, but not in the eastern white pine (*Pinus strobus*) (Roth & Lindroth, 1994).

The first reaction expected from herbivores to the increase of the C/N ratio is compensatory feeding, in other words they should eat more to accumulate enough nitrogen for their development. Thus, plant damage may increase, but the relative damage could remain stable if we assume that the plants exposed to high CO_2 grow

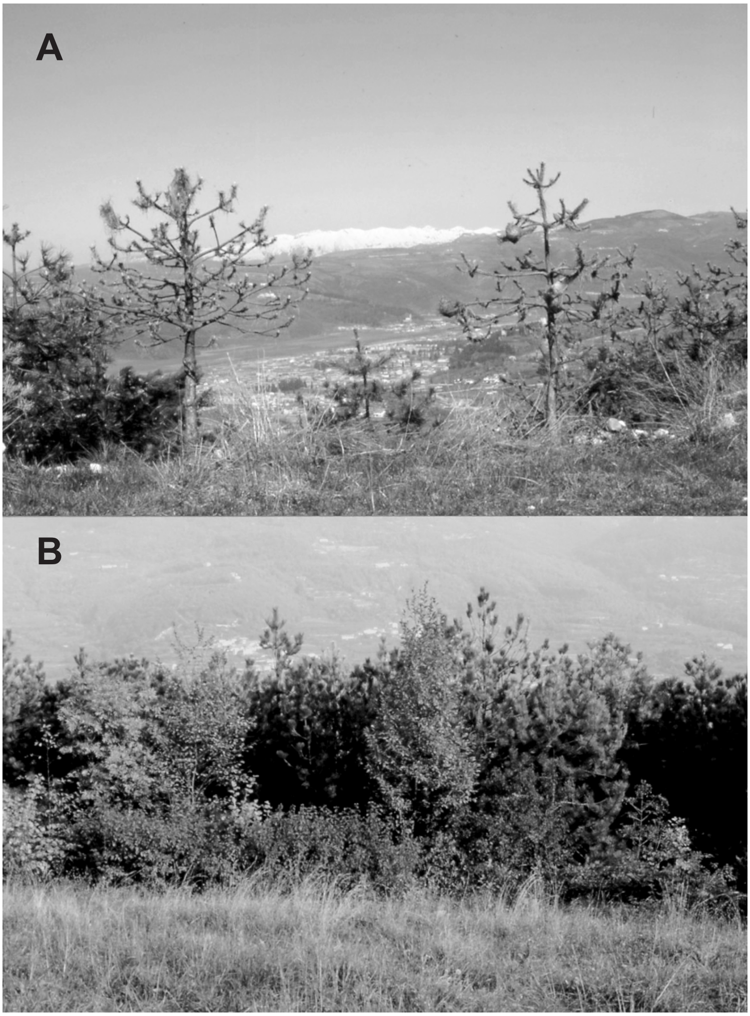

Figure 2. Defoliation by the pine processionary moth, Thaumetopoea pityocampa, *in the Southern Alps and changing of forest composition. Pure plantations of* Pinus nigra *are completely defoliated for 2-3 times in the age of 15 to 30 years (A). Native broadleaf species (*Quercus pubescens, Ostrya carpinifolia, Fraxinus ornus*) fill the gaps left by the defoliation (B). The defoliation becomes then less important and concentrates on the most prominent pine trees. This is a mechanistic example about how a defoliating insect can modify the stand composition, with a negative feed-back on the insect itself. Foresters can accelerate the process and reduce defoliation damage by favoring broadleaf species in plantations. Data from Battisti (1988).*

more. Phytophagous insects may also develop adaptations to overcome higher C/N ratios, such as the pine sawfly *Neodiprion lecontei*, which shows an increase in the efficiency of nitrogen utilization when reared on plants treated with high CO_2 concentration (Williams et al., 1994).

However, other insect species seem unable to compensate the lower nutritional quality of the plants by increasing the efficiency of nutrient utilization (Brooks & Whittaker, 1999; Stiling et al., 1999). The experiments of Lindroth et al. (1993), on three species of saturniid moths, show that the performance of the caterpillars is only marginally affected when the nitrogen content of the leaves is reduced by 23% and the C/N ratio increased by 13-28%.

Experiments combining different concentrations of both nitrogen and carbon dioxide supplied to Norway spruce showed that a high nitrogen level may compensate the effects of CO_2 on the concentration of nutrients and defense compounds in the shoots, limiting the negative effects on the test insect *Lymantria monacha* (Haettenschwiler & Schafellner, 1999).

The effects of a modified atmosphere on herbivore insects could also involve the third trophic level, i.e. their parasitoids and predators. As we are expecting a delay in the developmental time of the herbivores after exposure to high CO_2 (Fajer et al., 1989; Lindroth et al., 1993; Smith & Jones, 1998), the probability of parasitism and predation should increase as well. Experimental evidence of such a hypothesis is contradictory, as Roth & Lindroth (1995) did not find higher parasitism by the hymenopteran *Cotesia melanoscela* on the larvae of *Lymantria dispar* raised at high CO_2, whereas Stiling et al. (1999) found higher mortality of oak leaf miners by parasitoids on two species of oak (*Quercus myrtifolia*, *Q. geminata*) grown at high CO_2 level.

Laboratory or greenhouse experiments provide valuable data, but it is difficult to derive conclusions applicable to the natural environment. For example, high CO_2 levels are known to increase the temperature and, indirectly may affect the host-herbivore interaction. Dury et al. (1998) showed that an increase of 3°C of the temperature might lead to the same effects of an increase of CO_2 (decrease of nitrogen, increased of condensed tannins) on oak leaves. However, an increase of temperature may enhance the feeding of the herbivore and thus compensate for the negative effects of a lower food quality. An experiment that tested simultaneously the effects of different levels of CO_2, nitrogen and temperature on the monoterpene production of *Pseudotsuga menziesii* (Litvak et al., 2002), indicated that the synthesis of these defense compounds was more affected by individual tree variability than by the treatments.

The response of herbivore insects to increased CO_2 may also differ among the feeding guilds, as suggested by Bezemer and Jones (1998). Defoliators are generally expected to increase leaf consumption by about 30%, but leaf miners showed a much lower rate. Phloem-sucking insects appear to take the greatest advantage from increased CO_2, as they grow bigger and in a shorter time. In a FACE (Free Air Carbon Enrichment) experiment carried out in Wisconsin (Percy et al., 2002), the activity of all guilds of herbivores, combined with the effect of increased ozone, may be compensated by the beneficial consequences of enriched CO_2 on growth of *Populus tremuloides*.

3.3. Responses linked to forest management

Besides the modification of the tree species composition which may have dramatic consequences on the activity of insect herbivores in the forest ecosystem (see 3.1), another important management tool concerns the fate of dying or dead trees following storms, fires, pest outbreaks and other disturbances. It has been widely recommended that weakened and dying trees should be removed in order to avoid the breeding of insects which could later attack living trees (Speight & Wainhouse, 1989). However, dead trees offer a number of microhabitats and may therefore harbor a high diversity of species, among which there are several endangered and protected species (Speight et al., 1999).

A few studies have dealt with the assessment of the risk of attack of living trees related to the increase of dead wood in the forest. A good example comes from Scandinavia, where wind-felled spruce (*Picea abies*) trees have been harvested or retained over large areas and the effects on the attack of the bark beetle *Ips typographus* have been assessed (Schroeder & Lindelöw, 2003). Four years after the wind-felling, the difference in the number of trees killed by the bark beetle in stands with and without retained wind-felled spruces was only 6.2 trees/ha, as most of the bark beetles selected the wind-felled trees for breeding. In addition, the removal of wind-felled trees did not prevent the attack of living trees in the managed stands.

In another study, different numbers (1-5) of spruce trees were cut along forest edges and the attack of *Ips typographus* assessed over the two following years (Hedgren et al., 2003). Tree mortality was not higher at spruce stand edges with a small number of felled trees compared to edges without such trees, even though colonized trees increased the risk of the nearest tree being killed.

A possible conclusion from these studies is that small amounts of cut or wind-felled spruce trees colonized by *I. typographus* can be retained for conservation purposes, without increasing the risk that more living trees will be killed by the bark beetle. Of course this conclusion needs to be validated under different conditions of climate and forest type before finding a larger application.

3.4. Responses not linked to the tree or to the forest variation

The effects of global warming on living organisms have now been recognized from the level of individual species to communities, most notably in the form of temperature-related range shifts (Walther et al., 2002; Root et al., 2003). As the number of insects per unit area is inversely related to latitude and elevation (Speight et al., 1999), we may assume that the increase of temperature would allow the spreading of insect species northward and upward, especially for those species that have wide ranges, as many forest pests have.

With mean global temperatures increasing over the past 100 years by about 0.8°C and projected to continue (Houghton et al., 2001; Luterbacher et al., 2004), widespread climate-related changes in the biosphere can be expected. There are various ways by which the insects may react to climate change (Williams & Liebhold, 1995; Ayres & Lombardero, 2000; Harrington et al., 2001; Bale et al., 2002), and it seems reasonable to assume that an increase of temperature within the vital limits of a species implies a faster development.

Recently Parmesan and Yohe (2003) have provided a quantitative assessment of the biological impact of climatic change, using data from different types of organisms, including insects. This analysis concerned the spatial (range shift) and phenological (advancement of spring events) data, averaging 6.1 km/decade and 2.3 days/decade, respectively. Eighty percent of the studied species (n = 434) showed a consistent range shift and 87% an advancement of spring events, such as flowering or migration.

The response of insects to climatic change may not always be linear (Bale et al., 2002; Gaston, 2003). For example, the developmental stages of the insects can be differentially affected by the climate change, i.e. the growth can be accelerated by higher temperature, but at the same time the length of diapause may be extended. Those insects developing without winter diapause, which are active during this season and are protected from the low temperature, are the best candidates for range expansion if the winter temperature maintains the current increasing trend (Sinclair et al., 2003). A good example concerns the pine processionary moth *Thaumetopoea pityocampa*, which expanded considerably its range in southern Europe at higher latitude and altitude in the last three decades as a consequence of the increase of winter temperature (Battisti et al., unpublished data).

4. CONCLUSIONS

The material presented in this paper allows one to draw three main conclusions.

1. Forest sustainability and conversion in the temperate zone of Europe. The achievement of these goals seems to be compatible with reducing the risk of insect damage, at least for monophagous species which are notably the most important. However this may have a cost in term of yield of a given species, even if at the ecosystem level the loss of growth of one species can be compensated by higher growth of the unaffected species. The ageing of the stands may have some unpredictable consequences in terms of pest attacks, because of the limited knowledge about the behavior of pest species on old trees. In case of aggravation of the attacks with the age, there could be negative consequences on the carbon sink function of the stands, making these forests less sustainable.

2. Management for conservation. The new issues about conservation policy in the different types of protected areas imply a change in the management of bark and wood-boring insects, as more dead wood has to be retained in the forest. First results about the wood volume which can be retained without major risks for the living trees are encouraging, but more work is needed for exploring other situations and key insect pests. A possible increase of senescence feeders, as those commonly living in the old-growth and generally considered as endangered species (e.g. the oak longhorn beetles *Cerambyx* spp.) may also occur, but the consequences for the

living trees are hardly predictable. In addition, outbreaks of herbivores specialized on over-mature trees could also lead to loss of diversity at the ecosystem level.

3. Climate change and insect responses. There is little doubt that insect species range and performance are affected by the climate change, but the main objective is to understand the direction of the change. If the direct effect of the temperature on insects can be included in predictive models, the indirect effects due to the modification of the host plant quality by the climate change are more difficult to find and to predict. A further complication is given by the interaction of temperature and host plant quality, and by the response of the third trophic level or natural enemies to the changes occurring in the herbivores and their host plants.

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CHAPTER EIGHT

SYNECOLOGY OF *WASMANNIA AUROPUNCTATA*, AN INVASIVE ANT SPECIES (HYMENOPTERA: FORMICIDAE), IN CONTINUOUS AND FRAGMENTED AREAS IN THE BRAZILIAN ATLANTIC FOREST

1. INTRODUCTION

Ants have been considered as particularly important indicators of biodiversity (Alonso 2000; Bisevac & Majer 2002, Majer *et al.* 2004), disturbance (Brown 1997a, b; Andersen *et al.* 2002), and of rehabilitation or successional stages in ecosystems (Majer 1983, 1990; Majer & Nichols 1998). Ant communities are of key importance for regulating the abundance and composition of other arthropod communities, and even plants, in the ecosystems (Hölldobler & Wilson 1990; Davidson 1997; Davidson *et al.* 2003). However, there is also evidence that plant community structure influences ant distribution and occurrence. Certain human-made modifications inflict a persisting and remarkable effect on ant communities (Morais and Benson 1988; Schoereder & Coutinho 1990), qualifying ants to be intensively used in several studies as indicators of environmental conditions (Silva & Brandão 2000). The reasons for this ample utilization are: (i) ants are cosmopolitan, (ii) extremely abundant and diverse locally, (iii) ecologically important, (iv) taxonomically treatable, and (v) easily sampled.

The ant species of the genus *Wasmannia* are widely distributed throughout South America (Kempf 1972; Brandão 1991). They are considered omnivorous and true generalists in feeding habits, choice of nest sites and day/night preferences. There are ten valid nominal species for the genus, nine of them found only in the Neotropics. *Wasmannia auropunctata* (Roger), also known as "little fire ant", is the sole member of the genus recorded outside the Neotropics (Wetterer & Porter 2003). It is a "tramp species", disseminated by human transport, considered a pest in many places (Hölldobler & Wilson 1990; McGlynn 1999).

Wasmannia auropunctata shares many of the traits of other highly successful and disruptive invasive ant species that enable these ants to invade new areas, and to succeed once they arrive (Brandão & Paiva 1994). This syndrome, rarely seen in native ants, includes: generalist feeding and nesting habits, simple, superficial and replaceable nests, high colony mobility, polygyny, colony budding, low intraspecific

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aggression, high interspecific aggression, small size, and tending of extrafloral nectaries and/or Homoptera (Wetterer & Porter 2003). The sting of W. *auropunctata* is a highly efficient weapon, lethal against other ants and small animals, which effects are enhanced by the defensive secretion of the mandibular gland (Howard *et al.* 1982; Le Breton *et al.* 2002).

Wasmannia auropunctata is supposedly native to western South America and has been introduced into tropical and subtropical areas in other parts of the world, such as the Galapagos Islands, West Central Africa (Gabon and Cameroon), several islands of Melanesia and Polynesia, and some northern subtropical parts of the New World (Florida, California, Bermuda and Bahamas) (Wetterer & Porter 2003). Several populations have also been recorded in greenhouses in many temperate places (review by Wetterer & Porter 2003).

Here we focus on the abundance of *W. auropunctata* in fragmented and continuous Atlantic rain forest and its possible effects on the original ant litter assemblages. Since other *Wasmannia* species have not been reported as pests, we treat them as one taxonomic unit. This is further justified by the lack of recent revisional work and poor state of taxonomic knowledge of the genus. Our goal is to measure *Wasmannia* pest and non-pest species' effects on other ants in areas where the genus is supposedly native, and to compare the results with studies conducted in places they were reported as introduced.

The Atlantic Forest is considered as one of the most threatened ecosystems on Earth, now occupying only 7% or 98,000 Km^2 of its original range,of approximately 1,3000,000 Km^2 or 12% of the land surface of Brazil (SOS Mata Atlântica & INPE 1993; Ministério do Meio Ambiente 1999; Morellato & Haddad 2000). The Brazilian Atlantic forest is considered a megadiverse biome, classified among the top five ecosystems of the world regarding the number of species, and is considered a hot spot of biodiversity (Myers, 1988).

2. METHODS

2.1. *Study areas*

The study was carried out at the Atlantic forest along the Brazilian Atlantic coast (06°-30°S) as part of the project "Biodiversity of Hymenoptera and Isoptera: richness and diversity along a latitudinal gradient in the Mata Atlântica - the eastern Brazilian rain forest", within the Biota-FAPESP Program (www.biota.org).

The Atlantic forest is a very humid tropical forest, with the rainy season extending from December to March, and a "dry" (actually "less wet") season from June to August. The Atlantic forest covers the Serra do Mar range, with relatively high altitudes south of mid Espírito Santo, so the remnants we chose at high altitudes (between 650-100 m over sea level) are all in the southern portion of the biome. In the southern portion we also visited remnants in lower altitudes (0-200 m); remnants at the northern portion are all at relatively low altitudes. Localities were chosen as regularly spaced as possible, with all remnants larger than 400 ha.

All areas were sampled during the rainy season, between the years 2000-2004. Also we concentrated all collecting efforts in the evergreen dense forest subtype, expecting a richer fauna there as it is the most well preserved Atlantic forest subtype.

2.2. Sampling

The ant species richness and relative frequencies were evaluated by sifting and submitting to Winkler extractors 50 one square meter leaf litter samples at each locality, along a transect of 1250 m distant no less than 500 m from the forest edge. Every 50 meters along the trail (sample points), a pair of litter samples were collected, at the left and right sides of each point, 50 m distant from each other. In this way, 50 samples covered an estimated area of the 12,5 hectares.

All ants extracted from each leaf litter sample were kept in one vial, and transported to the Museu de Zoologia of the Universidade de São Paulo (MZUSP) ant laboratory in 70% ethanol. Identification to generic level follows Bolton (1994). Morph-species were separated in comparison with the MZUSP collection, where voucher specimens were deposited.

The ants were sorted to species level and species frequencies in 50 samples were recorded for each species. The areas were divided into two groups, fragmented and continuous, corresponding to northeast and south southeastern areas of Atlantic Forest, respectively.

2.3. Statistical Analyses

Expected species richness was estimated by Jacknife 1.

First, we asked if there is a correlation between *Wasmannia* spp. or *W. auropunctata* relative frequencies and species richness in each locality we visited, using linear correlation (Spearmann rank coefficient).

Next, we used data from the only locality where *W. auropunctata* was frequent enough to allow an evaluation whether its presence affects the within sample community structure, using variance analysis. The model was submitted to residual analysis and was tested for variance equality.

All statistical analyses were carried out using the R package (Ihaka & Gentleman, 1996).

3. RESULTS

The average richness of litter ant species in 18 surveyed areas in the Atlantic forest was 81 ± 15.55 (mean ± sd) with minimum of 58 species in Ilhéus, Bahia and maximum of 110 species in Tapiraí, São Paulo. We recorded 368 species total and estimate 491 ± 36.35 species in the litter of the Atlantic forest (Jackknife 1 estimator ± standard error).

Species of *Wasmannia* other than *W. auropunctata* were recorded in 17 out of 18 localities. Their summed frequencies are widely variable among localities (Table 1).

W. auropunctata occurs mostly in the northern, fragmented half of the Atlantic forest; other species of the genus were recorded in 16 localities (Fig. 1).

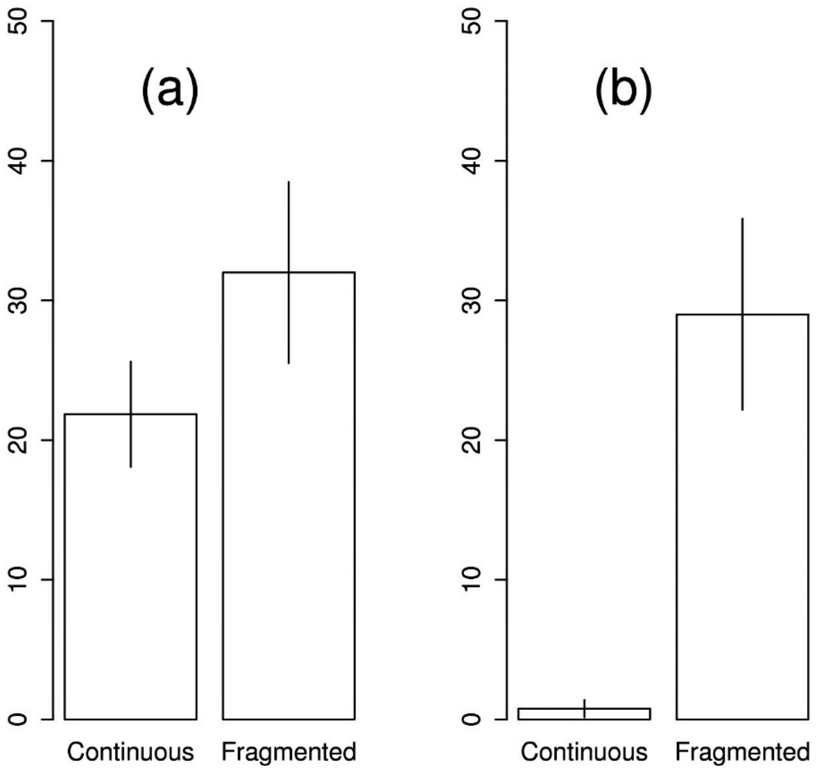

Figure 1. Boxplot with mean ± standard error of relative frequencies of Wasmannia *spp. (a) and* W. auropunctata *(b) in continuous and fragmented 18 Atlantic forest areas.*

There was no correlation between *Wasmannia* spp. and overall species richness in fragmented Atlantic forest areas (Spearman = 1033, rho = -0.06, p = 0.79). There was also no correlation between the overall species richness in fragmented Atlantic forest and *W. auropunctata* frequency in theses areas (Spearman = 1271, rho = -0.31, p = 0.21).

We found no evidence of a decline in ant species richness in 1m^2 samples with *W. auropuncta* in Sapiranga, BA, the only locality where the number of records yielded a meaningful analysis (ANOVA, $F_{1, 48}$= 0.34, p= 0.55).

4. DISCUSSION

Armbrecht & Ulloa-Chacon (2003) found a strongly significant negative correlation between Wasmannia auropunctata frequencies and the number of ant morph-species in 14 dry forest fragments located in southwestern Colombia. The fragments with highest dominance of the little fire ant showed the lowest number of other ant species. Our data, however, do not show the same pattern, because our study was conducted in the place from where this species has supposedly spread out.

Wasmannia auropunctata, like other ant tramp species (Passera, 1994), are able to invade undisturbed ecosystems, disrupting community structures and displacing native ants, affecting the guild of insectivorous lizards, populations of tortoises and birds, and those of other native arthropod communities in the Galapagos Archipelago and in sclerophyllic habitats in New Caledonia (Clark *et al.* 1982; Jourdan 1997; Jourdan & Chazeau 1999; Jourdan *et al.* 2001; Lubin 1984; Roque-Albelo & Causton 1999). There is also evidence suggesting serious impact in the Solomon Islands, Vanuatu, and Gabon (Jourdan *et al.* 2002; Wetterer & Porter 2003). Although here, *W. auropunctata* was recorded significantly more in fragmented areas, it does occur in two areas in the continuous southern half of the biome. Not surprisingly, these two localities are very close to the geographic limit between fragmented and continuous areas (see Table 1).

The data presented here suggest that fragmentation does not significantly affect the overall abundance of *Wasmannia* spp. in the forest floor, nor does *Wasmannia* spp. affect the leaf litter ant species richness in the samples. In contrast, *W. auropunctata* is negatively affected by fragmentation, albeit it does not affect leaf litter ant species richness. A possible explanation for the differences observed in our study with those conducted in other areas, is that native *W. auropunctata* frequencies may be controlled by other organisms in the Atlantic forest, while facing no natural enemies or competition where it occurs as an invasive species.

The generalist ecological attributes of *Wasmannia* may result in direct competition with a wide number of native ant species (Le Breton *et al.* 2003). However, it is possible that we were not able to reveal these effects in the Atlantic Forest, or that *Wasmannia* densities are too low in the sampled areas, because we carefully avoided collecting in places situated at less than 500 m from the forest edge. Thus, while trying to prevent border effects, we may have avoided recording *Wasmannia* effects on other ant species and community structure.

Notwithstanding, there is evidence from recent studies in New Caledonian sclerophyll forest (Jourdan *et al.*, 2001) that *Wasmannia* may not affect the native litter ant populations; yet most other ant guilds showed less species in zones invaded by *W. auropunctata*. The non-affected native ant fauna segment in these places included only few individuals of cryptic species such as those belonging to *Hypoponera*, *Oligomyrmex* and *Strumigenys* (Le Breton *et al.* 2003). So, perhaps a better way to reveal the effects of introduced or invasive species is to measure this influence in guild systems and not in the entire population.

In Neotropical lowland forests, where *W. auropunctata* is supposedly native, the species is often rather common, but usually does not dominate intact communities (Levings & Franks 1982; Tennant 1994; Alonso 1998). In fact, *W. auropunctata,* although invasive and dominant in many parts of the world, is not dominant in Neotropical intact ant communities. In contrast, in perturbed environments, *W. auropunctata* can be one of the most common and widespread ants in several sites, including areas in its native range in the Neotropics (Tennant 1994; McGlynn & Kirskey 2000).For example, *W. auropunctata* is among the dominant ant species in cacao plantations of Brazil (Medeiros *et al.* 1995; Majer *et al.* 1994; Souza *et al.* 1998), is very common in disturbed lowland habitats in Costa Rica (Longino & Hanson 1995; Roth *et al.* 1994; McGlynn & Kirksey 2000), rainforest in Chiapas, Mexico (MacKay *et al.* 1991), in the ant-mosaics of Colombian Choco rainforest (Armbrecht *et al.* 2001) and is dominant in coconut palms plantations in Trinidad, replacing other ant species nesting in the same palms (Way & Bolton 1997).

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Table 1. Ant species richness in 50 leaf litter samples of 1m^2, sifted and submitted to Winkler extractors for 48 hours for each of 18 Atlantic forest localities in Brazil. Localities in the northern half of the biome are represented by fragmented (F) remnants, while in the southern half, the forest is still continuous (C). Localities at highest altitudes (650 - 900 m over sea level) are recorded as H and in low altitudes (0 - 200 m) as L.

Locality/ State	Integrity	Altitude	Coordinates	Number of ant species	Samples with *Wasmannia* spp. records (N= 50)	Samples with *W. auropunctata* records (N= 50)
Itabaiana, SE	F	L	10.750 S 37.313 N	88	47	44
Crasto, SE	F	L	11.367 S 37.417 N	69	47	6
Sapiranga, BA	F	L	12.550 S 38.033 N	72	30	30
Ilhéus, BA	F	L	14.783 S 39.050 N	58	17	13
Porto Seguro, BA	F	L	16.383 S 39.167 N	69	19	14
Desengano, RJ	C	H	21.967 S 41.950 N	71	38	2
Cunha, SP	C	H	23.250 S 45.000 N	84	21	0
Picinguaba, SP	C	L	23.333 S 44.833 N	102	10	8

Table 1. (Continued)

Locality/ State	Integrity	Altitude	Coordinates	Number of ant species	Samples with *Wasmannia* spp. records (N= 50)	Samples with *W. auropunctata* records (N= 50)
Boracéia, SP	C	L	23.517 S 45.833 N	71	16	0
Cubatao, SP	C	L	23.967 S 46.533 N	70	16	0
Tapiraí, SP	C	H	24.016 S 47.450 N	110	39	0
Intervales, SP	C	H	24.300 S 48.350 N	66	42	0
Juréia, SP	C	L	24.533 S 47.233 N	73	14	0
Lauráceas, PR	C	H	24.850 S 48.717 N	105	0	0
Cananéia, SP	C	L	25.083 S 47.917 N	71	4	0
São Bento do Sul, SC	C	H	26.350 S 49.267 N	103	34	0
Blumenau, SC	C	H	27.100 S 49.150 N	90	22	0
Palhoça, SC	C	L	27.733 S 48.683 N	86	28	0

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LAWRENCE M. HANKS

CHAPTER NINE

CHANGING RELATIONSHIPS AMONG BIODIVERSITY, MANAGEMENT, AND BIOSECURITY IN MANAGED AND UNMANAGED FORESTS

1. INTRODUCTION

Natural forest ecosystems have long been, and continue to be greatly influenced by human activities, particularly through tree harvest, development and conversion of land for agriculture, suppression of natural disturbances such as fire, and environmental pollution (e.g., Carey, 2003a; Fuller et al., 1998; Hannon et al., 2000; Kanowski et al., 2003; Litvaitis, 2003; Moretti & Barbalat, 2004; Williams, 2003). Tropical forests are suffering the fastest rates of deforestation, and unfortunately also support the highest levels of species endemism and richness (Hall, Harris, Medjibe, & Ashton, 2003; Kellman & Tackaberry 1997; Thiollay, 2002). Forest ecosystems can be disrupted by spatial effects resulting from fragmentation by roads, power lines, and urban development (Fahrig, 2003; Godefroid & Koedam, 2003; Spellerberg, 1998). The nature of forest ecosystems is modified further when humans manipulate stand composition, such as by establishing native trees of uniform age and introducing exotic tree species (e.g., Brockerhoff et al., 2003; Ohsawa, 2004), or creating artificial ecosystems *de novo*, as in the case of many urban forests. With increasing urbanization worldwide and decimation of natural habitats (United Nations, 2003), it is essential that methods be developed for managing natural and man-made forests to sustain economic productivity and/or aesthetic quality while conserving biodiversity.

2. EXOTIC INVASIVE SPECIES

An ever more serious consequence of the development of global commerce is unintentional introduction of exotic species that can have an important impact on natural and man-made forests (US Congress 1993), particularly invasive plant species and wood-boring insects (e.g., Haack & Poland, 2001; Lavergne et al., 1999). Invasive species are thought to pose a serious risk to biodiversity (reviewed by Sax, 2002), and their detrimental impact in the United States is second only to habitat destruction (Enserink, 1999). Exotic insects that feed on woody plants in the

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United States are currently estimated to number in the hundreds of species, most of which having established within the last decade (see Haack & Poland, 2001). The potential impact of invasive exotic woodborers on North American forests is illustrated by recent introductions of Asian longhorned beetle, *Anoplophora glabripennis* Motsch. (Cerambycidae), and emerald ash borer, *Agrilus planipennis* Fairmaire (Buprestidae). *Anoplophora glabripennis* apparently was independently introduced into New York and Chicago in solid wood packing materials from China (Haack et al., 1997). This species is predicted to have a $600 billion impact in the United States because of its broad host range and ability to attack living trees (Nowak et al., 2001). *Anoplophora planipennis* was first detected in Michigan in 1998, but apparently has spread quickly (Haack et al., 2002) and is beyond any hope of containment. Although *A. planipennis* is more selective in its hosts, attacking only species of ash, it will likely have a severe impact on natural and urban forests over much of North America because it kills trees in any state of vigor, and because ash trees are important forest elements in many areas (Haack et al., 2002; USDA-APHIS, 2003).

3. ENVIRONMENTALISM AND CONSERVATION

People have a natural appreciation for trees and forest ecosystems, and degradation of forests by any agent elicits a knee-jerk public reaction (Spies, 2004). There is an inherent desire to conserve “nature” and “wildlife” (see Wilson, 1984), although there may be a general impression that the species to be conserved are charismatic vertebrates such as chipmunks, and not creatures like harvestmen that also play important ecological roles (see Jepson & Canney, 2001). Although “artificial” forests, such as urban forests and tree plantations, can be biologically diverse (Pickett et al. 2001), there is less concern over species composition and long-term sustainability. In fact, some such artificial forests rival adjacent natural forests in species richness and biodiversity of vertebrates and invertebrates, for example stands of exotic eucalypts compared to oak woodlands in the San Francisco Bay Area of California (Sax, 2002; also see Theodoropoulos, 2003). Thus, conservation of species in such artificial forests can be important for sustaining biodiversity over larger spatial scales.

The growth of environmentalism in recent decades has inspired interest in sustainable forestry practices that conserve biodiversity (e.g., see Carey, 2003a, 2003b; Hall et al., 2003; Jonsson & Jonsell, 1999). In fact, sustainability is intimately linked with biodiversity, since sustainability assumes ecological stability, and stability requires persistence of the diverse ecological interactions that comprise an intact food web (see Chapin et al., 2000; Ehrlich & Ehrlich, 1992; Holling, 2001). Thus, the desire to conserve large and mature trees, in “old growth” or “climax” forests (sensu Spies, 2004), is entirely consistent with conservation of biodiversity in general. For example, conservation of old growth results in accumulation of coarse woody debris (Spies, 2004) which plays a crucial role in preservation of many species of threatened forest arthropods (Jonsell et al., 1998; Speight, 1989). The factor that puts the teeth into public opinion, however, and that ultimately determines forest management policy, is the social assessment of what is to be gained by having "healthy" forests (Carey, 2003b; O'Brian, 2003; Sheppard et al., 2004; Weiss, 2004). Economic benefits are relatively easy to assess, including revenue for landowners and economic support of local communities through ecotourism and recreation (Sheppard et al., 2004). More difficult to assess are such factors as the value of forests in environmental function, such as carbon sequestration, and as sources of as yet undiscovered agricultural and medicinal plants (Myers, 1979). Even more difficult to assess are the health benefits for humans gained through clean air and water, relief of stress through spiritual contemplation of nature, and intellectual and ethical issues in forest management (Carey, 2003b; Jepson & Canney, 2001; Leopold, 1949; O'Brian, 2003; Spies, 2004; Wilson, 1984).

4. CHALLENGES FOR CONSERVATION OF BIODIVERSITY AND SUSTAINABILITY

Although conservation of biodiversity and preservation of natural forests clearly are desirable long-term goals, developing and evaluating the appropriate management strategies is problematical at many different levels. A primary stumbling block is identifying the level of biodiversity and ecosystem structure and composition that is "natural" and will be the ultimate objective. These qualities can be inferred on the basis of historical records of tree size, species, density, age, and geographic area (e.g., Litvaitis, 2003). Even in the absence of anthropogenic disturbance, however, forests are dynamic, subject to dramatic and unpredictable change by such stochastic processes as fire, wind and ice storms, short- and long-term shifts in climate, and outbreak of herbivorous insects and plant pathogens (e.g., Anagnostakis, 2001; Bormann & Kiester, 2004; Fuller et al., 1998; Hannon et al., 2000; Litvaitis, 2003; Lorimer & White, 2003; Moretti & Barbalat, 2004; Slik, 2004). Thus, knowledge of the early composition of a forest would not necessarily provide an accurate indication of its current state had it never been disturbed by humans.

Rehabilitation of forest ecosystems may not be achievable by reversing anthropogenic influence. For example, many areas of the world have been influenced by humans for so long that their original state is not completely known (e.g., Europe; Rackham, 1998; Spies, 2004). Anthropogenic disturbance of forest ecosystems can be subtle and difficult to document (Fuller et al., 1998; Hannon et al., 2000; Lorimer & White, 2003), and its impact can vary across taxa of plants and animals (Brouat et al., 2004; Godefroid & Koedam, 2003; Sax, 2002). In fact, the global reach of anthropogenic disturbance probably has eliminated any vestiges of virgin forest (Hannon et al., 2000; Thiollay, 2002). The difficulty in reversing anthropogenic disturbance can be illustrated by considering rehabilitation of eastern deciduous forests of the United States. Re-establishing dominance by chestnuts might be considered a desirable correction for decimation by chestnut blight, introduced by man in the early 1900s (Anagnostakis, 2001). The initial abundance of chestnuts, however, was due to their out competing other tree species in abandoned farmland (see Anagnostakis, 2001; Lorimer & White, 2003), also a consequence of human interference. Species dominance changed several times in forests of the northeastern United States independent of humans, passing from pines to hemlocks to oaks and spruce over the last 12,000 years (Anagnostakis, 2001). Thus, it is unclear which forest type should be the objective of a rehabilitation program.

Another stumbling block to rehabilitating forest ecosystems lies in assessing the current ecological state, and defining and evaluating "biodiversity". Biodiversity encompasses more than the mere number of species, but also the total genetic diversity within species, as well as the wealth of ecological interactions among species (Purvis and Hector 2000; Thiollay, 2002). A complete assessment of biodiversity therefore necessitates a comprehensive characterization of taxonomy, life history, and ecology (Jonsson & Jonsell, 1999), which currently is unobtainable (Bormann & Kiester, 2004; Jonsell et al., 1998). Choice of appropriate indices of biodiversity and species richness also is controversial (Purvis and Hector, 2000) and interpretation is complicated by spatial and temporal variation (Jonsson & Jonsell, 1999; Romero-Alcaraz & Ávila, 2000; Weber, Hintermann, & Zangger, 2004) and inconsistencies in effectiveness across taxa (Jonsson & Jonsell, 1999). Different methods of sampling and different biodiversity indices can yield dramatically different assessments of community structure, and also can vary with taxon focus (e.g., Onaindia et al., 2004; Ranius & Jansson, 2002). Still more difficult to evaluate are important measures of the suitability of forests to recreation and tourism, including such nebulous criteria as aesthetics (Sheppard et al., 2004).

Even with a clearly defined goal for forest management, and appropriate methods of assessing its progress, changes in forest structure may be unpredictable and the end product quite different from the expected or desired (e.g., see Brearley et al., 2004; Fuller et al., 1998; Kanowski et al., 2003; Ohsawa, 2004; Romero-Alcaraz & Ávila, 2000; Spies, 2004). Management of forests can have an unpredictable impact on community composition and biodiversity, and attempts at rehabilitation may not result in a resurrection of the original state (e.g., Bormann & Kiester, 2004; Brouat et al., 2004; Fuller et al., 1998; Kanowski et al., 2003; Nummelin & Zilihona, 2004). The classic example is fire suppression, which can result in diminished biodiversity in communities that are fire adapted (e.g., Moretti & Barbalat, 2004).

5. FOREST MANAGEMENT POLICY

Given the intrinsic difficulties in defining strategies for managing forests and assessing their effectiveness, forestry policy today calls for compromise and conciliation. Conservation of biodiversity and sustainability in forest ecosystems must be translated into coherent political process that guides management strategy and addresses economic and societal goals, "holistic management" (e.g., see Bormann & Kiester, 2004; Carey, 2003a,b; Hall et al., 2003; Litvaitis, 2003; O'Brian, 2003; Spies, 2004; Thiollay, 2002; Weiss, 2004). These policies must appease the public, stakeholders, interest groups, scientists, and authorities (see Dahlsten & Dreistadt, 1991; Litvaitis, 2003; O'Brian, 2003; Thiollay, 2002; Weiss, 2004). The policy also must be operationally and economically feasible (Bormann & Kiester, 2004). To achieve these goals, policymakers and forest managers require specific definitions: for example, what trees species are of concern?, what should the age structure be?, what geographic area should be targeted?, what research is needed?, and how should funding be allocated to support research? (Bormann & Kiester, 2004; Dahlsten & Dreistadt, 1991; Spies, 2004).

The many intangibles in forestry management, from defining goals to predicting outcomes, suggest that the optimal strategy may be to diversify management policies and strategies (e.g., Bormann & Kiester, 2004; Godefroid & Koedam, 2003; Moretti & Barbalat, 2004), the community-level equivalent to diversifying species composition within stands. For example, different areas within a contiguous forest, or different isolated stands, could be managed independently, varying logging practices, access for recreation, and methods of regulating forest pests. The ultimate goal would be to conserve habitat heterogeneity and maximize total biodiversity over large spatial scales (Jonsell et al., 1998; Romero-Alcaraz & Ávila, 2000).

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TIMOTHY D. PAINE

CHAPTER TEN

CHANGING THE MIX: NEW RULES IN REGULATING HERBIVORE POPULATIONS

1. INTRODUCTION AND HYPOTHESIS:

Plants, animals, and microorganisms (including pathogens) are moving around the planet and establishing new populations in new geographic distributions. Some of the movement is the result of natural range expansions as environmental conditions change or as community compositions change. For example, climate change may be a factor in the northward range expansion of collared peccaries in North America (Albert et al. 2004). Distributions of other species are intentionally expanded by human activities related to economic interests (e.g., planting *Eucalyptus* into plantations in North America or *Pinus* into plantations in Australia for fiber production), recreation (e.g., release of fox into Australia or brown trout into New Zealand), or a variety of other directed actions (e.g., classical biological control efforts [Clausen et al. 1977]). Human activities have also led to the unintentional introduction of plants and animals into new environments. While many of these introductions have not had serious consequences, some of the exotic invasive species have cause serious economic or ecological disturbance.

In many cases, the introduced plant or animal is not a problem in its native environment, but when released into the new geographic setting, the population grows rapidly and with few limits. One obvious hypothesis for observed differences in population growth is that when animals are introduced into new environments, the factors most critical for regulating the population size change in relative importance. That is, the factors holding the population within limits in the native range may be different or different in relative importance from the factors in the new geographic range. Note that this is a dynamic state and evolutionary processes will change the interactions between invasive species and the biotic and abiotic components of the novel environment over a variety of time scales (Lambrinos 2004).

T. D. Paine (ed.), Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems, 161–169.

2. POPULATION REGULATION

2.1. Density Dependent and Density Independent

Population regulation of insects in their native range is assumed to involve a range of dynamic processes that interact with the effect that populations are maintained within limits that fluctuate around some long-term or ecological mean. One approach to determining the relative strength of the various sources of stage specific mortality has been through key factor analysis (Casanova & do Prado 2002, Wakgari & Giliomee 2001, but also note concerns of Royama 1996). Following the introduction of insects to novel environments, populations may be regulated by ecological processes identified as important in the native range, but the relative effect of those processes may be different from what is observed in the native range. This assumption should be viewed with caution because there is evidence that populations may interact differently in different parts of their normal ranges, so some variation in the relative strength of the process should be considered to be normal (Bonsall et al. 2003). Alternatively, there may be mortality factors that are missing in the novel environment and the population of the introduced insect may achieve a higher equilibrium level than observed in the native environment.

Ecologists have categorized mortality factors in a variety of ways and have attempted to unravel the differential impacts of the different components. For example, competition and predation are often viewed as density dependent processes (although see Walker & Welter 2004), while factors associated with climate are considered density independent. Although the processes may be different, they frequently interact and the relative strength or importance of density dependent and density independent factors may change throughout the year (Leirs et al. 1997, Gonzalez-Megias & Gomez 2003, Stenseth et al. 2002, 2003).

However, it is not clear whether the impacts of density dependent and density independent factors act in the same interactive fashion in novel environments. For example, if herbivores are introduced in the absence of competitors or natural enemies, the roles of density dependent interspecific and intraspecific competition may become more critical. That is, there may be a release from interspecific competitive effects or the imposition of more severe intraspecific competitive effects in the novel environment. The distribution of available resources may be different from what is observed in native range. Consequently, the interaction among host distribution, stress and susceptibility, feeding pattern, dispersal, and population size (a function of the impact of other regulating factors) may have direct effect on strength of competition in novel environments.

Similarly, the climatic conditions and other density independent factors may exert a different relative strength in the novel environment. Abiotic stress can have direct effect on reproductive biology and life history of the insect. The environmental conditions may also have a direct effect on host plants and, consequently, a subsequent indirect effect on the insect herbivores. Alternatively, the novel environment may have a more moderate environment than the native range with subsequent release of introduced populations from environmental constraints.

2.2. Top-down and Bottom-up

Another way of classifying sources of population regulation is by trophic status. There are a large number of studies that have demonstrated that herbivore populations are limited by the suitability or susceptibility of their host plants (Kaitaniemi & Ruohomaki 2001; Hopkins & Memmott 2003; Steinbauer & Matsuki 2004). Availability of suitable plant tissues, hairs and trichomes, toughness and physical barriers, resins and latex, defensive chemistry, and nutritional suitability can cause significant mortality of insect herbivores (Zalucki et al. 2002). This type of regulation can be a powerful selection force in new environments (Garcia-Rossi et al. 2003). In addition, there can be important interactions between regulation from a lower trophic level and regulation from a higher trophic level (Cornell & Hawkins 1995; Stiling & Moon 2005). Volatiles produced following herbivore injury may attract natural enemies to the plant and enhance the impact of top-down regulation (Turlings et al. 1990; De Boer et al. 2004)

The mortality caused by predators and parasitoids is an important form of population regulation and underlies the practice of biological control of introduced pest species. The impact of natural enemies in native environments may be enhanced by a diverse community of herbivores and other natural enemies (Cardinale et al. 2003). However, there is increasing evidence that the interaction species in third and fourth trophic levels may actually reduce the impact of predation on herbivores (Rosenheim et al. 2004) and that natural enemies in native systems may have reduced effectiveness relative to the impact of natural enemies in exotic and simple food chains or webs (Hawkins et al. 1999; Montoya et al. 2003). Consequently, the impact of a narrow selected range of predators and parasitoids may be more important in regulating populations of introduced species in novel environments than more complex guilds in the native range.

3. EUCALYPTUS LONGHORNED BORERS: A CASE STUDY

Phoracantha semipunctata (F.) (Coleoptera: Cerambycidae) is widely distributed in Australia (Wang et al., 1996), but it is rarely considered to be an important factor in the mortality of *Eucalyptus* L'Heritier species (Duffy, 1963). Although the biology of the insect has not been extensively studied within the native range, there is a fundamental assumption that there is a complete range of factors that are important in regulating the population. For example, within the range of host eucalypts available for colonization, there are differences in susceptibility and suitability for beetle colonization which may provide bottom-up regulation (Paine et al. 2000a). Similarly, the availability of suitable resources may result in strong competitive interactions among colonizing larvae (Paine et al. 2001). A broad range of predators and parasitoids may also provide top down population regulation (Paine et al. 2000b; Hanks et al. 2001).

Although there are some earlier reports of beetle introductions (e.g., Tooke 1935), *P. semipunctata* has spread widely in the last forty years into most of the parts of the world where eucalypts have been planted (Drinkwater 1975; Ivory 1977). The beetle is causing significant tree mortality in many of those areas, and in particular, the regions around the Mediterranean (Chararas 1969; Mendel 1985; Gonzalez-Tirado 1987) and in California (Paine et al. 1993; 1995; 1997). Although now found in both Hawaii and Brazil, it is not considered to be a particularly significant problem in killing trees. These observations suggest that the beetle populations reach sizes that enable them to kill trees in some new environments but do not achieve significantly high levels in other new habitats and, therefore, must be regulated differently in some way in the different areas. In addition, the factors responsible for population in the new environments may not be the same or may not function at the same intensity as the factors in the native range.

In those areas where the beetle populations have reached very high levels and eucalypt mortality has been extensive, there has been a very limited level of local top-down population regulation. There have been rare reports of native predators killing a small proportion of the beetle population (Way et al. 1992). However, third trophic level control of the population has required the use of techniques of classical biological control and the introduction of natural enemies from Australia into new environments. The introduction of *Avetianella longoi* (Siscaro) (Hymenoptera: Encyrtidae) has been very effective in reducing the population of *P. semipunctata* in California (Hanks et al. 1995; 1996).

The reduction in *P. semipunctata* populations in California coincided with the rapid increase in population size of the *Phoracantha recurva* (Newman). Both species have overlapping geographical distributions in Australia (Wang et al. 1996), but their relative abundance across the range and in the areas of greatest overlap is undescribed. However, it is clear that while they do coexist in the native range, *P. recurva* has replaced *P. semipunctata* in at least two novel environments where both have invaded (Luhring et al. 2000; Di-Iorio 2004). The mechanisms for the replacement are unclear in Argentina, but in California, the combination of different seasonal emergence patterns between the beetle species (Bybee et al. 2004) and the preferential selection and increased fitness of *A. longoi* using *P. semipunctata* as a host (Luhring et al. 2000; 2004) may be responsible for the abundance patterns. The effects of a change in the biotic and abiotic mortality factors in the novel environments have altered the relative success of the congeners and resulted in a strikingly different pattern of population size compared to Australia.

In addition to the lack of native predators and parasites of the beetle in the new environments, there are few native competitors for the beetles in the exploitation of the tree resource. For example, despite growing in California for more than a century only one cerambycid, *Xylotrechus nauticus* (Mannerheim), is only rarely found colonizing dead eucalypt hosts. This observed lack of switching onto the introduced trees is not surprising, in part because the plant has high levels of terpene-based plant defenses. In addition, *Eucalyptus* is a member of the Myrtaceae, a plant family with representatives that are widely distributed in the southern hemisphere but with more limited representation in the northern hemisphere. Thus, there are few insects in the northern hemisphere that would be likely to switch from a closely related host species onto *Eucalyptus*. The exceptions have been observed in South Africa and in Brazil where there is a great diversity in myrtaceous plants.

If top-down regulation is limited in the new regions of the world where *P. semipunctata* has been introduced, but populations are low in some regions and high in others, then there must be some factor or factors that are acting with greater impact in different regions. Consequently, it is important to look at the impact of the plant host on beetle populations. There are two different aspects of host plant / beetle interactions that have been examined extensively and could exert bottom-up regulation.

It is clear that there are differences in the susceptibility and suitability of different *Eucaluptus* species for *P. semipunctata*. Hanks et al. (1995a) demonstrated that beetles preferentially colonized and killed highly preferred species while less preferred species suffered significantly lower levels of mortality. The most attractive species also were the most suitable for larval development, but paradoxically, these trees also had the highest level of intraspecific competition among the larvae and reduced emergence relative to the less preferred species (Hanks et al. 1993b). Despite the potential for differences in beetle performance in different host species, many of the same species are widely planted throughout the world, so it is unlikely that species differences, in themselves, could account for differences in beetle populations in different regions.

Alternatively, the mechanism of host plant resistance to the borer may explain the differences. The bark of many species of *Eucalyptus* is living and can have a very high moisture content. The beetles lay their eggs on the surface of the trunk under exfoliated bark or in tight places. The neonate larvae must penetrate through the outer bark to reach the cambium and outer layers of xylem to begin their larval feeding (Paine and Millar 2002). However, the ability of the neonate larvae to successfully penetrate the bark and establish feeding galleries is significantly reduced if the bark moisture content exceeds a critical level (approximately 55%) (Hanks et al. 1991b; 1999). Consequently, trees that are well hydrated have greater resistance to colonizing beetles than are trees that are suffering from moisture stress. The stressed trees are also highly attractive to host-seeking beetles (Hanks et al. 1991b).

Phoracantha semipunctata is active in California from late spring through early fall, but adults are not present during the late fall and winter months (Paine et al. 1995; Bybee et al. 2004). In parts of the world with Mediterranean climate patterns, including California, the winters are cool and wet and the summers are hot and very dry. The active period for the beetle corresponds to the time of year when the trees are subject to the most severe moisture stress, are most attractive to flying adults, and because of reduced bark moisture content, most susceptible to successful colonization. Thus, in areas with Mediterranean climates where tree mortality has been the highest, the insects are most active when host tree defenses and bottom-up regulation is least effective.

In contrast, many of the eucalypt forests in eastern Australia as well as plantations in Brazil and Hawaii grow in climates characterized by having rainfall throughout the year, including substantial summer rainfall. In these areas, the trees would typically not be subject to summer drought stress and bark moisture content would remain high during the time of highest beetle activity. The trees would be less attractive as hosts and if beetle larvae do attempt to penetrate, the bark moisture content above the critical threshold and larval success would be limited. Bottom-up regulation through host resistance could be the underlying mechanism for the observation of low beetle populations and low levels of tree mortality in Brazil and Hawaii where natural enemies are absent.

The test of this climate driven bottom-up regulation hypothesis will come in two ways. The first aspect has been demonstrated through modification of moisture regimes in areas with Mediterranean climates. Hanks et al. (1999) clearly reversed host susceptibility with supplemental irrigation in California. The second aspect has been initiated in an unanticipated field trial that will play out over the next decade. *Phoracantha semipunctata* is a particular problem in *E. globulus* (Hanks et al. 1995a), a species with great commercial importance as a source of cellulose fiber used for the manufacture of paper that has been introduced from Tasmania and Victoria to Mediterranean climates outside Australia. That species and others from regions with significant summer precipitation are now being commercially planted in significant numbers for the first time in parts of Western Australia, an area with a Mediterranean climate. The plantations are established on land formally used for unirrigated grain production and the trees receive minimal amounts of supplemental moisture. It remains to be seen what will happen in this grand experiment. An increase in *P. semipuntata* populations and high levels of tree mortality in those plantations will lend support to the hypothesis that host resistance is a key factor in population regulation.

4. CONCLUSIONS

Populations of herbivores in native or endemic environments are regulated by a broad range of factors that can include abiotic conditions and both top-down and bottom-up factors. It is possible to characterize the relative importance of each factor and the conditions where the balance among regulating factors can change. However, when those herbivores become established in novel environments, the factors regulating the populations and the balance among those forces can be drastically altered. The host plants are growing under very different conditions, often in association with very different communities with different composition and structure. These differences can change the bottom-up regulation of the herbivore populations. The herbivore may also be part of a very different community, either more simplified with fewer potential competitors, or more complex. The community of natural enemies may also be simplified or more complex. Consequently, the impact of top-down regulation on the population may be very different from what is observed in the native range. The differences in the impact of individual components that contribute to population regulation need to be carefully assessed in the context of the novel environment, host tree community, other herbivores, and complex of natural enemies.

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Keyword Index

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