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O. W. Van Auken
Editor

Western North American *Juniperus* Communities

A Dynamic Vegetation Type

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A Dynamic Vegetation Type

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Preface

Juniperus woodlands and savannas in western North America are both extensive and dynamic. They are influenced and perhaps controlled by fire and anthropogenic factors, specifically herbivory. Their recent expansion into many grasslands has been carefully documented (Norris et al. 2001). Some of these *Juniperus* communities have shown dramatic changes in response to very recent global-change-type droughts (Breshears et al. 2005). However, the future community response to these global-change-type conditions is unknown. These *Juniperus* communities seem to be very sensitive and possibly pivotal in understanding global-change-type phenomena, including droughts.

This volume has grown out of a symposium held in San Antonio, Texas, in April 2004. The symposium was associated with the annual meeting of the Southwestern Association of Naturalists. Much of the material included has been published in the open literature and in reports by state and national agencies, although it has not appeared in one place in one document. A synthesis of past, current, and proposed future research on *Juniperus* woodland and savanna ecosystems is presented.

It has been difficult to develop a comprehensive understanding of *Juniperus* communities because they are quite diverse. They occur on shallow limestone soils in the eastern United States, on steep slopes in the Great Plains, and at low to mid-altitudes in the western United States, Texas, and Mexico (McPherson 1997). They occur in areas with very low rainfall bordering arid grasslands and deserts, as well as early-successional woodlands embedded in deciduous forest communities and most communities in between. *Juniperus* communities appear to occur along an elevation gradient as well as a spatial rainfall gradient in western North America. The *Juniperus* communities change dramatically along these gradients. On one end, a few scattered *Juniperus* plants are embedded in a grassland matrix. On the other end, grassland is found as small patches that are embedded in a *Juniperus* woodland matrix. If succession is involved in determining community structure along this grassland–forest continuum, the *Juniperus* woodland patches may end up within a forest matrix, or they may be replaced by forest species from within or below the canopy. However, neither the mechanism nor the dynamics of the process is well understood.

Although *Juniperus* woodlands are intermediate successional communities in the development of deciduous forests in relatively mesic areas, the successional sequence in more arid regions is unclear (Howard and Lee 2002). In addition, the dynamics of woody plant replacement in many of these *Juniperus* woodlands and savannas has only been partially investigated (McKinley and Van Auken 2005). The future structure of these communities is unknown, especially as it relates to global change.

There are four general sections in this volume. The first section concerns the ecology of these western North American *Juniperus* communities and includes six chapters. Chapter 1 covers the distribution of the various *Juniperus* species and where the different communities are found. It also covers Pleistocene community distributions and long-term changes in community locations. Chapter 2 is concerned with the composition and structure of western North American *Juniperus* communities and the factors that seem to control the structure, composition, and location of these communities. Chapter 3 compares the various landforms where communities are found. Chapter 4 examines changes in the environment between canopy and intercanopy positions and how those abiotic changes alter the community structure. The herbaceous understory of various Juniperus communities is examined in Chapter 5, and the importance of mycorrhizae to *Juniperus* seedlings is examined in Chapter 6.

Community changes associated with *Juniperus* encroachment are included in the second section, and there are five chapters. The ecological importance of encroachment of *Juniperus* plants into grasslands is examined in Chapters 7 and 8; alterations in ecosystem processes are examined in Chapter 9. Modifications in water budgets and the water cycle are examined in Chapters 10 and 11. The third section concerns human impact on *Juniperus* ecosystems and includes four chapters: Chapters 12 through 15 cover effects of herbivory, fire, physical treatments, and combinations thereof on various *Juniperus* communities and their potential degradation, restoration, and recovery. The fourth and last section contains one chapter, Chapter 16, which covers future research needs and possible directions.

Finally, this volume represents a significant effort and represents many years of effort by the various authors. This specific project was started more than 3 years ago. These efforts came from all my co-authors, friends, and others. I appreciate all their help and patience.

San Antonio
November 2006 *O.W. Van Auken*

References

Breshears, D.D., Cobb, N.S., Rich P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.D., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., and Meyer, C.W. 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. U.S.A. 102:15144–15148.

Howard, L.F., and Lee, T.D. 2002. Upland old-field succession in southeastern new Hampshire. J. Torrey Bot. Soc. 129:60–76.

McKinley, D.C., and Van Auken, O.W. 2005. Influence of interacting factors on the growth and mortality of *Juniperus* seedlings. Am. Midl. Nat. 154:320–330.

McPherson, G.R. 1997. Ecology and Management of North American Savannas. Tucson: University of Arizona Press.

Norris, M.D., Blair, J.M., Johnson, L.C., and McKane, R.B. 2001. Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. Can. J. For. Res. 31:1940–1946.

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Section 1
Ecology

1
Western North American *Juniperus* Communities: Patterns and Causes of Distribution and Abundance

O.W. Van Auken and Fred Smeins

Introduction

About 60 species of *Juniperus* are found across the Northern Hemisphere, from near the equator in Africa and Central America and north to the Arctic Circle in Alaska, Canada, Greenland, Norway, and Russia (Hora 1981). In North America, 13 species of *Juniperus* have been reported (Little 1971; Elias 1980). *Juniperus communis* and *J.horizontalis* are found in the Far North across Alaska and Canada, while *J. flaccida* and *J. deppena* occur south into the mountains of southern Mexico. In the eastern United States, *J. virginiana* is the most common species of *Juniperus*, whereas in the intermountain West *J. monosperma, J. osteosperma*, and *J. scopulorum* are common. In Oregon and northern California, *J. occidentalis* is the major species of *Juniperus* and *J. californica* is largely confined to California. The distribution of *J. ashei* and *J. pinchotii* is mostly in central and western Texas, and *J. silicicola* occurs along the Atlantic and Gulf Coasts.

Juniperus communities cover approximately 30×10^6 ha in western North America (Figure 1; West 1988, 1999; Miller et al. 2005). They occur as savannas in areas with low rainfall bordering arid or semiarid grasslands (Figure 2). In central and western Texas, *Juniperus* species occupy an additional 20×10^6 ha in the Edwards Plateau, the Rolling Plains, and the Trans-Pecos Regions (Figure 3). The area covered by *Juniperus* communities in Mexico is not known (West 1999). Other *Juniperus* communities occur as early successional woodlands embedded in deciduous forest communities in eastern North America. In addition, some *Juniperus* species have encroached into grassland communities all across North America (Van Auken 2000).

Juniperus usually occur on shallow rocky soils in the eastern United States, on steep slopes in the Great Plains, and at low to midaltitudes in the western United States, Texas, and Mexico (Miller and Wigand 1994; McPherson 1997). Many *Juniperus* species have recently increased in density and area covered, especially in the central, western, and southwestern United States (Bray 1904; West 1984; Eddleman 1987; Smeins and Merrill 1988; Miller and Wigand 1994; McPherson 1997; Van Auken 2000; Norris et al. 2001; Briggs et al. 2002; Miller et al. 2005).

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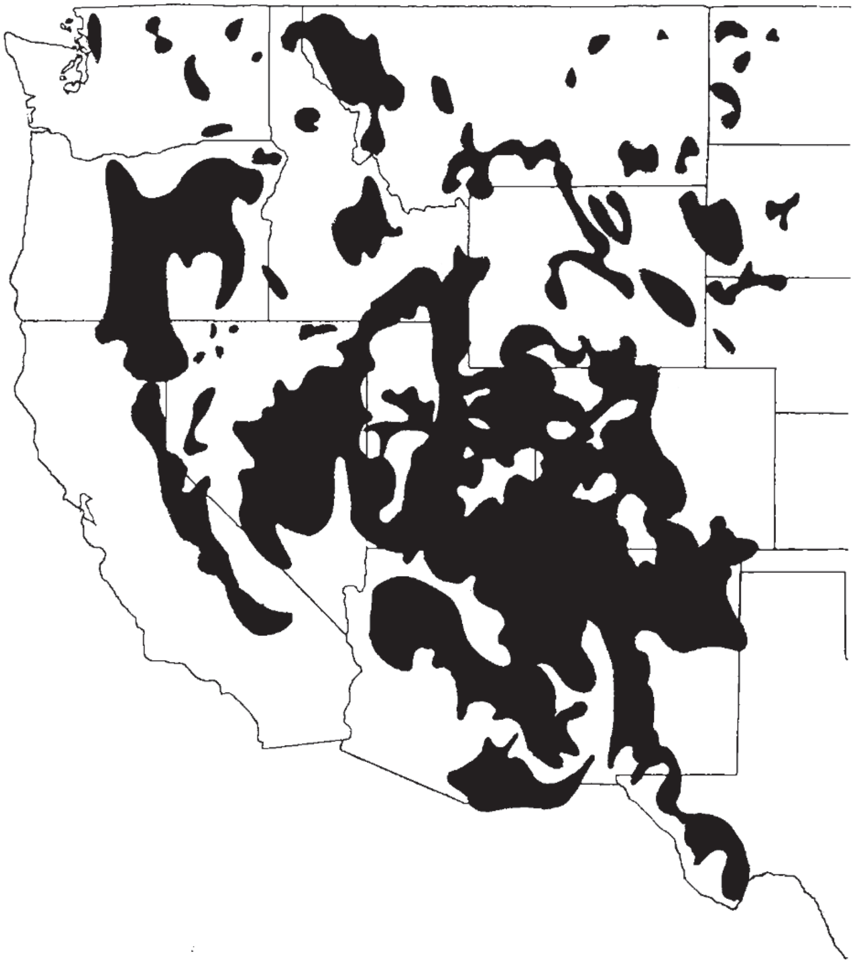

Figure 1 Map of western North America showing the approximate distribution of various *Juniperus* woodlands (*shaded areas*). (From Küchler 1970; West 1988)

This change has resulted in a decrease in areas of grassland and a concomitant increase in areas of savanna and woodland (Bahre 1991; McPherson 1997).

Causes of the increased density of these woody plants (brush encroachment) appear to be chronic high levels of domestic ungulate herbivory that alters the grass competitive abilities, leading to reduced fine fuel biomass, which alters fire frequency and intensity (Archer et al. 1995; Bush and Van Auken 1995; Fuhlendorf et al. 1996; Fuhlendorf and Smeins 1997; Van Auken and Bush 1997; Van Auken 2000). However, neither the mechanism nor the dynamics of the process is well understood, and these may be variable across environments.

Juniperus communities seem to be intermediate in the grassland–forest continuum (Belsky and Canham 1994; Breshears and Barnes 1999; House et al. 2003; Breshears

Figure 2 Photograph of a *Juniperus* savanna in western North America

2006; see Breshears, Chapter 4, this volume). On the dry end of the gradient, a few scattered *Juniperus* plants are embedded in a grassland matrix, whereas on the mesic end grassland is found as small patches that are embedded in a *Juniperus* woodland matrix, or *Juniperus* communities are embedded in a forest matrix. *Juniperus* patches in a forest matrix may be replaced by forest species from below the canopy.

In western North America, *Juniperus* communities occur along an elevation gradient as well as a spatial rainfall gradient (Miller and Wigand 1994). The *Juniperus* communities change dramatically along these gradients, and changes can occur relatively quickly (Allen and Breshears 1998) and over large areas (Breshears et al. 2005). In addition, superimposed on the elevation and spatial physical differences in these communities are the current worldwide global climate changes (Pimm et al. 1995; Dobson et al. 1997; Chapin et al. 1998; Mooney and Hobbs 2000; Mackenzie 2003; Yu 2003).

Changes in the populations of plants and animals of the communities of the American West and Southwest have been pieced together from pollen records and fossil packrat middens from a large number of localities (Betancourt et al. 1990; Miller and Wigand 1994; Van Devender 1995; Martin 1999). Organic carbon from these sites has been radiocarbon dated, and this material has been linked to oxygen isotope data from foraminifera shells in deep-sea cores and changes in global ice volume to develop a single time series to represent global changes (McDowell et al. 1995).

Although *Juniperus* woodlands are intermediate successional communities in the development of deciduous forests in relatively mesic areas, the successional sequence in more arid regions is unclear (Cadenasso et al. 2002; Joy and Young 2002; Howard

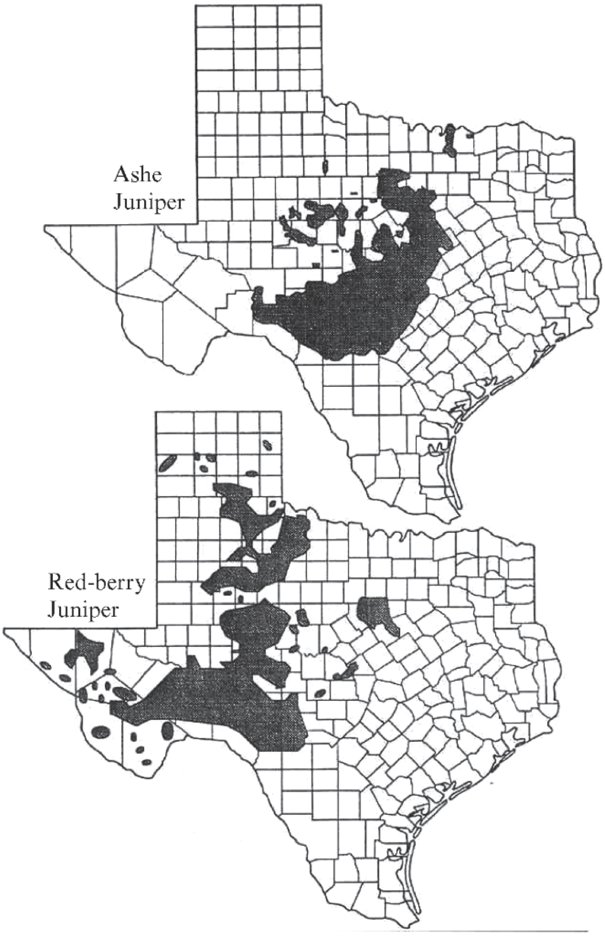

Figure 3 Map showing the state of Texas with the approximate distribution of *Juniperus ashei* (*top*) and *Juniperus pinchotii* (*bottom*)

and Lee 2002). In addition, the dynamics of woody plant replacement in many of these *Juniperus* woodlands and savannas has not been extensively investigated, and the future structure of these communities is only postulated (Van Auken et al. 2004).

Late Pleistocene *Juniperus* Distribution

Over most of the past 2 million years, during the Pleistocene, the climate of the Earth was much cooler than it is today (Martin 1999; McDowell et al. 1995; Van Devender 1995). Originally, there were thought to be four glacial periods with evidence from widespread sedimentary records. However, oxygen isotope studies from ocean floor sediments showed that there may have been 15 to 20 glacial periods with associated interglacials (Imbrie and Imbre 1979). The interglacial periods lasted 10,000 to 20,000 years and the glacial periods about 10 times longer.

Global climate has been warming since the late Pleistocene approximately 11,000–15,000 years B.P. (before present) and into the Holocene. We are currently in an interglacial; thus, the climate is warm compared to the glacial periods, and it has been warming during the past 15,000 years. As the glaciers melted, plant communities around the world moved. Increased global temperature during this period was a major factor controlling the northward migration of many species of *Juniperus*, including relatively recent fluctuations in distribution and density (Miller and Wigand 1994).

Deglaciation caused major fluctuations in plant populations and communities throughout the world, starting toward the end of the Pleistocene (11,000–15,000 years BP) with the retreat of the glaciers. During Pleistocene glacial advances, boreal forest with *Picea* (spruce), *Abies* (fir), and *Pinus* (pine) covered much of what is now mixed deciduous forest in the eastern United States (Delcourt et al. 1983; Davis 1981; Delcourt and Delcourt 1981). Subalpine woodlands were found in areas now covered with *Pinus-Juniperus* (piñon-juniper) woodlands in the Great Basin (Betancourt et al. 1990; Miller and Wigand 1994). *Picea* forests or open *Picea, Pinus*, and *Betula* (birch) parkland occurred in areas of tallgrass prairie in Kansas and in areas of *Juniperus* grassland or savanna in west central New Mexico. *Pinus* parkland was found in what is now shortgrass prairie in western Texas and in areas of desert grassland in southeastern Arizona (Sears and Clisby 1956; Halfsten 1961; Hevly and Martin 1961; Gruger 1973; Van Devender 1995). It is clear that many *Juniperus* woodlands and savannas had very different distributions compared to today.

Apparently these *Juniperus* communities and other communities migrated as the climate warmed or cooled without the influence of man or domesticated animals. During the current warming trend, in areas that are now semiarid grasslands or desert grasslands of southwestern North America, *Pinus* parkland and *Juniperus* woodlands and savannas were found. These communities moved mostly in a northern direction or upward in elevation to their current locations. The semiarid grasslands of the American Southwest, which were lower in elevation and probably more to the south, migrated to their approximate current location as well (Van Auken 2000). The current Chihuahuan and Sonoran Desert shrublands were restricted to lower elevations and more to the south. With the warming trend they migrated to their approximate, current locations.

Northward migration of *J. occidentalis* into Oregon and northern California occurred as temperatures increased during the early Holocene (Bedwell 1973; Mehringer and Wigand 1984; Wigand 1987; Miller et al. 2005). *Juniperus occidentalis* density and distribution fluctuated dramatically over the last 7500 years, but its general range seems to have remained relatively constant over the past 3000 years (Wigand et al. 1995). During this time period, *J. occidentalis* trees were apparently confined to rocky ridges and slopes, low *Artemisia* (sagebrush) flats, and areas with pumice soils with fine fuel levels too low to carry a fire and probably low tree density (Burkhardt and Tisdale 1976; Vasek and Thorne 1977; Holmes et al. 1986; Miller and Rose 1995; Waichler et al. 2001. These areas with low levels of fine fuel would have burned less frequently and with lower intensity compared to surrounding areas that burned more frequently at higher intensity, which would have reduced or eliminated nonsprouting *Juniperus* plants. Warming and drying during the Holocene in the Big Horn Basin of Wyoming and Montana caused replacement of *J. communis, J. horizontalis*, and *J. scopulorum* with the drought-tolerant *J. osteosperma* by 4700 years B.P. (Lyford et al. 2002). Increased aridity after 2700 years B.P. apparently initiated expansion of *J. osteosperma* in this area.

Recent Changes in *Juniperus* Distribution and Abundance

The postglacial warming trend is continuing, but it has been difficult to demonstrate during the past 150 years because of the short time span and considerable spatial and temporal heterogeneity (Crowley 2000). In addition, it has been difficult to link recent climatic changes to vegetation changes occurring at the same time because of other potential or interacting causes, in spite of the large number of sites around the world measuring climatic variables.

However, there does not seem to be conclusive evidence to demonstrate that changes in precipitation patterns or temperature in western or southwestern North America since the 1870s are linked to recent shrub or woody plant encroachment. The unevenness of *Juniperus* and other woody plant encroachment and dramatic differences in density in adjacent, fenced, edaphically similar areas would seem to rule out large-scale climatic influences as the major cause of woody plant increases (Bahre and Shelton 1993).

Another hypothesis that has been proposed is that the current elevated level of atmospheric CO_2 is the cause of shrub encroachment in western and southwestern North America (Mayeau et al. 1991; Idso 1992; Polley et al. 1992; Johnson et al. 1993). This is an interesting hypothesis because it could account for the synchronous, widespread encroachment of *Juniperus* and other woody plants into various grasslands and savannas throughout the world. It is based on observations that most woody plants have the C_3 photosynthetic pathway and that in the western and southwestern North American grasslands most of the grasses that are being replaced have the C_4 photosynthetic pathway.

The various *Juniperus* species and other plants with the C_3 photosynthetic pathway have a growth advantage at higher levels of CO_2 compared to plants with the C_4 photosynthetic pathway. However, there are some difficulties with this hypothesis (Archer et al. 1995). Quantum yields, photosynthesis rates, and water use efficiencies at current levels of CO_2 are comparable for a variety of C_3 and C_4 species. Many C_4 grasses are more responsive to increased levels of CO_2 than previously supposed. The encroachment of C_3 woody shrubs in the cold deserts and the replacement of C_3 grasses in this area are not explained by the elevated CO_2 hypothesis. Fences restricting constant grazing by domestic herbivores are enough to reduce the encroachment of C_3 woody shrubs in adjacent edaphically similar areas with C_4 grasses. Shifts in populations of C_4 grasses to C_3 grasses in these same areas have not occurred. There is a temporal disparity between the time of the greatest increase in CO_2 and the encroachment of woody plants. There have been many shifts in dominance of woody plants and grasses during the Holocene that do not appear to be related to elevated levels of CO_2. Finally, not all studies have shown a CO_2 fertilizer effect, suggesting other limitations or constraints. Thus, the CO_2 enrichment hypothesis does not seem to explain the encroachment of various *Juniperus* species or other woody plants into the grasslands and savannas of the American West and Southwest.

Compared to the Pleistocene, changes and rates of change of plant populations and communities in the past 150 years have been unparalleled (Pimm et al. 1995; Dobson et al. 1997; Chapin et al. 1998). Most recent changes in woody plant populations associated with grasslands or savannas do not appear to have been caused directly by deglaciation or to be considered invasions, as suggested by some, but are probably best considered encroachment, a phenomenon of movement from adjacent communities that have been in existence for a considerable time (Burkhardt and Tisdale 1976; Miller and Wigand 1994; Van Auken 2000; Jessup et al. 2003). At lower elevations in western North America, shrubby or woody species usually associated with the Chihuahuan or Sonoran Deserts have increased in density in areas previously covered by semiarid grassland (Buffington and Herbel 1965; Hastings and Turner 1965). At higher elevations, various species of *Juniperus* previously restricted to rocky outcrops, steep slopes, and shallow soils have spread down slope into semiarid grasslands and similar grasslands throughout western and southwestern North America (Johnsen 1962; Wells 1965; Blackburn and Tueller 1970; Eddleman 1987; West 1984; McPherson 1997; Miller and Wigand 1994).

These changes in density of woody plants have been attributed to climate change (Buffington and Herbel 1965; Hastings and Turner 1965; Neilson 1986). However, in the semiarid grasslands, climate change (warming) would suggest that the various species of *Juniperus* would move north and upward in elevation (Miller and Wigand 1994). Recent climatic or precipitation changes in the Southwest do not seem connected to recent vegetation changes in the semiarid grasslands (Bahre and Shelton 1993).

In the northwestern mid- and high-elevation forests, including *Pinus contorta* (lodgepole pine) and *Picea–Abies* forests, there are some interesting relationships. In these areas, with higher, larger-wildfire frequency and longer wildfire duration, there are strong associations with earlier spring snowmelt and increased spring and summer temperatures (Westerling et al. 2006). At lower elevations, the changes in *Juniperus* populations seem to be caused by reduced grass biomass and a concomitant reduction in fire frequency (Johnsen 1962; Blackburn and Tueller 1970; Burkhardt and Tisdale 1976; McPherson et al. 1988). Not all species have moved. For example, populations of *Quercus emoryi* that form woodlands above the semiarid grasslands in parts of Arizona and northern Mexico apparently have been rather stable for many years, not migrating up or down in elevation (Weltzin and McPherson 1999), which seems to be because seedling establishment has been restricted to the area below the adult tree canopy by dispersal and specific seedling requirements (Germain and McPherson 1999; Weltzin and McPherson 1999).

Anthropogenic forces have apparently caused most of the recent changes in semiarid grasslands, either directly or indirectly, thus allowing considerable *Juniperus* and other woody plant population expansion in North America and throughout the world (Hastings and Turner 1965; Buffington and Herbel 1965; Blackburn and Tueller

1970; Van Vegten 1983; Harrington et al. 1984; Van Auken and Bush 1985; Bush and Van Auken 1986; Smith and Goodman 1987; Archer et al. 1988; Archer 1989; Adamoli et al. 1990; Grover and Musick 1990; Schlesinger et al. 1990; Bahre 1991; Archer 1994; Miller and Wigand 1994; McClaran 1995; Reynolds et al. 1999; Schmutz et al. 1991; Scholes and Archer 1997; McPherson 1997; Van Auken 2000). What has occurred is an increase in density or cover of local woody species, including many *Juniperus* species, that have been present in various parts of western and southwestern North America for thousands of years (Humphrey 1958; Johnston 1963; Van Devender and Spaulding 1979; Vasek 1980).

Evidence that demonstrates recent, rapid *Juniperus* population expansion comes from old surveys, sequential photographs, pollen analysis, old stumps or logs, soil isotopic analysis, packrat middens, and tree-ring chronologies (Lyford et al. 2002; Jessup et al. 2003; Miller et al. 2005). The best evidence that shows the relatively recent, rapid population expansion of *J. occidentalis* is from tree-ring chronologies. When a large number of *Juniperus* communities are aged and the ages of the communities are examined as a function of time, there is an obvious large and rapid increase in the number or percent of *Juniperus* communities that have established recently (Figure 4). The increase in the number of new *Juniperus* communities started in the mid- to late 1800s and continued through most of the 1900s. This increase in *Juniperus* community establishment coincided with the introduction of season-long grazing by large numbers of domestic livestock and a concomitant reduction in fine fuel loads and fire frequency (Miller et al. 2005). Mean fire return intervals or fire-free intervals (time without fire) in these communities were highly variable and in the early 1800s were probably 12 to 15 years. However, the fire-free interval increased to more than 70 years after the introduction of season-long grazing by large numbers of domestic livestock and the concomitant reduction in fine fuel loads.

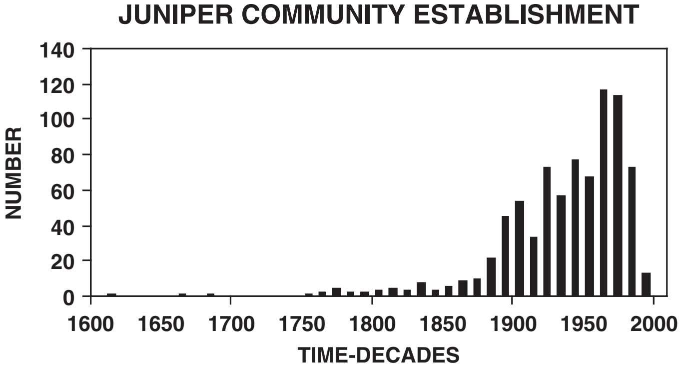

Figure 4 Number of new *Juniperus occidentalis* communities establishing per decade from 1600 to 2000. Total number of communities examined was 801. The area studied was the Lava Beds National Monument in northern California. (Data were modified from Miller et al. 2005)

Gradients

Elevational and spatial gradients are two major gradients present in western North America that must be considered when examining the distribution of *Juniperus* communities. In general, *Juniperus* woodlands exist along the lower part of the elevation gradients in many areas in the mountainous regions of western North America (West 1988, 1999; Miller and Wigand 1994). These *Juniperus* communities are usually found in locations with 17 to 50 cm of total annual precipitation and range in elevation from approximately 200 to 2800 m (West 1988, 1999; Gedney et al. 1999). The elevation range where the *Juniperus* communities are found depends on the aspect (lower on north-facing slopes and higher on south-facing slopes). In addition, when moving from south to north, the elevation where the *Juniperus* communities are found decreases.

These gradients would include increased moisture and decreased temperature as elevation and latitude increases. In addition, certainly other abiotic factors would change along an elevation gradient. Photographs easily show some of these population or community differences (Figure 5). There are very few *Juniperus* trees in the semiarid grassland on the low side of the elevation gradient in areas with lower rainfall and higher temperatures. The density and basal diameter of the *Juniperus* trees increases with elevation to a maximum and then decreases as *Pinus edulis* (or other piñon pine species) becomes the dominant species in the communities (Phillips 1909; Woodbury 1947; West 1988, 1999; Padien and Lajtha 1992;

Figure 5 Photograph of *Juniperus* plants along an elevation gradient. Higher elevation is to the *right center* and lower elevation is to the *left center*

Martens et al. 2001). Unfortunately, the structure of the *Juniperus* communities along the east–west spatial rainfall gradients where various *Juniperus* species are found is more difficult to understand and has not been examined or compared as carefully.

Some interesting studies have been carried out that demonstrate local biotic and abiotic changes that occur from woodland gaps or intercanopy spaces into *Juniperus* woodlands. In central Texas *Juniperus ashei* (Ashe juniper) woodlands, surface light, soil temperature, and soil moisture vary both temporally and spatially. Mean values for light and soil surface temperature were highest in August and lowest in December, whereas soil moisture was the reverse. Lowest light levels and soil surface temperatures were below the woodland canopy, and highest values were in the gaps, whereas soil moisture was highest below the woodland canopy and lowest in the gaps (Wayne and Van Auken 2002, 2004). The canopy edge values were intermediate to the canopy and intercanopy values for all factors. Apparently the *Juniperus* canopy intercepts incoming light and reduces the light levels and soil surface temperature in the understory.

Similar trends in surface light levels and surface soil temperatures have been reported in New Mexico *Pinus edulis–Juniperus monosperma* (piñion-juniper) woodlands and in *Juniperus virginiana* (eastern red cedar) woodlands in eastern North America (Breshears et al. 1997, 1998; Martens et al. 2000, 2001; Joy and Young 2002). The greatest differences in surface light levels in these communities are related to canopy–intercanopy patch variation or overstory–no overstory. Although trends for soil moisture in all these woodlands were similar, there were a few interesting differences in the New Mexico *Pinus edulis–Juniperus monosperma* woodlands (Breshears et al. 1997, 1998; this volume). In some of these New Mexico woodlands, at certain times of the year, there was more moisture in the soil in the intercanopy space than there was below the canopy. It is unclear if this is the result of interception of rainfall and/or differential evapotranspiration.

Other factors change as *Juniperus* woodlands encroach into various grasslands. Soil carbon storage changes dramatically, as do soil mineralization, nitrogen storage, and the types of nitrogen present in the soil (Miller et al. 2005; see McKinley et al., Chapter 9, this volume). Higher concentrations of soil nutrients and soil organic matter are usually found below the canopy in *Juniperus* woodlands compared to adjacent grasslands or gaps (Norris et al. 2001; Jessup et al. 2003). The levels of these factors may be the driving force for future community change.

Summary

Juniperus communities are widely distributed throughout the Northern Hemisphere, especially in western North America. Various species are found near the Arctic Circle in Alaska, Canada, and Greenland while other species are found south into the mountains of Central America. In the past, most *Juniperus* species appeared confined to rocky outcrops with thin soils associated with grassland communities or on slopes above the desert grasslands and in disturbances in forest communities. Recently, many of these *Juniperus* species have expanded their distribution by encroaching into adjacent grasslands. Their cover and density have increased, and other community properties have changed as well. The structure of these *Juniperus* communities is diverse but seems to be intermediate in the grassland–forest continuum. These communities occur in areas with very low rainfall bordering semiarid grasslands and deserts, as well as in early successional woodlands embedded in deciduous forests and in various communities between these. *Juniperus* communities appear to occur along an elevation gradient as well as a spatial rainfall gradient in parts of western North America. Species composition and community structure change along these gradients depending on biotic and abiotic conditions. In addition to elevation, spatial and temporal differences in these *Juniperus* communities are anthropogenically induced changes. Many of the recent changes in *Juniperus* populations seem to be caused by heavy and continuous grazing by domestic ungulates, coupled to reduced levels of light fluffy fuel and reduced fire frequency and intensity. Although global climate change is cited as a cause and may be a factor involved in *Juniperus* community distribution and spread, it does not seem to be the main factor. Global climate change in the late Pleistocene and Holocene was a major factor controlling the northern migration of various species of *Juniperus*. Thus, the structure, density, and composition of these savannas and woodlands seem to be controlled by rainfall and temperature, but reduction of the competing grass biomass by constant high levels of introduced domestic herbivores has reduced the fire frequency and is a major factor modifying the distribution and structure of these *Juniperus* communities.

References

Allen, C.D., and Breshears, D.D. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proc. Natl. Acad. Sci. U.S.A. 95:14839–14842.

Adamoli, J., Sennhauser, E., Acero, J.M., and Rescia, A. 1990. Stress and disturbance: vegetation in the dry Chaco region of Argentina. J. Biogeogr. 17:491–500.

Archer, S.R. 1989. Have southern Texas savannas been converted to woodlands in recent history? Am. Nat. 134:545–561.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: Ecological implications of livestock herbivory in the West, eds. M. Vavra, W.A. Laycock, and R.D. Pieper, pp 13–69. Denver: Society of Range Management.

Archer, S., Scifres, C., Bassham, C.R., and Maggio, R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecol. Monogr. 52:111–127.

Archer, S., Schimel, D.S., and Holland, E.A. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2? Clim. Change 29:91–99.

Bahre, C.J. 1991. A legacy of change: historic human impact on vegetation of the Arizona Borderlands. Tucson: University of Arizona Press.

Bahre, C.J., and Shelton, M.L. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. J. Biogeogr. 20:489–504.

Bedwell, S.F. 1973. Fort Rock Basin prehistory and environment. Eugene: University of Oregon Books.

Belsky, A.J., and Canham, C.D. 1994. Forest gaps and isolated savanna trees. BioScience 44:77–84.

Betancourt, J.L., Van Devender, T.R., and Martin, P.S. 1990. Synthesis and prospectus. In: Packrat middens: the last 40,000 years of biotic change, eds. J.L. Betancourt, T.R. Van Devender, and P.S. Martin, pp 435–447. Tucson: The University of Arizona Press.

Blackburn, W.H., and Tueller, P.T. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. Ecology 51:841–848.

Bray, W.L. 1904. The timber of the Edwards Plateau of Texas: its relation to climate, water supply, and soil. Bulletin no. 47. Washington, DC: United States Department of Agriculture, Bureau of Forestry.

Breshears, D.D. 2006. The grassland–forest continuum: trends in ecosystem properties for woody plant mosaics? Front. Ecol. Environ. 4:96–104.

Breshears, D.D., and Barnes, F.J. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landsc. Ecol. 14:465–478.

Breshears, D.D., Rich, P.M., Barnes, F.J., and Campbell, K. 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecol. Appl. 7:1201–1215.

Breshears, D.D., Nyhan, J.W., Heil, C.E., and Wilcox, B.P. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. Int. J. Plant Sci. 159:1010–1017.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.D., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., and Meyer, C.W. 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. U.S.A. 102:15144–15148.

Briggs, J.M., Knapp, A.K., and Brock, B.L. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. Am. Midl. Nat. 147:287–294.

Buffington, L.C., and Herbel, C.H. 1965. Vegetation changes on a semidesert grassland range from 1858 to 1963. Ecol. Monogr. 35:139–164.

Burkhardt, J.W., and Tisdale, E.W. 1976. Causes of juniper invasion in Southwestern Idaho. Ecology 57:472–484.

Bush, J.K., and Van Auken, O.W. 1995. Woody plant growth related to planting time and clipping of a C_4 grass. Ecology 76:1603–1609.

Cadenasso, M.L., Pickett, S.T.A., and Morin, P.J. 2002. Experimental test of the role of mammalian herbivores on old field succession: community structure and seedling survival. J. Torrey Bot. Soc. 129:228–237.

Chapin, F.S., III, Sala, O.E., Burke, I.C., Grime, J.P., Hooper, D.U., Lauernroth, W.K., Lombard, A., Mooney, H.A., Mosier, A.R., Naeem, S., Pacala, S.W., Roy, J., Steffen, W.L., and Tilman, D. 1998. Ecosystem consequences of changing biodiversity. BioScience 48:45–52.

Crowley, T.J. 2000. Causes of climate change over the past 1000 years. Science 289:270–277.

Davis, M.B. 1981. Quaternary history and stability of forest communities. In: Forest succession: concepts and applications, eds. D.C. West, H.H. Shugart, and D.B. Botkin, pp 132–153. New York: Springer-Verlag.

Delcourt, P.A., and Delcourt, H.R. 1981. Vegetation maps for the eastern United States: 40,000 yr B.P. to present. In: Geobotany, vol. II, ed. R.C. Romans, pp 123–165. New York: Plenum Press.

Delcourt, P.A., Delcourt, H.R., and Webb, T. 1983. Dynamic plant ecology: the spectrum of vegetation change in space and time. Quat. Sci. Rev. 1:153–175.

Dobson, A.P., Bradshaw, A.D., and Baker, A.J.M. 1997. Hopes for the future: restoration ecology and conservation biology. Science 277:515–522.

Eddleman, L.E. 1987. Establishment and stand development of western juniper in central Oregon. In: Proceedings of the pinyon-juniper cnference, ed. R.L. Everett, pp 255–259. General technical report INT-215. Ogden, UT: United States Forest Service.

Elias, T.S. 1980. The complete trees of North America. New York: Van Nostrand Reinhold.

Fuhlendorf, S.D., and Smeins, F.E. 1997. Long-term vegetation dynamics mediated by herbivory, weather and fire in a *Juniperus-Quercus* savanna. J. Veg. Sci. 8:819–828.

Fuhlendorf, S.D., Smeins, F.E., and Grant, W.E. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecol. Model. 90:245–255.

Gedney, D.R., Azuma, D.L., Bolsinger, C.L., and McKay, N. 1999. Western juniper in eastern Oregon. General technical report NW-GTR-464. Washington, DC: United States Forest Service.

Germain, H.L., and McPherson, G.R. 1999. Effects of biotic factors on emergence and survival of *Quercus emoryi* at lower tree line. Ecoscience 6:92–99.

Grover, H.D., and Musick, H.B. 1990. Shrubland encroachment in southern New Mexico, USA: an analysis of desertification processes in the American Southwest. Clim. Change 17:305–330.

Gruger, J. 1973. Studies on the vegetation of northwestern Kansas. Geol. Soc. Am. Bull. 84:239–250.

Halfsten, U. 1961. Pleistocene development of vegetation and climate in the southern high plains as evidenced by pollen. In: Paleoecology of the Llano Estacato, ed. F. Wencorf, pp 59–91. Fort Burgwin Research Center report I. Albuquerque: University of New Mexico Press.

Harrington, G.N., Wilson, A.D., and Young, M.D. 1984. Management of Australia's rangelands. Melbourne: Commonwealth Scientific Industrial Research Organization.

Hastings, J.R., and Turner, R.M. 1965. The changing mile. Tucson: University of Arizona Press.

Hevly, R.H., and Martin, P.S. 1961. Geochronology of pluvial Lake Cochise, southern Arizona. I. Pollen analysis of shore deposits. J. Ariz. Acad. Sci. 2:24–31.

Holmes, R.L., Adams, R.K., and Fritts, H.C. 1986. Tree ring chronologies of western North America: California, eastern Oregon and northern Great Basin. Chronology Series VI. Laboratory of Tree Ring Research. Tucson: University of Arizona Press.

Hora, B. 1981. The Oxford encyclopedia of trees of the world. New York: Oxford University Press.

House, J.I., Archer, S.R., Breshears, D.D., and Scholes, R.J. 2003. Conundrums in mixed woody-herbaceous plant systems. J. Biogeogr. 30:1763–1777.

Howard, L.F., and Lee, T.D. 2002. Upland old-field succession in southeastern new Hampshire. J. Torrey Bot. Soc. 129:60–76.

Humphrey, R.R. 1958. The desert grassland: a history of vegetation change and an analysis of causes. Bot. Rev. 24:193–252.

Idso, S.B. 1992. Shrubland expansion in the American southwest. Clim. Change 22:85–86.

Imbrie, J., and Imbrie, K.P. 1979. Ice Ages: solving the mystery. Short Hills: Enslow.

Jessup, K.E., Barnes, P.W., and Boutton, T.W. 2003. Vegetation dynamics in a *Quercus-Juniperus* savanna: an isotopic assessment. J. Veg. Sci. 14:841–852.

Johnsen, T.N. 1962. One-seed juniper invasion of Northern Arizona grasslands. Ecol. Monogr. 32:187–207.

Johnson, H.B., Polley, H.W., and Mayeux, H.S. 1993. Increasing CO_2 and plant–plant interactions: effects on natural vegetation. Vegetatio 104–105:157–170.

Johnston, M.C. 1963. Past and present grasslands of southern Texas and northeastern Mexico. Ecology 44:456–466.

Joy, D.A., and Young, D.R. 2002. Promotion of mid-successional seedling recruitment and establishment by *Juniperus virginiana* in a coastal environment. Plant Ecol. 160:125–135.

Küchler, A.W. 1970. Potential natural vegetation map. In: The National Atlas of the U.S., pp 90–91. Washington, DC: United States Government Printing Office.

Little, E.L. 1971. Atlas of United States trees, vol. 1. Conifers and important hardwoods. Miscellaneous publication 1146. Washington, DC: United States Department of Agriculture.

Lyford, M.E., Betancourt, J.L., and Jackson, S.T. 2002. Holocene vegetation and climatic history of the northern Big Horn Basin, Southern Montana. Quat. Res. 58:171–181.

Mackenzie, F.T. 2003. Our changing planet: an introduction to Earth systems science and global environmental change. Upper Saddle River, NJ: Pearson Education.

Martens, S.N., Breshears, D.D., and Meyer, C.W. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial patterns of tree canopies. Ecol. Monogr. 126:79–93.

Martens, S.N., Breshears, D.D., and Barnes, F.J. 2001. Development of species dominance along an elevational gradient: population dynamics of *Pinus edulis* and *Juniperus monosperma*. Int. J. Plant Sci. 162:777–783.

Martin, P.S. 1999. Deep history and a wilder West. In: Ecology of the Sonoran Desert plants and plant communities, ed. R.H. Robichaux, pp 255–290. Tucson: University of Arizona Press.

Mayeux, H.S., Johnson, H.B., and Polly, H.W. 1991. Global change and vegetation dynamics. In: Noxious range weeds, eds. L.F. James, J.O. Evans, M.H. Ralphs, and B.J. Sigler, pp 62–74. Boulder: Westview Press.

McClaran, M.P. 1995. Desert grasslands and grasses. In: The desert grasslands, eds. M.P. McClaran and T.R. Vandevender, pp 1–30. Tucson: University of Arizona Press.

McDowell, P.F., Webb, T., III., and Bartlein, P.J. 1995. Long-term environmental change. In: Ecological time series, eds. T.M. Powell, and J.H. Steele, pp 327–370. New York: Chapman & Hall.

McPherson, G.R. 1997. Ecology and management of North American savannas. Tucson: University of Arizona Press.

McPherson, G.R., Wright, H.W., and Wester, D.B. 1988. Patterns of shrub invasion in semiarid Texas grasslands. Am. Midl. Nat. 120:391–397.

Mehringer, P.J., and Wigand, P.E. 1984. Prehistoric distribution of western juniper. In: Proceedings, western juniper management short course. Bend: Oregon State University Agricultural Extension Service.

Miller, R.F., and Rose, J.A. 1995. Historic expansion of *Juniperus occidentalis* (western juniper) in south eastern Oregon. Great Basin Nat. 55:37–45.

Miller, R.F., and Wigand, P.E. 1994. Holocene changes in semiarid pinyon-juniper woodlands: response to climate, fire, and human activities in the Great Basin. BioScience 44:465–474.

Miller, R.F., Bates, J.D., Svejcar, T.J., Pierson, F.B., and Eddleman, L.E. 2005. Biology, ecology and management of western juniper (*Juniperus occidentalis*). Technical bulletin 152. Corvallis: Agriculture Experiment Station, Oregon State University.

Mooney, H.A., and Hobbs, R.J. 2000. Invasive species in a changing world. Covelo, CA: Island Press.

Neilson, R.P. 1986. High-resolution climatic analysis and southwest biogeography. Science 232:27–34.

Norris, M.D., Blair, J.M., Johnson, L.C., and McKane, R.B. 2001. Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. Can. J. For. Res. 31:1940–1946.

Padien, D.J., and Lajtha, K. 1992. Plant spatial pattern and nutrient distribution in pinyon-juniper woodlands along an elevational gradient in northern New Mexico. Int. J. Plant Sci. 153:425–433.

Pimm, S.L., Russell, G.J., Gittleman, J.L., and Brooks, T.M. 1995. The future of biodiversity. Science 269:347–350.

Phillips, F. 1909. A study of pinion pine. Bot. Gaz. 48:216–223.

Polley, H.W., Johnson, H.B., and Mayeux, H.S. 1992. Carbon dioxide and water fluxes of C_3 annuals and C_3 and C_4 perennials at subambient CO_2 concentrations. Funct. Ecol. 6:693–703.

Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soyza, A.G., and Tremmel, D.C. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecol. Monogr. 69:69–106.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., and Whitford, W.G. 1990. Biological feedbacks in global desertification. Science 247:1043–1048.

Schmutz, E.M., Smith, E.L., Ogden, P.R., Cox, M.L., Klemmedson, J.O., Norris, J.J., and Fierro, L.C. 1991. Desert grasslands. In: Natural grasslands: introduction and Western Hemisphere, ed. R.T. Coupland, pp 337–362. Amsterdam: Elsevier.

Scholes, R.J., and Archer, S.R. 1997. Tree-grass interactions in savannas. Annu. Rev. Ecol. Syst. 28:517–544.

Sears, P.B., and Clisby, K.H. 1956. San Agustin Plains–Pleistocene climate changes. Science 124:537–539.

Smeins, F.E., and Merrill, L.B. 1988. Long term change in a semiarid grassland. In: Edward's Plateau vegetation: plant ecological studies in central Texas, eds. B.B. Amos and F.R. Gehlbach, pp 101–114. Waco, TX: Baylor University Press.

Smith, T.M., and Goodman, P.S. 1987. Successional dynamics in an *Acacia nilotica–Euclea divinorum* savannah in southern Africa. J. Ecol. 75:603–610.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–215.

Van Auken, O.W., and Bush, J. K. 1985. Secondary succession on terraces of the San Antonio River. Bull. Torrey Bot. Club 112:158–166.

Van Auken, O.W., and Bush, J.K. 1997. Growth of *Prosopis glandulosa* in response to changes in aboveground and belowground interference. Ecology 78:1222–1229.

Van Auken, O.W., Jackson, J.T., and Jurena, P.N. 2004. Survival and growth of *Juniperus* seedlings in *Juniperus* woodlands. Plant Ecol. 175:245–257.

Van Devender, T.R. 1995. Desert grassland history: changing climates, evolution, biography, and community dynamics. In: The desert grassland, eds. M.P. McClaran and T.R. Van Devender, pp 68–99. Tucson: University of Arizona Press.

Van Devender, T.R., and Spauling, W.G. 1979. Development of vegetation and climate in the southwestern United States. Science 204:701–710.

Van Vegten, J.A. 1983. Thornbush invasion in a savanna ecosystem in eastern Botswana. Vegetatio 56:3–7.

Vasek, F.C. 1980. Creosote bush: long-lived clones in the Mojave Desert. Am. J. Bot. 67:246–255.

Vasek, F.C., and Thorne, R.F. 1977. Transmontane coniferous vegetation. In: Terrestrial Vegetation of California, Special Publication No. 9, eds. M.G. Barbour and J. Major, pp 797–832. Berkley: California Native Plant Society.

Waichler, W.S., Miller, R.F., and Doescher, P.S. 2001. Community characteristics of old-growth western juniper woodlands in the pumice zone of central Oregon. J. Range Manag. 54:518–527.

Wayne, R., and Van Auken, O.W. 2002. Spatial and temporal patterns of xylem water potential in *Juniperus ashei* seedlings. Southwest. Nat. 47:153–161.

Wayne, R., and Van Auken, O.W. 2004. Spatial and temporal abiotic changes along a canopy to intercanopy gradient in central Texas *Juniperus ashei* woodlands. Tex. J. Sci. 56:35–54.

Wells, P.V. 1965. Scarp woodlands, transported grassland soils, and concept of grassland climate in the Great Plains Region. Science 148:246–249.

Weltzin, J.F., and McPherson, G.R. 1999. Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. Ecol. Monogr. 69:513–534.

West, N.E. 1984. Successional patterns and productivity potentials of pinyon-juniper ecosystems. In: Developing strategies for range management, ed. National Research Council/National Academy of Sciences, pp 1301–1332. Boulder: Westview Press.

West, N.E. 1988. Intermountain deserts, shrub steppes, and woodlands. In: North American terrestrial vegetation, eds. M.C. Barbour and W.D. Billings, pp 210–230. Cambridge: Cambridge University Press.

West, N.E. 1999. Juniper-piñon savannas and woodlands of western North America. In: Savannas, barrens, and rock outcrop plant communities of North America, eds. R.C. Anderson, J.S. Fralish, and J.M. Baskin, pp 288–308. Cambridge: Cambridge University Press.

Westerling, A.L., Hidalog, H.G., Cayan, D.R., and Swetnam, T.W. 2006. Warming and earlier spring increases western U.S. forest wildfire activity. Science 1126:1–10.

Wigand, P.E. 1987. Diamond Pond, Harney County, Oregon: vegetation history and water table in the eastern Oregon desert. Great Basin Nat. 47:427–458.

Wigand, P.E., Hemphill, M.L., Sharpe, S., and Patra, S. 1995. Great Basin semi-arid woodland dynamics during the late Quaternary. In: Proceedings: climate change in the Four Corners and adjacent regions: implications for environmental restoration and land-use planning, ed. W.J. Waugh, pp 51–70. Washington, DC: United States Department of Energy.

Woodbury, A. M. 1947. Distribution of pygmy conifers in Utah and northeastern Arizona. Ecology 28:113–126.

Yu, Z.C. 2003. Late Quaternary dynamics of tundra and forest vegetation in the southern Niagara Escarpment, Canada. New Phytol. 157:365–390.

2
Structure and Composition of *Juniperus* Communities and Factors That Control Them

O.W. Van Auken and D.C. McKinley

Introduction

Most *Juniperus* communities are savannas, evergreen woodlands, and, in some cases, evergreen forests. They are found above the arid deserts of the American West and Southwest or above the various grasslands found in this region (Coupland 1979; Sims 1988; West 1988, 1999; Van Auken 2000a). They are usually below the diverse high-elevation evergreen forests that are found here as well (West 1988, 1999). Rainfall in *Juniperus* woodland communities is usually 17 to 80 cm per year, and elevation is 200 to 2800 m, depending on latitude (West 1988, 1999; Jackson and Van Auken 1997; Gedney et al. 1999). In mountain ecosystems, lower-elevation *Juniperus* communities interdigitate with associated deserts and grasslands and are fairly open communities. At higher elevations, they grade into the evergreen forests and may have a closed canopy. In many grassland communities in central North America, *Juniperus* encroachment has converted large areas of contiguous grassland into savannas, woodlands, or closed-canopy forests (Briggs et al. 2002; also see Chapter 8, this volume).

Comparisons presented are primarily of various *Juniperus* and associated communities in western and southwestern North America with a few examples from the central plains. However, many of the studies reported here were conducted in central Texas along the southern edge of the Edwards Plateau near the Balcones Escarpment (Diamond et al. 1995). This area of central Texas includes upland and riparian communities that are representative of the region and have not been grazed for more than 50 years. The regional climate for this central Texas area is subtropical–subhumid with a mean annual temperature of 20°C (Arbingast et al. 1976) and annual precipitation of approximately 80 cm with peaks in May (11 cm) and September (9 cm). Monthly and annual precipitation is highly variable with very little occurring during June and July. Low temperature is in January (9.6°C) and high temperature is in July (29.4°C). These temperatures are higher than reported for more northern and western continental *Juniperus* communities (National Oceanic and Atmospheric Administration 2004).

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Soils of many of the *Juniperus* communities in western North America are shallow, derived from various limestone or dolomite substrates, but there is considerable variation (West 1988, 1999). Soils of the upland central Texas sites are generally clayey-skeletal, smectitic, thermic lithic calciustolls in the Glen Rose, Edwards, or the Tarrant association, and rolling, with a slope of 4.5° to 13.5°. The surface horizon ranges from 0 to 25 cm in thickness over a subsurface of heavily fractured limestone over limestone bedrock (Sellards et al. 1932; Taylor et al. 1962). Floodplain soils are deep (>150 cm), well-drained, coarse-loamy, carbonatic, thermic fluventic ustochrepts of the Boerne series (Soil Conservation Service 1979).

Woodland Community Structure

Juniperus woodlands vary considerably in structure and composition and are usually found with one or more species of *Pinus*, usually *P. edulis, P. monophyla, P. cembroides*, or *P. juarezensis* (West 1988, 1999). In addition, various *Quercus* sp. are fairly common associates in southwestern woodlands (Peet 1988). Variation in the herbaceous communities in the understory of these woodlands is even greater and is probably best described as similar to the adjacent grasslands (West 1988).

Comparison of some of the woodlands of southwestern Texas (the Davis Mountains) and similar communities in central New Mexico (the Manzano Mountains) demonstrates some of the variation in species present, density, and basal area of these communities (Table 1). Four species of *Juniperus*, two species of *Pinus*, and three species of *Quercus* were reported. Total density of these communities was 400–600 stems/ha, and total basal area was 4.5 m^2/ha in western Texas and 13.3 m^2/ha in central New Mexico. Only stems greater than 10 cm in diameter at 0.3 m in height were measured. Consequently, only plants with a fairly large basal diameter were included in the study. Because of this constraint, both basal area and density were probably underestimated.

The *Juniperus* woodlands found in central Texas and in other areas are presumably controlled by broad climatic and edaphic factors including the amount of precipitation, temperature, soil characteristics, and amount and availability or nutrients. Hilltop central Texas *Juniperus* woodlands are relatively simple communities. The number of woody species in any given community is relatively low (10–20) with one or two dominants. *Juniperus ashei* density in these areas is usually 400–1000 plants/ha depending on the area studied and the procedure used (Table 2). However, much higher densities have been reported, including densities as high as 3500 plants/ha in some communities (Van Auken et al. 1979, 1980; Briggs et al. 2002).

Another high-density shrub or small tree in these central Texas *Juniperus* communities is *Diospyros texana* (Texas persimmon). Other species found at lower densities were *Quercus virginiana* (=*Q. fusiformis*, live oak), *Sophora secundiflora* (mountain laurel), *Q. glaucoides* (Lacy oak), *Rhus virens* (evergreen sumac), *Berberis trifoliata* (agarito), and *Acacia romeriana* (cat-claw acacia). The various species of piñon pines that are common in the more western *Juniperus* woodlands

Table 1 Comparison of density and basal area of woody plants found in evergreen woodlands in the Davis Mountains of the southwestern part of Texas and the Manzano Mountains of central New Mexico

	Density (plants/ha)		Basal area (m^2/ha)	
Species	Texas	New Mexico	Texas	New Mexico
Juniperus deppeana	181	—	2.2	—
Pinus cembroides	128	—	1.0	—
Quercus grisea	94	—	0.9	—
Quercus emoryi	40	—	0.3	—
Juniperus erythrocarpa	21	—	0.2	—
Juniperus monosperma	—	346	—	9.8
Pinus edulis	—	162	—	2.9
Quercus undulatus	—	24	—	—[a]
Juniperus scopulorum	—	18	—	0.6
Rhus trilobata	—	9	—	—[a]
Cercocarpus montanus	—	6	—	—[a]
Total	464	565	4.6	13.3

[a] Less than 0.1 m^2/ha.
Source: Woodin and Lindsey (1954).

Table 2 Mean density and basal area (±SE) of woody plants found in evergreen woodlands in the southern part of the Edwards Plateau of central Texas

Species	Density (plants/ha)	Basal area (m^2/ha)
Juniperus ashei	668 ± 150[a]	38.6 ± 5.4
Diospyros texana	207 ± 39	1.0 ± 0.4
Quercus virginiana	39 ± 19	0.9 ± 0.8
Sophora secundiflora	10 ± 8	< 0.1 ± 0.1
Quercus glaucoides	7 ± 6	0.2 ± 0.1
Other (seven species)	39	0.1
Total	970	40.8

[a] Mean ± SE.
Source: Van Auken et al. (1981).

are usually not present in these central Texas *Juniperus* communities. However, limited populations of *P. ramota*, a localized species of piñon pine, have been reported in some places in south-central Texas and northeastern Mexico (Lundell 1966; Olson et al. 1997).

The species with the highest basal area or dominance in these central Texas woodlands was usually *J. ashei* (see Table 2) with a basal area more than three times higher than the New Mexico woodlands. Other species such as *Q. virginiana, Berberis trifoliata*, and *Diospyros texana* sometimes have high basal areas in these central Texas woodlands (Van Auken et al. 1979, 1980; Terletzky and Van Auken 1996). *Juniperus* basal areas ranged from about 20 to 45 m^2/ha in these Texas woodlands. In northeastern Kansas, *J. virginiana* breast height areas were 21–36 m^2/ha (McKinley, unpublished data). Some of the reported differences are

Figure 1 Photograph of encroachment and early establishment of various ages and sizes of *Juniperus* plants in a heavily grazed, unburned grassland in central Texas

caused by habitat or environmental conditions, but some are the result of different techniques used to estimate the population parameters (i.e., quadrate versus the point-centered quarter method or basal versus breast-height measurements). Many of these *Juniperus* woodlands and savannas are quite open (Figure 1). Some differences in the communities appear to be caused by limited and variable rainfall, but some are related to shallow soils, geological substrate, or anthropogenic factors (Marsh and Marsh 1993a,b; Wilding 1993; Terletzky and Van Auken 1996; Van Auken 2000a).

Gaps or Patches

Many of the central Texas *Juniperus* woodlands are fairly open with numerous gaps or open patches (Van Auken 2000b), which is true for other *Juniperus* woodlands as well (Breshears et al. 1998; also see Chapter 4, this volume). There seem to be at least two types of gaps or patches. Narrow central Texas hillside intercanopy gaps or patches have low plant cover, and annuals are usually dominates (Figure 2) (Terletzky and Van Auken 1996). These gaps appear similar to the more thoroughly studied intercanopy patches or cedar glades in the southeastern and south-central United States (Kucera and Martin 1957; Quarterman 1950a,b; Baskin and Baskin 1978, 1985a,b). The central Texas hillside intercanopy gaps are narrow bands of herbaceous vegetation that alternate with bands of *Juniperus ashei* woodlands (Figures 2, 3). When viewed from the air, these bands form a “bulls-eye” around the hill. They seem to correspond to “stair-step” topography (Figure 4) commonly seen in parts of central Texas (Riskind and Diamond 1988; Woodruff 1993; Terletzky and Van Auken 1996). The gaps or patches are usually found on

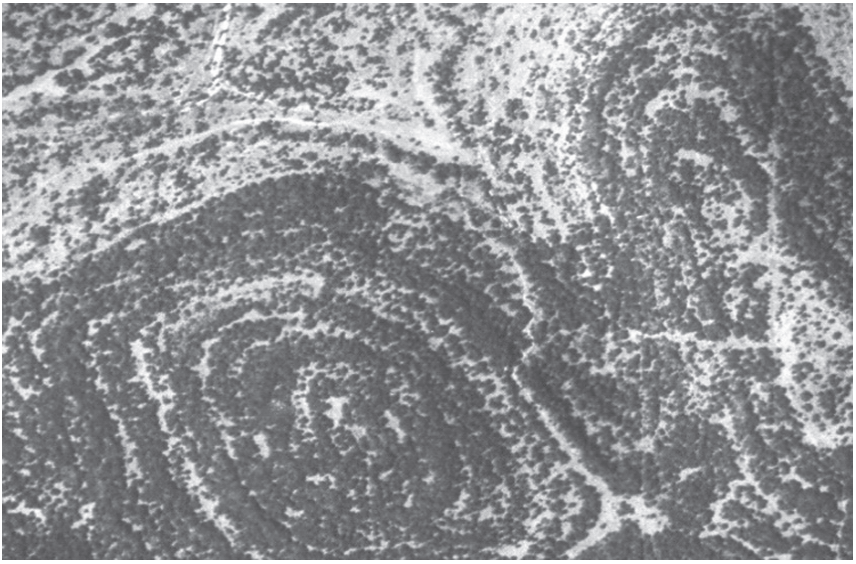

Figure 2 Aerial photograph of a hilltop found in the southern part of the Edwards Plateau in central Texas. The bulls-eye structure represents a series of alternating bands of vegetation. The *dark bands* are *Juniperus* woodlands and the *lighter bands* are the grassy open gaps or patches within the woodlands

Figure 3 Photograph of a hillside gap or opening and associated *Juniperus* woodland in central Texas. The photograph was taken in one of the grassy patches with woodland on both sides

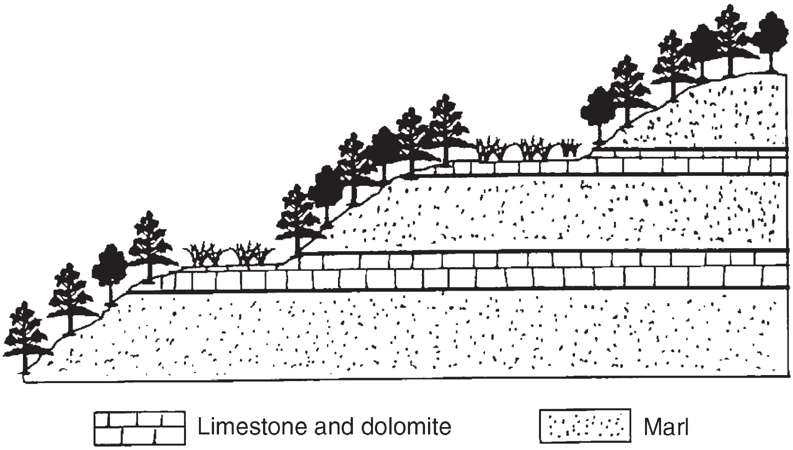

Figure 4 Schematic cross-sectional drawing of *Juniperus* woodlands and hillside intercanopy gaps or patches in the southern part of the Edwards Plateau Region. This figure represents several of the alternating vegetational bands shown in the aerial view of the bulls-eye structure shown in Figure 3

the outer edge of the steps whereas the *Juniperus* woodland occurs on the inner edge (see Figure 4). This topography is the result of differential weathering and erosion of the alternating bands of soft marl and hard limestone and dolomite that compose the Glen Rose Formation (Woodruff 1993). Similar "stair-step" topography and vegetation banding are associated with the open cedar glades and *Juniperus* woodlands in Missouri and Arkansas (Kucera and Martin 1957; Hendrickson and Davis 1980; Gates et al. 1982; Ware 2002) but have not been reported from western or southwestern North America.

The surface light levels in the gaps or open patches were 10 times higher (1990 ± 9 µmol/m^2/s, mean ± SD) compared to below the woodland canopies (189 ± 46 µmol/m^2/s), and soils were shallow (3.4 ± 1.1 cm) compared to the woodlands (8.1 ± 1.2 cm). The soils were also slightly basic, high in calcium, and variable in organic matter (Terletzky and Van Auken 1996). The mean total herbaceous plant cover in the gaps was 13% compared to the associated woodlands at 3%. The vegetative structure of the gaps seems to be influenced primarily by shallow soils and intermittent, low soil moisture levels. However, soil fertility and the type of bedrock may be important (Freeman 1933; Erickson et al. 1942; Quarterman 1950b; Kucera and Martin 1957).

In addition to the hillside gaps or patches, others gaps are found on level terrain. These gaps can include bare patches that are small, relatively circular communities with an exposed central bedrock, shallow soil, and low plant cover; they can occur in a grassland or woodland matrix. The bare patches are dominated by nonvascular plants, annual grasses, and annual forbs (Van Auken 2000b). These patches are relatively common in the grassland matrix of central Texas woodlands and savannas. Mean cover ± SD of plant, litter, rock, and bare soil in these patches was

23% ± 3%, 23% ± 5%, 44% ± 9%, and 10% ± 4%, respectively. Approximately 50% of the total relative plant cover consisted of forbs with 25% grasses and 25% non-vascular plants. Fifty-seven species of flowering plants from 30 families were identified, including 27 annuals (Table 3) and 30 perennials (Table 4). The most

Table 3 Relative occurrence and relative cover of the common annual species found in the intercanopy bare patches in the southern Edwards Plateau Region of central Texas

Species	Occurrence (%)	Cover (%)
Chaetopappa bellidifolia	100	15.3 ± 0.6
Evax prolifera	100	2.5 ± 0.2
Croton monanthogynus	92	4.2 ± 0.2
Spermolepis inermis	92	4.8 ± 0.5
Centaurium texense	83	1.3 ± 0.1
Galium virgatum	83	1.9 ± 0.2
Astragalus nuttallianus	67	1.2 ± 0.2
Euphorbia serpens	67	1.2 ± 0.1
Heliotropium tenellum	58	3.9 ± 0.6
Lesquerella recurvata	58	0.8 ± 0.1
Sporobolus vaginaeflorus	58	2.2 ± 0.2
Other[a]		6.5
Total		45.8

Relative cover values are means ± SE.
[a] Sixteen species with occurrence values of 50% or less and cover values of 1.0% or less.
Source: Van Auken (2000b).

Table 4 Relative occurrence and relative cover of the common herbaceous perennial species found in the intercanopy bare patches in the southern Edwards Plateau Region of central Texas

Species	Occurrence (%)	Cover (%)
Sida abutifolia	83	1.3 ± 0.1
Schizachyrium scoparium	83[a]	3.1 ± 0.2
Allium drummondii	58	0.7 ± 0.1
Chaerophvllum tantorii	58	1.8 ± 0.2
Aristida purpurea	58[a]	0.9 ± 0.1
Carex planostachys	50	0.5 ± 0.1
Cooperia peduneulata	50	0.5 ± 0.1
Phyla incisa	50	0.6 ± 0.1
Hilaria berlangeri	50[a]	1.5 ± 0.2
Other[b]		7.8
Total		17.8

Relative cover values are means ± SE.
[a] Grass species.
[b] Fourteen species with occurrence values less than 50% and relative cover less than 1.5%.
Source: Van Auken (2000b).

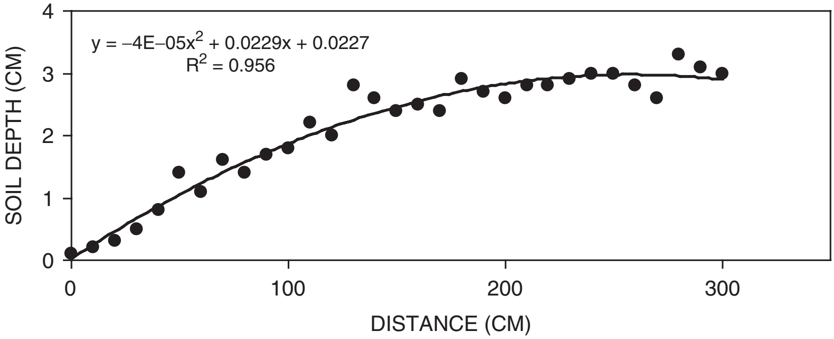

Figure 5 Mean soil depth (cm) is presented as a function of distance (cm) from the central bedrock of an intercanopy bare patch. Measurements were made every 10 cm and are averaged over 12 intercanopy bare patches examined in central Texas. The line is a best-fit function, and the coefficient of determination (R^2) is significant ($P < 0.001$). (Data from Van Auken 2000b)

common families were the Poaceae (9 species), Asteraceae (5 species), Euphorbiaceae (5 species), and Labiatae (4 species).

Nostoc commune, a common soil blue-green algae, was found in every intercanopy bare patch. Nonvascular plant cover was highest near the edge of the central bedrock and decreased with distance. Total plant and litter cover increased with distance from the central bedrock. Total annual cover was five times higher than total perennial cover, and both increased with distance from the central bedrock. The mean number of species found per intercanopy patch was 31 ± 4. Soil depth increased with distance from the central bedrock, whereas rock cover decreased. Total plant, annual, and perennial cover, as well as litter cover, were positively related to soil depth, whereas rock cover was negatively related to soil depth. The mean soil depth was 0 cm in the central bedrock area and increased to 3.3 cm near the outer edge of the patches (Figure 5). Ninety-six percent of the variation in mean soil depth was explained by distance ($R^2 = 0.96$, $P < 0.001$, using a second-order quadratic equation) (Van Auken 2000b). Soils were slightly basic, high in calcium, and low in nitrogen and organic matter. Shallow soil depth and intermittent water availability are probably the main factors that determine the composition of the bare patches, including low cover and the high proportion of annuals (Van Auken 2000b).

Embedded Deciduous Forest Structure

Within the *Juniperus* woodlands of central Texas there are limited areas of deciduous forest (Van Auken et al. 1981). These deciduous forests are found on north-facing slopes just below a hard limestone cap rock. They seem to be similar to the “Cove” forests reported from eastern North America (Barbour and Billings 1988). The dominant genera found in these communities were *Quercus, Prunus,*

Table 5 Mean density and basal area (±SE) of common woody plants found in deciduous woodlands in the southern part (Hill Country) of the Edwards Plateau of central Texas

Species	Density (plants/ha)	Basal area (m^2/ha)
Juniperus ashei	502 ± 93	1.9 ± 0.5
Aesculus pavia	296 ± 106	0.8 ± 0.4
Quercus texana	263 ± 24	12.8 ± 2.0
Quercus glaucoides	236 ± 77	8.9 ± 2.4
Diospyros texana	207 ± 39	1.0 ± 0.4
Prunus serotina	80 ± 19	4.8 ± 1.2
Fraxinus texensis	69 ± 21	3.6 ± 0.9
Ugnadia speciosa	34 ± 13	0.2 ± 0.1
Juglans nigra	44 ± 9	4.5 ± 1.7
Sophora secundiflora	29 ± 12	< 0.1 ± 0.1
Quercus virginiana	1 ± 1	< 0.1 ± 0.1
Other (7 species)	40	0.3
Total	1851	38.6

Source: Van Auken et al. (1981).

Juglans, and *Fraxinus* (Table 5), although *Juniperus ashei* and *Diospyros texana* were present at relatively high densities but low basal areas (see Table 5). Nineteen woody species were found, and 48% were exclusive to these deciduous forests.

Soils in the deciduous forests were deeper than the soils in the *Juniperus* woodland (103.8 ± 6.7 cm vs. 21.4 ± 2.8 cm) and had higher organic content and water retention capacity (19.2% ± 1.3% vs. 13.7% ± 3.7%, and 103.7% ± 3.8% vs. 93.9% ± 8.5%, respectively). Consequently, the potential field capacity for the deciduous forest soils was 3.5 times higher than for the *Juniperus* woodland soils. The factors regulating the distribution and composition of these deciduous forest communities appear to be the amount of insolation reaching the communities and the water available in the soil, which results in part from differences in soil composition, depth, and topographic position.

The woodland and forest communities found in this area of central Texas appear to be part of a soil moisture gradient (Van Auken et al. 1981). This gradient affects the extent, density, basal area, and species composition of these communities. The mesic end of this gradient would be the floodplain forests found along the major rivers crossing the region (Van Auken et al. 1979; Ford and Van Auken 1980; see following). Intermittent creek or stream fringe forest would be drier, followed by the upland deciduous forests and the canyon floor forests. The xeric end of the gradient would be the open south-facing slope woodlands, followed by hilltop savannas of this region or farther west. The gradient for these communities is similar to that reported for the woodland communities of southeastern Arizona (Whittaker 1975).

Many of the species present in the deciduous forest communities of central Texas are either endemics or eastern species that have their western limit of distribution in this area (Van Auken et al. 1981). Apparently the microclimate of these protected deciduous communities is such that it can accommodate some eastern and western species and has allowed the development and maintenance of several endemics as well. The structure of these communities may be changing, but unfortunately there is little documentation of the changes or of the direction of these changes.

Riparian Forest Structure

Riparian forests or woodlands transect all the *Juniperus* communities in western and southwestern North America (Barbour and Billings 1988). They are not *Juniperus* communities but are adjacent to them. These communities are narrow, ribbon-like gallery communities. They cover small areas, but their structure and composition are very different from that of the surrounding *Juniperus* communities. The low-elevation streamside or riverside forests of central Texas and western North America are botanically and ecologically quite interesting. In many cases, they are the first true forests encountered in the region, but they are probably the least typical of the region as a whole. They are composed mostly of deciduous species, including several truly invasive species such as the salt cedars or *Tamarix* (Van Auken 2000a). In some areas, the river and stream banks are covered with a heavy growth of *Tamarix*.

The native species that are usually fairly common in these riparian forests are *Populus* (cottonwoods) and *Salix* (willows), and these species change from east to west and from north to south (Peet 1988; West 1988). In addition, there are also elevational gradients to which these species respond, with cold-tolerant species at the higher elevations. Smaller creeks have fewer truly riparian species and usually a lower density and basal area of these species (Van Auken et al. 1979). In the madrean region of the southwestern United States and northern Mexico, low-elevation riparian forests usually have one or more species of *Platanus, Juglans*, and *Fraxinus*.

Just below the *Juniperus* communities on some of the more extensive floodplains, along some of the larger rivers, are fairly extensive stands of *Prosopis* (mesquite). These communities are probably successional, resulting from heavy grazing by domestic ungulates and lack of fires (Van Auken 2000a). *Prosopis* communities can be found over broad areas, but these usually occur at lower elevations compared to the *Juniperus* communities. Some *Juniperus* species can establish in these areas that are currently undergoing succession, and the communities will not be the same in the future, but at this time their projected composition is unknown.

The riparian forests of the Guadalupe River floodplain in central Texas are typical of the region. A high diversity of deciduous plants including many eastern forest species are present (Table 6) (Ford and Van Auken 1982). Total density was 1396 plants/ha including some vines and shrubs. The high-density species included *Celtis laevigata* and *Carya illinoinensis. Juniperus ashei* was found infrequently, but occurred near the upper edge of the riparian community and is probably capable of encroachment. Total basal area was 67.5 m^2/ha, which was 1.7 times greater than the total basal area of the upland *Juniperus* woodlands. *Taxodium distichum* had the greatest basal area at 35.5 m^2/ha. Riparian community total density, basal area, and number of species were highest at the edge of the river and decreased as one proceeded away from the river and upslope.

Table 6 Mean density and basal area of common woody plants found in riparian forests on the floodplain along the Guadalupe River in the southern part of the Edwards Plateau of central Texas

Species	Density (plants/ha)	Basal area (m^2/ha)
Celtis laevigata	274	5.6
Carya illinoinensis	249	17.0
Diospyros texana	172	0.2
Parthenocissus quinquefolia	137	0.3
Acer negundo	69	0.2
Ulmus crassifolia	59	3.0
Taxodium distichum	46	35.5
Cornus drummondii	41	0.1
Morus rubra	32	1.2
Ulmus americana	31	1.2
Vitus mustangensis	24	0.2
Juglans nigra	22	0.8
Other (15 species)	240	2.3
Total	1396	67.6

Source: Ford and Van Auken (1982).

The species composition of these riparian forests resembles the communities described in early reports, which suggests lack of change or constant change, indicating that these communities are probably stable (Hill and Vaughan 1898; Bray 1904; Palmer 1920). There are certainly species that have been recent introductions, including *Melia azedarach* (Chinaberry) and probably *Rhus toxicodendron* (poison ivy) and *Sapium sebiferum* (Chinese tallow) (Van Auken 2000a). The extent of the spread of these woody species, their expected density and basal area, and their effects on these central Texas communities are unstudied and unknown. Community ordination showed that the forests of the intermittent creeks and rivers are similar, but both these communities are quite different compared to the *Juniperus* woodlands of this area (Van Auken 1988).

Succession in *Juniperus* Woodlands

In many parts of central, western, and southwestern North America, populations of various *Juniperus* species have increased in density and area covered (Bray 1904; West 1984; Eddleman 1987; Smeins and Merrill 1988; Miller and Wigand 1994; McPherson 1997; Norris et al. 2001; Briggs et al. 2002; also see Chapter 8, this volume). Increased density of *Juniperus* has occurred in the grasslands, savannas, and woodlands in this area during the past 150 to 300 years, but most of the information reported is anecdotal (see Inglis 1962; Bahre 1991; Bahre and Shelton 1993). These changes have resulted in a decrease in grassland and a concomitant increase in savanna and woodland (Bahre 1991; McPherson 1997; Norris et al. 2001; Briggs et al. 2002). This encroachment (Van Auken 2000a) is a form of succession from grassland to savanna, woodland, or forest. The stable point or the stable community in the successional process or the time required to get to a stable point is undetermined. Although *Juniperus* woodlands are known to be intermediate successional communities in the development of deciduous forests in relatively mesic areas, the successional sequence and the time line in more arid regions is unclear (Cadenasso et al. 2002; Joy and Young 2002; Howard and Lee 2002). In addition, the dynamics of replacement in these *Juniperus* woodlands and savannas have not been extensively investigated; consequently, the future structure of these communities is unknown (Van Auken et al. 2004).

Certain plant community analyses can suggest stability or lack of stability in a population. In addition, some of these measurements can suggest previous community structure and composition as well as future community changes (Horn 1975; Van Auken 1993; Bush and Van Auken 1987; Ryniker et al. 2006). Size of woody plants is easy to measure, and it is tempting to equate size and age, which is not necessarily true (Harper 1977). However, it is probably better to use size as an indicator of maturity because reproductive behavior is more closely related to plant size (Harper 1977). Consequently, size-frequency distributions can be prepared and can be used to evaluate community successional status, including stability (Bailey and Dell 1973; Lorimer and Krug 1983; Baker et al. 2005; Ryniker et al. 2006).

Studies of the structure of *Juniperus* woodlands in the past used composite data pooled from a series of communities (Van Auken et al. 1979, 1980; Van Auken 1988; Ahmed et al. 1990; Gardner and Fisher 1994). These frequency plots demonstrated populations with negative exponential functions (Figure 6), which have been interpreted as expanding populations (Whittaker 1975). When more standard techniques were used (Mohler et al. 1978) and *Juniperus* stands were examined independently, several different population patterns emerged (Van Auken 1993). Some example frequency distribution plots demonstrated expanding populations of *Juniperus* plants, including negative exponential functions or inverted "J" frequency distributions (Whittaker 1975; Sokol and Rohlf 1981). A large number of small individuals were found in the smallest size-class, suggesting recruitment into the populations after a disturbance and that these communities might be relatively young.

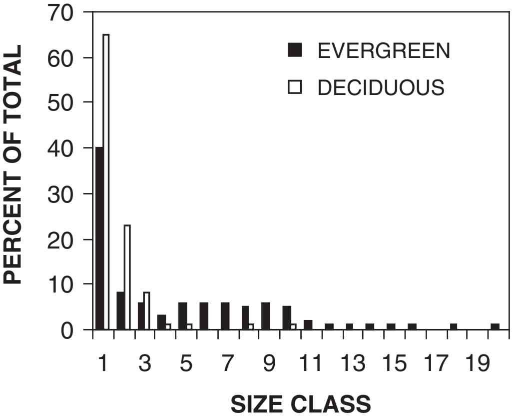

Figure 6 Frequency diameter size-class distributions for *Juniperus ashei* in upland *Juniperus* evergreen woodlands (forests) on Edwards limestone and in north slope deciduous forests on the Edwards Plateau of central Texas. Each size-class represents 5 cm of stem diameter. (Data from Van Auken 1988)

The population frequency distribution from another representative stand appeared to have a population that was in the self-thinning stage of growth (Mohler et al. 1978; Van Auken 1993). This population of *Juniperus* plants had a normal size-frequency distribution and was not skewed or peaked. The smallest individuals sampled in this community were 2 cm in diameter, and there were only three, suggesting no new seedlings entering the population. Total density decreased as total basal area increased in these communities, with no juveniles in the community with the largest total basal area. These results suggest that this community was the oldest or most mature community examined (Van Auken 1993). Trends in *J. virginiana* size-frequency distributions (Figure 7A) closely resemble those reported for *J. ashei* (Van Auken 1993). It seems that most of the *Juniperus* communities

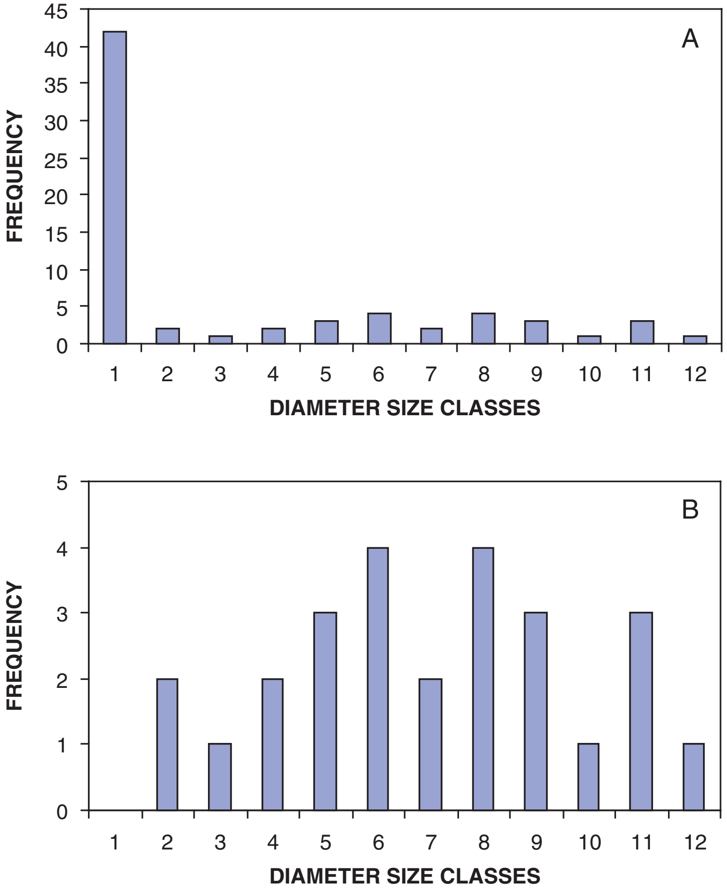

Figure 7 Mean (±SE) frequency diameter (cm at breast height) size-class distributions for *Juniperus virginiana* in four representative Flint Hills, Kansas, forest communities. The population of each stand was apportioned into equal size-classes by dividing the diameter of the largest tree by 12. **A** shows all size-classes; **B** does not include the smallest size-class, the juveniles, to better show the adult tree size-class distributions. (From McKinley, unpublished data)

examined in central Texas and northeastern Kansas were relatively young stands with expanding populations. In central Texas, this is probably because of constant thinning or cutting, but in Kansas it is the result of recent encroachment.

It has been difficult to find communities of mature *Juniperus* plants in central Texas. Mature *Juniperus* plants and communities are a valuable resource because of the properties of the wood and associated value. *Juniperus* trees of various sizes are harvested for posts, lumber, and natural oils (Diamond et al. 1995). These trees were harvested for building materials when the earliest settlers arrived in the West, and the harvest continues today. Evidence of harvest can be easily seen in aerial photographs where fences mark various property or pasture limits and the limits of the harvests.

Juniperus spp. have been considered pioneer woody species in succession in some areas (Whittaker 1975; Ormsbee et al. 1976). Underrepresentation of *Juniperus ashei* seedlings or saplings in the smallest size-class could certainly be interpreted as the future loss of this species from some woodland ecosystem (Van Auken 1993). However, this does not seem to be a reasonable conclusion based on the current widespread distribution and high density of *Juniperus* in southwestern and western North America. Changes in some of these *Juniperus* woodlands seem to be taking place. Reduced *Juniperus* density will occur as communities mature and self-thin (Harper 1977; Van Auken 1993). Certainly, there are other interpretations of the population structure of these *Juniperus* woodlands. It is possible that there is constant age-specific mortality, resulting in nonnormal size distributions, which has been reported in some *Juniperus* communities (Van Auken et al. 2004). However, this may be a temporary phenomenon, and difficult to see, because it takes 25 to 35 years for complete replacement of the seedlings and saplings. Constant mortality and replacement may occur until canopy closure (or later), with the potential self-replacement of adult trees when mortality occurs, until other species start to replace the *Juniperus* trees. Most of the *Juniperus* stands in central Texas are probably not mature stands because of past cutting and possibly the presence of fire, but unfortunately almost no evidence is available to support this claim. Some western *Juniperus* trees, and possibly their communities, are quite old, but future replacement at this time is undefined (Miller et al. 2005).

The ambiguity associated with the underrepresentation of seedlings or saplings of *Juniperus* plants in the smallest size-classes during the maturation of some *Juniperus* woodlands is not true for many deciduous species in the same areas. Populations of upland species such as *Quercus virginiana* (live oak) and *Diospyros texana* (Texas persimmon) show evidence of recruitment (Van Auken et al. 1980). However, other upland deciduous species such as *Q. texana* (=*Q. buckleyi*, Texas red oak), *Q. glaucoides* (Lacy oak), *Prunus serotina* (black cherry), *Fraxinus texensis* (Texas ash), and *Juglands nigra* (black walnut) have few or no new individuals in the smallest size-classes examined (Van Auken 1988, 1993). This observation is true for other North American deciduous species in many forested areas (Ryniker et al. 2006). Thus, for many species there is little or no recruitment of juveniles of these species into the adult populations. Possible reasons for this lack of recruitment are changes in local environment (shading), changes in the disturbance regime, or increases in herbivore populations, or establishment may be episodic and reflect local environmental conditions (Auclair and Cottam 1971; Harper 1977; Harcombe and Marks 1978; Ryniker et al. 2006). Populations of many species of plants may be adjusting to such changes. Records do not indicate local climate changes. However, in central Texas, populations of *Odocoileus virginianus* (white-tailed deer) have increased dramatically in the past 75 years (Doughty 1983). These large deer or other herbivore populations have been implicated in the lack of recruitment of many deciduous species in this and other areas (Russell and Fowler 1999, 2002, 2004; Ryniker et al. 2006).

Seedling Emergence and Survival

Understanding the current and potential future structure of woodlands and forests requires knowing something about the survival and growth of the seedlings of the species that are present in the community of concern. Consequently, it is important to understand the dynamics of the replacement process of the species present (Harper 1977; Fenner 1985). The source of seeds for a given cohort of *Juniperus* seedlings is the mature female canopy trees and has only recently been identified for one species as coming from seed crops of previous years (Van Auken et al. 2004). The seedlings emerging during the winter and spring of a given year are from the fruit or seeds produced at least 1 full year before the appearance of the seedlings. The seeds must survive in or on the soil through the summer until the following winter and spring before emergence occurs. Others have reported low *J. ashei* seed viability (0%–5%), but with approximately 18 million fruit/ha/year produced, a large number of viable seeds would still be present in the soil for emergence 1 or more years following production (Chavez-Ramirez and Slack 1994; Owens and Schliesing 1995; Smeins and Fuhlendorf 2001).

Juniperus ashei seedlings in central Texas woodlands began to emerge in November–February and continued to emerge into April–June, depending on the year and thus the conditions (Figure 8A). No new seedlings emerged in the study area before November or after June, and survival was 12% to 42% through the initial summer after emergence. Thus, 58% to 88% of the seedlings died during the initial summer after emergence (Figure 8B). Emergences were in the cool, wet months, and mortalities were highest in the warm, dry months (see Figure 8). Only 11 of the emerging seedlings were in the grassland; 84 were in the edge habitats, and 1967 seedlings, or 96%, were beneath the *J. ashei–Q. virginiana* canopy. Total mortality was 100% in the unburned grassland, approximately 78% in the edge, and 60% below the woodland canopy.

Although most *Juniperus* fruit fall below or near the parent tree (Owens and Schliesing 1995), long-distance dispersal into associated grassland communities by mammals and birds has been reported (Holthuijzen et al. 1987; Chavez-Ramirez and Slack 1994). Emergence and early survival in associated communities, especially grasslands, does occur, but seem to be low and probably occurs infrequently. Emergence and establishment in the grassland may require unusual conditions. These conditions could include high and persistent rainfall for one or several annual

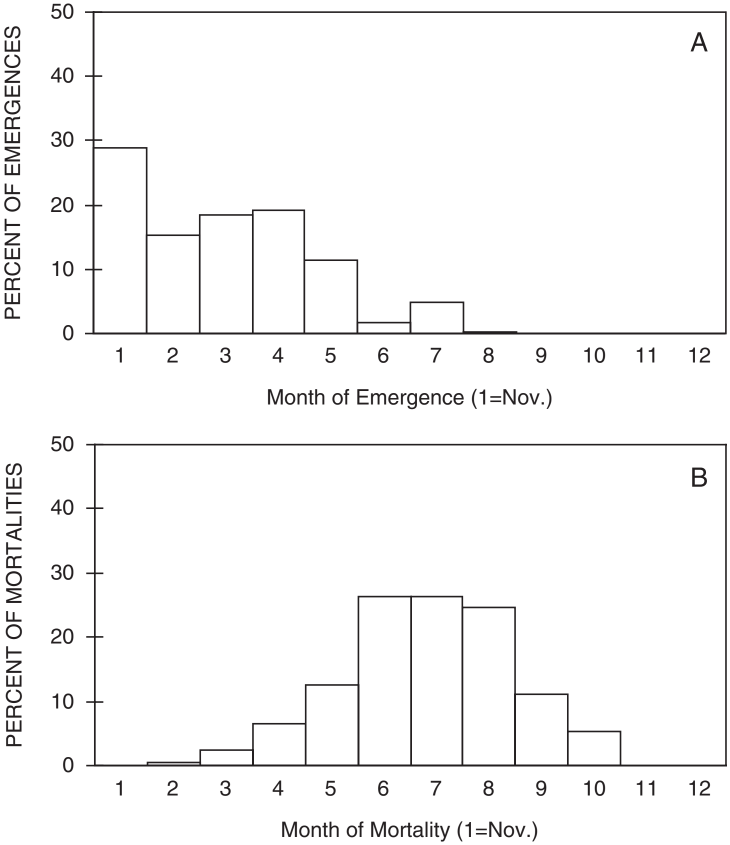

Figure 8 Mean percent of total emergences (**A**) and mortalities (**B**) per month for the 1994 and 1995 cohorts of newly emerged *Juniperus ashei* seedlings for 21 months (two growing seasons). Number 1 on the *x*-axis = November. (Data from Van Auken et al. 2004)

growth cycles, providing high herbaceous biomass and shading of the soil surface, allowing *Juniperus* seedling emergence, survival, and growth, followed by normal or below-normal rainfall conditions and limited grass growth or few grazing effects. Roots of the *Juniperus* seedlings would now be deep enough in the soil, below the grass root zone and beyond the grass root zone of influence. Also, seedlings may grow tall enough to overcome shading imposed by herbaceous plants. Therefore, the survival of the *Juniperus* seedlings in the grassland would be assured providing there were no fires.

The replacement dynamics of *J. ashei* below *Juniperus* canopies in semiarid woodlands has only recently been reported, and there is no information for other *Juniperus* species (Van Auken et al. 2004). Seedling location and small seedling size seem to be associated with most *Juniperus* mortalities (Jackson and Van Auken 1997), which occurred during the hot and dry months and seem to be consistent with other species of *Juniperus*. Survival and growth of the seedlings was

Table 7 Means and standard deviations for absolute basal diameter growth (mm/year), absolute height growth (mm/year), and absolute new branch growth (number/year) in both the edge and canopy habitats for surviving *Juniperus ashei* seedlings from the 1994 and 1995 cohorts

	1994		1995		
Variable	Edge	Canopy	Edge	Canopy	ANOVA
Basal diameter[a]	0.7 ± 0.2	0.5 ± 0.1	0.5 ± 0.3	0.3 ± 0.1	H*** C***
Height[b]	77.3 ± 17.2	53.2 ± 13.6	41.9 ± 15.0	38.0 ± 9.7	H*** C*** HC***
Number of branches[c]	5 ± 3	1 ± 1	3 ± 0	0 ± 0	H*** C*** HC*

Results of three analyses of variance (ANOVAs, SAS Institute 1989) of the effects of habitat (H = edge vs. canopy), cohort (C = 1994 vs. 1995), and the interaction between habitat and cohort (HC) are shown on the right. Sample size for the 1994 edge and canopy were 5 and 13, respectively; for 1995, these were 17 and 763, respectively.

[a] Basal diameter growth (mm/year).

[b] Height growth (mm/year).

[c] New branch growth (number/year).

Significance levels for the separate ANOVAs are as follows: $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

dependent on the spatial as well as the temporal cohort of the seedlings (Table 7). The highest growth rates were in the edge habitats; this has not been previously reported, although high irradiance is a suggested requirement for the growth of *Juniperus* seedlings (Burkhardt and Tisdale 1976; McKinley and Van Auken 2005). The conditions present beneath the canopy of an adult tree or shrub should be less extreme compared to associated open areas (see Chapter 9, this volume). Consequently, these sites are apparently more favorable for the survival of newly emerging seedlings (Breshears et al. 1997, 1998; Breshears and Barnes 1999; Anderson et al. 2001; Wayne and Van Auken 2002; Phillips and Barnes 2003; Wayne and Van Auken 2004). However, growth is greatest in the edge habitats.

Precipitation and temperature seemed to have a major influence on the emergence and mortality of *J. ashei* seedlings but have only recently been investigated. Most emergences occurred in late fall, winter, and early spring months, periods of lower temperature and usually higher precipitation than the summer and early fall months when emergences do not take place. The months that had the highest mortalities were usually warmer and drier than months in which mortality was low. Simple linear correlations of the relationships between mortalities/month and emergence/month of *J. ashei* seedlings and mean monthly temperature and monthly precipitation were completed.

Emergence was significantly inversely related to temperature but not to precipitation. There was also a significant multiple linear correlation between the number of emergences/month and mean monthly temperature and monthly rainfall, but the relationship was not strong (Van Auken et al. 2004). If lags were used (1–4 months), significant linear correlations were found (Table 8; Van Auken et al. 2004). The highest number of emergences occurred at the coolest time of the year, 1 to 4 months after a period of high rainfall.

Table 8 Results of correlation analyses of the relationships between monthly emergence totals of *Juniperus ashei* seedlings by cohort (year) and monthly precipitation from the month of the emergences and then 1, 2, 3, or 4 previous months of precipitation (lag). Bold indicates the significant correlations

	1994 Cohort		1995 Cohort	
Lag in months	*r*	*P*	*r*	*P*
0	–0.17	>0.05	–0.32	>0.05
1	–0.25	>0.05	**0.81**	**<0.05**
2	–0.26	>0.05	0.52	>0.05
3	–0.70	>0.05	0.45	>0.05
4	**0.95**	**<0.05**	0.00	>0.05

Similar difficulties were encountered attempting to relate mortality to temperature or precipitation. However, when rainfall was examined and data were considered by year with only the months having mortalities correlated with rainfall, for the 1994 cohort there was a significant, inverse logarithmic relationship, and for 1995 there was a significant, inverse exponential relationship. The coefficients of determination suggest that rainfall explained 85% and 55% of the variation in seedling mortality for the 1994 and 1995 cohorts, respectively. When the sum of mortalities for 1994 was correlated with monthly temperature, using only the sequence of months with mortalities, there was a significant linear correlation, and the same was true for the 1995 data. The coefficients of determination suggested that temperature explained 77% and 92% of the variation in the sum of seedling mortality for the 1994 and 1995 cohorts, respectively. The highest number of mortalities occurred at the hottest, driest time of the year.

Juniperus seedlings may require a nurse plant, possibly the parent or other species, for initial survival of the newly emerged seedlings in arid or semiarid environments, as has been suggested for the establishment of some woody seedlings in grassland habitats and for some arid land species (Turner et al. 1966; Phillips and Barnes 2003). To be effective, the nurse plant has to be a perennial, remaining in place long enough to allow for development of the seedling to a size that it could independently survive the harsh environmental conditions present. However, the best conditions for seedling survival are not necessarily the best conditions for seedling growth, and as such further maturation depends upon loss of the shading affects of the nurse plant or the overstory tree (Turner et al. 1966; McKinley and Van Auken 2005).

We measured a decline in density of all *Juniperus* seedling cohorts below the canopy with known emergence dates, with 1.0% to 3.4% surviving for 8 or 9 years, depending on the cohort (Van Auken et al. 2004). However, the cause of seedling mortality was not determined. Annual survival was a significant, inverse, exponential function for each cohort, with coefficients of determination (R^2) of 0.86, 0.98, and 0.99 for the 1994, 1995, and preexisting cohorts, respectively (Van Auken et al. 2004). Kaplan–Meier survival analyses (Allison 1995) showed the percent survival distributions of the populations over the 8 or 9 years they were followed (see Van Auken et al. 2004). The lowest first-year survival was 12% for the 1994 cohort. The first-year survival for the 1995 cohort was 42%, followed by 79% survival for the first year the preexisting cohort was monitored (Van Auken et al. 2004). After nine growing seasons, 1.0% of the seedlings from the 1994 cohort remained alive. After eight growing seasons, 3.4% of the seedlings from the 1995 cohort remained alive. After nine growing seasons, 17% of the seedlings from the preexisting cohort remained alive.

The high survival of the preexisting cohort suggests the production of a seedling bank, a large number of suppressed seedlings waiting to be released after a disturbance (Harper 1977; Marks and Gardescu 1998). The preexisting cohort of seedlings (mixed-age cohort) seems to have a constant mortality, with about 8% of the population dying every year, and they are presumably being replaced. However, these seedlings could start to grow immediately if the overstory canopy was removed, and a relatively rapid replacement of the overstory would be ensured by the seedlings that are present (Owens and Schliesing 1995; Marks and Gardescu 1998; Smeins and Fuhlendorf 2001; McKinley and Van Auken 2005).

Few seedlings were physically removed by herbivores or lost, and mortalities were highest for the hottest and driest months, suggesting desiccation as a contributing, if not major, factor for these mortalities. Interference from neighboring plants, especially the overstory trees, which formed the canopies over the majority of these seedlings, did not appear to increase mortality, as survival was the same under the canopy as at the inside canopy edge while seedlings on the outside edge showed lower survival. However, interference from these larger woody plants probably resulted in suppressed growth rates because individuals present under these canopies showed little growth over the 21 months that growth rates were measured (Van Auken et al. 2004), but canopy removal and higher light levels promoted seedling growth (McKinley and Van Auken 2005).

Factors Important for Seedling Growth

The growth and survival of *Juniperus* seedlings in the savannas and woodlands where they are found, and the replacement dynamics of the adult *Juniperus* trees, are presently unknown. In addition, the factors that control seedling growth and survival in these woodlands have not been well documented. We hypothesized that competition from the adult *Juniperus* trees is manifested by altered light, water, or nutrient levels, resulting in modified growth and mortality of the *Juniperus* seedlings, eventually affecting replacement dynamics. Understanding the potential for adult replacement can provide insight to the long-term viability and maintenance of these *Juniperus* communities and their potential role in succession or other global-change phenomena, such as carbon storage.

A characteristic of *Juniperus* seedling emergence and establishment in woodlands and savannas is that it occurs primarily in partially shaded areas under herbaceous canopies or the canopies of shrubs or trees (Johnsen 1962; Burkhart and Tisdale 1976; Jackson and Van Auken 1997; Gass and Barnes 1998; Van Auken et al.

2004). Factors that may promote seedling survival below various canopy types could include subtle differences in surface temperatures, soil moisture, and light levels. However, increased survival may be simply the result of reduced transpiration demand and thermal stress, which improves water relationships in the shade (Tiedemann and Klemmedson 1977; Frost and McDougald 1989; Holmgren et al. 1997; Anderson et al. 2001). In some savanna ecosystems the shade provided by isolated trees can reduce or minimize high temperature and water stress in understory plants (Belsky et al. 1989; Belsky and Canham 1994; Gass and Barnes 1998) and enhance germination and seedling survival (Callaway 1992; Fulbright et al. 1995).

Others suggest that there may be improved nutrient availability under canopy trees (Kellman 1979; Bush and Van Auken 1986; Belsky et al. 1989; Jurena and Van Auken 1998). Hydraulic lift by overstory trees has also been implicated in increasing soil moisture below the canopy (Richards and Caldwell 1987). *Juniperus* seedlings may need some amelioration of extreme environments or increased resource availability created by the adult *Juniperus* trees or other species to establish (Jackson and Van Auken 1997; Gass and Barnes 1998). It is likely that not one factor, but several factors acting in combination, are responsible for reduced seedling growth and mortality below the canopy. In addition, the conditions responsible for increased growth of *Juniperus* seedlings at the canopy edge are not necessarily the same as those responsible for reduced seedling mortality below the canopy (Jackson and Van Auken 1997; Van Auken et al. 2004).

Juniperus seedling growth and survival seems to be governed by a dynamic interaction of biotic and abiotic factors. If the canopy, light levels, soil nutrient levels, and soil water levels are manipulated, the most important factor seems to be light (Figure 9). If light levels are experimentally reduced in the field, the relative growth rate (RGR) for all response variables measured for *Juniperus* seedlings were reduced 55% to 90%. Complementing the significant main effect of light in the field was a two-way interaction between light and nutrient treatments (see Figure 9) and two significant three-way interactions (McKinley and Van Auken 2005). The interactions demonstrate the complexity of understanding *Juniperus* seedling growth. Generally, the RGR for the *Juniperus* seedlings were highest in the high light levels when water and nutrients were added and lowest in the low light levels without added water. At higher light levels, both water and nutrient levels interact to support both the growth and survival of the *Juniperus* seedlings (Figure 10; McKinley and Van Auken 2005).

Several studies suggest that mature *Juniperus* plants are shade intolerant, in part because they occur and grow rapidly in high light environments (Baker 1991; Ormsbee et al. 1976). This conclusion may be a misinterpretation, because there is opposing evidence suggesting that at least seedlings of some *Juniperus* spp. may be shade tolerant. Seedling survival can be high over a considerable time in low light conditions. For example, high densities of seedlings and saplings of *J. ashei* and *J. virginiana* have been reported in low light conditions below various canopy trees (Lassoie et al. 1983; Jackson and Van Auken 1997; Gass and Barnes 1998). Highest survival is also below these canopy trees relative to open areas, but growth rates are

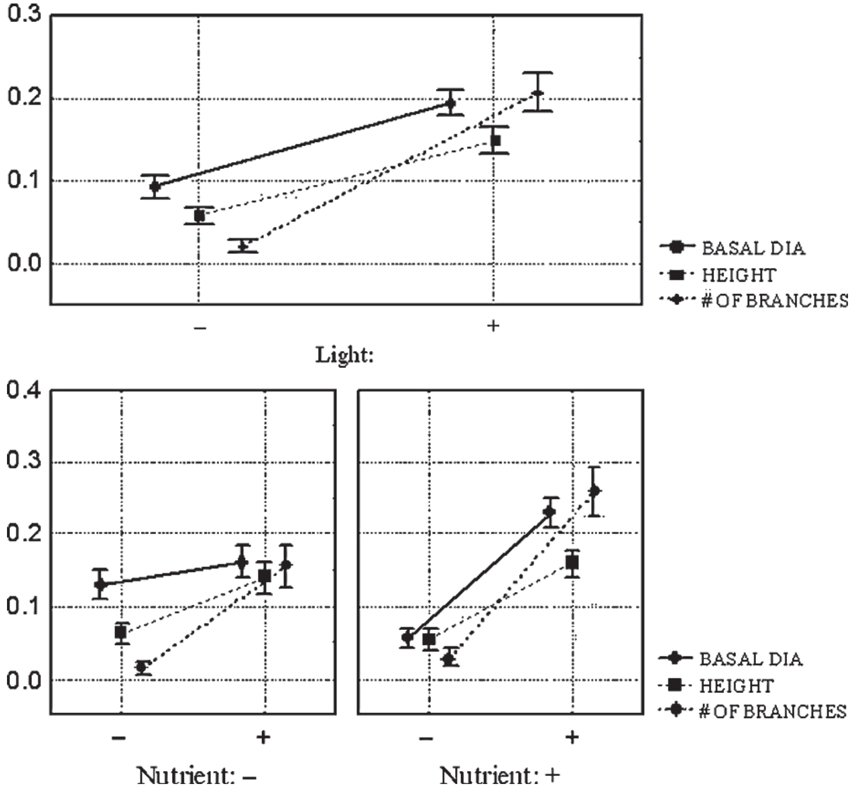

Figure 9 Three-way MANOVA interaction plot of relative growth rates (y-axis) for basal diameter, height and number of branches for *Juniperus ashei* seedlings grown in light and shaded conditions in *Juniperus* woodlands in central Texas. *Upper panel* shows growth response to low light (–) and ambient light (+). *Lower left panel* shows relative growth rates with ambient nutrients (native soil) at low and ambient light (–, +); *lower right panel* shows relative growth rates with native soil supplemented with a complete nutrient mixture at low and ambient light levels (–, +). (Data from McKinley and Van Auken 2005)

lowest below the canopy (Van Auken et al. 2004). Additionally, photosynthetic response curves suggest that *J. ashei* seedlings may be shade tolerant (McClean 1985; Wayne et al. 2002). *Juniperus ashei* seedlings can grow in low light below the adult canopy, but that growth is much slower under intact canopies and increases considerably with canopy removal (see Figure 9). This effect appears to be associated with higher light levels and may be enhanced by increased availability of water and soil nutrients. Additionally, *J. virginiana* carbon uptake is higher below a deciduous canopy in winter when leaves have fallen (Lassoie et al. 1983).

The removal of adult canopy trees increased surface light levels, reducing aboveground competition, and may reduce belowground competition for water and nutrients (McKinley and Van Auken 2005). However, the lack of a strong response of seedlings to supplemental water may be the result of above-average rainfall (~8%) recorded for the study period.

Juniperus plants, similar to other evergreen conifers, have low nutrient requirements (Ormsbee et al. 1976). Generally, evergreens (i.e., *J. ashei*) have lower nutrient requirements and greater nutrient retention compared to herbaceous plants in savannas (Aerts 1995; Scholes and Archer 1997). Soil nutrient levels appear to limit *J. ashei* seedling growth, but only when light levels are relatively high. In a similar savanna system in central Texas, herbaceous productivity under *Q. virginiana* canopies was not positively related with soil nutrient availability (Anderson et al. 2001).

Because overall mortality of *Juniperus* seedlings can be considerable, it was necessary to examine seedling mortalities carefully to fully explore the response of the seedlings to experimental treatments. McKinley and Van Auken (2005) reported a lack of significant differences in seedling mortality among the single canopy treatments used, which suggests that the varying abiotic and biotic conditions created by different canopy treatments were insufficient to independently explain patterns of seedling mortality. However, examination of the seedling treatments after pooling the mortality data across all canopy treatments demonstrated clear patterns (see Figure 10). Increased mortality in the low light treatments (1–4) suggests the modified environment does not facilitate seedling survival, probably a result of the inability of seedling to meet metabolic requirement with photosynthetic products at low light levels. Although higher light levels seem to be an important factor governing the survival of the seedlings, light levels did not affect seedling survival unless coupled with other factors such as water and nutrients.

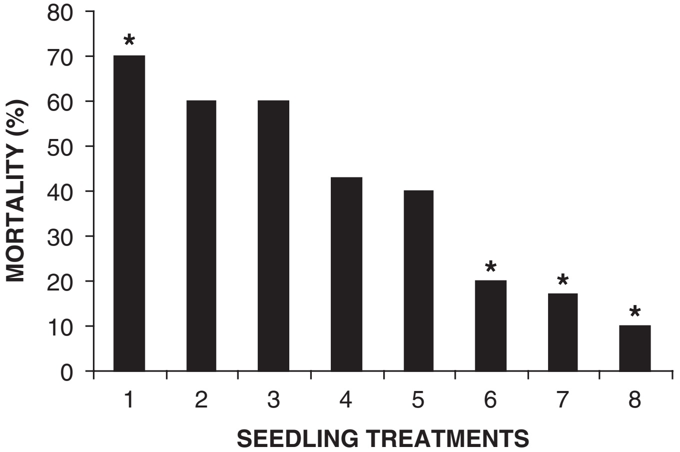

Figure 10 Relative mortality of *Juniperus ashei* seedlings grown in various conditions in *Juniperus* woodlands in central Texas. Low light treatments are indicated by 1–4 and ambient light treatments by 5–8. Actual treatments were as follows: *1*, low light, no added water, added nutrients; *2*, low light, added water, added nutrients; *3*, low light, added water, no added nutrients; *4*, low light, no added water, no added nutrients; *5*, ambient light, no added water, no added nutrients; *6*, ambient light, added water, no added nutrients; *7*, ambient light, no added water, added nutrients; *8*, ambient light, added water, added nutrients. (Data from McKinley and Van Auken 2005)

Facilitation and competition do not seem to be acting independently but may be acting in sequence to promote *Juniperus* seedling growth and survival (Holmgren et al. 1997). A canopy species may facilitate growth and survival of seedlings in dry conditions (reducing water stress), whereas the same shade conditions inhibit seedlings in wet conditions (increasing competition for light). This conceptual model seems to help explain the apparent sequential facilitative yet competitive role that adult *Juniperus* trees appear to have on *Juniperus* seedling growth.

The positive–negative resource balance between seedlings and adults is probably subject to frequent temporal shifts as the light–water interaction changes based on moisture and light availability, which is influenced by local conditions. The positive resource balance may be enough to support initial seedling establishment under intact *J. ashei* canopies in terms of germination and survival (Batchelor and Fowler 2004). Eventually as *J. ashei* seedlings mature, they seem to succumb to the low light levels in these woodlands, as evidenced by a negative logarithmic survival of seedlings below the canopy (Van Auken et al. 2004). However, mortality seems to be reduced when the constraints of the adult trees are removed (Owens and Schleising 1995). The growth of understory seedlings and the rate of replacement of the adult trees after adult plant mortality (assuming higher light levels) is probably regulated by water limitations, whereas light is the main constraint under the intact adult canopy.

Because intact canopies appear to confer little long-term growth or survival advantage to the seedlings below intact *Juniperus* woodlands, a facilitative relationship is not indicated for these seedlings. However, if a facilitative relationship exists it may be transitory and benefit newly germinated first-year seedlings by reduced water stress and interspecific competition (Batchelor and Fowler 2004; Van Auken et al. 2004). Older seedlings are ostensibly constrained by interactions of light, water, and nutrients, at least partially attributable to adult trees, providing strong evidence for intraspecific competition. The adult trees must be removed by attrition to perpetuate seedling growth, allowing replacement of individual adult trees by seedlings of the same species in these contiguous woodlands or savanna systems.

Summary

The structure of *Juniperus* communities today is probably different from the *Juniperus* communities of the past. However, it is difficult to make this type of comparison. It is especially difficult because of limited preservation and temporal changes occurring in many of these *Juniperus* communities. Composition and structure are postulated from a few communities. Factors that control the structure and composition of these *Juniperus* communities seem to be amount and seasonality of rainfall, temperature, fire frequency and intensity, and possibly other anthropogenic factors.

Juniperus seedling emergence and establishment in the south-central part of North America occur in the cool and wet months of winter. The months of emergence and establishment may change in other areas, but emergence and establishment would probably still occur during the cool and wet months. *Juniperus* seedling establishment in grasslands seems to occur with or without grazing by domestic ungulates. If juvenile plants are going to survive, fire exclusion seems to be paramount at this early stage of *Juniperus* plant establishment and community development. Without fire, most *Juniperus* juvenile mortality occurs during the hot and dry months.

The density and basal area of savanna *Juniperus* communities are generally low. Both factors increase as the canopy closes and evergreen woodlands develop. Density then decreases, and basal area continue to increase as the communities mature. One or more species of *Juniperus* are present in these communities depending on location, along with one or more species of *Pinus*, usually a piñon pine. In the Southwest, various species of *Quercus* are *Juniperus* associates, whereas in the north and at higher elevations, various *Pinus, Picea*, and *Abies* replace *Quercus*. The successional species present in these *Juniperus* communities depend on the latitude and the elevation. At this time, the next stage in the succession of western and southwestern North American *Juniperus* communities is only speculative.

The herbaceous species associated with the *Juniperus* communities are also highly variable but are similar to the species found in the associated grasslands. Density of annuals would be high in gaps, probably because of the limited, intermittent supply of water associated with shallow soils or the presence of the *Juniperus* plants. Below the canopy, herbaceous cover would be low in most areas, but in some localities, species of drought-tolerant *Carex* are common.

The dynamics of *Juniperus* community development is mostly unknown. Diameter distributions of most *Juniperus* population are frequently steeply descending monotonic functions, suggesting expanding populations. Juvenile plants can be long lived, and survival for *J. ashei* juveniles is highest below the adult *Juniperus* canopy. However, juvenile growth is greatest at the canopy edge, not below the canopy. Replacement of adult *Juniperus* plants by juveniles seems to require adult mortality, and surface light level is a major factor controlling juvenile plant growth. However, soil moisture and nutrients would modify growth and mortality at high light levels. Apparently *Juniperus* savanna and woodland structure is controlled by the interaction with the adult canopy, surface light levels, soil moisture, and soil nutrients. Structure of many of these woodlands will change in time with the continued modification of biotic and abiotic conditions.

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References

Aerts, R. 1995. The advantages of being evergreen. Trends Ecol. Evol. 10:402–407.

Ahmed, M., Shaukat, S.S., and Buzdar, A.H. 1990. Population structure and dynamics of *Juniperus excelsa* in Balouchistan, Pakistan. J. Veg. Sci. 1:271–276.

Allison, P.O. 1995. Survival analysis using SAS system: a practical guide. Cary, NC: SAS Institute.

Anderson, L.J., Brumbaugh, S.M., and Jackson, R.B. 2001. Water and tree-understory interactions: a natural experiment in a savanna with oak wilt. Ecology 82:33–39.

Arbingast, S.A., Kennamer, L.G., Ryan, R.H., Buchanan, J.R., Hezlep, W.L., Ellis, L.T., Jordan, T.G., Granger, C.T., and Zlatkovich, C.P. 1976. Atlas of Texas. Austin, TX: Bureau of Business Research, University of Texas.

Auclair, A.N., and Cottam, G. 1971. Dynamics of black cherry (*Prunus serotina* Erhr.) in Southern Wisconsin oak forests. Ecol. Monogr. 41:153–177.

Bailey, R.L., and Dell, T.R. 1973. Quantifying diameter distributions with the Weibull function. For. Sci. 19:97–104.

Bahre, C.J. 1991. A legacy of change: historic human impact on vegetation of the Arizona Borderlands. Tucson: University of Arizona Press.

Bahre, C.J., and Shelton, M.L. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. J. Biogeogr. 20:489–504.

Baker, C.J. 1991. A revised tolerance table. J. For. 49:179–181.

Baker, P.J., Bunyavejchewin, S., Oliver, C.D., and Ashton, P.S. 2005. Disturbance history and historical stand dynamics of a seasonal tropical forest in western Thailand. Ecol. Monogr. 75:317–343.

Barbour, M.G., and Billings, W.D. 1988. North American terrestrial vegetation. New York: Cambridge University Press.

Baskin, J.M., and Baskin, C.C. 1978. Plant ecology of cedar glades in the Big Barrens region of Kentucky. Rhodora 80:545–557.

Baskin, J.M., and Baskin, C.C. 1985a. A floristic study of a cedar glade in Blue Licks Battlefield State Park, Kentucky. Castanea 50:19–25.

Baskin, J.M., and Baskin, C.C. 1985b. Life cycle ecology of annual plant species of cedar glades of the southeastern United States. In: The population structure of vegetation, ed. J. White, pp 371–398. Dordrecht: Junk.

Batchelor, M.E., and Fowler, N.L. 2004. Intraspecific facilitation of *Juniperus ashei* in Texas savannas. In: Proceedings, 89th annual meeting, Ecological Society of America, Portland, OR, p 33.

Belsky, A.J., and Canham, C.D. 1994. Forest gaps and isolated savanna trees. BioScience 44:77–84.

Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Ali, A.R., and Mwonga, S.M. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. J. Appl. Ecol. 26:1005–1024.

Bray, W.L. 1904. The timber of the Edwards Plateau of Texas: its relation to climate, water supply, and soil. Bulletin no. 47. Washington, DC: Bureau of Forestry, United States Department of Agriculture.

Breshears, D.D., and Barnes, F.J. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landsc. Ecol. 14:465–478.

Breshears, D.D., Rich, P.M., Barnes, F.J., and Campbell, K. 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecol. Appl. 7:1201–1215.

Breshears, D.D., Nyhan, J.W., Heil, C.E., and Wilcox, B.P. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. Int. J. Plant Sci. 159:1010–1017.

Briggs, J.M., Knapp, A.K., and Brock, B.L. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. Am. Midl. Nat. 147:287–294.

Burkhardt, J.W., and Tisdale, E.W. 1976. Causes of juniper invasion in Southwestern Idaho. Ecology 57:472–484.

Bush, J.K., and Van Auken, O.W. 1986. Changes in nitrogen, carbon and other surface soil properties during secondary succession. Soil Soc. Am. J. 50:1597–1601.

Bush, J.K., and Van Auken, O.W. 1987. Some demographic and allometric characteristics of *Acacia smallii* (Mimosaceae) in successional communities. Madroño 34:250–259.

Cadenasso, M.L., Pickett, S.T.A., and Morin, P.J. 2002. Experimental test of the role of mammalian herbivores on old field succession: community structure and seedling survival. J. Torrey Bot. Soc. 129:228–237.

Callaway, R.M. 1992. Effect of shrubs on recruitment of *Quercus douglassii* and *Quercus lobata* in California. Ecology 13:2118–2128.

Chavez-Ramirez, F., and Slack, R.D. 1994. Effects of avian foraging and post-foraging behavior on seed dispersal patterns of Ashe juniper. Oikos 71:40–46.

Coupland, R.T. 1979. Grassland ecosystems of the world: analysis of grassland and their uses. Cambridge: Cambridge University Press.

Diamond, D.D., Rowel, G.A., and Keddy-Hector, D.P. 1995. Conservation of ashe juniper (*Juniperus ashei* Buchholz) woodlands of the central Texas Hill Country. Nat. Areas J. 15:189–197.

Doughty, R.W. 1983. Wildlife and man in Texas: environmental change and conservation. College Station: Texas A & M University Press.

Eddleman, L.E. 1987. Establishment and stand development of western juniper in central Oregon. In: Proceedings of the pinyon-juniper conference, ed. R.L. Everett, pp 255–259. General Technical report INT-215. Ogden, UT: United States Forest Service.

Erickson, R.O., Brenner, L.G., and Wraight, J. 1942. Dolomitic glades of east-central Missouri. Ann. Mo. Bot. Gard. 29:89–101.

Fenner, M. 1985. Seed ecology. New York: Chapman & Hall.

Freeman, C. 1933. Ecology of the cedar glade vegetation near Nashville, Tennessee. J. Tenn. Acad. Sci. 8:142–228.

Ford, A.L., and Van Auken, O.W. 1982. Distribution of woody species in the Guadalupe River flood plain in the Edwards Plateau of Texas. Southwest. Nat. 27:392–393.

Frost, W.E., and McDougald, N.K. 1989. Tree canopy effects on herbaceous production of annual rangelands during drought. J. Range Manag. 42:281–283.

Fulbright, T.E., Kuti, J.O., and Tipton, A.R. 1995. Effects of nurse-plant canopy temperatures on shrub seed germination and seedling growth. Acta Oecol. 16:621–632.

Gardner, A.S., and Fisher, M. 1994. How the forest lost its trees: just so storytelling about *Juniperus excelsa* in Arabia. J. Arid Environ. 26:299–301.

Gass, L., and Barnes, P. 1998. Microclimate and understory structure of live oak (*Quercus fusiformis*) clusters in central Texas, USA. Southwest. Nat. 43:183–184.

Gates, J.A., Awra, M., Settergren, C.D., Henderson, G.S., and Krstansky, J.J. 1982. Hydrology of a south-central Missouri cedar glade. Water Soil Manag. 1:36–41.

Gedney, D.R., Azuma, D.L., Bolsinger, C.L., and McKay, N. 1999. Western juniper in eastern Oregon. General technical report NW-GTR-464. Washington, DC: United States Forest Service.

Harcombe, P.A., and Marks, P.L. 1978. Tree diameter distributions and replacement processes in southeast Texas forests. For. Sci. 24:153–166.

Harper, J.L. 1977. Population biology of plants. New York: Academic Press.

Hendrickson, B., and Davis, W. 1980. Ozark glades: prairie islands in the wilderness. In: Proceedings, 7th North American prairie conference, ed. C.L. Kucera, pp 85–86. Springfield: Southwest Missouri State University.

Hill, R.T., and Vaughan, T.W. 1898. Geology of the Edwards Plateau and Rio Grande Plain adjacent to Austin and San Antonio, Texas, with reference to the occurrence of underground waters. U.S. Geol. Surv. Annu. Rep. 18:193–322.

Holmgren, M., Scheffer, M., and Huston, M.A. 1997. The interplay of facilitation and competition in plant communities. Ecology 78:1966–1975.

Holthuijzen, A.M.A., Shank, T.L., and Fraser, J.D. 1987. Dispersal of eastern red cedar (*Juniperus virginiana*) into pastures: an overview. Can. J. Bot. 65:1092–1095.

Horn, H.S. 1975. Markovian properties of forest succession. In: Ecology and evolution of communities, eds. M.L. Cody and J.M. Diamond, pp 196–211. Cambridge: Harvard University Press.

Howard, L.F., and Lee, T.D. 2002. Upland old-field succession in southeastern New Hampshire. J. Torrey Bot. Soc. 129:60–76.

Inglis, J. 1962. A history of vegetation on the Rio Grande Plain. Bulletin 45. Austin, TX: Texas Parks and Wildlife Department.

Jackson, J.T., and Van Auken, O.W. 1997. Seedling survival, growth and mortality of *Juniperus ashei* (Cupressacae) in the Edwards Plateau Region of central Texas. Tex. J. Sci. 49:267–278.

Johnsen, T.N. 1962. One-seed juniper invasion of Northern Arizona grasslands. Ecol. Monogr. 32:187–207.

Joy, D.A., and Young, D.R. 2002. Promotion of mid-successional seedling recruitment and establishment by *Juniperus virginiana* in a coastal environment. Plant Ecol. 160:125–135.

Jurena, P.N., and Van Auken, O.W. 1998. Woody plant recruitment under canopies of two acacias in a southwestern Texas shrubland. Southwest. Nat. 43:195–203.

Kellman, M. 1979. Soil enrichment by neotropical savanna trees. J. Ecol. 67:565–577.

Kucera, C.L., and Martin, S.C. 1957. Vegetation and soil relationships in the glade region of the southwestern Missouri Ozarks. Ecology 8:285–291.

Lassoie, J.P., Dougherty, P.M., Reich, P.B., Hinckley, T.M., Metcalf, C.M., and Dina, S.J. 1983. Ecophysiological investigations of understory eastern redcedar in central Missouri. Ecology 64:1355–1366.

Lorimer, C.G., and Krug, A.G. 1983. Diameter distributions in even-aged stands of shade-tolerant and midtolerant tree species. Am. Midl. Nat. 109:331–345.

Lundell, C.L. 1966. Flora of Texas, vol. I. Renner, TX: Texas Research Foundation.

Marks, P.L., and Gardescu, S. 1998. A case study of sugar maple (*Acer saccharum*) as a forest seedling bank species. J. Torrey Bot. Soc. 125:287–296.

Marsh, W.M., and Marsh, N.L. 1993a. Juniper trees, soil loss, and local runoff processes. In Soil, landforms, hydrologic processes, and land-use issues: Glen Rose limestone terrains, Barton Creek watershed, Travis County, Texas, eds. C.M. Woodruff, Jr., W.M. Marsh, and L.P. Wilding, pp 4:1–14. Austin, TX: Society of Independent Professional Earth Scientists, Central Texas Chapter.

Marsh, W.M., and Marsh, N.L. 1993b. Hydrographic considerations in road location and stormwater management in small basins tributary to Barton Creek. In: Soil, landforms, hydrologic processes, and land-use issues:-Glen Rose limestone terrains, Barton Creek watershed, Travis County, Texas, eds. C.M. Woodruff, Jr., W.M. Marsh and L.P. Wilding, pp 6:1–11. Austin, TX: Society of Independent Professional Earth Scientists, Central Texas Chapter.

McClean, T.M. 1985. Environmental and physiological factors affecting the establishment of *Juniperus ashei* on the Edwards Plateau of Texas. M.S. thesis. Southwest Texas State University, San Marcos, TX.

McKinley, D.C., and Van Auken, O.W. 2005. Influence of interacting factors on the growth and mortality of *Juniperus* seedlings. Am. Midl. Nat. 154:320–330.

McPherson, G.R. 1997. Ecology and management of North American savannas. Tucson: University of Arizona Press.

Miller, R.F., and Wigand, P.E. 1994. Holocene changes in semiarid pinyon-juniper woodlands: response to climate, fire, and human activities in the Great Basin. BioScience 44:465–474.

Miller, R.F., Bates, J.D., Svejcar, T.J., Pierson, F.B., and Eddleman, L.E. 2005. Biology, ecology and management of western juniper (*Juniperus occidentalis*). Technical bulletin 152. Corvallis, OR: Agriculture Experiment Station, Oregon State University.

Mohler, C.L., Marks, P.M., and Sprugel, D.G. 1978. Stand structure and allometry of trees during self-thinning of pure stands. J. Ecol. 66:599–614.

National Oceanic and Atmospheric Administration. 2004. Asheville, NC: National Climatic Data Center.

Norris, M.D., Blair, J.M., Johnson, L.C., and McKane, R.B. 2001. Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. Can. J. For. Res. 31:1940–1946.

Olson, D.W., Olson, M.S., Doescher, R.L., Lambert, L.L., Lemke, D.E., Carl, A.M., Johnson, R., Smith, S.D., and Trede, K.H. 1997. Piñion pines and the route of Cabeza de Vaca. Southwest. Hist. Q. 101:175–186.

Ormsbee, P., Bazzaz F.A., and Boggess, W.R. 1976. Physiological ecology of *Juniperus virginiana* in old-fields. Oecologia (Berl.) 23:75–82.

Owens, M.K., and Schliesing, T.G. 1995. Invasive potential of ashe juniper after mechanical disturbance. J. Range Manag. 48:503–507.

Palmer, E.J. 1920. The canyon flora of the Edwards Plateau of Texas. J. Arnold Arbor. Harv. Univ. 1:233–239.

Peet, R.K. 1988. Forests of the Rocky Mountains. In: North American terrestrial vegetation, eds. M.C. Barbour and W.D. Billings, pp 63–101. Cambridge: Cambridge University Press.

Phillips, P.L., and Barnes, P.W. 2003. Spatial asymmetry in tree-shrub clusters in a subtropical savanna. Am. Midl. Nat. 149:59–70.

Quarterman, E. 1950a. Major plant communities of Tennessee cedar glades. Ecology 31:234–254.

Quarterman, E. 1950b. Ecology of cedar glades. I. Distribution of glade flora in Tennessee. Bull. Torrey Bot. Club 77:1–9.

Richards, J.H., and Caldwell, M.M. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia (Berl.) 73:486–489.

Riskind, D.H., and Diamond, D.D. 1988. An introduction to environments and vegetation. In: Edwards Plateau vegetation: plant ecological studies in central Texas, eds. B.B. Amos and F.R. Gehlbach, pp 1–15. Waco, TX: Baylor University Press.

Russell, F.L., and Fowler, N.L. 1999. Rarity of oak saplings in savannas and woodlands of the eastern Edwards Plateau, Texas. Southwest. Nat. 44:31–41.

Russell, F.L., and Fowler, N.L. 2002. Failure of adult recruitment in *Quercus buckleyi* populations on the eastern Edwards Plateau, Texas. Am. Midl. Nat. 148:201–217.

Russell, F.L., and Fowler, N.L. 2004. Effects of white-tailed deer on the population dynamics of acorns, seedlings and small saplings of *Quercus buckleyi*. Plant Ecol. 173:59–72.

Ryniker, K.A., Bush, J.K., and Van Auken, O.W. 2006. Structure of *Quercus gambelii* communities in the Lincoln National Forest, New Mexico, USA. For. Ecol. Manag. 233:69–77.

SAS Institute. 1989. SAS user's guide. Cary, NC: SAS Institute.

Scholes, R.J., and Archer, S.R. 1997. Tree–grass interactions in savannas. Annu. Rev. Ecol. Syst. 28:517–544.

Sellards, E.H., Adkins, W.S., and Plummer, F.B. 1932. The geology of Texas, vol. I. Stratigraphy. Bulletin number 3232. Austin: University of Texas, Bureau of Economic Geology.

Sims, P.L. 1988. Grasslands. In: North American terrestrial vegetation, eds. M.C. Barbour and W.D. Billings, pp 265–286. Cambridge: Cambridge University Press.

Smeins, F.E., and Fuhlendorf, S.D. 2001. Biology and ecology of Ashe (blueberry) juniper. In: Juniper symposium, 2001 proceedings, ed. C.A. Taylor, pp 23–37. College Station, TX: Texas Agriculture Experiment Station.

Smeins, F.E., and Merrill, L.B. 1988. Long-term change in a semiarid grassland. In: Edwards Plateau vegetation: plant ecological studies in central Texas, eds. B.B. Amos and F.R. Gehlbach, pp 101–114. Waco, TX: Baylor University Press.

Soil Conservation Service. 1979. Soil survey interpretation for Kendal County, Texas. Washington, DC: United States Department of Agriculture, Soil Conservation Service.

Sokol, R.R., and Rohlf, F.J. 1981. Biometry. San Francisco: Freeman.

Taylor, F.B., Hailey, R.B., and Richard, D.L. 1962. Soil survey of Bexar County, Texas. Washington, DC: United States Department of Agriculture, Soil Conservation Service.

Terletzky, P.A., and Van Auken, O.W. 1996. Comparison of cedar glades and associated woodlands of the southern Edwards Plateau. Tex. J. Sci. 48:55–67.

Tiedemann, A.R., and Klemmedson, J.O. 1977. Effect of mesquite trees on vegetation and soils in the desert grasslands. J. Range Manag. 30:361–367.

Turner, R.M., Alcorn, S.M., Olin, G., and Booth, J.A. 1966. The influence of shade, soil, and water on saguaro seedling establishment. Bot. Gaz. 127:95–102.

Van Auken, O.W. 1988. Woody vegetation of the southeastern escarpment and Plateau. In: Edwards Plateau vegetation: plant ecological studies in central Texas, eds. B.B. Amos and F.R. Gehlbach, pp 43–55. Waco, TX: Baylor University Press.

Van Auken, O.W. 1993. Size distribution patterns and potential population change of some dominant woody species of the Edwards Plateau region of Texas. Tex. J. Sci. 45:199–210.

Van Auken, O.W. 2000a. Shrub invasions of North American semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–215.

Van Auken, O.W. 2000b. Characteristics of intercanopy bare patches in *Juniperus* woodlands of the southern Edwards Plateau, Texas. Southwest. Nat. 45:95–110.

Van Auken, O.W., Ford, A.L., and Stein, A. 1979. A comparison of some woody upland and riparian plant communities of the southern Edwards Plateau. Southwest. Nat. 24:165–180.

Van Auken, O.W., Ford, A.L., Stein, A., and Stein, A.G. 1980. Woody vegetation of upland plant communities in the southern Edwards Plateau. Tex. J. Sci. 32:23–35.

Van Auken, O.W., Ford, A.L., and Allen, J.L. 1981. An ecological comparison of upland deciduous and evergreen forests of central Texas. Am. J. Bot. 68:1249–1256.

Van Auken, O.W., Jackson, J.T., and Jurena, P.N. 2004. Survival and growth of *Juniperus* seedlings in *Juniperus* woodlands. Plant Ecol. 175:245–257.

Ware, S. 2002. Rock outcrop plant communities (glades) in the Ozarks: a synthesis. Southwest. Nat. 47:585–597.

Wayne, R., and Van Auken, O.W. 2002. Spatial and temporal patterns of xylem water potential in *Juniperus ashei* seedlings. Southwest. Nat. 47:153–161.

Wayne, R., and Van Auken, O.W. 2004. Spatial and temporal abiotic changes along a canopy to intercanopy gradient in central Texas *Juniperus ashei* woodlands. Tex. J. Sci. 56:35–54.

Wayne, E.R., Jurena, P.N., and Van Auken, O.W. 2002. Light response of *Juniperus ashei* and its role in spatial differences of seedlings beneath the woodland canopy and canopy edge. In: Ecological Society of America 87th annual meeting, August 2–7, 2002, Tucson, AZ, p 293.

West, N.E. 1999. Juniper-piñon savannas and woodlands of western North America. In: Savannas, barrens, and rock outcrop plant communities of North America, eds. R.C. Anderson, J.S. Fralish, and J.M. Baskin, pp 288–308. Cambridge: Cambridge University Press.

West, N.E. 1988. Intermountain deserts, shrub steppes, and woodlands. In: North American terrestrial vegetation, eds. M.C. Barbour and W.D. Billings, pp 210–230. Cambridge: Cambridge University Press.

West, N.E. 1984. Successional patterns and productivity potentials of pinyon-juniper ecosystems. In: Developing strategies for range management, ed. National Research Council/National Academy of Sciences, pp 1301–1332. Boulder, CO: Westview Press.

Whittaker, R.H. 1975. Communities and ecosystems. New York: MacMillan.

Wilding, L.P. 1993. Soils of tributary sub-basins in the Barton Creek Watershed: implications for a reappraisal of Hill Country soils. In: Soil, landforms, hydrologic processes, and land-use issues: Glen Rose limestone terrains, Barton Creek watershed, Travis County, Texas, eds. C.M. Woodruff, Jr., W.M. Marsh, and L.P. Wilding, pp 3:1–12. Austin, TX: Society of Independent Professional Earth Scientists, Central Texas Chapter.

Woodin, H.E., and Lindsey, A.A. 1954. Juniper-pinyon east of the continental divide analyzed by the line-strip method. Ecology 35:473–489.

Woodruff, Jr., C.M. 1993. Geology and physiography of Glen Rose limestone terrains, Barton Creek Watershed, central Texas. In: Soil, landforms, hydrologic processes, and land-use issues: Glen Rose limestone terrains, Barton Creek watershed, Travis County, Texas, eds. C.M. Woodruff, Jr., W.M. Marsh, and L.P. Wilding, pp 2:1–21. Austin, TX: Society of Independent Professional Earth Scientists, Central Texas Chapter.

3

Distribution of *Juniperus* Woodlands in Central Texas in Relation to General Abiotic Site Type

David D. Diamond and C. Diane True

Introduction

Most of the focus on North American *Juniperus* species has been related to efforts to reduce their abundance through mechanical or chemical methods or via prescribed fire (Grumbles 1989; Rasmassan and Wright 1989; Scifres 1980; Lyons et al. 1998; Taylor 1997; Wright 1980). Recently, more workers have investigated *Juniperus* species from the point of view of understanding their basic biology, rather than developing control methods (Van Auken 2000). Workers have investigated the biology of *Juniperus ashei* and have described woodlands with *Juniperus ashei* as a component or a dominant factor (Fuhlendorf et al. 1996; Gass and Barnes 1998; Smeins and Fuhlendorf 1997; Van Auken 2000; Yager and Smeins 1999). *Juniperus ashei* community types have also been related to geolandforms or ecological site types within the Hill Country (Amos and Gehlbach 1988; Diamond et al. 1995). For example, uplands with relatively deep, continuous soils often support grasslands or Ashe juniper shrublands, shallow soils over massive limestone support glade-like communities, and canyon slopes and valleys often support Ashe juniper or mixed juniper–deciduous woodlands (Diamond et al. 1995; Terletzky and Van Auken 1996; Van Auken 1988). The composition of communities varies across more than 250 km from east to west (Diamond et al. 1995). However, no evaluation of the distribution of abiotic site types of the Hill Country has been done, and few or none of these types of studies have been conducted on other *Juniperus* communities across North America. Without this type of study, knowledge about the distribution of vegetation cannot be related to landscapes in a quantitative way. Hence, we selected *Juniperus ashei*, the primary *Juniperus* species in the Central Texas Hill Country, as a case study.

Recent advances in geographic information systems (GIS) software, computer hardware, and the availability of digital data, including digital elevation models (DEMs) and satellite-derived land cover such as the national land cover database (NLCD), allow for better quantification and analysis of abiotic site types and vegetation. Our goals are to (1) provide a quantitative description of the major abiotic site types of the Texas Hill Country, (2) provide a quantitative evaluation of current land cover in relation to site type, (3) model historic vegetation based on site type, and (4) evaluate the current distribution of vegetation in relation to the historic distribution by site type.

O.W. Van Auken (ed.), *Western North American Juniperus Communities: A Dynamic Vegetation Type.*

Methods

We defined the Edwards Plateau and the Hill Country by referring to digital delineations of ecological sections and subsections provided by Bailey et al. (1994; digital version available for download at http://www.fs.fed.us/land/ecosysmgmt/ecoreg1_home.html) and to the state soil geographic (STATSGO) database (USDA 1991; downloads available from National Resource Conservation Service at http://www.nrcs.usda.gov/technical/techtools/stat_browser.html). We defined the exterior boundaries of the Hill Country and the Edwards Plateau using Bailey's ecoregions, and we modified the boundaries of the Hill Country by overlaying STATSGO soil polygons, which are drafted at finer resolution (Figure 1). We then divided the Hill Country into northeast, central, and western regions based on watershed divides. The northeast region separates the Brazos River drainage to the north from the Colorado River drainage to the south. The central region is separated from the western region at the divide between the Colorado River to the northeast and the Medina River to the southwest.

We acquired 30-m resolution (900-m^2 pixels) DEMs for the Edwards Plateau from the USGS National Elevation Dataset (Gesch et al. 2002; downloads available at http://gisdata.usgs.net/NED/default.asp), and 30-m resolution satellite-derived land cover from the national land cover dataset (NLCD; Vogelmann et al. 2001; downloads available at http://landcover.usgs.gov/natllandcover.asp). Finally, we

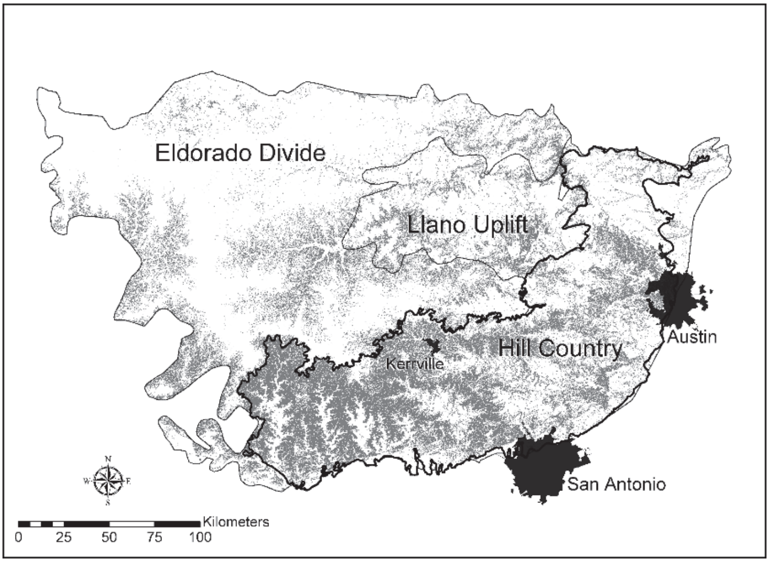

Figure 1 The Edwards Plateau ecological section and the Hill Country, Llano Uplift, and Eldorado Divide subsections. The section and subsection lines are based on Bailey et al. (1994), and the final delineation of the Hill Country is based on overlays of state soil geographic (STATSGO) (USDA 1991) soil polygons on the subsection lines

acquired other standard digital data layers, such as hydrology and streams, from standard, nationally available sources (see summary for Texas at the Texas Natural Resource Information Service website http://www.tnris.state.tx.us/).

We defined flat abiotic site types as having less than 8% slope and separated these from site types with slopes greater than 8%. We defined slopes that face north or northeast (315° to 135°) as protected from the direct rays of the sun and those that face south or southwest (135° to 315°) as exposed.

To separate river floodplains, valley bottoms, and low flats from higher flats, we used 30-m resolution DEMs to first create a coverage of 372 watersheds in the Hill Country with a catchment size of 40,000 30-m cells (average size, 7668 ha). Next, we selected all 30-m pixels with less than 8% slope (e.g., flats), and placed each pixel into one of nine classes corresponding to different elevations, including 10% of the highest elevation within the watershed, then 20%, 30%, and so on to 90%. Each class was color coded for on-screen analysis. Hence, all 30-m pixels in flats with an elevation equal to or less than 10% of the highest elevation within a watershed were one color, pixels with an elevation between 10% and 20% of the maximum for the watershed were a second color, and so on. Finally, we selected and zoomed to each of the 372 catchments on screen against a backdrop of a topographic hill shade and stream network, and separated high flats from floodplains and low flats by selecting a cutoff point for pixel elevation (e.g., 10% of the highest elevation within the watershed represents floodplains and low flats, or 20%, and so on). The cutoff value was set such that floodplains and low flats were captured based on visual inspection of the hill shade and stream network. Finally, we merged results for all 372 catchments and viewed these on screen against a topographic hill shade, and with overlays of STATSGO soil polygons, some of which correspond to alluvial soils, and made adjustments to approximately 20 catchments to form the final floodplain and low flats data layer.

We summarized the area of each abiotic site type by region for the Hill Country, and then overlaid the 30-m resolution NLCD on site types to summarize land cover by site type for each region. We combined land cover classes from the NLCD into six classes: water, urban, deciduous woodland, evergreen or mixed woodland, grassland or shrubland, and cropland. Finally, we modeled historic vegetation by assigning slopes and floodplains as historic woodland and high flats as grassland. We then overlaid the results from this model, and the NLCD current land cover, on site types to evaluate land cover change by site type and region.

Results

The Hill Country is 35% of the Edwards Plateau (see Figure 1), but contains 61% of the area with slopes greater than 8%. Thus, the Hill Country is more rugged than the main body of the Edwards Plateau. The western region is composed of 53.3% slopes and hence is more rugged than the central and northeast region (Table 1, Figure 2). The northeast region is composed of relatively more high flats, 88.6%, than either of the

Table 1 Area of four major abiotic site types by region for the Texas Hill Country based on analysis of 30-m resolution digital elevation models (DEMs; Gesch et al. 2002)

	Abiotic site type by region							
	Northeast Region		Central Region		Western Region		Hill Country Total	
Landform	Area (ha)	%	Area (ha)	%	Area (ha)	%	Area (ha)	%
High flats	156,863	88.6%	553,532	55.9%	208,675	24.5%	919,070	45.5%
Protected slopes	8,964	5.1%	183,664	18.5%	224,005	26.3%	416,632	20.6%
Exposed slopes	6,367	3.6%	174,224	17.6%	230,435	27.0%	411,025	20.3%
Low flats and floodplains	4,760	2.7%	78,971	8.0%	189,414	22.2%	273,145	13.5%
Regional total	176,953	100.0%	990,391	100.0%	852,529	100.0%	2,019,873	100.0%

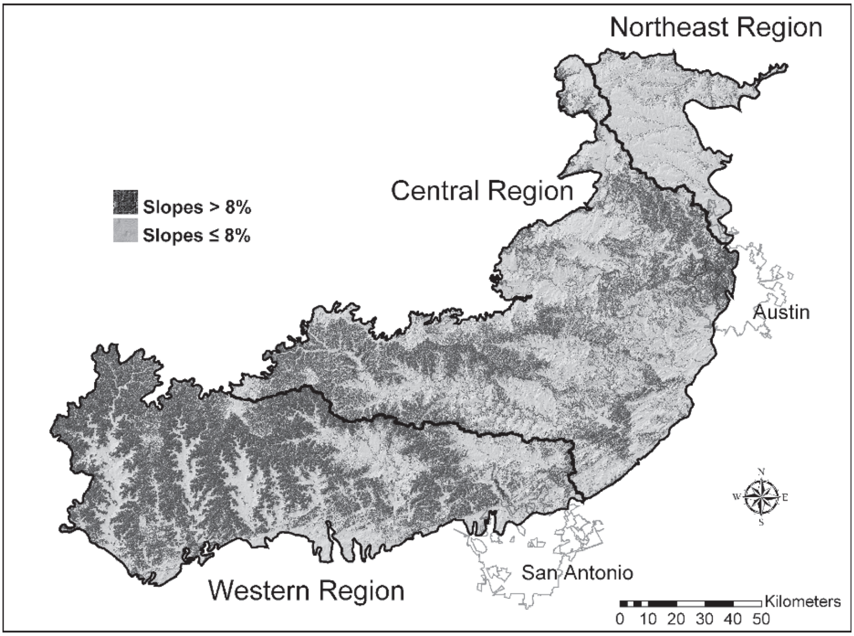

Figure 2 Topographic hill shade of the Hill Country with northeast, central, and western subdivisions based on river divides. Slopes >8% were defined using 30-m resolution digital elevation models (DEMs; Gesch etal. 2002)

other regions. In relative terms, the western region comprises 10 times more low flats than the northeast region and almost 3 times more than the central region. The western region of the Hill Country is relatively rugged with more low flats, the northeast region is mainly high flats, and the central region is intermediate (Table 1, Figure 3).

A total of 5.2%, or 105,033 ha, of the natural vegetation of the Hill Country has been lost to reservoirs, urban development, or cropland (Table 2). Among these, the loss to urban development is highest, at 2.5% or 50,497 ha. Grasslands make up 37.6% of the land cover and woodland 57.2%. Thus, the Hill Country supports

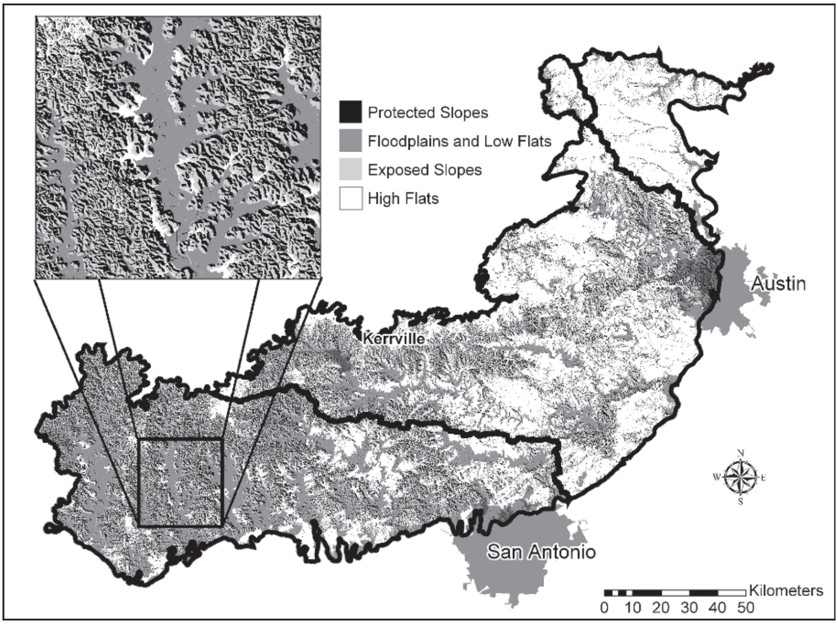

Figure 3 Major abiotic site types for the Hill Country from modeling using 30-m resolution digital elevation models (DEMs; Gesch et al. 2002). For historic vegetation modeling, high flats were grassland, and all slopes and floodplains and low flats were woodland

mainly seminatural land cover types, with little conversion to strictly anthropogenic land cover overall.

Slopes have 68.0% woodland and 29.8% grassland, whereas high flats have 50.1% woodland and 45.1% grassland (see Table 2). Low flats have 36.1% grassland and 47.7% woodland. Low flats have the highest relative total anthropogenic land cover at 16.2%, versus 4.8% for high flats and 2.1% for slopes. Anthropogenic land cover on low flats includes 7.4% cropland, 5.1% water, and 3.7% urban land. Thus, Hill Country slopes support more than twice as much woodland as grassland, high flats have slightly more woodland than grassland, and low flats have significant anthropogenic land cover, with seminatural land cover consisting of more woodland than grassland.

A total of 45.5% of the Hill Country was modeled as grassland and 54.5% as woodland (see Table 1, Figure 3). Currently, 57.2% of the Hill country is woodland, a 5.0% gain over what was modeled, and 32.7% is grassland, a 28.2% loss over what was modeled. Overall, 54.9% of the modeled grassland has been converted, mainly to woodland, and 37.0% of modeled woodland has been converted, mainly to grassland. On floodplains and low flats, 37.5% of the modeled woodland has been converted, whereas on slopes, 31.9% of the modeled woodland has been converted. In the flat northeast region of the Hill Country, 39.5% of the grassland has been lost

Table 2 Regional summary (hectares) of land cover, modeled historic land cover, and loss by abiotic site type within region for the Texas Hill Country

		Land cover class from the National Landcover Dataset							
Abiotic site type	Water	Urban	Deciduous woodland	Evergreen or mixed woodland	Grassland or shrubland	Cropland	Modeled land cover	Area lost (ha)	Percent loss
Northeast region									
High flats	502	2,915	9,833	46,767	94,927	1,930	Grassland	61,946	39.5%
Protected slopes	76	36	888	3,144	4,809	10	Woodland	4,931	55.0%
Exposed slopes	45	27	700	2,223	3,366	6	Woodland	3,443	54.1%
Low flats and floodplains	214	15	614	786	2,915	217	Woodland	3,360	70.6%
Total	837	2,993	12,034	52,920	106,016	2,163			.
Central Region									
High flats	1,254	15,114	39,556	236,035	252,186	9,381	Grassland	301,340	54.4%
Protected slopes	1,357	4,044	13,141	93,987	70,442	693	Woodland	76,535	41.7%
Exposed slopes	1,179	4,397	14,607	91,036	62,439	568	Woodland	68,583	39.4%
Low flats and floodplains	10,654	4,365	7,560	19,682	28,861	7,848	Woodland	51,728	65.5%
Total	14,444	27,920	74,865	440,741	413,927	18,490			
Western Region									
High flats	407	9,440	9,268	119,203	67,345	3,006	Grassland	141,323	67.7%
Protected slopes	282	1,705	5,216	166,804	49,502	493	Woodland	51,982	23.2%
Exposed slopes	305	1,784	6,424	165,474	55,891	554	Woodland	58,535	25.4%
Low flats and floodplains	3,085	5,671	7,475	94,144	66,902	12,143	Woodland	87,801	46.4%
Total	4,079	18,599	28,383	545,624	239,641	16,196			
Hill Country Total									
High flats	2,163	27,469	58,657	402,005	414,458	14,317	Grassland	504,610	54.9%
Protected slopes	1,716	5,785	19,246	263,935	124,752	1,196	Woodland	133,449	32.0%
Exposed slopes	1,529	6,208	21,731	258,733	121,696	1,128	Woodland	130,561	31.8%
Low flats and floodplains	13,953	10,051	15,649	114,612	98,678	20,208	Woodland	142,890	52.3%
Total	19,361	49,512	115,282	1,039,285	759,584	36,849			

Land cover is from the National Land Cover Dataset (Vogelmann et al. 2001); modeled abiotic site types are from analyses of 30-m resolution digital elevation models (DEMs; Gesch et al. 2002) compared to that which was modeled, whereas 54.5% of the woodland on slopes has been lost and 70.6% of the woodland on floodplains and low flats has been lost. In the rugged western region of the Hill Country, 67.7% of the grassland modeled on high flats has been lost, 24.4% of the woodland on slopes, and 46.4% of the woodland on floodplains and low flats. Relative losses from historic modeled land cover by landform are intermediate in the central region. Thus, relatively more woodlands and fewer grasslands remain intact where they were modeled in the western region, and more grasslands and fewer woodlands remain intact in the northeast region.

Discussion

Results from the current land cover analysis and the abiotic site type classification carry with them inaccuracies from input data. The reported user's accuracy of NLCD land cover data for the southwest region of the United States is 91% for water, 66% for woodland, 75% for grassland and shrubland combined, 82% for agricultural land cover classes combined, and 71% for urban land cover classes (Vogelmann 2001). The low flats and floodplains data layer were interpreted from on-screen analysis on a watershed-by-watershed basis. For some large watersheds, relatively high flats downstream in watersheds may have been included as floodplains and some areas of low flats and floodplains upstream in watersheds may have been counted as high flats. Digital elevation models (DEMs) from which the abiotic site types were derived are as accurate as the hypsography information from USGS 1:24,000 scale quadrangles. Nonetheless, the digital data used are the best available, and on-screen viewing of results reveals few errors.

Modeling of historic vegetation to site type for analyses was simplistic. We will never know the exact land cover of the Hill Country at any given point in time, even the present (see local estimates and discussion in Bray 1904; Buechner 1944; Huss 1954; Solcher 1927). Historic land cover depended on factors such as the timing, intensity, and frequency of fire, which in turn depend on variables such as drought cycles and landscape position (e.g., patch size of fire-prone flats within rugged landscapes; fire shadows), and on geological or edaphic variables such as massive limestone at the surface that reduced fine fuel (see Bray 1904; Diamond et al. 1995; Fuhlendorf et al. 1996; Smeins 1980; Smeins and Merrill 1988). For example, small patches of high flats within a rugged, largely wooded, more "fireproof" landscape may have seldom burned. High flats over massive limestone may have lacked the fine fuel to carry frequent ground fires, and might instead have experienced a decades-long fire return interval in which Ashe juniper woodlands were burned via a crown fire and then recovered only to be burned again. Similarly, small patches of slopes within a largely flat, grassy, fire-prone landscape may have burned often enough to be kept free of woody vegetation. Using this logic, we could have modeled small patches of high flats less than 50 ha, which make up 20.4% of all high flats in the rugged western region of the Hill

Country, as woodland; and we could have mapped small patches, less than 50 ha, of slopes more than 8%, which make up 76.7% of all slopes in the flat northeast region, as grassland. Similarly, low flats and floodplains may have experienced a cycle of catastrophic flooding followed by development of mature woodlands, and some large patches of low flats may have been kept clear of woody vegetation by frequent ground fires. Thus, comparisons of modeled versus existing land cover by abiotic site type show broad trends for interpretation and are not meant to be taken as estimates with a known accuracy.

We showed a slight gain overall in woodland and loss in grassland for the Hill Country. The loss in grassland corresponds to many modern interpretations, but some interpretations also assert a large increase in woodland, which was not shown under our modeling assumptions (Van Auken 2000). Indeed, the general perception is that woody species have increased overall worldwide, but these notions should be tempered by more specific studies, because the human tendency is to assume that less desirable vegetation types have replaced more desirable types. We did not show a great loss of seminatural land cover (e.g., grassland and woodland) to anthropogenic land cover (e.g., cropland, reservoirs, and urban land cover). The NLCD land cover data we used were from circa 1992, and some further loss of natural land cover may have occurred since then. Diamond and Blodgett (2003) showed an increase in urban land cover for the St. Louis area of 17.8% between 1987 and 1999. Using this value for urban land cover increase from 1992 to 2004, an additional 0.44% of the Hill Country has been converted to urban land cover, for a total of 2.9%. Overall, the increase in woodland, loss in grassland, and increase in urban areas within the Hill Country are not dramatic.

Land cover of the Hill Country appears to be relatively similar to historic conditions, although the species composition (e.g., greater abundance of grazing-tolerant and introduced species) and the character of the communities (e.g., few or no old-growth woodlands; loss of highly palatable and grazing-intolerant species) have changed (Almos and Gehlback 1988; Diamond 1997). This lack of dramatic land cover change is evident even 200 years since European settlement and after long-term, vigorous, expensive efforts to change the vegetation, mainly via removal of Ashe juniper (Taylor 1997). These proven failures of the past are doomed to be repeated unless managers take a more realistic view of vegetation management. For example, most of the slopes greater than 8% in the Hill Country are woodland and cannot be converted to grassland without repeated clearing. These areas, including more than half of the western region of the Hill Country and 41% overall, are best managed for their wildlife and woodland resources. Some portion of uplands, such as those lying over massive, cracked limestone that currently support mainly woody plant communities, also are best managed for wildlife habitat rather than grazing by domestic livestock, because the latter requires ongoing, and ultimately futile, expenditures of time, energy, and money. Thus, we suggest that land stewards should match management goals to realistically attainable results by understanding abiotic site potentials as these interact with current community composition.

Summary

Juniperus ashei Buchholz (Ashe juniper) communities are important components of the Central Texas Hill Country, a kidney-shaped region that comprises 35% of the southern and eastern portion of the Edwards Plateau. We used digital elevation models (DEMs) to define abiotic site types and overlaid land cover from the national land cover dataset (NLCD) to analyze the distribution of woodlands in relation to site type. We modeled the historic distribution of woodlands and grasslands and compared the modeled historic extent to the modern extent. The Hill Country is more dissected than the rest of the Edwards Plateau, with 41% of the area on slopes greater than 8% versus 24% for the entire plateau. Woodlands currently occupy 68% of slopes greater than 8% in the Hill Country, 50.2% of high flats, and 47.7% of floodplains. Grasslands currently make up 37.6% of the land cover of the region, and cropland, urban land, and water together cover 5.2%. The historic vegetation of the Hill Country was modeled as 54.5% woodland and 45.5% grassland. Woodlands apparently have decreased on slopes and floodplains, and may have increased on high flats, whereas grasslands may have decreased on high flats and increased on slopes and floodplains. Overall changes in land cover have not been dramatic since European settlement, despite long-term attempts to reduce Ashe juniper cover. Land management designed to reduce or eliminate *Juniperus ashei* woodland has failed, and more realistic and attainable goals and management regimes related to abiotic site types and current conditions should be adopted.

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References

Amos, D.D., and Gehlbach, F.R., eds. 1988. Edwards Plateau vegetation. Plant ecological studies in Central Texas. Waco, TX: Baylor University Press.

Bailey, R.G., Avers, P.E., King, T., and McNab, W.H., eds. 1994. Ecoregions and subregions of the United States (map). Washington, DC: USDA Woodland Service. 1:7,500,000. With supplementary table of map unit descriptions, compiled and edited by W.H. McNab and R.G. Bailey.

Bray, W.L. 1904. The timber of the Edwards Plateau of Texas; its relation to climate, water supply and soil. Bulletin 49. Washington, DC: United States Department of Agriculture.

Buechner, H.K. 1944. The range vegetation of Kerr County, Texas in relation to livestock and white-tailed deer. Am. Midl. Nat. 31:697–713.

Diamond, D.D. 1997. An old-growth definition for western juniper woodlands: Texas Ashe juniper dominated or codominated communities. General technical report SRS-15. Washington, DC: United States Department of Agriculture, Southern Research Station.

Diamond, D.D., and Blodgett, C. 2003. Urban remote sensing for land use change and impacts. Final report. Las Vegas: U.S. Environmental Protection Agency, Office of Research and Development.

Diamond, D.D., Rowell, G.A., and Keddy-Hector, D.P. 1995. Conservation of Ashe juniper (*Juniperus ashei* Buchholz) woodlands of the Central Texas Hill Country. Nat. Areas J. 15:189–197.

Fuhlendorf, S.D., Smeins, F.E., and Grant, W.E. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecol. Model. 90:245–255.

Gass, L., and Barnes, P.W. 1998. Microclimate and understory structure of live oak (*Quercus fusiformis*) clusters in central Texas, USA. Southwest. Nat. 43:183–194.

Gesch, D., Oimoen, M., Greenlee, S., Nelson, C., Steuck, M., and Tyler, D. 2002. The national elevation dataset. Photogram. Remote Sens. 68:5–33.

Grumbles, J.B. 1989. Control of eastern redcedar and Ashe juniper with soil spot applications of picloram. Down Earth 45:13–16.

Huss, D.L. 1954. Factors influencing plant succession following fire in Ashe juniper woodland types in Real County, Texas. Ph.D. dissertation. College Station, TX: Texas A&M University.

Lyons, R.K., Owens, M.K., and Machen, R.V. 1998. Juniper biology and management in Texas. Technical report B-6074, 9-98. College Station, TX: Texas Agricultural Extension Service, Texas A&M University System.

Rasmussen, G.A., and Wright, H.A. 1989. Succession of secondary shrubs on Ashe juniper communities after dozing and prescribed burning. J. Range Manag. 42:295–298.

Scifres, C.J. 1980. Brush management: principles and practices for Texas and the Southwest. College Station, TX: Texas A&M University Press.

Smeins, F.E. 1980. Natural role of fire on the Edwards Plateau. In: Prescribed burning in the Edwards Plateau, ed. L.D. White. College Station, TX: Texas Agricultural Extension Service, Texas A& M University System.

Smeins, F.E., and Fuhlendorf, S.D. 1997. Biology and ecology of Ashe (blueberry) juniper. In: Juniper symposium, 1997 proceedings, ed. C.A. Taylor. Technical report 97-1. College Station, TX: Texas Agricultural Experiment Station, Texas A&M University System.

Smeins, F.E., and Merrill, L.B. 1988. Longterm change in a semiarid grassland. In: Edwards Plateau vegetation: plant ecological studies in Central Texas, eds. B.B. Amos and F.R. Gehlbach, pp 101–114. Waco, TX: Baylor University Press.

Solcher, E.A. 1927. An analysis of the plant associations of Bexas County, Texas. M.A. thesis. Austin, TX: University of Texas.

Taylor, C.A., ed. 1997. 1997 juniper symposium. Technical report 97-1. College Station, TX: Texas Agricultural Experiment Station, Texas A&M University System.

Terletzky, P.A., and Van Auken, O.W. 1996. Comparison of cedar glades and associated woodlands of the southern Edwards Plateau. Tex. J. Sci. 48:55–67.

USDA. 1991. States soil geographic (STASGO) data base. Data use information. Miscellaneous publications 1492. Washington, DC: United States Department of Agriculture, Natural Resource Conservation Service, National Soil Survey Center.

Van Auken, O.W. 1988. Woody vegetation of the southeastern escarpment and plateau. In: Edwards Plateau vegetation: plant ecological studies in Central Texas, eds. B.B. Amos and F.R. Gehlbach, pp 43–55. Waco, TX: Baylor University Press.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–215.

Vogelmann, J.E., Howard, S.M., Yang, L., Larson, C.R., Wylie, B.K., and Van Driel, N. 2001. Completion of the 1990s national land cover data set for the conterminous United States from Landsat Thematic Mapper data and ancillary data sources. Photogram. Eng. Remote Sens. 67:650–662.

Wright, H.A. 1980. Techniques and procedures for safe use of prescribed fire. In: Prescribed range burning in the Edwards Plateau of Texas. Proceedings of a symposium, ed. L.D. White, pp 51–61. College Station, TX: Texas A&M University System, Texas Agricultural Extension Service.

Yager, L.Y., and Smeins, F.E. 1999. Ashe juniper (*Juniperus ashei*: Cupressaceae) canopy and litter effects on understory vegetation in a juniper-oak savanna. Southwest. Nat. 44:6–16.

4

Structure and Function of Woodland Mosaics: Consequences of Patch-Scale Heterogeneity and Connectivity Along the Grassland–Forest Continuum

David D. Breshears

Introduction

A large fraction of the terrestrial biosphere can be viewed as gradients of varying amounts of cover by woody plants, referred to as the grassland–forest continuum, (Figure 1; Belsky and Canham 1994; Breshears and Barnes 1999; Breshears 2006). Over such gradients, the proportion of cover from woody vegetation generally increases from grasslands to savannas to woodlands to forests. The ecosystems along the grassland–forest continuum vary with respect to their proportions of woody and herbaceous plants. Understanding and predicting the dynamics of mixed woody-herbaceous systems remain a major challenge (House et al. 2003). The juniper woodlands that are the focus of this volume represent one such system that is widely distributed in North America as well as elsewhere (McPherson 1997; Anderson et al. 1999).

Here I summarize the findings from an intensively studied woodland site, the Mesita del Buey Piñon-Juniper Site, located within the Los Alamos National Environmental Research Park at Los Alamos National Laboratory in northern New Mexico, USA. Research at this site has focused in large part on relating structure to function in a manner that could have implications for other systems along the grassland–forest continuum (Figure 2). In particular, much of the research has focused on (1) quantifying heterogeneity between canopy patches of woody plants and intercanopy patches, (2) quantifying connectivity among patches, and (3) relating patch-scale heterogeneity and connectivity to structure and dynamics at the ecosystem scale and along gradients of woody vegetation. A theme of the research has been the important relationship between ecological and hydrological processes, a focus of the emerging area of ecohydrology (Newman et al. 2006). The patch-scale approach has lead to the development of several related conceptual models applicable to gradients of woody vegetation. In this chapter, I provide an overview of the study site and the diverse set of properties and processes that have been evaluated at the site in the context of patch-scale heterogeneity and connectivity. These findings are related to resulting conceptual models and current understanding of juniper woodlands within the context of the grassland–forest continuum. The research highlights the

O.W. Van Auken (ed.), *Western North American Juniperus Communities:
A Dynamic Vegetation Type.*

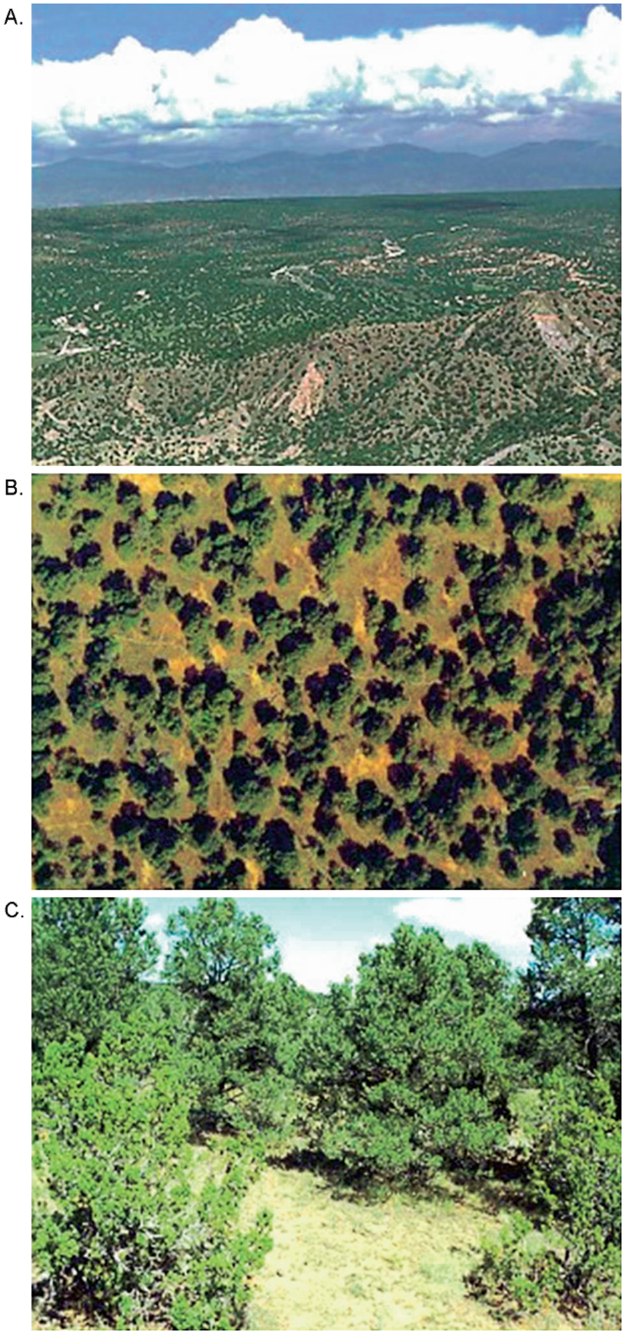

Figure 1 Woodland patches on the ground (**A**), from above (**B**), and as the matrix for vegetation gradients across landscapes (**C**). (Reprinted from Breshears 2006, with permission from the Ecological Society of America)

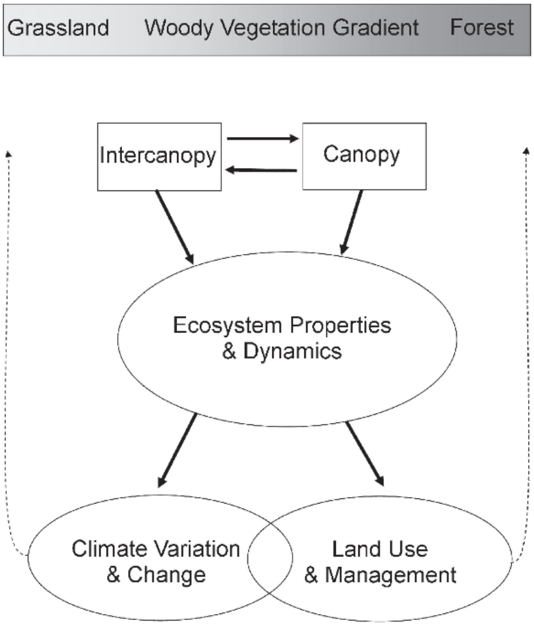

Figure 2 Conceptual framework for viewing the grassland–forest continuum as a mosaic of the canopy patches of woody plants and the intercanopy patches that separate them. Heterogeneity and connectivity among patches determine key ecosystem properties and dynamics, which in turn relate to issues of climate variation and change and of land use and management

importance of understanding and quantifying patch-scale relationships in juniper woodlands and of the potential for juniper woodlands to serve as model systems for better understanding the grassland–forest continuum.

The Mesita del Buey Study Site

The Mesita del Buey Woodland study site is located in northern New Mexico within Technical Area 51 of the Los Alamos National Environmental Research Park (Figure 3: latitude 35°50’ N, longitude 106°16’ W; the geographical coordinates for this location previously reported erroneously in Breshears et al. 1997b, 1998; Martens et al. 1997; and Martens et al. 2000). Site elevation is approximately 2140 m. The area has a temperate montane climate, with annual precipitation of approximately 40 cm, mainly in the form of winter snowfall and late-summer precipitation (Bowen 1996; Figure 4; see Bowen 1990 for a more expansive description of site climate). Soils at Mesita del Buey are predominantly sandy loam or loam at the surface, but graded to an argillic horizon in texture with a clay loam underlying in the Bt horizon (Davenport et al. 1996). Fifty-five percent of the soils are Typic Haplustalfs (median thickness of 85 cm, divided by horizon as 10 cm of

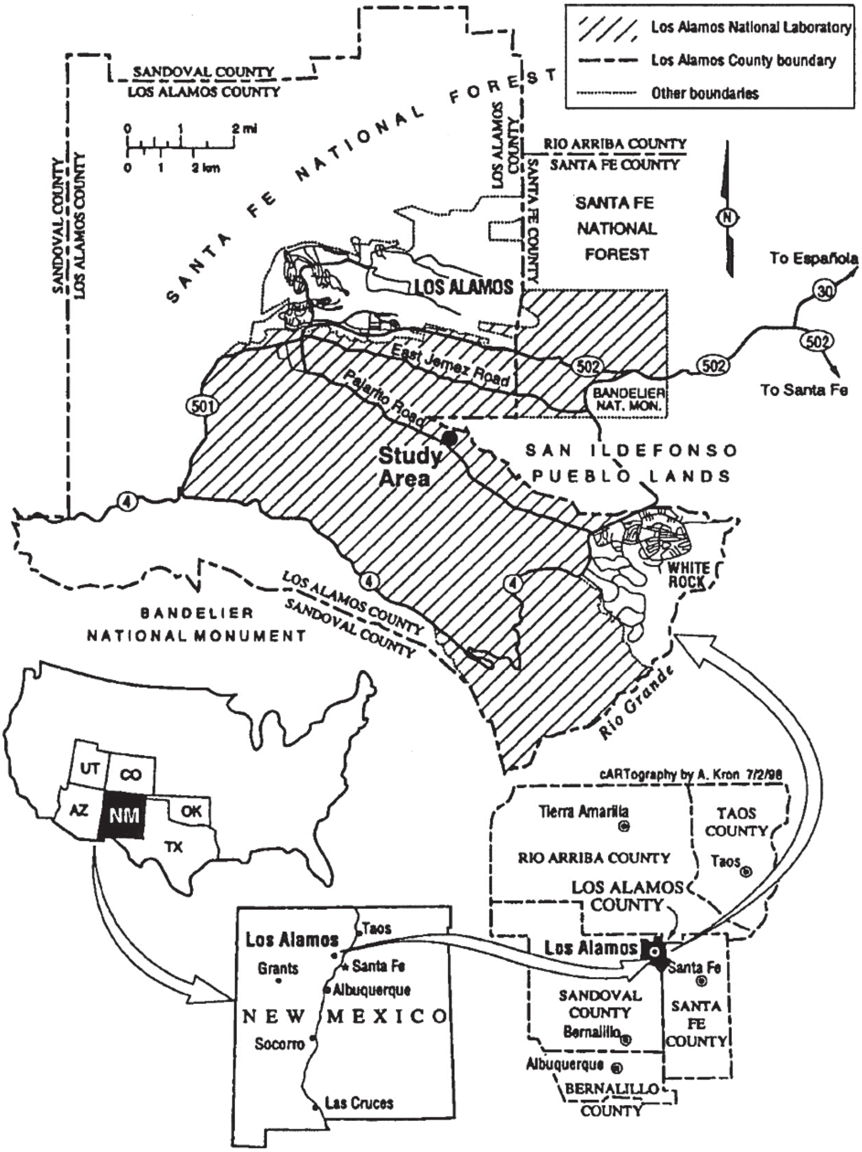

Figure 3 Location of the Mesita del Buey research site. (Reprinted from Reid et al. 1999, with permission from the Soil Science Society of America)

A, 25 cm of Bt, and 48 cm of Cr), and 34% are Typic Ustochrepts (median thickness of 80 cm, divided by horizon as 8 cm of A, 23 cm of Bw, and 47 cm of Cr; Davenport et al. 1996). The larger unit encompassing the area was described as Hackroy clay loam, derived from volcanic tuff (Nyhan et al. 1978). The landscape ecology of this encompassing area, including historical land use and disturbances such as fire,

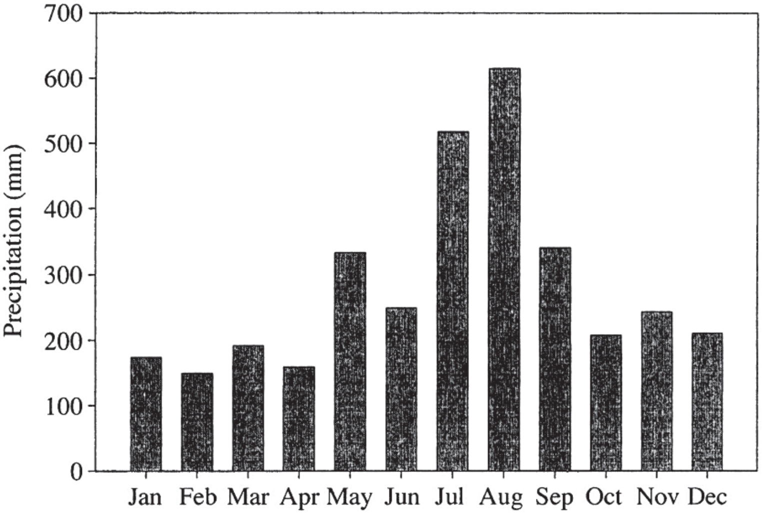

Figure 4 Mean monthly site precipitation (1991–1998). (Reprinted from Wilcox et al. 2003a, with permission from the Ecological Society of America)

Table 1 Study characteristics for Mesita del Buey

Characteristic	Value	Reference
Elevation	2140	
Slope	~6%	
Soil types	Typic Haplustalfs, Typic Ustrochrepts	Davenport et al. 1996
Canopy cover, nonoverlapping (%)	43 (from 50 × 50 m plot)	Martens et al. 2000
Overlapping cover (%)	56 (from 50 × 50 m plot)	Martens et al. 2000
Mean tree height (m)	3.8	Martens et al. 2000
Spatial pattern: Hopkins index	2.3 (aggregated)	Martens et al. 2000

drought, and insect infestations, was described by Allen (1989). The dominant overstory species are piñon pine, *Pinus edulis* Engelm., and one-seed juniper, *Juniperus monosperma* (Engelm.) Sarg. The density of *P. edulis* and J. *monosperma* is just over 500 woody individuals/ha, yielding an overstory canopy coverage of ~50% (Table 1), with near-equal densities of the two species. Average size of piñons exceeds that of junipers (Figure 5), and hence piñons contribute a much larger fraction to site biomass. Trees have a clumped distribution of individual crowns (Padien and Lajtha 1992), with a strong aggregation of crowns at 2 to 4 m, indicating the scale of canopy patches (Martens et al. 1997). Canopy patches are composed of individuals of both woody species, with younger trees of one species being associated with older trees of the other species (Martens et al. 1997). The average age of piñons in the stand in 1992 was about 110 years, with the oldest piñon being about 220 years (Davenport et al. 1996). The junipers at the site have not been aged because

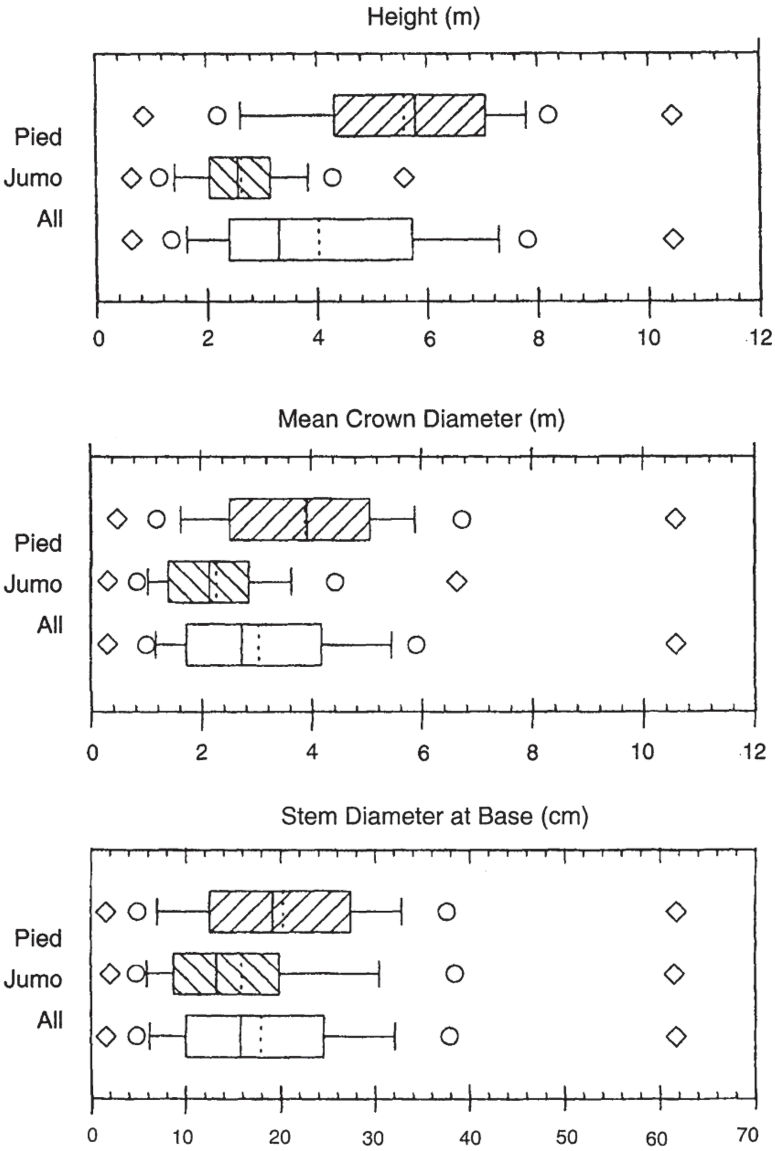

Figure 5 Summary statistics for crown height (m), mean canopy diameter (m), and stem diameter at base (cm) for piñon, *Pinus edulis* (*Pied, n* = 249), and juniper, *Juniperus monosperma* (*Jumo, n* = 278), for the central 70 m × 115 m section of the study site. Means indicated with *dashed lines within boxes*, medians as *solid lines within boxes*, 25th and 75th percentiles as *box ends*, 10th and 90th percentiles as *error bars*, 5th and 95th percentiles as *circles*, and minima and maxima as *diamonds*. (Reprinted from Martens et al. 1997, with permission from Opulus Press)

they are very difficult to core and *Juniperus* species often have false rings, making them difficult to age. Ground cover in intercanopy areas adjacent to the study site is about 85%, with approximately 50% from cryptogamic crust, 13% from grass (primarily blue grama, *Bouteloua gracilis* (H.B.K.) Lag.), 2% semishrub, 1% forb, and 18% litter (Wilcox 1994); canopy areas are covered with litter and contain few herbaceous plants (Reid et al. 1999). The overstory vegetation produces a large degree of variation in key abiotic properties such as near-ground solar radiation and soil water content within the woodland (Figure 6).

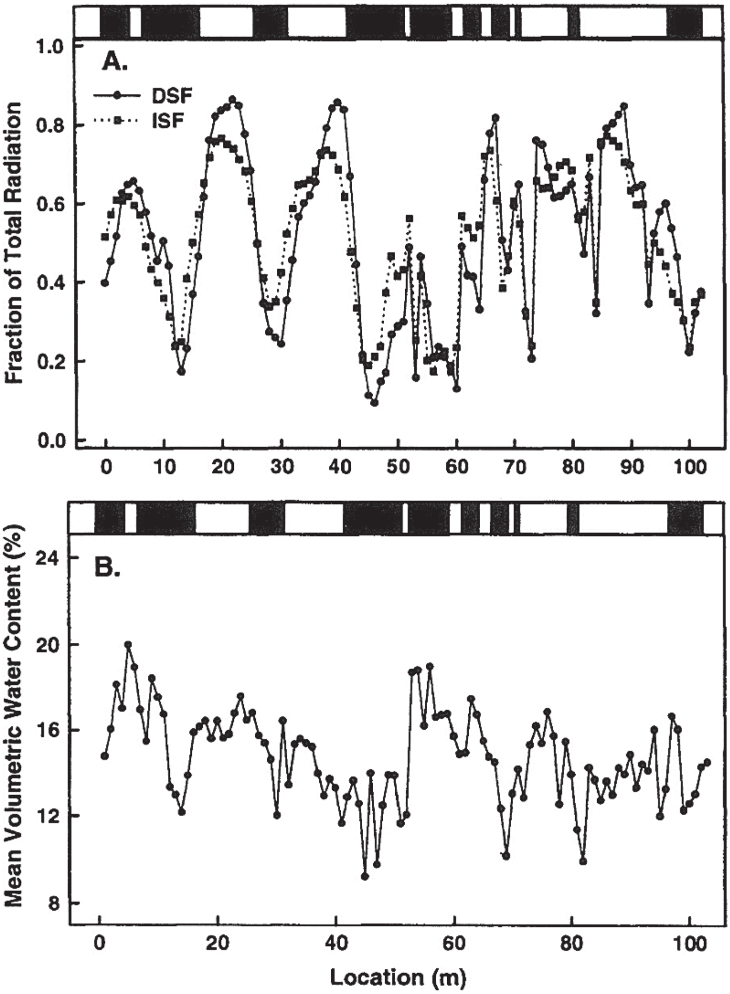

Figure 6 A transect across the site. The overstory along the transect is represented by the *bar across the top* for each site (*black* = canopy; *white* = intercanopy). **A** Site factors for near-ground solar radiation direct-beam only (*DSF*) and indirect as well as direct (*ISF*) for the fraction of total annual solar radiation received at a given location. **B** Three-year mean soil water content (0–15 cm measured monthly by time domain reflectometry). (Reprinted from Breshears et al. 1997b, with permission from the Ecological Society of America)

Patterns and Implications of Patch-Scale Heterogeneity and Connectivity

Soils

Canopy Versus Intercanopy Heterogeneity for Soils

Most soil morphological properties at Mesita del Buey do not differ between the canopy patches of woody plants and the intercanopy patches that separate the canopy patches (Table 2). Canopy patches have an O horizon of litter that is lacking for intercanopy patches. Intercanopy patches have a significantly thicker Bt horizon and less coarse fragments (Davenport et al. 1996). Mean saturated hydraulic conductivity, driving soil infiltration rates, is ~2 times higher for canopy patches than intercanopy patches, although large variances within each patch type render this difference insignificant based on sample sizes to date (note that these estimates are obtained excluding the O horizon of litter; Wilcox et al. 2003c). Soil pH is slightly more basic in intercanopy locations (Davenport et al. 1996). There are quite substantial biogeochemical differences between the two patch types: organic carbon is ~4.5 times greater in canopy versus intercanopy patches (Davenport et al. 1996). Nitrification and mineralization rates in the field are roughly 3 times greater in canopy than in intercanopy patches (Padien and Lajtha 1992).

Within-Patch Heterogeneity for Soils

Significant differences in soil properties beneath canopy patches have not been documented for piñon versus juniper patches (Davenport et al. 1996; Wilcox et al. 2003c). Saturated hydraulic conductivity for juniper canopies spans a larger range than that for piñons, a difference that has been attributed to the more shallow rooting distribution of juniper (Wilcox et al. 2003c). Within intercanopy patches, mean saturated

Table 2 Selected properties of canopy and intercanopy patches

Property	Intercanopy	Canopy		Reference
Total soil thickness	76	80	NS	Davenport et al. 1996
A horizon thickness, % of total	12	11	NS	Davenport et al. 1996
Bt horizon thickness, % of total profile	34	30	*	Davenport et al. 1996
Cr horizon thickness, % of total profile	59	58	NS	Davenport et al. 1996
Coarse fragments, volume %	10	12	*	Davenport et al. 1996
Soil pH	7.4	6.9	*	Davenport et al. 1996
Saturated hydraulic conductivity (mm/h)	73	150	NS	Wilcox et al. 2003c

NS, not significant.
*Significant difference ($P < 0.05$).

hydraulic conductivity of bare locations may exceed that for herbaceous locations, but significant differences have not been detected with sample sizes utilized to date (Wilcox et al. 2003c). Within intercanopy patches, soil carbon is slightly higher under herbaceous than bare locations (Reiley 2003).

Solar Radiation Inputs and Soil Temperature

Canopy Versus Intercanopy Heterogeneity and Connectivity for Solar Radiation

Much of the variation in near-ground solar radiation at the site (see Figure 6) is associated with heterogeneity between canopy and intercanopy patches. The fraction of direct-beam solar radiation reaching near-ground remains relatively constant in canopy patches throughout the year relative to intercanopy patches, for which near-ground solar radiation varies by a factor of 2 throughout the year (Figure 7).

Within-Patch Heterogeneity and Connectivity for Solar Radiation

Near-ground solar radiation varies predictably within canopy and intercanopy patch types on the basis of sun angle (Figure 8). The center locations of intercanopy patches received an average of about 65% of the potential direct radiation, whereas the center of canopy patches received <40% of the potential. However, the differences are less dramatic near the canopy–intercanopy edges. The north sides of intercanopy patches

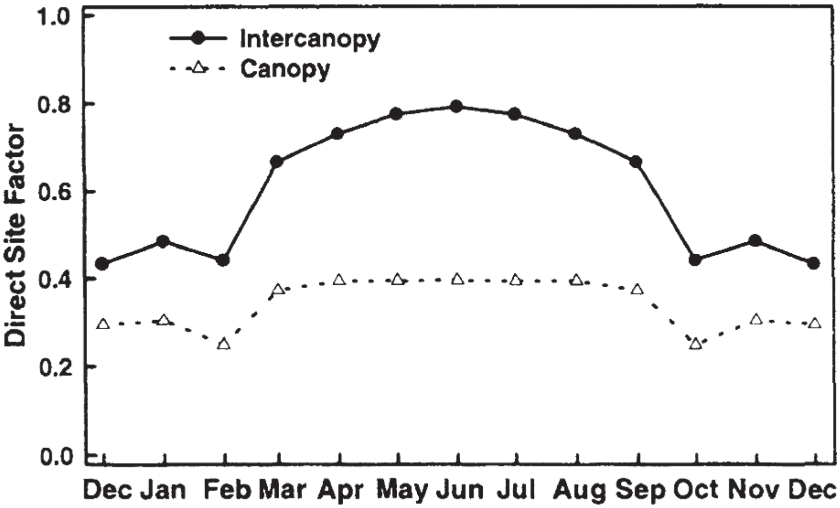

Figure 7 Direct site factor (DSF) indicating fraction of monthly potential solar radiation within each patch type by month. (Reprinted from Breshears et al. 1997b, with permission from the Ecological Society of America)

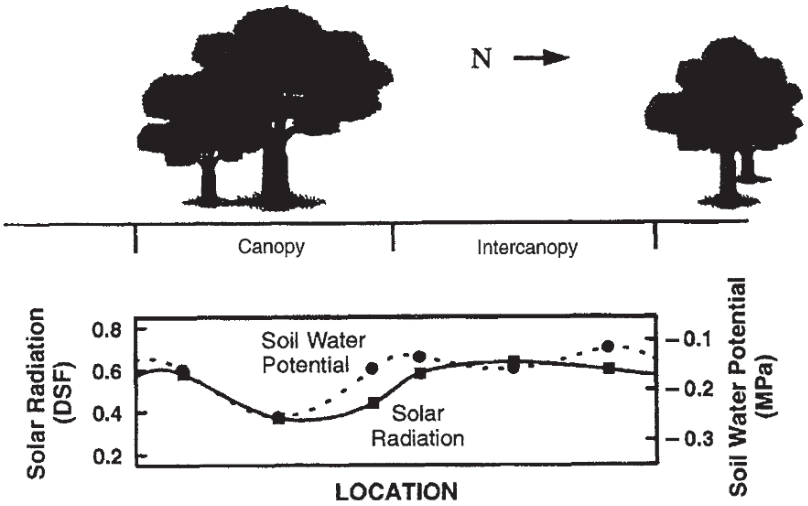

Figure 8 Mean values for patch-scale gradients of solar radiation and soil water potential along a north–south transect through a canopy and intercanopy patch. Solar radiation is the direct site factor (*DSF*), indicating fraction of annual potential solar radiation, and soil water potential is calculated from 3-year averages of soil water content data. (Reprinted from Breshears et al. 1997b, with permission from the Ecological Society of America)

receive less solar radiation than the south sides because of the shading effects of canopy patches. Similarly, the south sides of canopy patches receive more solar radiation than north sides of canopy patches because of lesser self-shading effects by the canopy itself. The shading of locations within intercanopy patches is an important mode of connectivity between the two patch types.

Larger-Scale Implications of Patch-Scale Heterogeneity and Connectivity for Solar Radiation

General patterns of near-ground solar radiation within and across sites along the grassland–forest continuum emerge as a result of the mosaic pattern of canopy and intercanopy patches within a woodland. Modeling near-ground solar radiation using a ray-tracing model, Martens et al. (2000) systematically evaluated how patterns of canopy coverage affect distributions at a site overall and within either patch type. The set of simulations varied three components of woody plant canopy structure: amount of ground covered, height, and spatial pattern. Ground cover ranged from no woody plant cover, corresponding to grassland, to nearly complete woody plant cover, corresponding to closed-canopy forest. Height was based on varying the height distribution of woody plants at the Mesita del Buey site by either doubling or halving them. Spatial pattern was manipulated to evaluate differences among random, aggregated, and regular spacing. These factors were varied individually and collectively to reflect how they concurrently change along an elevational gradient.

For the gradient studied, height increases with cover and pattern shifted from random to aggregated. The simulations highlight how the distribution of near-ground solar radiation changes dramatically over an intermediate range of canopy cover, from 21% to 43% in this case, and how these changes relate to distributions within each patch type (Figure 9). For example, at canopy cover of 43%, nearly all the locations with the highest light levels for canopy cover of 21% have been eliminated. Mean plot solar radiation is sensitive to height as well as cover, with taller woody plants producing larger reductions in near-ground solar radiation (Figure 10A); spatial pattern does not have a large effect on the plot mean. Spatial variance in near-ground solar radiation is also sensitive to the amount of cover and to height. Variance peaks at an intermediate value that is

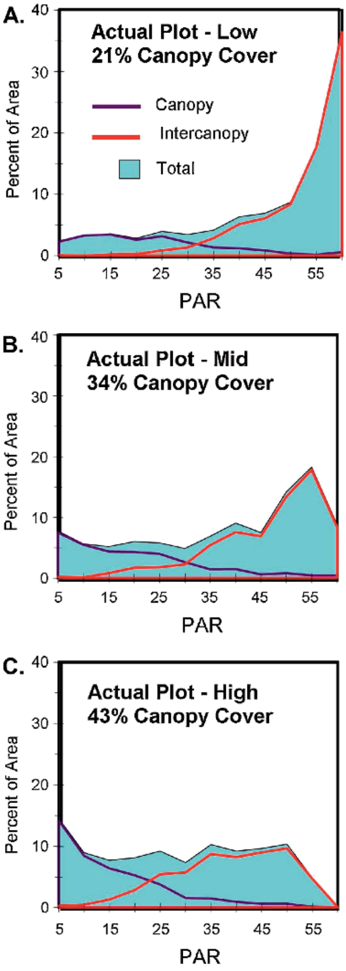

Figure 9 Histograms for spatial variation in transmitted photosynthetically active radiation (*PAR*; mol m^{-2}) integrated over the growing season for three plots along an elevational gradient that vary in woody plant cover, height, and spatial pattern (**A–C**). Estimates are presented for canopy locations, intercanopy locations and total (overall for plot). The "High" plot (**C**) is Mesita del Buey. (Reprinted from Martens et al. 2000, with permission from Elsevier)

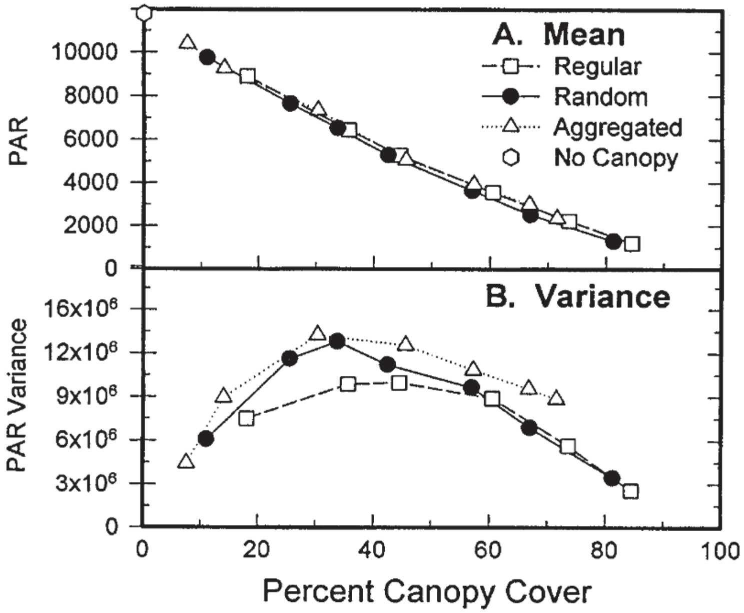

Figure 10 Effect of height and canopy cover on transmitted photosynthetically active radiation (*PAR*; mol m^{-2}) integrated over the growing season for regular, random, and aggregated canopy patterns. (Reprinted from Martens et al. 2000, with permission from Elsevier)

less than 50% woody plant cover (Figure 10B); this results from the connectivity among patches due to shading. The magnitude of the peak and the amount of cover to which it corresponds are related to woody plant height, with taller woody plants producing a higher peak that occurs at a lower amount of woody plant coverage.

These results lead to one of several sets of hypotheses about the grassland–forest continuum generated by research at the Mesita del Buey research site (Table 3). Near-ground solar radiation and associated transmitted photosynthetically active radiation are expected to decrease with canopy cover in a nearly linear fashion as height is held constant but in a more sigmoid fashion when height increases (Figure 11A). Plot variance peaks at an intermediate level of cover that is less than 50%, and the relative amplitude of the peak is greater if woody plant height increases with cover (Figure 11B).

Interception of Precipitation

Woody plant canopies intercept not only solar radiation but also precipitation. Studies at Mesita del Buey have not directly quantified interception, although several relevant studies have been conducted elsewhere (Skau 1964; Collings 1966; see also Wilcox et al. 2003b; and Chapter 10, this volume). Annually, interception for canopy patches can range from 5% to 46% of precipitation input. On an event basis, a larger

Table 3 Conceptual models and hypotheses stemming from research at the Mesita del Buey Woodland Site

Concept	Description
Trends in near-ground solar radiation as a function of woody plant cover, height, and spatial pattern (Martens et al 2000).	Plot-scale near-ground solar radiation decreases nearly linearly with increasing woody plant cover for plants of constant height; the decrease is very sensitive to plant height, with taller plants providing more shading; spatial pattern (random, regular, or aggregated) does not have a large effect on plot mean. Plot-scale variance peaks at an intermediate value less than 50% cover, with the location of the peak sensitive to plant height and spatial pattern. For gradients in which height increases with cover—a common feature of elevational/climatic gradients—means and variances change more curvilinearly than if height remains constant.
Runoff and erosion as a function of spatial scale (Wilcox et al. 2003a).	Runoff and erosion decrease with increasing scale as a result of storage at different scales, including grassy areas within intercanopy patches, canopy patches, and microtopographic variation. For disturbed systems in which herbaceous areas are eliminated and woody plants become mounded, runoff does not decrease with increasing scale.
Erosion thresholds with changing cover (Davenport et al. 1998).	The threshold for transitioning from a low to high erosion system can be viewed in the context of mathematical percolation theory, in which patches are categorized into two types—runoff and erosion generating patches (bare areas) and runoff and erosion storage areas (grassy areas and woody plant canopy patches); the system crosses a threshold from low to high connectivity among bare patches that corresponds from low to high erosion with a small change in the proportions of the two patch types. It can be difficult to return to a low-connectivity state, and hence the relationship can be viewed as a catastrophe cusp surface.
Soil water heterogeneity and composition by plant functional type (Breshears and Barnes 1999).	Community composition as a function of plant functional type can be related to soil water heterogeneity. The conceptual model builds off the Walter (1971) two-layer model, which assumes the ratio of herbaceous to woody biomass is proportional to the ratio of shallow to deep soil-moisture, and the Schlesinger et al. (1990) model of desertification, which implicitly assumes that multiple ratios of woody to herbaceous vegetation are possible at the site. The model assumes soil water varies horizontally between woody plant canopy and intercanopy patches, as well as vertically between shallow and deeper soil layers, and it distinguishes among three plant functional types: herbaceous plants, shallow-extracting woody plants, and deeper-extracting woody plants. The model unifies the key concepts of the two models above and the concept that increases in woody plants can be difficult to reverse.
Diverging differential rooting depth with woody plant size (Martens et al. 2001)	The difference in rooting depth between a shallow-and deeper-extracting woody plant species increases with age, leading to increasing mortality-related divergence with increasing age.

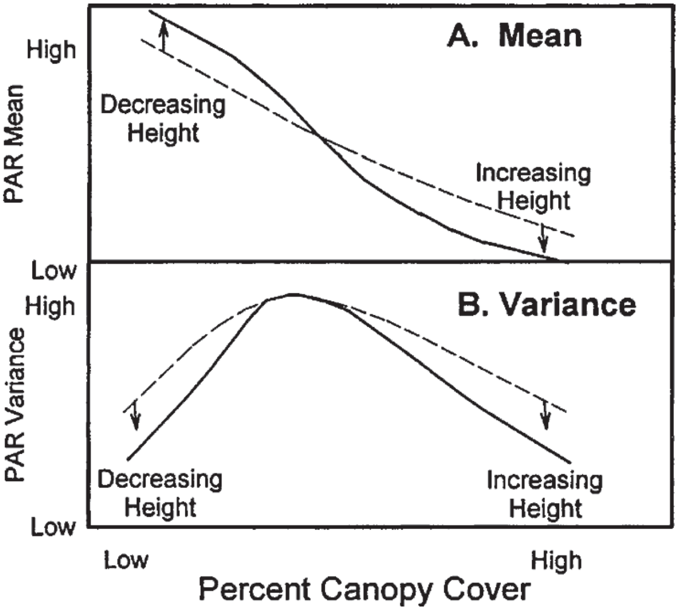

Figure 11 Generalizations of the relationship between transmitted *PAR* (mol m^{-2}) and percent canopy cover: predicted trend for plots with constant woody plant height (*dashed lines*) and variation in trend for grassland–forest continuum in which height increases with increasing canopy cover (*solid lines*). (Reprinted from Martens et al. 2000, with permission from Elsevier)

fraction of the total is intercepted for smaller precipitation events (Loik et al. 2004), as is reflected in more general modeling studies. The effects of precipitation interception, however, are reflected in measurements of snow cover at Mesita del Buey, quantifying the large reduction in snow input beneath canopy patches (Figure 12). The interception of precipitation by canopies impacts subsequent runoff and soil dynamics, as indicated next. Notably, junipers can use intercepted rainfall through foliar absorption, especially when they are water stressed (Breshears et al. in press).

Runoff and Runon

Canopy Versus Intercanopy Heterogeneity for Runoff

Runoff patterns are influenced by a number of factors that can vary at the scale of canopy and intercanopy patches. These factors include both plant and litter cover, soil morphology, and antecedent soil water content. Initial study of runoff at Mesita del Buey focused on intercanopy patches and assumed that canopy patches contributed insignificant amounts of runoff. Based on field measurements of runoff following actual precipitation events, as opposed to rainfall simulation studies, Wilcox (1994) found that runoff from intercanopy patches accounted for 10% to

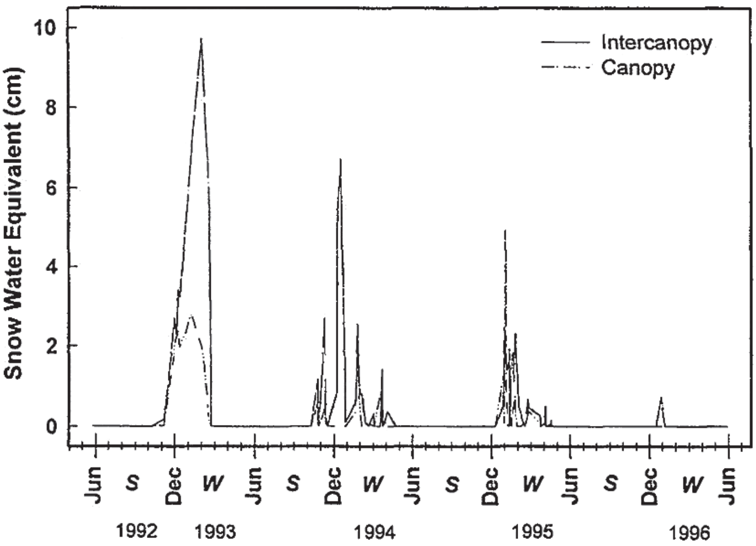

Figure 12 Snow water equivalent for canopy (*dashed line*) and intercanopy (*solid line*) locations at the Mesita del Buey site. (Reprinted from Breshears et al. 1997b, with permission from the Ecological Society of America)

28% of the water budget over a 2-year period; this study included both disturbed and undisturbed plots. Runoff was produced not only in conjunction with intense storms during the summer monsoon season but also in response to snowmelt events and rain-on-snow events (rainfall that occurs while the ground still has snow cover). Most of the erosion was associated with intense thunderstorms. In a follow-up study, Reid et al. (1999) compared runoff in intercanopy and canopy positions and found that runoff and erosion were indeed much greater in intercanopy than canopy patches. However, canopy patches generated runoff in response to longer-lasting frontal storms. These infrequent storms can be a substantial fraction of annual precipitation, and Reid et al. (1999) found that runoff from canopy patches was about 25% to 35% of that in intercanopy patches of different types (discussed next). Spatial differences in runoff can produce amplified differences in erosion, which are reflected in the finding that erosion from canopy patches was 4% to 13% of that in intercanopy patches that had varying amounts of herbaceous cover. The differences in runoff between canopy and intercanopy patches at Mesita del Buey appear to be caused not by differences in soil morphology alone but rather by the effects of woody plant cover and associated litter cover (Wilcox 2003c).

Within-Patch Heterogeneity and Connectivity for Runoff

Runoff varies not only between canopy and intercanopy patches but also within intercanopy patches between bare and herbaceous locations. Reid et al. (1999)

found that runoff was more than 40% greater and erosion was more than 300% greater for bare locations relative to herbaceous locations within intercanopy patches. The responses varied among convective, frontal, and minor storms. Interestingly, many minor storms generated runoff within intercanopy patches, particularly in bare locations.

Generated runoff can either leave the system or be redistributed within the system. In other mixed woody-herbaceous systems, particularly those with low slope and banded patterns of vegetation, runoff generated from intercanopy patches can produce substantial runon to the canopy patches. This process results in a reconcentration of a large pulse of water beneath canopy patches (Ludwig et al. 2005). We would expect plants to obtain a larger fraction of water from large pulses, with a smaller fraction being lost to evaporation (Loik et al. 2004). The redistribution of water from canopy to intercanopy patches has not been measured directly at Mesita del Buey and remains a matter of debate among site researchers. Indirect measures related to runoff such as how runoff varies with increasing scale (discussed in detail next), coupled with the high infiltration capacity of the litter layer of the canopy patches, suggest that some fraction of the runoff generated in intercanopy patches may be redistributed to canopy patches (Wilcox et al. 2003a).

A large fraction of runoff generated within intercanopy patches at Mesita del Buey is redistributed from bare to herbaceous locations within the intercanopy. Reid et al. (1999) used a divided plot design to compare the amount of runoff leaving an intercanopy patch composed of bare and herbaceous locations with the total amount leaving the corresponding herbaceous and bare locations. The amount of runon redistributed to herbaceous locations increases with precipitation amount up to a threshold at which the storage capacity of the intercanopy patches is exceeded (Figure 13). The phenomena of runoff being redistributed to vegetated

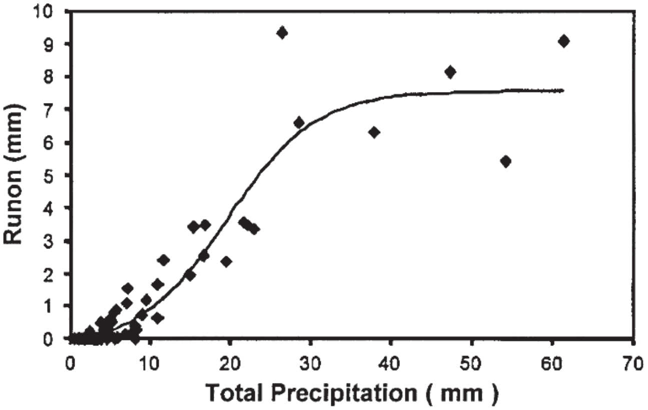

Figure 13 Runon within intercanopy patches from bare to herbaceous locations as a function of total precipitation by event. (Reprinted from Reid et al. 1999, with permission from the Soil Science Society of America)

patches now appears to be a much more widely operating process than previously thought (Ludwig et al. 2005).

Larger-Scale Implications of Patch-Scale Heterogeneity and Connectivity for Runoff

The patterns of runoff and runon for canopy and intercanopy patches have implications for patterns of runoff and ecosystem or hillslope storage. Building on the results of Reid et al. (1999) in quantifying runoff and runon between and within patches, Wilcox et al. (2003a) obtained runoff measurements at two larger scales: large intercanopy plots (3 × 10m) and a whole hillslope (Figure 14). Little runoff and associated erosion leave the largest scale of the hillslope (Figure 15). Hence, most of the runoff is being redistributed within the hillslope. The scale-dependent differences in runoff provide insights into where storage is occurring. The scale dependency differs for small, medium, and large precipitation events. For small events, the rapid decrease in runoff with increasing scale indicates that most of the runon is being stored within intercanopy herbaceous locations. For larger events, the main decrease in runoff occurs at scales greater than that of intercanopy

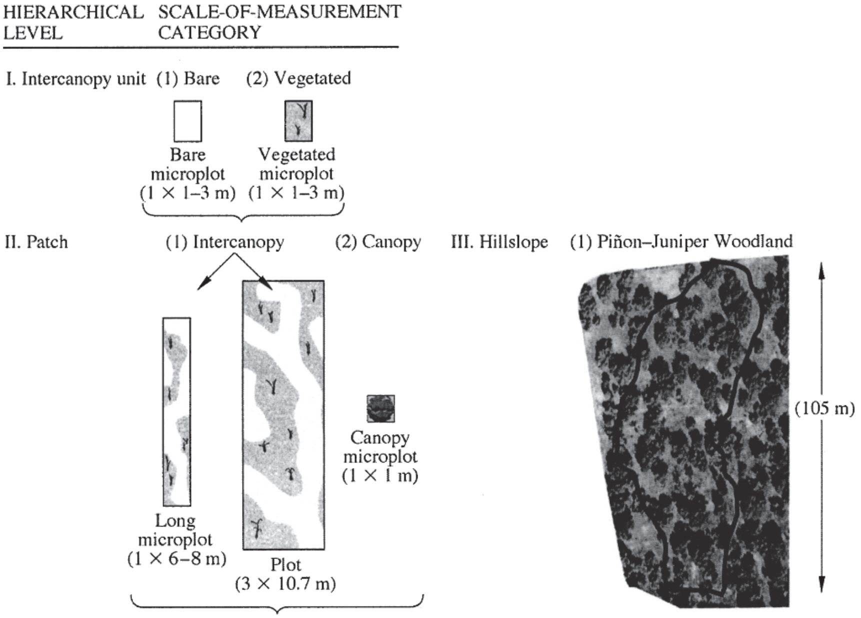

Figure 14 Design of multiscale studies of runoff and erosion at Mesita del Buey. (Reprinted from Wilcox et al. 2003a, with permission from the Ecological Society of America)

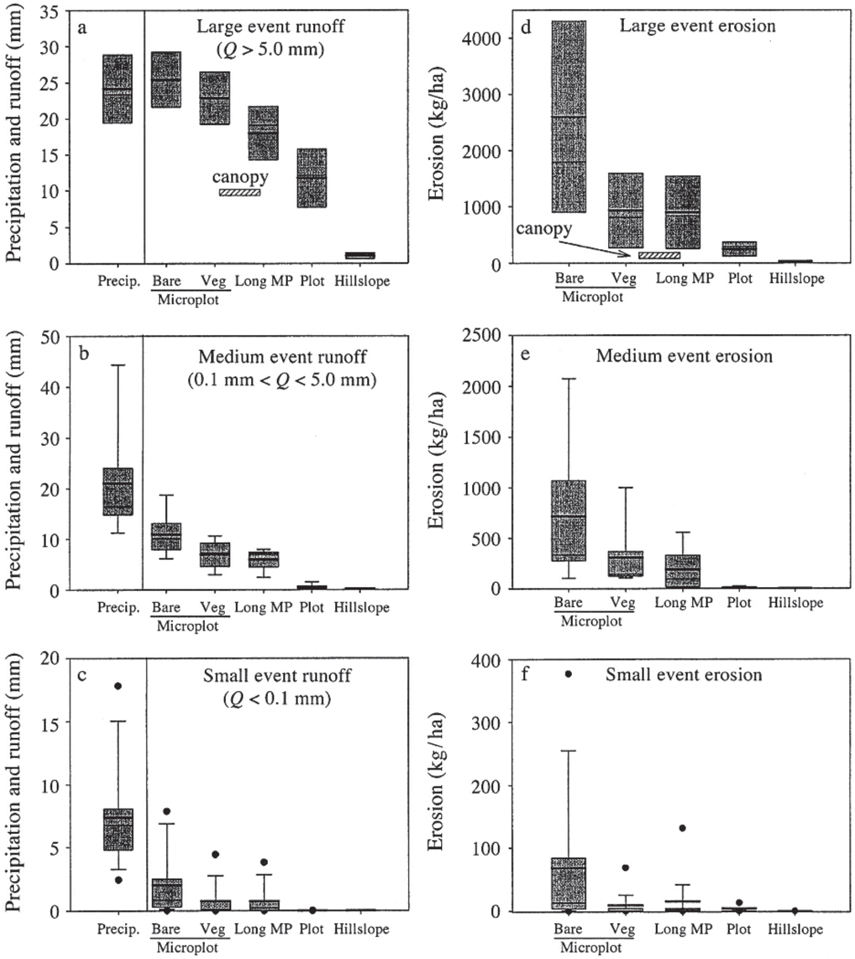

Figure 15 Multiscale observations of runoff at Mesita del Buey, sorted as a function of precipitation event size (Q); MP: microplot. (Reprinted from Wilcox et al. 2003a, with permission from the Ecological Society of America)

patches and may be associated with microtopographic variation that was not explicitly incorporated into the study design.

These results indicate that the connectivity among intercanopy bare locations is a key determinant of how runoff and erosion change as a function of scale. These concepts were integrated with percolation theory to develop a conceptual model about erosion thresholds in semiarid woodlands (see Table 3). The degree of connectivity among bare locations can cross a threshold at which the hillslope rapidly transitions from a low degree of connectivity among bare locations to a high degree of connectivity that results in a larger yield of runoff and associated erosion from the hillslope (Figure 16).

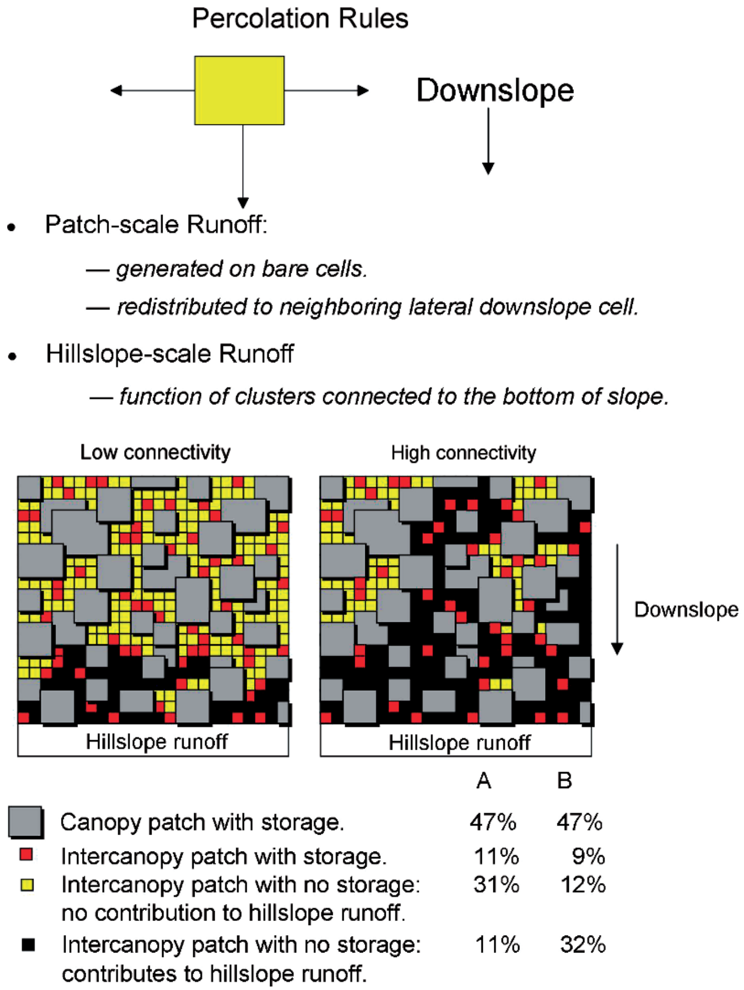

Figure 16 Runoff and erosion threshold conceptual model based on percolation theory relating patch-scale to hillslope-scale runoff using a simple connection rule. A small change in the percent of patches with no storage (A versus B) can trigger a transition from low to high connectivity at the hillslope scale. (Modified from Davenport et al. 1998)

Soil Water and Plant Water Use

Canopy Versus Intercanopy Heterogeneity for Soil Water

Soil water is perhaps the most central component of the water budget and arguably the most direct driver of ecosystem processes in arid and semiarid ecosystems. Soil water variation is affected by several input factors and several output factors. Interception of precipitation, as presented earlier, results in reduced inputs to canopy patches. Also, as already noted, it is currently unclear the extent to which runoff is redistributed to canopy patches. The effects of stemflow have also not been quantified for the Mesita del Buey site, although stemflow has been shown to be important for other juniper species (Skau 1964).

The large effect of woody canopy patches on near-ground solar radiation, as described here, has important implications for evaporation of soil water. Estimated potential evaporation for canopy patches, based on near-ground solar radiation estimated by the direct site factor, can be less than half of that for intercanopy patches (Figure 17). As expected, mean monthly soil temperatures differ between the two patch types for many months throughout the year (Figure 18). When evaluated within diurnal cycles, temperature of intercanopy patches can exceed canopy patches by more than 10°C (Figure 19). During winter months, canopy patches can be warmer then intercanopy patches (Figure 19), likely the result of insulating effects of the canopy litter layer. The temperature differences yield predicted differences in soil water content of as much as 2% volumetric water content within a 24-h cycle and associated changes in soil water potential (Figure 20). When these differences are integrated over monthly intervals, they produce substantial time-integrated values of differences in water potential between the two patch types (Figure 21).

Soil water content varies between canopy and intercanopy patches, with the direction and the magnitude of the difference varying with time (Figure 22). On average, canopy locations are drier than intercanopy locations in terms of soil water content, and this difference becomes amplified in terms of soil water potential (see Figures 8, 22). This result suggests that the interception effect, in which inputs to canopy patches are reduced (see Figure 12), apparently exceeds the evaporation effect, in which intercanopy patches have greater evaporative losses than canopy patches (Breshears et al. 1997b). Additional studies of soil water dynamics indicate

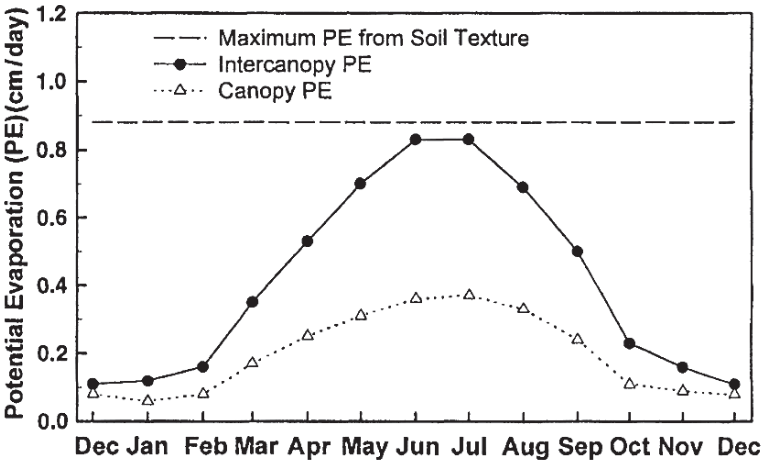

Figure 17 Differences in site potential evaporation (*PE*) for canopy and intercanopy based on differences in the direct site factor (DSF). (Reprinted from Breshears et al. 1997b, with permission from the Ecological Society of America)

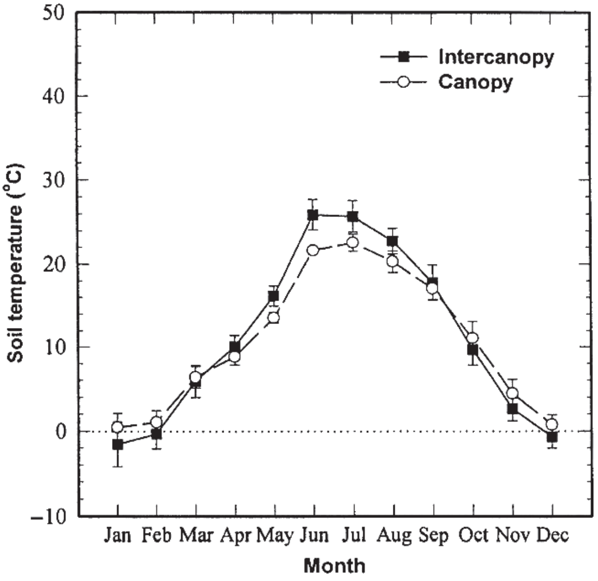

Figure 18 Mean monthly soil temperature at 2 cm below soil surface for intercanopy patches and 2 cm below O horizon for canopy patches. (Reprinted from Breshears et al. 1998, with permission from the University of Chicago Press)

that the canopy versus intercanopy heterogeneity varies with depth, and therefore both horizontal and vertical heterogeneity in soil water content may be important to consider (Williams et al. 2003, Loik et al. 2004).

Within-Patch Heterogeneity and Connectivity for Soil Water

Soil water content also varies significantly within patch type (see Figure 8). Edge locations within both patch types have much more soil water than the central portion of the patch of the corresponding type, likely because of canopy drip (Breshears et al. 1997b). However, differences in soil water content among piñon versus juniper canopy patches or bare versus herbaceous locations within intercanopy patches have not been evaluated to date.

An important mode of connectivity between canopy and intercanopy patches is the use of intercanopy water by the woody plants that comprise the canopy patches. Woody plants can have substantial lateral roots that extend into intercanopy areas, as demonstrated in an experiment in which water was added to intercanopy locations (Breshears et al. 1997a). Both woody species, *Pinus edulis* and *Juniperus monosperma*, were able to effectively extract shallow intercanopy water (at 0–30 cm, most of which was located at 0–15 cm) intercanopy water (Figure 23). Notably, juniper was more effective at extracting shallow intercanopy water than piñon, suggesting a more shallow root distribution for juniper. This result is consistent with measurements of the temporal dynamics of plant water potential of both species, which show juniper is

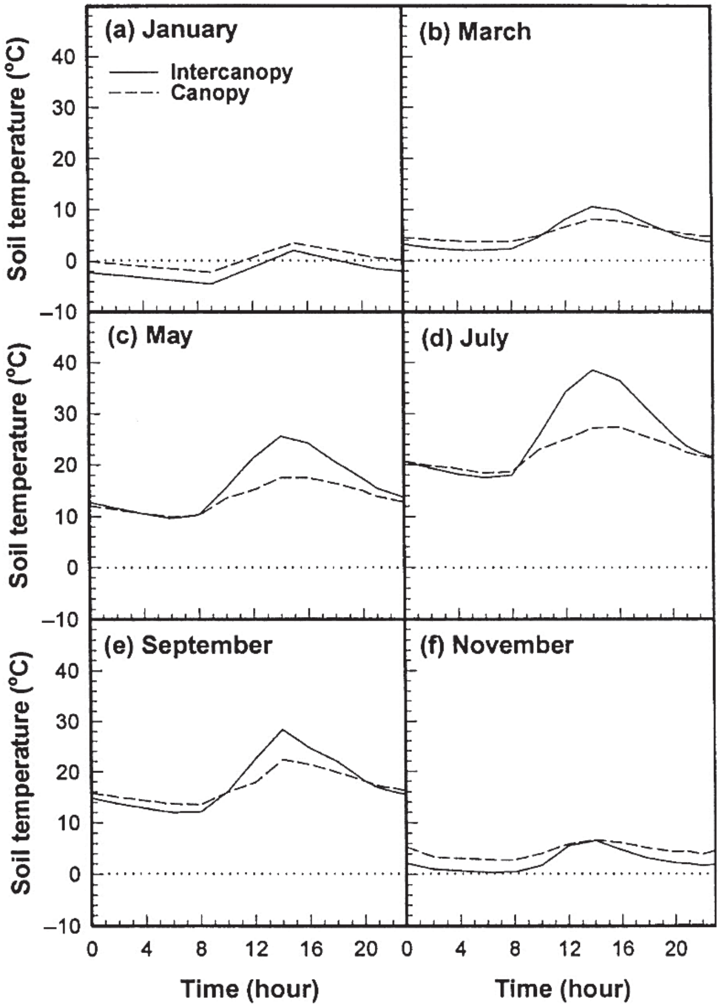

Figure 19 Diurnal soil temperature at 2 cm below soil surface for intercanopy patches and 2 cm below O horizon for canopy patches. (Reprinted from Breshears et al. 1998, with permission from the University of Chicago Press)

more temporally variable and responsive to precipitation events (Barnes and Cunningham 1987; Breshears 1993). Conversely, the most common herbaceous species at Mesita del Buey is *Bouteloua gracilis*, blue grama, which is sparse beneath woody plant canopies and does not have extensive lateral roots (Coffin and Lauenroth 1990).

There are several important physiological differences between the two common woody species that also affect patterns of plant water use. Piñons have a higher rate of transpiration under wet conditions but cease to transpire much sooner as soils dry than junipers do (Barnes 1986; Lajtha and Barnes 1991; Lajtha and Getz 1993). Instantaneous water use efficiency is greater for juniper than for piñon, but piñon has a greater seasonally integrated plant water use efficiency.

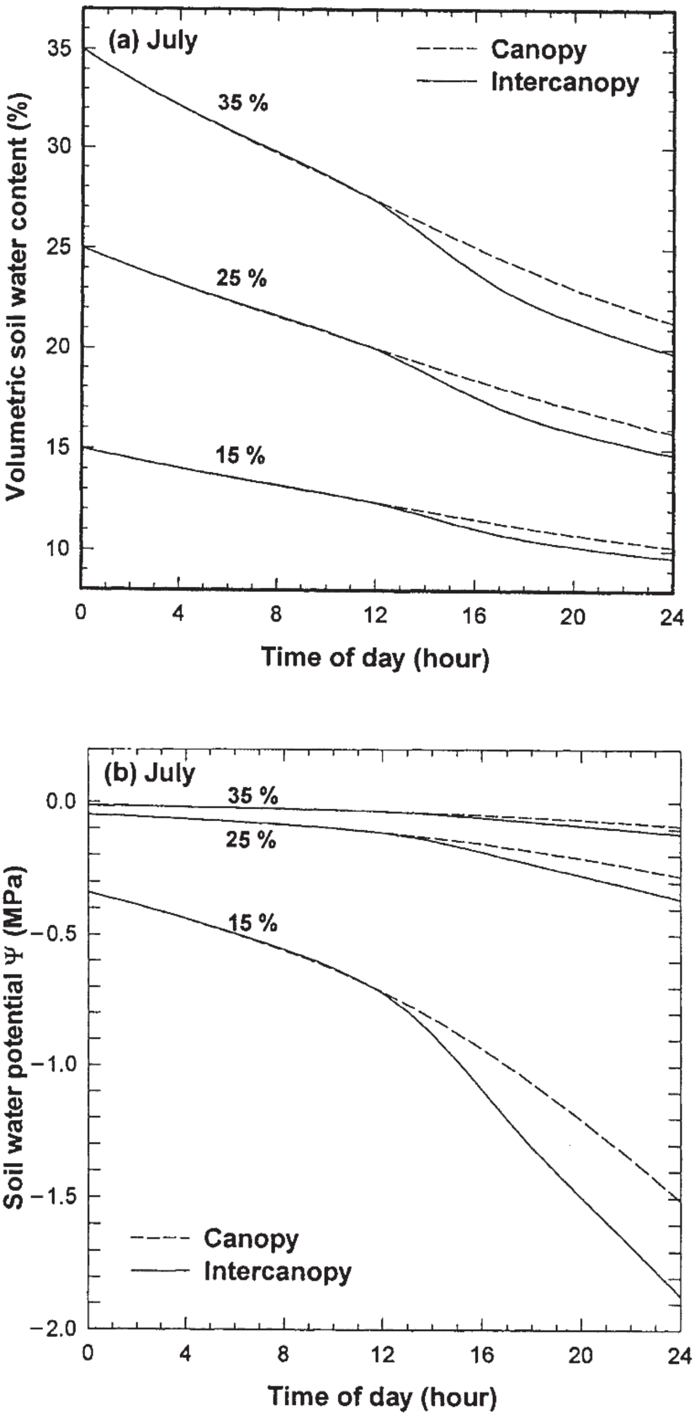

Figure 20 Diurnal soil drying rates by evaporation in terms of soil water content and soil water potential. (Reprinted from Breshears et al. 1998, with permission from the University of Chicago Press)

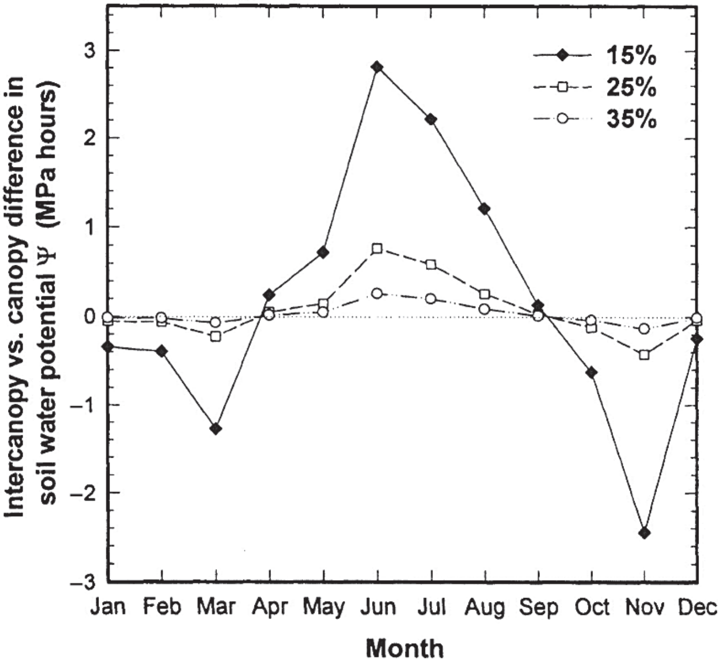

Figure 21 Summary of differences integrated over 1 day in soil water potential for intercanopy and canopy patches for each month of the year for various initial water content values. Positive values are associated with intercanopy evaporation rates that exceed canopy evaporation rates, whereas negative values equal the converse. (Reprinted from Breshears et al. 1998, with permission from the University of Chicago Press)

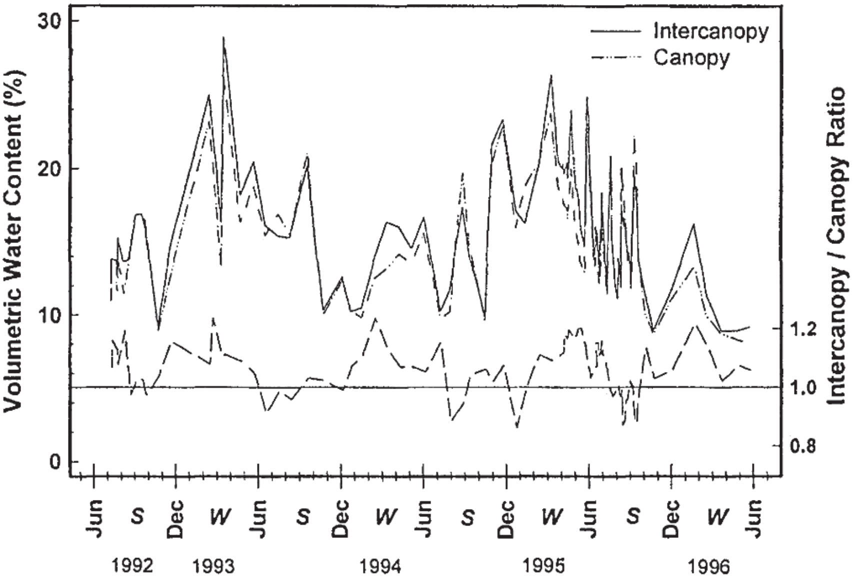

Figure 22 Variation in soil water content (0–15 cm) between canopy and intercanopy patches at the Mesita del Buey site. (Reprinted from Breshears et al. 1997b, with permission from the Ecological Society of America)

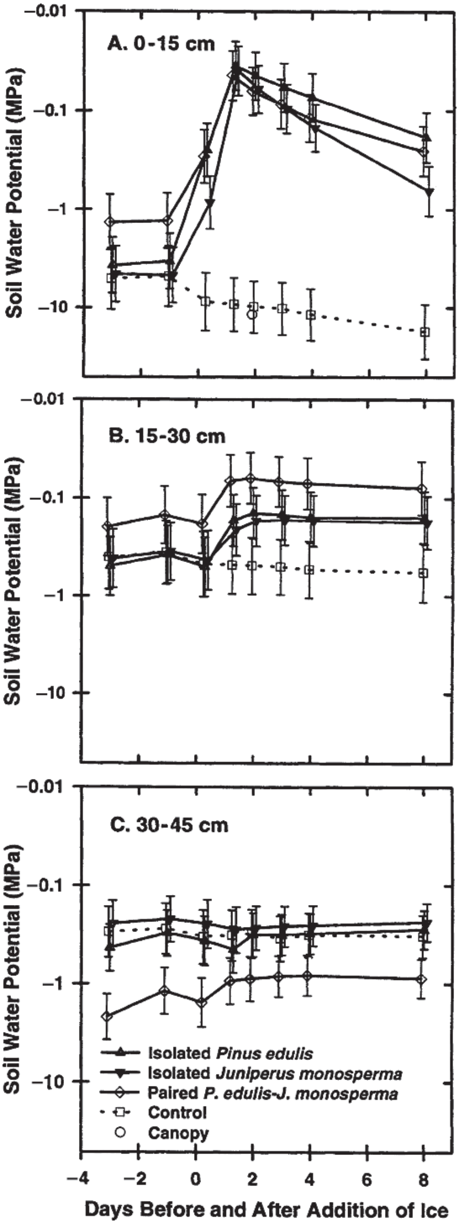

Figure 23 Soil water response on experimental plots following water addition to isolated *Pinus edulis* trees, isolated *Juniperus monosperma* trees, and paired *Pinus edulis–Juniperus monosperma* trees. (Reprinted from Breshears et al. 1997a, with permission from Blackwell Publishing)

Larger-Scale Implications of Patch-Scale Heterogeneity and Connectivity of Soil Water

Predominant theories about plant community composition in semiarid environments focus on relating soil water heterogeneity to the relative proportions of herbaceous and woody plant biomass at a site (Breshears and Barnes 1999). These theories focus on one or the other of two fundamentally different concepts: (1) differences between two or more relatively undisturbed sites are a function of differences in climate and/or soil profile; or (2) the same site can change over time as a consequence of disturbance. The first conceptual model, proposed by Walter (1971), focuses on vertical heterogeneity in soil water content. In this model, two soil layers are differentiated on the basis of differences in root distributions of woody and herbaceous plants. Herbaceous plants are assumed to be much more efficient at utilizing shallow soil moisture, while woody plants are assumed to have sole access to the deeper layer. The ratio of herbaceous to woody biomass is assumed to be a function of the ratio of soil water content in the upper to lower soil layers. For a given soil profile and climate, only one ratio of woody to herbaceous biomass occurs. The second conceptual model, proposed by Schlesinger et al. (1990) for desertification, focuses on horizontal heterogeneity in soil water content between canopy and intercanopy patches that results from disturbance. The model assumes that land use disturbances cause reductions in herbaceous vegetation. In conjunction with the reduction in herbaceous vegetation, intercanopy soils become compacted, both these phenomena lead to an increase in runoff from intercanopy areas, and woody plants effectively use the extra water that runs off into canopy areas.

The results of the Mesita del Buey research on soil water heterogeneity and plant water use were integrated with existing theory to develop a unified perspective of relationships along the grassland–forest continuum (see Table 3). Two of the major findings from the research at Mesita del Buey are (1) that soil water content varies horizontally between canopy and intercanopy patches, as well as vertically with depth, and (2) that woody species can be differentiated with respect to water use into shallow-extracting (e.g., juniper) and deeper-extracting (e.g., piñon) plants. These findings were incorporated into an expanded conceptual model that unifies the two foregoing conceptual models (Breshears and Barnes 1999). The unified model was developed by relaxing two assumptions of Walter's model: (1) soil moisture varies horizontally between canopy and intercanopy patches, not only because of land use disturbance (as assumed by Schlesinger et al. 1990) but also because of the physical nature of the canopy itself; and (2) although woody plants generally obtain soil moisture from deeper depths than herbaceous plants, woody plants are also differentiated on the basis of those that extract a substantial proportion of their moisture from shallower versus deeper soil depths. The unified model recognizes four soil compartments (upper canopy, upper intercanopy, lower canopy, and lower intercanopy) and three plant functional types (herbaceous, shallow-extracting woody, and deeper-extracting woody) (Figure 24). Combinations of the three plant functional types are then

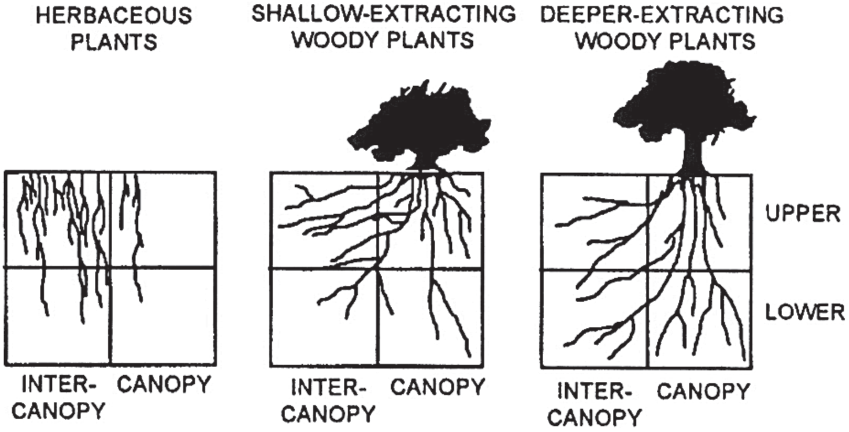

Figure 24 Conceptual model relating soil moisture heterogeneity to differences in plant uptake. Four soil compartments result from distinguishing between upper and lower layers and canopy and intercanopy patches. (Reprinted from Breshears and Barnes 1999, with permission from Springer)

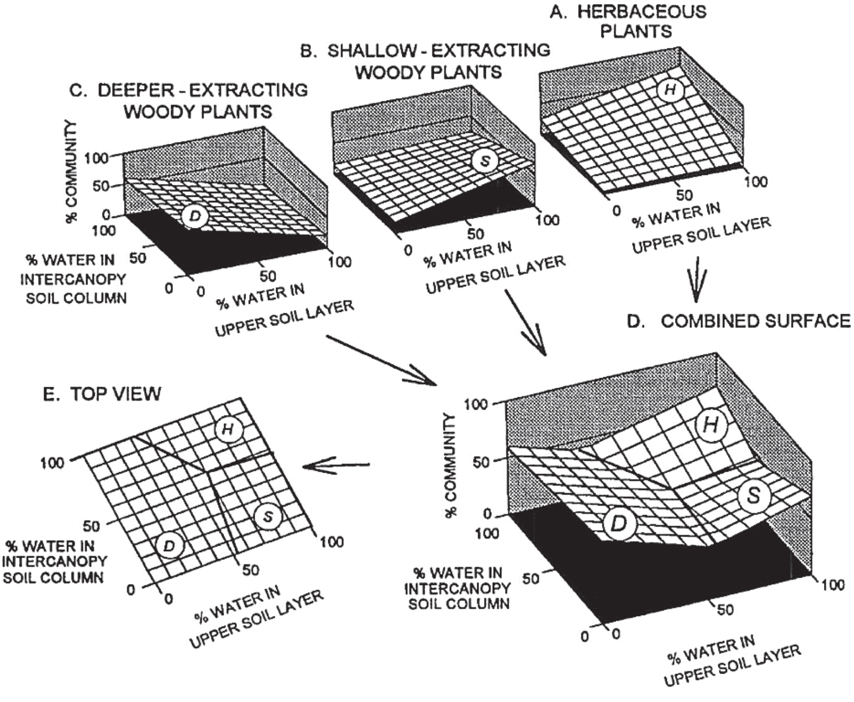

Figure 25 Model predictions for percent of community biomass for three plant types based on location of soil moisture. Predictions are presented for each plant type individually (**A–C**) and for dominant plant type (**D–E**). (Reprinted from Breshears and Barnes 1999, with permission from Springer)

interrelated with soil water heterogeneity (Figure 25). The model integrates three key concepts in semiarid ecology:

- The proportion of woody cover generally increases as soil water in the deeper layer increases (Walter's two-layer hypothesis for the coexistence of herbaceous and woody plants).
- Land use practices that cause a reduction in herbaceous vegetation and compaction of intercanopy soils lead to a long-term increase in the proportion of woody plants (the concept of Schlesinger and colleagues, or, more generally, that at a given site multiple combinations in the proportions of herbaceous and woody plant biomass are possible).
- Changes in the ratios of herbaceous to woody plant biomass exhibit complex behavior (changes can happen quickly and are not directly reversible without intensive management).

This integration is the result of the assumption that there is an interdependence between soil water heterogeneity and plant community composition: soil water heterogeneity constrains plant community composition, which in turn modifies soil water heterogeneity. The model, which is based on patch-scale connectivity and heterogeneity for canopy and intercanopy patches, provides an integrated picture of both dimensions of soil water heterogeneity—horizontal and vertical—and the interdependence between that heterogeneity and plant community composition. The model can be applied to provide insight into plant community dynamics for sites along the grassland–forest continuum and the individual and combined effects of climate and land use on plant communities.

The importance of plant water use and soil water dynamics in determining plant community composition is underscored by patterns of vegetation along gradients and by mortality-related responses. A severe drought during the 1950s caused extensive mortality of dominant woody plants at the lower end of the distribution for each species (Allen 1989; Betancourt et al. 1993; Allen and Breshears 1998). In addition, vegetation patterns along the gradient are consistent with the predictions for a portion of the conceptual model: herbaceous cover remains nearly constant across the gradient, whereas the ratio of shallow- to deeper-extracting woody plants decreases when moving to higher elevations, where plant water potentials indicate more water is available (Breshears 1993).

The stand structure across the elevational gradient spanning Mesita del Buey also suggests drought-induced mortality may be important. A canonical correspondence analysis of both piñon and juniper as a function of size indicates a major gradient associated with elevation (Martens et al. 2001). Along that axis, smaller trees of both species overlap but diverge through intermediate sizes such that large trees are highly separated along the elevation-related axis (Figure 26). Large junipers are associated with lower elevations, whereas large piñons are associated with higher elevations, a pattern that is consistent with expected differences in soil water as a function of depth and species differences in rooting depth (Breshears et al. 1997a), as well as plant physiological differences. The pattern is consistent with density-dependent mortality. These findings led to the

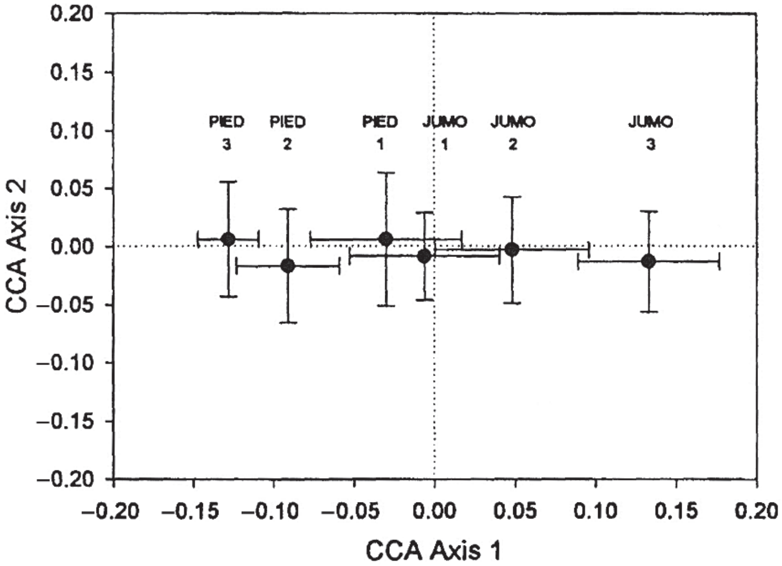

Figure 26 Centroids for three size-classes of *Pinus edulis* (PIED) and *Juniperus monosperma* (JUMO) along cannonical correspondence analysis (*CCA*) axes. Size-classes increase from *1* (smallest/youngest) through *3* (largest/oldest). *CCA axis 1* is associated with elevation. *Error bars* represent two standard errors in each of four directions. (Reprinted from Martens et al. 2001, with permission from Opulus Press)

proposal of a simple conceptual model in which differences between the two woody species in resource acquisition increase with age and size (Figure 27). This conceptual model implies that as woody plants mature, differences among them in resource acquisition play a greater role in determining species dominance along resource gradients (see Table 3). A subsequent drought spanning 2000–2003 that was warmer than the previous drought of the 1950s resulted in >90% mortality of piñons at the Mesita del Buey site and along the gradient (Breshears et al. 2005, Fair and Breshears 2005; Stimson et al. 2005), which was followed by an increase in herbaceous vegetation after the drought (Rich et al. 2008).

General Hypotheses for Gradients

The conceptual models and hypotheses based on the Mesita del Buey research (see Table 3) provide a basis for placing woodland studies within the broader context of the grassland–forest continuum. Building on these findings, a set of more general hypotheses was also posed for the grassland–forest continuum (Figure 28; Breshears 2006). Soil surface energy inputs are expected to decrease with increasing canopy cover, as highlighted by the model simulations by Martens et al. (2000). Conversely, in the water budget, plant uptake and the associated ratio of transpiration

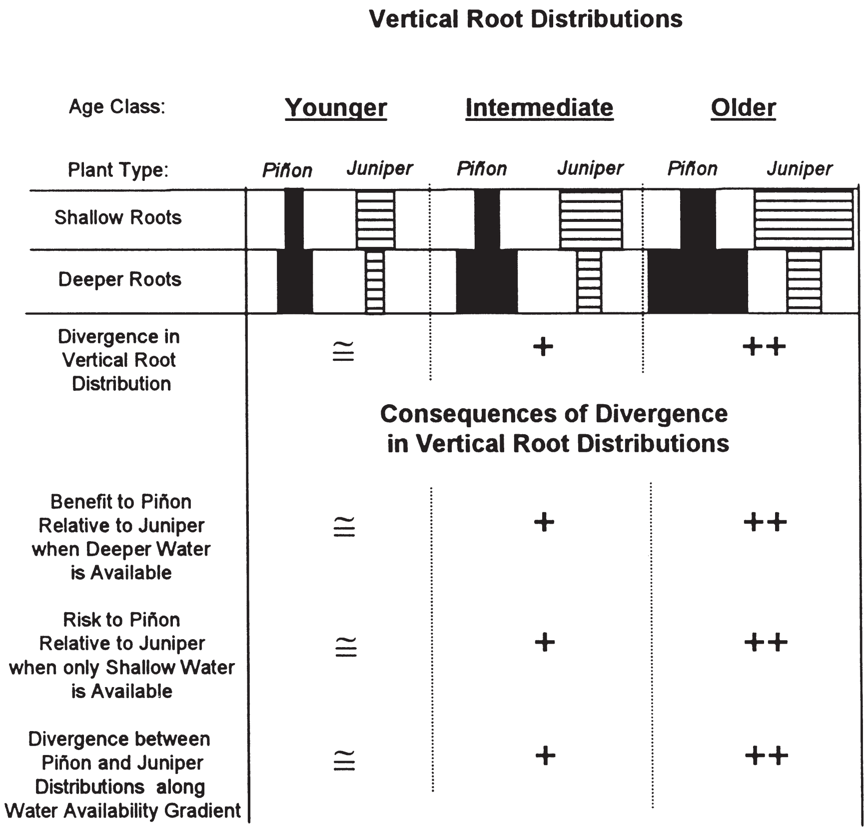

Figure 27 Conceptual model for species- and size- (age)-dependent differences in vertical root distributions between piñon and juniper as a function of increasing age. (Reprinted from Martens et al. 2001, with permission from Opulus Press)

to evapotranspiration are expected to increase (building on Huxman et al. 2005). Carbon in both aboveground and belowground components is also expected to increase with woody plant coverage (Muñoz-Erickson et al. 2004). For all these patterns, variance is expected to be greatest at an intermediate portion of the grassland–forest continuum, and the peak in the variance should occur at a value less than 50% cover as a result of various modes of patch-scale connectivity, particularly woody plant shading of intercanopy patches and uptake of intercanopy resources (see Figure 28).

These hypotheses, which require further testing, contribute to a larger set of perspectives on trends along the grassland–forest continuum (Belsky and Canham 1994). Related hypotheses specific to piñon–juniper woodland gradients have been posed by Muñoz-Erickson et al. (2004) with respect to erosion, percent of soil carbon, soil moisture, herbaceous ground cover, native plant diversity, exotic plant establishment, aboveground net primary productivity, belowground net primary productivity, and water use efficiency of carbon fixation. Related studies in

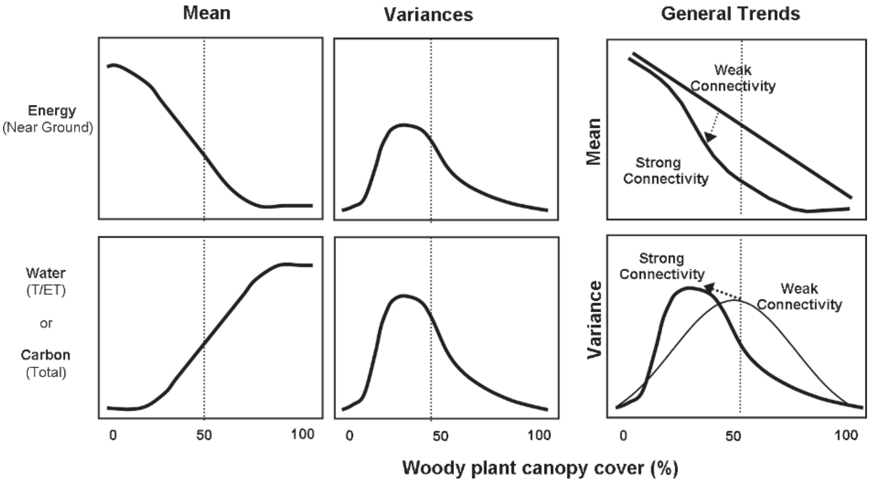

Figure 28 General hypotheses for the grassland–forest continuum for means (left column) and variances (center column) in properties related to energy, water, and carbon. The relationships are dependent on the degree to which canopy patches provide connectivity through their effects on intercanopy patches (right column). (Modified from Breshears 2006)

other systems also indicate that there may be predictable patterns related to energy, water, and biogeochemistry along gradients of woody plants (Reich et al. 2001; Hibbard et al. 2003).

The conceptual models posed here are insufficient to assess many ecosystem patterns and dynamics. Disturbance magnitude and frequency can overwhelm hypothesized relationships. Nutrient limitations may follow patterns similar to that for carbon or may alter predicted relationships. Nonetheless, woody plants have direct physical effects on the environment that creates the structure of the canopy–intercanopy mosaic, and these physical effects have biological implications. Site-specific factors remain crucial to understanding patterns and dynamics at certain sites, but a general framework that provides a means for relating the diverse set of sites along the grassland–forest continuum will more readily facilitate comparisons and contrasts for a larger fraction of terrestrial ecosystems. In conclusion, woodlands dominated by piñon and juniper can be viewed within the broader context of the grassland–forest continuum, in which explicit study of heterogeneity and connectivity among patches yields trends that may be possible to generalize across broad gradients and diverse terrestrial ecosystems.

Summary

Woodlands dominated by species of juniper, and often co-occurring with species of piñon, are regionally extensive and similar to other types of dryland woodlands globally. Research from the Mesita del Buey Woodland site in northern New

Mexico provides examples of interrelationships between structure and function that are widely relevant for woodlands. A key characteristic of these woodlands is the mosaic pattern composed of the canopy patches of woody plants and the intercanopy patterns that separate them. These two patch types differ in a wide variety of properties related to energy, water, and biogeochemistry. Yet, although they are heterogeneous, they are not isolated, but rather are connected in many important ways, including shading, runoff redistribution, and plant water uptake. Understanding these aspects of heterogeneity and connectivity can provide important insights into the structure and functioning of these ecosystems and associated gradients, such as those related to elevation or encroachment, and highlights how rate of change and magnitude of variance are often greatest for intermediate portions of a continuum of woody plant cover ranging from grassland to forest.

Acknowledgments This chapter is a synthesis of my past 15 years of study within the Mesita del Buey Piñon-Juniper Woodland site and is dedicated to my late great uncle, Harold R. Young—a naturalist with a depth of knowledge that has never ceased to amaze me and an enthusiasm for life and the environment which has inspired my research. I also thank my coauthors and collaborators over the past 15 years who contributed to the work embodied in this synthesis, including Craig D. Allen, Fairley J. Barnes, Katherine Campbell, Christopher E. Heil, David W. Davenport, Michael H. Ebinger, Jeanne M. Fair, Susan R. Johnson, Scott N. Martens, Lee MacDonald, Nathan G. McDowell, Clifton W. Meyer, Orrin B. Myers, Kevin D. Reid, David K. Reiley, Paul M. Rich, Hugh G. Stimson, H. J. Turrin, Susan L. Ustin, Bradford P. Wilcox, Paul M. Zedler, and Chris B. Zou. This work was supported by various funds from Los Alamos National Laboratory and the Department of Energy over the past 15 years, most recently by Los Alamos National Laboratory Directed Research.

References

Allen, C.D. 1989. Changes in the landscape of the Jemez Mountains, New Mexico. Ph.D. dissertation. University of California at Berkeley, Berkeley.

Allen, C.D., and Breshears, D.D. 1998. Drought induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proc. Natl. Acad. Sci. U.S.A. 95:14839–14842.

Anderson, R.C., Fralish, J.S., and Baskin, J.M., eds. 1999. Savannas, barrens, and rock outcrop plant communities of North America. New York: Cambridge University Press.

Barnes, F.J. 1986. Carbon gain and water relations in pinyon-juniper habitat types. Ph.D. dissertation. New Mexico State University, Las Cruces, NM.

Barnes, F.J., and Cunningham, G.L. 1987. Water relations and productivity in pinyon-juniper habitat types. In: Proceedings, pinyon-juniper conference, ed. R.L. Everett, pp 406–411. General technical report INT-215. Ogden, UT: United States Forest Service.

Belsky, A.J., and Canham, C.D. 1994. Forest gaps and isolated savanna trees. BioScience 44:77–84.

Betancourt, J.L., Pierson, E.A., Rylander, K.A., Fairchild-Parks, J.A., and Dean, J.S. 1993. Influence of history and climate on New Mexico pinyon-juniper woodlands, In: Proceedings, managing pinyon-juniper ecosystems for sustainability and social needs, pp 42–62. General technical report RM-236. Fort Collins, CO: United States Forest Service.

Bowen, B.M. 1990. Los Alamos climatology. LA-11735-MS; UC-902. Springfield, VA: National Technical Information Service.

Bowen, B.M. 1996. Rainfall and climate variation over a sloping New Mexico plateau during the North American monsoon. J. Clim. 9:3432–3442.

Breshears, D.D. 1993. Spatial partitioning of water use by herbaceous and woody lifeforms in semiarid woodlands. Ph.D. dissertation. Colorado State University, Fort Collins, CO.

Breshears, D.D. 2006. The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? Front. Ecol. Environ. 4:96–104.

Breshears, D.D., and Barnes, F.J. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landsc. Ecol. 14:465–478.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., and Meyer, C.W. 2005. Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad. Sci. U.S.A.* 102:15144–15148.

Breshears, D.D., McDowell, N.G., Goddard, K.L., Dayem, K.E., Martens, S.N., Meyer, C.W. and Brown, K.M. 2008. Foliar absorption of intercepted rainfall improves plant water status and enables drought recovery. *Ecology*: in press.

Breshears, D.D., Myers, O.B., Johnson, S.R., Meyer, C.W., and Martens, S.N. 1997a. Differential use of heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*. J. Ecol. 85:289–299.

Breshears, D.D., Rich, P.M., Barnes, F.J., and Campbell, K. 1997b. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecol. Appl. 7:1201–1215.

Breshears, D.D., Nyhan, J.W., Heil, C.E., and Wilcox, B.P. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. Int. J. Plant Sci. 159:1010–1017.

Coffin, D.P., and Lauenroth, W.K. 1990. A gap dynamics simulation model of succession in a semiarid grassland. Ecol. Model. 49:229–266.

Collings, M.R. 1966. Throughfall for summer thunderstorms in a juniper and pinyon woodland, Cibecue Ridge, Arizona. Geological Survey professional paper 485-B. Washington, DC: United States Government Printing Office.

Davenport, D.W., Wilcox, B.P., and Breshears, D.D. 1996. Soil morphology of canopy and intercanopy sites in a piñon-juniper woodland. Soil Sci. Soc. Am. J. 60:1881–1887.

Davenport, D.W., Breshears, D.D., Wilcox, B.P., and Allen, C.D. 1998. Viewpoint: Sustainability of piñon-juniper ecosystems—a unifying perspective of soil erosion thresholds. J. Range Manag. 51:229–238.

Fair, J.M., and Breshears, D.D. 2005. Drought stress and fluctuating asymmetry in *Quercus undulata* leaves: confounding effects of absolute and relative amounts of stress? *J. Arid Environ*. 62:235–249.

Hibbard, K.A., Schimel, D.S., Archer, S., Ojima, D.S., and Parton, W. 2003. Grassland to woodland transitions: integrating changes in landscape structure and biogeochemistry. Ecol. Appl. 13:911–926.

House, J.I., Archer, S., Breshears, D.D., Scholes, R.J., and NCEAS Tree-Grass Interactions Participants. 2003. Conundrums in mixed woody-herbaceous systems. J. Biogeogr. 30:1763–1777.

Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Snyder, K.A., Small, E.E., Hultine, K., Pockman, W.T., and Jackson, R.B. 2005. Ecohydrological implications of woody plant encroachment. Ecology 86:308–319.

Lajtha, K., and Barnes, F.J. 1991. Carbon gain and water use in pinyon pine-juniper woodlands of northern New Mexico: field versus phytotron chamber measurements. Tree Physiol. 9:59–67.

Lajtha, K., and Getz, J. 1993. Photosynthesis and water-use efficiency in pinyon-juniper communities along an elevation gradient in northern New Mexico. Oecologia (Berl) 94:95–101.

Loik, M.E., Breshears, D.D., Lauenroth, W.K., and Belnap, J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology in western USA. Oecologia (Berl) 141:269–281.

Ludwig, J.A., Wilcox, B.P., Breshears, D.D., Tongway, D.J., and Imeson, A.C. 2005. Vegetation patches and runoff-erosion as interacting eco-hydrological processes in semiarid landscapes. Ecology 86:288–297.

Martens, S.N., Breshears, D.D., Meyer, C.W., and Barnes, F.J. 1997. Scales of above- and below-ground competition differ in a semiarid woodland as detected from spatial pattern. J. Veg. Sci. 8:655–664.

Martens, S.N., Breshears, D.D., and Meyer, C.W. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. Ecol. Model. 126:79–93.

Martens, S.N., Breshears, D.D., and Barnes, F.J. 2001. Development of species dominance along an elevational gradient: population dynamics of *Pinus edulis* and *Juniperus monosperma*. Int. J. Plant Sci. 162:777–783.

McPherson, G.R. 1997. Ecology and management of North American Savannas. Tucson: University of Arizona Press.

Muñoz-Erickson, T.A., Loeser, M.R., and Aguilar-González, B.J. 2004. Identifying indicators of ecosystem health for semiarid ecosystems: a conceptual approach. In: The Colorado Plateau: cultural, biological, and physical research, eds. C. van Riper, III and K.L. Cole, pp 139–152. Tucson: University of Arizona Press.

Nyhan, J.W., Hacker, L.W., Calhoun, T.E., and Young, D.L. 1978. Soil survey of Los Alamos County, New Mexico. LA-6779-MS; UC-11. Springfield, VA: National Technical Information Service.

Padien, D.J., and Lajtha, K. 1992. Plant spatial pattern and nutrient distribution in pinyon-juniper woodlands along an elevational gradient in northern New Mexico. Int. J. Plant Sci. 153:425–433.

Reich, P.B., Peterson, D.A., Wrage, K., and Wedin, D. 2001. Fire and vegetation effects on productivity and nutrient cycling across a forest-grassland continuum. Ecology 82:1703–1719.

Reid, K.D., Wilcox, B.P., Breshears, D.D., and MacDonald, L. 1999. Runoff and erosion in a piñon-juniper woodland: influence of vegetation patches. Soil Sci. Soc. Am. J. 63:1869–1879.

Reiley, D.K. 2003. Land use history and effects of soil carbon storage patterns in a pinyon-juniper woodland in northern New Mexico. M.S. thesis. University of Wisconsin at Madison, Madison.

Rich, P.M., Breshears, D.D. and White, A.B. 2008. Phenology of mixed woody-herbaceous ecosystems following extreme events: net changes from differential responses. *Ecology: in press*.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., and Whitford, W.G. 1990. Biological feedbacks in global desertification. Science 247:1043–1048.

Skau, C.M. 1964. Interception, throughfall, and stemflow in Utah and alligator juniper cover types in northern Arizona. For. Sci. 10:283–287.

Stimson, H.C., Breshears, D.D., Ustin, S.L., and Kefauver, S.C. 2005. Spectral sensing of foliar water conditions in two co-occurring conifer species: *Pinus edulis and Juniperus monosperma. Remote Sens. Environ.* 96:108-118.

Walter, H. 1971. Ecology of tropical and subtropical vegetation. Edinburgh: Oliver and Boyd.

Wilcox, B.P. 1994. Runoff and erosion in intercanopy zones of pinyon-juniper woodlands. J. Range Manag. 47:285–295.

Wilcox, B.P., Breshears, D.D., and Allen, C.D. 2003a. Resource conservation in a semiarid woodland: effects of scale and disturbance. Ecol. Monogr. 73:223–239.

Wilcox, B.P., Breshears, D.D., and Seyfried, M.S. 2003b. Water balance on rangelands. In: Encyclopedia of water science, pp 791–794. New York: Dekker.

Wilcox, B.P., Breshears, D.D., and Turrin, H.J. 2003c. Hydraulic conductivity in a piñon-juniper woodland: influence of vegetation. Soil Sci. Soc. Am. J. 67:1243–1249.

Williams, D.G., and Ehleringer, J.H. 2000. Intra- and interspecific variation for summer precipitation. Ecol. Monogr. 70:517–537.

5
Comparisons of the Understory Vegetation of *Juniperus* Woodlands

E.R. Wayne and O.W. Van Auken

Introduction

Fifty to 70 *Juniperus* species occur in the subtropical and temperate regions of the Northern Hemisphere (Johnsen and Alexander 1974). Most *Juniperus* woodlands are adjacent to various grassland communities and, in addition, are usually closely associated with small grasslands that are embedded in the woodland matrix (Baskin and Baskin 1978; Terletzky and Van Auken 1996). These glade-like areas lack an overstory and are referred to as intercanopy patches (Baskin and Baskin 1978; Breshears et al. 1997a,b; Van Auken 2000a; Ware 2002).

In central Texas, *J. ashei* woodlands occur mostly on the 10 million hectares (ha) of the Edwards Plateau (Little 1971; Correll and Johnston 1979; Diamond 1997). *Juniperus ashei* is a fire-sensitive (Foster 1917; Johnsen and Alexander 1974; Fuhlendorf et al. 1996), drought-tolerant (Fonteyn et al. 1985; Wayne and Van Auken 2002), evergreen, aromatic shrub reaching heights to 9 m (Correll and Johnston 1979). Soils in this area are thin, limestone-derived soils over shallow, heavily fractured limestone bedrock (Taylor et al. 1962). On the southern Edwards Plateau, *J. ashei* co-occurs with *Quercus virginiana* (=*Q. fusiformis*) (Hatch et al. 1990) and is a dominant species in these woodlands (Van Auken et al. 1979, 1980, 1981; Amos and Gehlbach 1988; Diamond et al. 1995; Smeins and Fuhlendorf 1997). Canopy cover is estimated at 40% to 90% (Van Auken et al. 1981; Smeins and Merrill 1988) and density is estimated at about 1500 plants/ha (Van Auken et al. 1979, 1981). However, both density and cover change with rainfall.

Distribution of *J. ashei*, similar to that of other *Juniperus* species (Johnsen 1962; Schott and Pieper 1987; Padien and Lajtha 1992; Baskin and Baskin 2000), is found across a variety of gradients (Diamond et al. 1995; Diamond 1997). *Juniperus ashei* occurs on xeric slopes with shallow soils as well as other habitats on deeper soils of flat topography. During the past 100 to 150 years, *J. ashei* has encroached into many associated grasslands (Bray 1904; Foster 1917; Diamond 1997; Scholes and Archer 1997; Smeins and Fuhlendorf

O.W. Van Auken (ed.), *Western North American Juniperus Communities: A Dynamic Vegetation Type.*

1997). Encroachment appears to be initiated by disturbances such as continuous heavy grazing by domestic herbivores, which causes a reduction in fine, fluffy fuel and decreased fire frequency (Ellison 1960; Johnsen 1962; McPherson et al. 1988; Miller and Wigand 1994; Diamond et al. 1995; Fuhlendorf et al. 1996; Van Auken 2000b; Jessup et al. 2003). It is generally believed that grassland cover has been reduced by *Juniperus* encroachment in many regions of North America (Johnsen 1962; Coppedge et al. 2001; Briggs et al. 2002). In addition, in many of these woodlands, the herbaceous layer of vegetation below the canopy has also been virtually eliminated (Schott and Pieper 1985; Briggs et al. 2002). Suspected causes for the reduction or elimination in the herbaceous layer are decreased light levels, change is soil moisture, and deeper litter, which interferes with seedling emergence (Johnsen 1962; Sydes and Grime 1981; Schott and Pieper 1985; Pieper 1990; Bates et al. 1998; Yager and Smeins 1999; Briggs et al. 2002).

Spatial and temporal gradients of surface light, soil temperature, and soil moisture have been demonstrated in *J. ashei* woodlands (Wayne and Van Auken 2002, 2004) and may be responsible for patchy *J. ashei* seedling distribution and growth. *Juniperus ashei* seedling emergence and survival is highest below the *Juniperus* canopy, intermediate at the canopy edge, and lowest in the intercanopy patches or gaps (Jackson and Van Auken 1997; Van Auken et al. 2004). Growth rates of *J. ashei* seedlings, however, are greater at the canopy edge (Jackson and Van Auken 1997; Van Auken et al. 2004). In addition, most germination occurs in early winter and spring, whereas most mortality occurs in late spring and summer. Suspected causes for these differences are available light levels, soil moisture, soil temperature, and surface litter (Wayne and Van Auken 2002; McKinley and Van Auken 2004; Wayne and Van Auken 2004; McKinley and Van Auken 2005). Surface light and surface soil temperature are highest in the intercanopy, intermediate at the canopy edge, and reduced below the canopy; soil moisture follows a reverse trend (Wayne and Van Auken 2002, 2004). During summer, surface light and soil temperatures are maximal and soil moisture is minimal. During winter, surface light and soil temperatures are minimal and soil moisture is maximal (Wayne and Van Auken 2004).

On the southern half of the Edwards Plateau, *J. ashei* woodlands have been studied fairly well. However, the herbaceous vegetation below the *J. ashei* canopy and community demography is less well understood (Van Auken et al. 1979, 1980, 1981, 2000a; Terletzky and Van Auken 1996; Smeins and Fuhlendorf 1997; Barnes et al. 2000). Most of these studies have focused on woody plants and possible encroachment with few observations of the herbaceous understory. However, there are a few studies of the herbaceous vegetation found in *J. ashei* communities, but these studies did not focus on the canopy understory (Lynch 1971; Fowler 1986; Fowler and Dunlap 1986).

In the intercanopy patches of *J. ashei* woodlands on the southern Edwards Plateau, 26 annual species with a total cover of about 46% were reported along with 23 perennials with a cover of about 18% (Terletzky and Van Auken 1996; Van Auken 2000a). Woody plant cover was less than 3% in the intercanopy patch. Below the understory of the woodland canopy, grass-like plant cover was estimated at about 3% (Terletzky and Van Auken 1996). On the eastern Edwards Plateau, Fowler and Dunlap (1986) identified 27 grass species, 14 forbs, and 7 woody and succulent species in open grasslands associated with *Juniperus* woodlands. Grass cover was estimated at about 8% to 21% (Miller et al. 1995), whereas cover of a given species could be quite high, and there was considerable variation (Fowler and Dunlap 1986). Barnes et al. (2000) reported high canopy and intercanopy species richness for woody and herbaceous plants. In the intercanopy patches or grassland, they found 75 forbs and 45 grass species with a total cover of 65%. The remaining ground cover was bare soil, rocks, and a few woody seedlings, consistent with other woodlands on the Edwards Plateau (Fowler and Dunlap 1986; Terletzky and Van Auken 1996; Van Auken 2000a).

Most reports indicate understory herbaceous cover in these central Texas *Juniperus* woodlands is low or absent (Terletzky and Van Auken 1996; Barnes et al. 2000). However, this may be an oversight resulting from the methodology used or time of sampling (Tremblay and Larocque 2001). In the study by Terletzky and Van Auken (1996), five paired transects or replicates were sampled. The sample size used could increase the likelihood that the true herbaceous cover is underestimated (Barbour et al. 1987). Fowler and Dunlap (1986) indicated a herbaceous presence in the understory, although they gave no details. An additional complication in sampling occurs in communities where distributions of the target plant species may have a patchy distribution and routine random sampling may underreport the true cover of the species in question (Vellend et al. 2000).

All the studies of herbaceous cover in *J. ashei* woodlands report the presence of sedge (Cyperaceae). This sedge, usually *Carex planostachys* (cedar sedge; nomenclature follows Correll and Johnson 1979), was reported at low cover values: <1% (Terletzky and Van Auken 1996), <5% (Fowler and Dunlap 1986), and <3% (*Carex* spp.; Barnes et al. 2000). However, this central Texas sedge may be a dominate understory herbaceous species in some of these *J. ashei* woodlands (Figure 1; personal observation). Cursory studies report populations of *C. planostachys* over dry limestone-derived soils on the Edwards Plateau of central Texas, in the mountains of the Trans-Pecos to the west, on cuestas of the Rio Grande Plains, areas of north Texas in Tarrant and Dallas counties, and in Arkansas (Correll and Johnston 1979; Hatch et al. 1990). Isolated populations of *C. planostachys* have also been reported in Arizona and northern Guatemala (Herman 1970, 1974). Some of these reports suggest high cover or abundance.

Carex L. includes 2000 herbaceous perennial species found in a diverse range of habitats from the tropics to the high artic (Ball 1990; Bernard 1990; Ball et al. 2001). The largest populations of *Carex* are toward the high latitudes where cooler climates prevail (Ball 1990), but they also occur in low latitudes at higher elevations (Herman 1970; Harper 1977). In North America, *Carex* L. is estimated to include 500 to 600 species (Herman 1970; Bernard 1990). *Carex* has received moderate attention as a widespread species dominating wetlands (see Bernard 1990), but has otherwise received little attention (Major 1971; Bernard 1990). In addition, sedges,

Figure 1 *Carex planostachys* plants in the *Juniperus ashei* woodland understory on the south central Texas Edwards Plateau. The plants are located about 10 m inside the woodland understory. The quadrat outlined by string was established in 1997 to measure the effect of watering on *C. planostachys* plants

including *Carex*, may be the most ecologically important vascular plant in wetlands and possibly grasslands (Reznicek 1990). Many individual *Carex* spp. can occur across a range of diverse habitats.

It is hypothesized that variation in surface light and soil water are primary causes of the suspected spatial trends in *C. planostachys* cover and biomass in some *J. ashei* woodlands. However, surface litter and soil temperature may also play an important role. The objective of this study was to examine the herbaceous vegetation of the understory of *J. ashei* woodlands on the southern Edwards Plateau. The focus of this study was the herbaceous ground cover and changes in biotic factors from below the canopy into the intercanopy patch, as well as changes in abiotic factors along the same gradient. A final goal was to compare the understory herbaceous vegetation of *J. ashei* woodlands with that of other Northern Hemisphere *Juniperus* woodlands.

Methods

To understand the distribution of *C. planostachys* in central Texas *J. ashei* woodlands, a study was conducted to measure surface light, soil temperature, and soil moisture along a canopy-to-intercanopy gradient. An additional study was conducted along the same gradient to estimate herbaceous species cover and biomass. Both these studies were conducted in Eisenhower Park, a 128.3-ha city park located in San Antonio, Texas, in northern Bexar County (98°34'26" W, 29°37'19" N). The park is on the southern edge of the Edwards Plateau and near the Balcones fault zone, about 5 km east of the University of Texas at San Antonio campus. No domestic livestock have been reported in the area for more then 50 years, and the park is currently maintained as a natural area with little disturbance to off-trail locations. Soil is a clayey-skeletal, smectitic, thermic lithic Calciustoll in the Tarrant association, rolling, with a slope of 4.5° to 13.5° (NRCS 2004). Three horizons occur that consist of shallow, clayey, weakly calcareous soil, developed over hard limestone with scattered stones and gravel. The surface horizon ranges from 0 to 25 cm in thickness. The subsurface is about 20 cm thick, heavily fractured limestone over limestone bedrock (Taylor et al. 1962). Regional climate is classified as subtropical–subhumid with a mean annual temperature of 20°C (Arbingast et al. 1976). Monthly mean temperature ranges from 9.6°C in January to 29.4°C in July (NOAA 2004). Annual precipitation in the study area is 78.7 cm, with two peaks occurring in May and September (monthly means of 10.7 cm and 8.7 cm, respectively). During the 1997 study, precipitation was above normal at 85.6 cm, with a low of 0.0 cm in July and a high of 18.5 cm in June (NOAA 2004). Precipitation in February 2004 was 4.1 cm.

The area vegetation is *Juniperus–Quercus* woodland, representative of woodlands found throughout this region (Van Auken et al. 1979, 1980, 1981). The dominant woody species are *J. ashei* and *Q. virginiana* (live oak). Associated with these woodlands are sparsely vegetated intercanopy patches or small open grasslands (Terletzky and Van Auken 1996; Van Auken 2000a). The major herbaceous species below the canopy is *Carex planostachys* (cedar sedge), and in the open grassland *Aristida longiseta* (red three-awn), *Bouteloua curtipendula* (side-oats grama), various other C_4 grasses, and a variety of herbaceous annuals are common (Fowler and Dunlap 1986; Van Auken 2000a).

A site consisting of a mostly closed-canopy *J. ashei* woodland and associated intercanopy patches (Figure 2) was used in both projects. The spatial and temporal trends for surface light, soil temperature, and soil moisture have been measured; however, only spatial trends for surface light levels, soil temperature, and soil water are presented here. The site was about 2000 m^2 and located about 200 m from a trail, in an area that appeared to be relatively undisturbed and rarely accessed by humans.

Surface light levels, surface soil temperature, and surface soil moisture were measured temporally along a suspected woodland canopy to intercanopy patch gradient. Six parallel, northeasterly transects (41° azimuth), 15 m in length, were

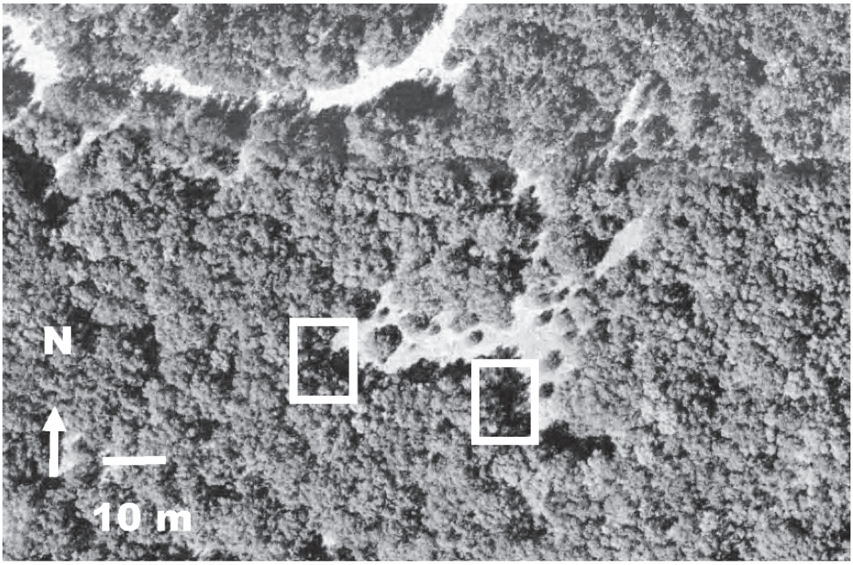

Figure 2 Aerial view of the research site in Eisenhower Park, San Antonio Texas. The intercanopy patch is located in the center of the image. Transects established are located within the outlined rectangles. Map units are indicated in the lower left. Map provided by City of San Antonio's Interactive Remote Sensing http://imageserver.sanantonio.gov/?res=1280&ver=true

established perpendicular to the canopy edge and extended 10 m into the woodland canopy and 5 m into the intercanopy patch, with respect to the canopy edge (drip line). One position was established at the end of each transect, the canopy patch and the intercanopy patch. Three additional positions were established along each transect: the canopy edge at 0 m, the mid-intercanopy at 2.5 m outside the canopy edge, and the midcanopy at 5 m inside the canopy edge.

Surface light (photosynthetically active radiation, PAR; λ = 400–700 nm) was measured at solar noon on cloudless days in July, August, October, and December (n = 4 months, 120 total samples) with a LI-COR LI-190 SA integrating quantum sensor linked to a LI-COR LI-1000 data logger (LI-COR, Lincoln, NE, USA). Instantaneous measurements were averaged over 60 s at 5-s intervals. The quantum sensor was placed level on bare ground at each position, and no attempt was made to move or disrupt herbaceous or woody vegetation near the sensor.

Soil temperature was measured within 2 h after solar noon on dates coinciding with soil moisture measurements. Measurements were made in April, July, August, September, October, and December (n = 6 months, 360 total samples) by inserting a 15-cm, probe-type, analogue thermometer 1 to 2 cm into the upper soil surface (Broadbent 1965; Larcher 1995). Soil temperatures were recorded after allowing 5 min for equilibration.

Surface soil moisture was measured on the same dates as soil temperature and two additional dates in May and December ($n = 8$ months, 480 total samples) using the gravimetric procedure (Pearcy 1989; Jackson et al. 2000). Soil moisture is reported as percent water on a dry mass basis. Before measurements, stones and organic litter were removed from the surface, and then the top 2 cm of soil was collected into plastic bags for transport. Approximately 40 g soil was placed into aluminum planchets and oven dried at 100°C to a constant mass.

Standing crop biomass (Catchpole and Wheeler 1992) was measured in February 2004 at four positions: 10 m inside the *Juniperus* canopy, 0.2 m inside the canopy edge, 0.2 m outside the canopy edge, and 5 m outside the canopy edge (intercanopy). At each canopy position, ten 0.1-m^2 quadrats (20 cm × 50 cm) were randomly placed with the long axis of the quadrat set parallel to the canopy edge. In addition, quadrats were not placed in areas with succulents or woody plants greater than 20 cm in height. Before biomass harvest, ground cover (cover/m^2) for each quadrat was visually estimated (Vellend et al. 2000). Cover was estimated for herbaceous, rock, litter, and bare areas. A 20 cm × 50 cm frame was divided into subsections and used to estimate cover. In addition, herbaceous cover was categorized as *Carex*, grass, and other herbaceous species. To estimate standing crop biomass, all herbaceous material 1 cm above ground level was clipped and bagged for transport. Herbaceous material was separated by cover type: *Carex*, grass, and other herbaceous. Clippings were oven dried at 80°C to a constant mass and weighed to the nearest 0.01 g. To test for sample adequacy, a running mean was calculated as new quadrats were added. Stabilization occurred between 6 and 8 quadrats (Figure 3). Percent standing crop biomass was determined for each position and plant type on a dry mass basis.

Below the canopy, six additional quadrats were clipped to estimate the proportion of live and senescent *C. planostachys* aboveground biomass. Only the canopy understory was measured at this time because all grass species were dormant (nongreen). Cover for each quadrat (0.1 m^2) was first estimated and all herbaceous material clipped 1 to 2 cm aboveground and bagged. The material was separated into live and dead biomass. Any leaf that was all green or had a portion of green was considered live. Fresh mass was recorded, and material was dried to a constant mass at 80°C. Total cover and standing crop biomass were calculated by adding *Carex*, grass, and other species cover and biomass at each position.

The experimental design for abiotic factors was factorial (position by date). Data were transformed as needed before analysis. Significant main effects were detected with analysis of variance (ANOVA) (SAS 1989), as well as temporal and spatial effects (Wayne and Van Auken 2002, 2004). Mean surface values were pooled temporally for each transect position to demonstrate the overall spatial differences for surface light, soil temperature, and soil moisture. Cover and biomass data analysis was performed using Excel and SAS (SAS 1989). Before analysis, cover data were inverse arcsine transformed. Individual *t* tests were used to test for differences between *Carex* standing crop biomass and total herbaceous standing crop biomass within each position. ANOVA and the Scheffé multiple comparison tests ($\alpha = 0.05$) were used to test for significant differences in percent cover and biomass across positions.

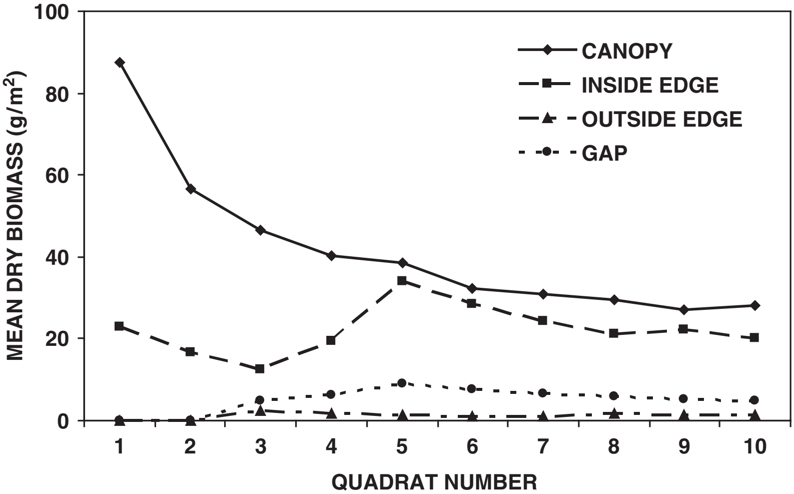

Figure 3 Standing-crop biomass quadrat stabilization curve. A cumulative mean for standing-crop biomass (g/m^2) was derived as new quadrats were added and plotted as a function of quadrat number

Results

In general, surface light ($F = 6.67$, $P \leq 0.0001$), soil temperature ($F = 36.90$, $P \leq 0.0001$) and soil moisture ($F = 23.77$, $P \leq 0.0001$) varied significantly both temporally and spatially. Mean values for light and temperature were highest in August and lowest in December, whereas soil moisture followed a reverse trend. The overall yearly trend in surface light ranged from 219 ± 77 μmol·m^{-2}·s^{-1} (mean ± SE) below the midcanopy to a high of 1183 ± 149 μmol·m^{-2}·s^{-1} in the intercanopy patchv (Figure 4A). The overall spatial trend in soil temperature mostly tracked surface light and ranged from 27.6° ± 1.4°C at the canopy edge to 32.6° ± 2.1°C in the intercanopy patch (Figure 4B). Annually, soil moisture was highest below the canopy at 43.4% ± 3.0% and lowest in the intercanopy at 30.3% ± 2.1% (Figure 4B). The canopy edge values were intermediate to the canopy and intercanopy values for all factors measured.

Litter cover and rock cover did not vary significantly by position ($F = 2.51$, $P > 0.05$ and $F = 0.38$, $P > 0.05$, respectively). Mean litter cover ranged from 60% ± 10% below the canopy to 9% ± 4% in the intercanopy; rock cover ranged from 12% ± 9% to 5% ± 4% (data not shown). Other species cover was less than 1% for all positions. *Carex planostachys* cover varied significantly between positions ($F = 10.45$, $P < 0.0001$). Total grass cover also varied significantly by position ($F = 13.57$, $P < 0.001$). Below the canopy, mean *Carex* cover was 29% ± 7% and grass cover was < 1% (Figure 5A). At the inside canopy edge, *Carex* cover was 39% ± 11% and grass cover was 5% ± 4%. At the outside canopy edge, *Carex* cover increased to 43% ± 4% and grass cover increased to 16% ± 6%. In the intercanopy patch, *Carex* cover decreased to 1% ± 0% and grass cover increased to 78% ± 7%. With respect to *Carex* cover, the Scheffé

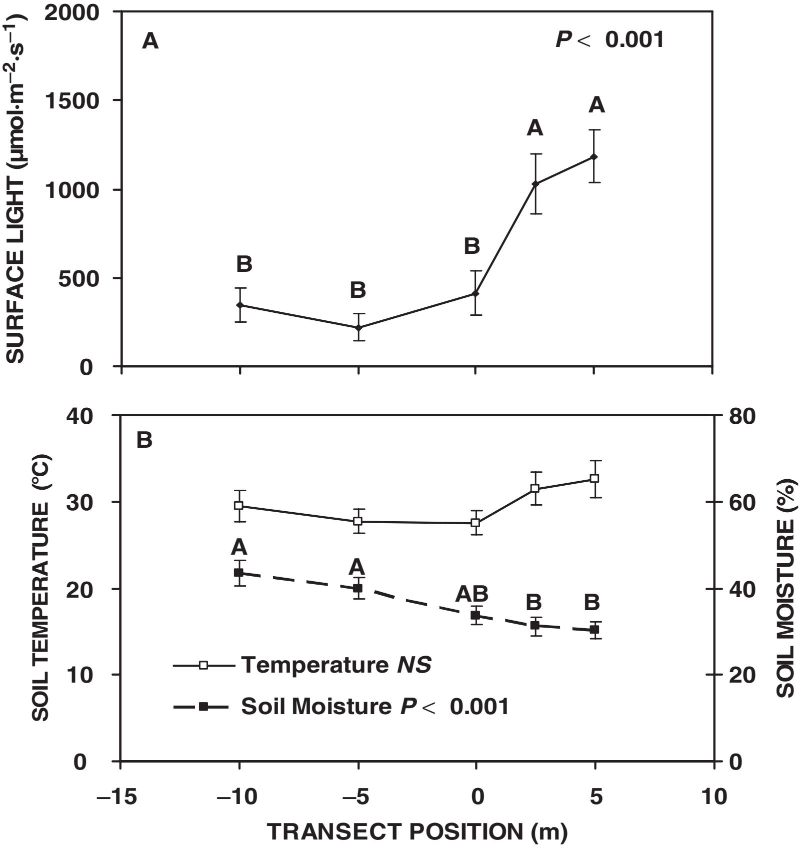

Figure 4 Yearly mean (±SE) surface gradient ($n = 6$ transects) from below the *Juniperus* canopy into the associated intercanopy ($n = 5$ positions) for (**A**) surface light levels ($\mu mol \cdot m^{-2} \cdot s^{-1}$) and (**B**) surface soil temperature (°C) and surface soil moisture (%). Light levels were measured at solar noon on cloudless days and represent the pooled measurements taken in July, August, October, and December ($n = 4$). Temperature measurements were made within 2h after solar noon and represent the pooled measurements taken in April, July, August, September, October, and December 1997 ($n = 6$). Soil moisture measurements represent the pooled measurements taken in April, May, July, August, September, October, and twice in December ($n = 8$). Transect position (x-axis) is in meters from the canopy edge: canopy (−10), mid-canopy (−5), canopy edge (0), mid-intercanopy (2.5), and intercanopy (5). *P* values are indicated; *NS* indicates no significant difference. Means with different letters indicate significant differences by Scheffé multiple comparison test. (Reprinted from Wayne and Van Auken 2004, with permission from the Texas Journal of Science)

multiple comparison tests indicated that only the intercanopy position was significantly different from all other positions (see Figure 5A). The Scheffé multiple comparison test indicated that grass cover at the canopy position and inside the canopy edge was significantly different from the intercanopy position. Grass cover at the outside canopy edge was not significantly different from the inside canopy edge or the intercanopy position. Total cover did not vary by position (see Figure 5A, $F = 1.3$, $P > 0.05$).

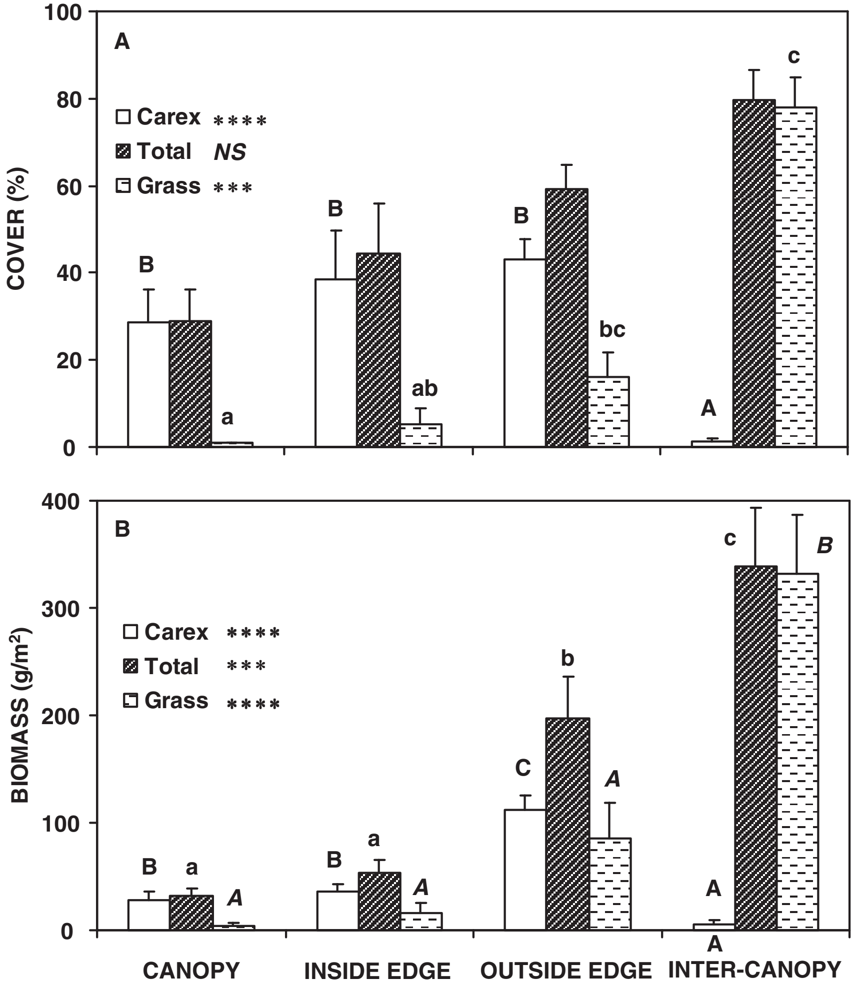

Figure 5 Positional differences in (**A**) cover (%) and (**B**) standing crop biomass (g/m^2) along a gradient from below a *Juniperus* canopy into an associated intercanopy patch. Cover and biomass (±SE) are indicated for *Carex planostachys*, total herbaceous, and grasses at each position. Total herbaceous is the product of *Carex*, grasses, and other herbaceous plants. The canopy position is 10 m inside the woodland, the inside edge is between 0 and 1 m inside the canopy edge, the outside edge is between 0 and 1 m outside the canopy edge, and the intercanopy is 5 m into the intercanopy. Ten 0.1-m^2 quadrats were sampled for each position. Significant positional differences are indicated adjacent to the legend. Means for *Carex*, total herbaceous, and grass with different letters are significantly different between positions (Scheffé multiple comparison tests). The proportion of *Carex* biomass to total biomass is indicated as the percent (%) of *Carex* biomass to total biomass. *t* tests were performed to detect differences in *Carex* biomass and total biomass. *NS*, not significantly different; *BS*, borderline significance; ***, $P < 0.001$; ****, $P \leq 0.0001$

Carex standing crop biomass varied significantly by position ($F = 27.49$, $P < 0.0001$), as did grass biomass ($F = 22.67$, $P < 0.001$) and total biomass. Live *Carex* standing crop biomass was 67% ± 4% of the total *Carex* biomass (data not shown). Below the canopy, *Carex* biomass was 28.0 ± 7.4 g/m^2, and grass biomass was 3.7 ± 2.7 g/m^2 (see Figure 5B). Other species biomass was 0.1 ± 0.0 g/m^2 (data not shown). At the inside canopy edge, *Carex* biomass increased to 36.3 ± 6.9 g/m^2, grass biomass was 15.4 ± 10.2 g/m^2, and other species biomass was 2.0 ± 0.9 g/m^2. At the outside edge, *Carex* biomass was 111.6 ± 13.9 g/m^2, grass biomass increased to 85.4 ± 33.0 g/m^2, and other species biomass was 0.1 ± 0.1 g/m^2. In the intercanopy patch, *Carex* biomass decreased to 5.8 ± 3.6 g/m^2, grass biomass reached a high of 332.5 ± 54.2 g/m^2, and other species biomass was 0.5 ± 0.2 g/m^2. The Scheffé multiple comparison tests indicated that for *Carex* biomass the outside canopy edge and the intercanopy positions were significantly different from all other positions (see Figure 5B). For grass biomass, the Scheffé multiple comparison test indicated that the intercanopy position was significantly different from all other positions.

Total standing-crop biomass varied significantly by position ($F = 17.51$, $P < 0.0001$) and the Scheffé multiple comparison tests indicated that the outside canopy and intercanopy positions were significantly different from each other and all other positions (see Figure 5B). The comparisons of *C. planostachys* biomass to total standing crop biomass indicated that *Carex* below the canopy was 88% of the total biomass and was not significantly different ($t = 0.34$, $P > 0.05$). At the inside canopy edge, *Carex* biomass was 68% of the total biomass, and the values were not significantly different ($t = 1.26$, $P > 0.05$). At the outside canopy edge, *Carex* was 57% of the total biomass and was borderline significantly different ($t = 2.10$, $P = 0.0595$). The *Carex* biomass in the intercanopy patch was 2% of the total biomass and was significantly different from the total biomass ($t = 6.07$, $P < 0.0001$).

Discussion

Carex apparently evolved as forest floor species (Ball 1990), and their occurrence in some woodlands should be expected. In many communities, *Carex* are considered important components of the woodland understory (Zavitkovski 1976; Gehring and Bragg 1992; Naumburg and DeWald 1999), but these woodlands tend to be more mesic than these central Texas woodlands. *Carex* have been reported in some *J. ashei* woodlands (Barnes et al. 2000; Jessup et al. 2003), but the location in relation to the overstory was not reported. Although herbaceous growth in the understory is reported for some *J. virginiana* woodlands, it may be transient (Gehring and Bragg 1992).

In the present study, *Carex planostachys* cover and biomass were mostly high below the *Juniperus* woodland canopy and canopy edge but greatly reduced in the intercanopy. The reason *C. planostachys* cover and biomass are high is probably related to its tolerance of low light levels. *Carex planostachys* photosynthetic light compensation point ranges from about 4 to 15 μmol·m^{-2}·s^{-1} and the light saturation point is about 200 to 600 μmol·m^{-2}·s^{-1} (Wayne, unpublished data). Grass cover and biomass followed a reverse trend, being high in the intercanopy patch and absent below the canopy. Grass cover was also present at the canopy edge, but *C. planostachys* contributed the higher proportion of total cover and total biomass. Grass biomass was higher at the outside canopy edge than the inside canopy edge (~43% cover vs. ~32% cover) where available surface light levels are elevated. In the intercanopy, grass cover was a significantly higher proportion of the total cover (~98% cover) where light levels are highest and soil moisture lowest. Most grasses are intolerant of low light conditions, similar to the values found below the canopy (Larcher 1995; Crawley 1997).

Gradients of surface light levels, soil temperature, and soil moisture were detected within these *J. ashei* woodlands and have been reported previously (Wayne and Van Auken 2002, 2004). These gradients are similar to abiotic gradients found in other *Juniperus* woodlands and associated grasslands (Schott and Pieper 1985; Breshears et al. 1997a,b, 1998; Breshears and Barnes 1999; Joy and Young 2002). In addition, these gradients are influenced by the canopy structure and the surface litter (Gass and Barnes 1998; Yager and Smeins 1999; Wayne and Van Auken 2004). At the same time, these gradients may also be important in determining juniper–grassland community structure (Everett et al. 1983; Gehring and Bragg 1992; Axmann and Knapp 1993; Fuhlendorf et al. 1997; Breshears et al. 1998; Bates et al. 2000).

A high amount of intercanopy grass cover is not unexpected, and this result is similar to other studies of *J. ashei* woodlands (Lynch 1971; Fowler 1986; Fowler and Dunlap 1986; Fuhlendorf et al. 1997). In addition, it is similar to what has been reported for grasslands associated with other *Juniperus* communities (Gehring and Bragg 1992; Knapp 1993; Knapp et al. 1993; Turner et al. 1995; Turner and Knapp 1996; Briggs et al. 2002). Grasses dominate in areas that lack an overstory to intercept light (Schott and Pieper 1985; McPherson et al. 1991; Yager and Smeins 1999). Several studies have suggested that the relative growth rate for various grass species in woodlands is dependent on available light (McPherson et al. 1991; Knapp 1993; Turner and Knapp 1996; Naumburg and DeWald 1999; Naumburg et al. 2001). For example, the relative growth rates of some C_4 grasses are positively correlated with increasing light levels, while some C_3 grasses respond favorably at decreased light levels (Gehring and Bragg 1992; Turner and Knapp 1996).

Many C_4 grasses are also tolerant of high soil temperatures, which are induced by elevated levels of solar radiation in open grasslands, and they maintain higher growth at these temperatures (Rice and Parenti 1978). On the central Texas Edwards Plateau, C_4 grasses such as *B. rigidiseta* and *A. longiseta* are most likely favored in the high light environment of the intercanopy, whereas the C_3 grass *Stipa leucotricha* is usually only found in the low light canopy and canopy edge environments (Fowler 1990). Grass species were not identified in this study, but *B. rigidiseta, A. longiseta*, and *S. leucotricha* have been reported in this area (Terletzky and Van Auken 1996; Van Auken 2000a; Wayne 2000).

Soil moisture is no less important than light levels or soil temperature and is often considered the principal limiting factor of productivity in C_4-dominated grasslands (Knapp 1993; Turner et al. 1995; Crawley 1997). However, it is difficult, if not impossible, to separate these factors and assign specific causes (Crawley

1997). The same is true for grasslands associated with *J. ashei* woodlands where water is certainly one of the limiting growth factors (Lynch 1971; Fuhlendorf and Smeins 1998). Decreased soil moisture in the intercanopy patch is also related to the increases in soil temperatures that occur in positions which lack an overstory (Breshears et al. 1997a,b, 1998; Wayne and Van Auken 2002, 2004). In most temperate grasslands, the C_4 grasses are considered tolerant of water stress (Fowler 1990; Knapp et al. 1993; Turner et al. 1995; Turner and Knapp 1996). For example, on the Konza Prairie in Kansas, the C_4 grass *Andropogon gerardii* maintains maximal photosynthetic activity at high xylem water potential during wet midsummers when light levels are high ($>1500\,\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and has moderate declines during soil water stress in late summer (Turner et al. 1995). Plants with the C_4 pathway have greater water use efficiency than C_3 grasses, providing the C_4 grasses a competitive advantage (Knapp 1993).

In most *Juniperus* woodlands, once the canopy overstory is established herbaceous growth is reduced or eliminated (Moir 1979; Clary and Jameson 1981; Engle et al. 1987; Pieper 1990; Gehring and Bragg 1992; Dye et al. 1995; Peek et al. 2001; Briggs et al. 2002). These trends have been reported in *J. deppeana, J. monosperma, J. occidentalis, J. pinchotii*, and *J. virginiana* communities (Table 1). The primary cause for the reduction of the herbaceous cover and biomass has been attributed to reduced levels of light because of the interception of light by the canopy. However, this may be a temporary phenomenon depending on the time since canopy establishment; consequently, this low herbaceous cover and biomass is probably not true for all closed-canopy woodlands. It has also been suggested that the light levels within the *J. ashei* understory are sufficient to support some herbaceous growth, especially those species with low light requirements (Fowler 1990; Fuhlendorf and Smeins 1997).

Another factor that may influence herbaceous recruitment and/or survival in the *J. ashei* understory is surface litter, which has a negative effect on some germination and emergence (Sydes and Grime 1981; Fowler 1990; Fuhlendorf et al. 1997; Yager and Smeins 1999). The influence of litter has been reported in various *Juniperus* and/or *Pinus* woodlands (Everett et al. 1983; Bates et al. 1998; Harrington and Edwards 1999). In this study, litter cover was highest below the canopy and decreased by about 85% in the intercanopy. It does not appear that *C. planostachys* has a problem establishing in the litter below the canopy, but no data are available concerning establishment for this species. However, once *C. planostachys* is established in the understory it does not appear to be affected by litter accumulation, likely because *C. planostachys* and most *Carex* spp. are clonal and propagation is by rhizome (Ball 1990; Bernard 1990; van Groenendael et al. 1996).

The presence of the relatively high herbaceous cover and biomass of *C. planostachys* below the canopy appears to make these central Texas *J. ashei* woodlands unique. However, the extent and commonness of this phenomenon in the Edwards Plateau *Juniperus* woodlands is unknown at this time. In addition, the timing of the establishment and development of the understory *Carex* community is unknown. Furthermore, the occurrence of *Carex* communities in other *Juniperus* woodlands is unreported.

Carex planostachys appears to have greater cover and biomass in the intermediate light and intermediate soil moisture environment of the canopy edge, but it also

Table 1 Other studies and date of study describing the change in herbaceous ground cover without a *Juniperus* canopy present or after the establishment of a *Juniperus* woodland with a closed canopy

Study author	Location	*Juniperus* species	No canopy	Canopy
Engle et al. 1987	OK	*J. virginiana*	350 g/m^2	25 g/m^2
Pieper 1990	NM	*J. monosperma*	80 g/m^2	0.2 g/m^2
Peek et al. 2001	OR	*J. occidentalis* and *J. monosperma*	15 g/m^2	4 g/m^2
Moir 1979	NM/AZ	*J. monosperma*	16%	3%
Clary and Jameson 1981	AZ	*J. monosperma*	35%	0.30%
Briggs et al. 2002	KS	*J. virginiana*	35 species	4 species

The state where the study was conducted is included along with the *Juniperus* species discussed. No canopy and canopy refer to the absence or presence of a *Juniperus* overstory. Measurements indicated are for herbaceous ground cover in g/m^2, % cover, or number of species/10 m^2.
The study by Clary and Jameson (1981) indicates the effect of canopy removal on herbaceous ground cover

seems tolerant of the low light and higher soil moisture environment of the *J. ashei* canopy. However, the low cover and biomass of this species in the intercanopy suggest intolerance to a high light environment or low seasonal water availability or a combination of these factors.

Summary

Juniperus woodlands occur in many regions of the Northern Hemisphere, mostly on thin, xeric soils of limestone derivation. In many areas *Juniperus* woodlands have increased their cover as a consequence of reduced fire frequency and concomitant encroachment and growth of their seedlings into associated grasslands. In the understory of many of these central and western North American *Juniperus* woodlands, herbaceous cover and biomass are reduced or even eliminated compared to associated grasslands. However, there appear to be some exceptions. *Carex planostachys* (cedar sedge) is an herbaceous species found in the understory of some central Texas *Juniperus* woodlands. *Carex planostachys* cover (mean ± SE) ranged from 29% ± 7% below the canopy to a high of 43% ± 4% at the outside canopy edge. In the intercanopy, cover was 1% ± 0% for *Carex* and 78% ± 7% (total) for several grass species. *Carex* biomass ranged from 28.0 ± 7.4 g/m^2 below the canopy to a high of 111.6 ± 13.9 g/m^2 at the outside canopy edge. In the intercanopy, biomass was 5.8 ± 3.6 g/m^2 for *Carex* and 332.5 ± 54.2 g/m^2 (total) for several grass species. *Carex planostachys* cover and biomass were higher below the *Juniperus* canopy where photosynthetic active radiation (PAR) was reduced and soil moisture was higher, whereas grass cover and biomass were higher in the intercanopy at elevated levels of PAR and soil moisture was lower. The spatial distribution of *C. planostachys* with greater cover and biomass below the canopy in some of these *J. ashei* woodlands suggests that this *Carex* sp. is tolerant of shade and may require a canopy presence.

References

Amos, B.B., and Gehlbach, F.R. 1988. Forests and woodlands of the northeastern Balcones escarpment. In: Edward's Plateau vegetation: plant ecological studies in central Texas, eds. B.B. Amos and F.R. Gehlbach, pp 57–78. Waco, TX: Baylor University.

Arbingast, S.A., Kennamer, L.G., Buchanan, J.R., Hezlep, W.L., Ellis, L.T., Jordan, T.G., Granger, C.T., and Zlatkovich, C.P. 1976. Atlas of Texas, 5th edition. Austin: University of Texas.

Axmann, B.D., and Knapp, A.K. 1993. Water relations of *Juniperus virginiana* and *Andropogon gerardii* in an unburned tallgrass prairie watershed. Southwest. Nat. 38:325–330.

Ball, P.W. 1990. Some aspects of the phytogeography of *Carex*. Can. J. Bot. 68:1462–1472.

Ball, P.W., Reznicek, A.A., and Murray, D.F. 2001. Magnoliophyta: Commelinidae (in part): Cyperaceae. London: Oxford University Press.

Barbour, M.G.,Burk, J.H. and Pitts, W.D. 1987. Terrestrial plant ecology. New York: Benjamin/Cummings.

Barnes, P.W., Liang, S., Jessup, K.E., Ruiseco, L.E., Phillips, P.L., and Reagan, S.J. 2000. Soils, topography and vegetation of the Freeman Ranch. San Marcos: Southwest Texas State University.

Baskin, J.M., and Baskin, C.C. 1978. Plant ecology of cedar glades in the Big Barrens region of Kentucky. Rhodora 80:545–557.

Baskin, J.M., and Baskin, C.C. 2000. Vegetation of limestone and dolomite glades in the Ozarks and Midwest regions of the United States. Ann. Mo. Bot. Gar. 87:286–294.

Bates, J.D., Miller, R.E., and Svejcar, T.J. 1998. Understory patterns in cut western juniper (*Juniperus occidentalis* spp. *occidentalis* Hook.) woodlands. Great Basin Nat. 58:363–374.

Bates, J.D., Miller, R.F., and Svejcar, T.J. 2000. Understory dynamics in cut and uncut western juniper woodlands. J. Range Manag. 53:119–126.

Bernard, J.M. 1990. Life history and vegetative reproduction in *Carex*. Can. J. Bot. 68:1441–1448.

Bray, W.L. 1904 The timber of the Edwards Plateau of Texas: its relation to climate, water supply, and soil. Washington, DC: U.S. Department of Agriculture, Bureau of Forestry.

Breshears, D.D., and Barnes, F.J. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landsc. Ecol. 14:465–478.

Breshears, D.D., Myers, O.B., Johnson, S.R., Meyers, C.W., and Martens, S.N. 1997a. Differential use of spatially heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*. J. Ecol. 85:289–299.

Breshears, D.D., Rich, P.M., Barnes, F.J., and Campbell, K. 1997b. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecol. Appl. 7:1201–1215.

Breshears, D.D., Nyhan, J.W., Heil, C.E., and Wilcox, B.P. 1998. Effects of woody plants on microclimate in a semi-arid woodland: soil temperature and evaporation in canopy and intercanopy patches. Int. J. Plant Sci. 159:1010–1017.

Briggs, J.M., Hoch, G.A., and Johnson, L.C. 2002. Assessing the rate, mechanisms and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578–586.

Broadbent, F.E. 1965. Organic matter. In: Methods of soil analysis, part 2. Chemical and microbiological properties, ed. C.A. Black, pp 1397–1400. Madison, WI: American Society of Agronomy.

Catchpole, W.R., and Wheeler, C.J. 1992. Estimating plant biomass: a review of techniques. Aust. J. Ecol. 17:121–131.

Clary, W.P., and Jameson, D.A. 1981. Herbage production following tree and shrub removal in the pinyon-juniper type of Arizona. J. Range Mang. 34:109–113.

Coppedge, B.R., Engle, D.M., Fuhlendorf, S.D., Masters, R.E., and Gregory, M.S. 2001. Landscape cover type and pattern dynamics in fragmented southern Great Plains grasslands, USA. Landsc. Ecol. 16:677–690.

Correll, D.S., and Johnston, M.C. 1979. Manual of the vascular plants of Texas. Renner, TX: Texas Research Foundation.

Crawley, M.J. 1997. Plant ecology, 2nd edition. Oxford: Blackwell Science.

Diamond, D.D. 1997 An old-growth definition for western Juniper woodlands: Texas Ashe Juniper dominated or codominated communities. General technical report SRS-15. Asheville, NC: United States Forest Service.

Diamond, D.D., Rowell, G.A., and Keddy-Hector, O.P. 1995. Conservation of Ashe Juniper (*Juniperus ashei* Buchholtz) woodlands of the central Texas hill country. Nat. Areas J. 15:189–197.

Dye, K.L., Ueckert, D.N., and Whisenant, S.G. 1995. Redberry juniper-herbaceous understory interactions. J. Range Manag. 48:100–107.

Ellison, L. 1960. Influence of grazing on plant succession of rangelands. Bot. Rev. 26:1–78.

Engle, D.M., Stritzke, J.F., and Claypool, F.I. 1987. Herbage standing crop around eastern redcedar trees. J. Range Manag. 40:237–239.

Everett, R.L., Sharrow, S.H., and Meeuwig, R.O. 1983. Pinyon-juniper woodland understory distribution patterns and species associations. Bull. Torrey Bot. Club 110:454–463.

Fonteyn, P.J., McClean, T.M., and Akridge, R.E. 1985. Xylem pressure potentials of three dominant trees of the Edwards Plateau of Texas. Southwest. Nat. 30:141–146.

Foster, J.H. 1917. The spread of timbered areas in central Texas. J. For. 15:442–445.

Fowler, N.L. 1986. Density-dependent population regulation in a Texas grassland. Ecology 67:545–554.

Fowler, N.L. 1990. The effects of competition and environmental heterogeneity on three coexisting grasses. J. Ecol. 78:389–402.

Fowler, N.L., and Dunlap, D.W. 1986. Grassland vegetation of the eastern Edwards Plateau. Am. Midl. Nat. 115:146–155.

Fuhlendorf, S.D., and Smeins, F.E. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus–Quercus* savanna. J. Veg. Sci. 8:819–828.

Fuhlendorf, S.D., and Smeins, F.E. 1998. The influence of soil depth on plant species response to grazing within a semi-arid savanna. Plant Ecol. 138:89–96.

Fuhlendorf, S.D., Smeins, F.E., and Grant, W.E. 1996. Simulation of a fire-sensitive ecological threshold: a case study of ashe juniper on the Edwards Plateau of Texas. Ecol. Model. 90:245–255.

Fuhlendorf, S.D., Smeins, F.E., and Taylor, C.A. 1997. Browsing and tree size influences on ashe juniper understory. J. Range Manag. 50:507–512.

Gass, L., and Barnes, P.W. 1998. Microclimate and understory structure of live oak (*Quercus fusiformis*) clusters in central Texas, USA. Southwest. Nat. 43:183–194.

Gehring, J.L., and Bragg, T.B. 1992. Changes in prairie vegetation under eastern redcedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie. Am. Midl. Nat. 128:209–217.

Harper, J.L. 1977. Population biology of plants. New York: Academic Press.

Harrington, T.B., and Edwards, M.B. 1999. Understory vegetation, resource availability, and litterfall responses to pine thinning and woody vegetation in longleaf pine plantations. Can. J. For. Res. 29:1055–1064.

Hatch, S.L., Gandhi, K.N., and Brown, L.E. 1990. Checklist of the vascular plants of Texas (MP-1655). College Station: Texas Agricultural Experimental Station.

Herman, F.J. 1970. Manual of the *Carices* of the Rocky Mountains and Colorado Basin. Washington, DC: Forest Service, United States Department of Agriculture.

Herman, F.J. 1974. Manual of the genus *Carex* in Mexico and Central America. Washington, DC: Forest Service, United States Department of Agriculture.

Jackson, J.T., and Van Auken, O.W. 1997. Seedling survival, growth and mortality of *Juniperus ashei* (Cupressaceae) in the Edwards Plateau region of central Texas. Tex. J. Sci. 49:2267–2278.

Jackson, R.B., Anderson, L.J., and Pockman, W.T. 2000. Measuring water availability and uptake in ecosystem studies. In: Methods in ecosystem science, eds. O.E. Sala, R.B. Jackson, H.A. Mooney, and R. Howarth, pp 199–214. New York: Springer-Verlag.

Jessup, K.E., Barnes, P.W., and Boutton, T.W. 2003. Vegetation dynamics in a *Quercus–Juniperus* savanna: an isotopic assessment. J. Veg. Sci. 14:841–852.

Johnsen, T.N. 1962. One-seed juniper invasion of northern Arizona grasslands. Ecol. Monogr. 32:187–207.

Johnsen, T.N., and Alexander, R.A. 1974. *Juniperus* L. In: Seeds of woody plants in the United States, ed. C.S. Schopmeyer, pp 460–469. Agricultural handbook 450. Washington, DC: Forest Service, United States Department of Agriculture.

Joy, D.A., and Young, D.R. 2002. Promotion of mid-successional seedling recruitment and establishment by *Juniperus virginiana* in a coastal environment. Plant Ecol. 160:125–135.

Knapp, A.K. 1993. Gas exchange dynamics in C_3 and C_4 grasses: consequences of differences in stomatal conductance. Ecology 74:113–123.

Knapp, A.K., Fahnestock, J.T., Hamburg, S.P., Statland, L.B., Seastedt, T.R., and Schimel, D.S. 1993. Landscape patterns in soil–plant water relations and primary production in tallgrass prairie. Ecology 74:549–560.

Larcher, W. 1995. Physiological plant ecology: ecophysiology and stress physiology of functional groups, 3rd edition. New York: Springer-Verlag.

Little, E.L. 1971. Atlas of the United States, vol. 1. Conifers and important hardwoods. Washington, DC: Forest Service, United States Department of Agriculture.

Lynch, D. 1971. Phenology, community composition, and soil moisture in a relict grassland at Austin, Texas. Ecology 52:890–897.

Major, J. 1971. *Carex* for the ecologist. Ecology 52:539.

McKinley, D.C., and Van Auken, O.W. 2004. Growth and survival of *Juniperus ashei* (Cupressaceae) seedlings in the presence of *Juniperus ashei* litter. Tex. J. Sci. 56:3–14.

McKinley, D.C., and Van Auken, O.W. 2005. Influence of interacting factors on the growth and mortality of *Juniperus* seedlings. Am. Midl. Nat. 154:320–330.

McPherson, G.R., Wright, H.W., and Wester, D.B. 1988. Patterns of shrub invasion in semi-arid Texas grasslands. Am. Midl. Nat. 120:391–397.

McPherson, G.R., Rasmussen, G.A., Wester, D.B., and Masters, R.A. 1991. Vegetation and soil zonation patterns around *Juniperus pinchotii* plants. Great Basin Nat. 51:316–324.

Miller, R.E., Ver Hoef, J.M., and Fowler, N.L. 1995. Spatial heterogeneity in eight central Texas grasslands. J. Ecol. 83:919–928.

Miller, R.F., and Wigand, P.E. 1994. Holocene changes in semiarid pinyon-juniper woodlands. Bioscience 44:465–474.

Moir, W.H. 1979. Soil-vegetation patterns in the central Peloncillo Mountains, New Mexico. Am. Midl. Nat. 102:317–331.

Naumburg, E., and DeWald, L.E. 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. For. Ecol. Manag. 124:205–215.

Naumburg, E., De Wald, L.E., and Kolb, T.E. 2001. Shade responses of five grasses native to southwestern U.S. *Pinus ponderosa* forests. Can. J. Bot. 79:1001–1009.

NOAA. 2004. Meteorological data. Asheville, NC: National Oceanic and Atmospheric Administration.

NRCS. 2004. Official soil series descriptions. Washington, DC: Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture.

Padien, D.J., and Lajtha, K. 1992. Plant spatial pattern and nutrient distribution in pinyon-juniper woodlands along an elevational gradient in northern New Mexico. Int. J. Plant Sci. 153:425–433.

Pearcy, R.W. 1989. Plant physiological ecology: field methods and instrumentation. New York: Chapman & Hall.

Peek, J.M., Korol, J.J., Gay, D., and Herhsey, T. 2001. Overstory-understory biomass over a 35-year period in southcentral Oregon. For. Ecol. Manag. 150:267–277.

Pieper, R.D. 1990. Overstory-understory relations in pinyon-juniper woodlands in New Mexico. J. Range Manag. 43:413–415.

Reznicek, A.A. 1990. Evolution in sedges (*Carex*, Cyperaceae). Can. J. Bot. 68:1409–1432.

Rice, E.L., and Parenti, R.L. 1978. Causes of decreases in productivity in undisturbed tall grass prairie. Am. J. Bot. 65:1091–1097.

SAS. 1989. SAS/STAT user's guide, version 6, 4th edition. Cary, NC: SAS Institute, Inc.

Scholes, R.J., and Archer, S.R. 1997. Tree-grass interactions in savannas. Annu. Rev. Ecol. Syst. 28:517–544.

Schott, M.R., and Pieper, R.D. 1985. Influence of canopy characteristics of one-seed juniper on understory grasses. J. Range Manag. 38:328–331.

Schott, M.R., and Pieper, R.D. 1987. Succession of pinyon-juniper communities after mechanical disturbance in southcentral New Mexico. J. Range Manag. 40:88–94.

Smeins, F.E., and Fuhlendorf, S.D. 1997 Biology and ecology of ashe (blueberry) juniper. In: Juniper symposium 1997 proceedings, ed. C.A. Taylor, pp 3.33–3.47. San Angelo, TX: Texas A & M Research and Extension Center.

Smeins, F.E., and Merrill, L.B. 1988. Long-term change in semi-arid grassland. In: Edwards Plateau vegetation, eds. B.B. Amos and F.R. Gehlbach, pp 101–114. Waco, TX: Baylor University Press.

Sydes, C., and Grime, J.P. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland: I. Field investigations. J. Ecol. 69:237–248.

Taylor, F.B., Hailey, R.B., and Richmond, D.L. 1962. Soil survey of Bexar County, Texas. Washington, DC: Soil Conservation Service, United States Department of Agriculture.

Terletzky, P.A., and Van Auken, O.W. 1996. Comparison of cedar glades and associated woodlands of the southern Edwards Plateau. Tex. J. Sci. 48:55–67.

Tremblay, N.O., and Larocque, G.R. 2001. Seasonal dynamics of understory vegetation in four eastern Canadian forest types. Int. J. Plant Sci. 162:271–286.

Turner, C.L., and Knapp, A.K. 1996. Responses of a C_4 grass and three C_3 forbs to variation in nitrogen and light in tallgrass prairie. Ecology 77:1738–1749.

Turner, C.L., Kneisler, J.R., and Knapp, A.K. 1995. Comparative gas exchange and nitrogen responses of the dominant C_4 grass *Andropogon gerardii* and five C_3 forbs to fire and topographic position in a tallgrass prairie during a wet year. Int. J. Plant Sci. 156:216–226.

Van Auken, O.W. 2000a. Characteristics of intercanopy bare patches in *Juniperus* woodlands of the southern Edwards Plateau, Texas. Southwest. Nat. 45:95–110.

Van Auken, O.W. 2000b. Shrub invasion of North American semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–215.

Van Auken, O.W., Ford, A.L., and Stein, A.G. 1979. A comparison of some woody upland and riparian plant communities of the southern Edwards Plateau. Southwest. Nat. 24:165–180.

Van Auken, O.W., Ford, A.L., and Stein, A.G. 1980. Woody vegetation of upland plant communities in the southern Edwards Plateau. Tex. J. Sci. 32:23–35.

Van Auken, O.W., Ford, A.L., and Allen, J.L. 1981. An ecological comparison of upland deciduous and evergreen forests of central Texas. Am. J. Bot. 68:1249–1256.

Van Auken, O.W., Jackson, J.T., and Jurena, P.N. 2004. Survival and growth of *Juniperus* seedlings in *Juniperus* woodlands. Plant Ecol. 175:245–257.

van Groenendael, J.M., Klimes, L., Klimesova, J., and Hendriks, R.J. 1996. Comparative ecology of clonal plants. Philos. Trans. R. Soc. Lond. Biol. Sci. 351:1331–1339.

Vellend, M., Lechowicz, M.J., and Waterway, M.J. 2000. Environmental distribution of four *Carex* species (Cyperaceae) in an old-growth forest. Am. J. Bot. 87:1507–1516.

Ware, S. 2002. Rock outcrop plant communities (glades) in the Ozarks: a synthesis. Southwest. Nat. 47:585–597.

Wayne, E.R. 2000. Water relations of *Juniperus ashei* seedlings and changes in biotic and abiotic factors along an environmental gradient on the Edwards Plateau from under a *Juniperus* woodland canopy into an intercanopy patch. M.S. thesis. University of Texas, San Antonio.

Wayne, E.R., and Van Auken, O.W. 2002. Spatial and temporal patterns of *Juniperus ashei* seedling xylem water potential. Southwest. Nat. 47:153–161.

Wayne, E.R., and Van Auken, O.W. 2004. Spatial and temporal abiotic changes along a canopy to intercanopy gradient in Central Texas *Juniperus ashei* woodlands. Tex. J. Sci. 56:35–54.

Yager, L.Y., and Smeins, F.E. 1999. Ashe juniper (*Juniperus ashei*: Cupressaceae) canopy and litter effects on understory vegetation in a juniper-oak savanna. Southwest. Nat. 44:6–16.

Zavitkovski, J. 1976. Ground vegetation biomass, production, and efficiency of energy utilization in some northern Wisconsin forest ecosystems. Ecology 57:694–706.

6

The Potential Role of Mycorrhizae in the Growth and Establishment of *Juniperus* Seedlings

J.K. Bush

Introduction

Approximately 95% of all terrestrial plant families have species that have mycorrhizal associations (Trappe 1987). The relationships are usually symbiotic, and typically mutualistic, but can also be parasitic (Allen 1991; Allen et al. 2003). The three most common types of mycorrhizae are the orchid mycorrhizae, arbuscular mycorrhizae (AM), and ectomycorrhizae (EM). There are distinct characteristics for fungi that can be defined as mycorrhizal: (1) the fungal hypha extends into a root or rhizoid and outward into the surrounding substrate, (2) the fungi acquire carbon from a host, and, in the case of mutualism, (3) the fungi provide soil resources to the host plant (Allen et al. 2003). Arbuscular mycorrhizae are a monophyletic group known as the Glomales, which contains six genera (Schwarzott et al. 2001). Ectomycorrhizae are found in three different fungal groups: Zygomycetes, Ascomycetes, and Basidiomyctes (Allen et al. 2003).

Mycorrhizae improve mineral nutrition and water transport in their host plants. It has been well established that mycorrhizal roots uptake several nutrients more efficiently than nonmycorrhizal roots, especially at low soil fertility levels (Marschner and Dell 1994; Smith and Read 1997; Clark and Zeto 2000; Liu et al. 2000). The arbuscular mycorrhizal hyphae increase the volume of soil explored for nutrients by more efficiently growing beyond the roots, where nutrients are depleted (Allen et al. 2003). In addition, small soil pores and microsites that roots cannot reach can be reached by the small-diameter hyphae (Egerton-Warburton et al. 2003). Ectomycorrhizal hyphae increase the total absorbing surface by several orders of magnitude, are responsible for much of the nutrient uptake, and have a high affinity for phosphorus when soil phosphorus is low (Cress et al. 1979; Allen et al. 2003; Haskins and Gehring 2004; Wallander 2004).

Except for a few rare instances (Andersen et al. 1988), arbuscular mycorrhizae have been shown to improve the water status of the host plant (Andersen et al. 1988; Kothari et al. 1990; Cui and Nobel 1992; Auge 2001; Marulanda et al. 2003). Arbuscular mycorrhizal plants are often less susceptible to drought than nonarbuscular mycorrhizal plants (Ibrahim et al. 1990; Michelsen and Rosendahl 1990; Davies et al. 1992) and mycorrhizal hyphae play an active role in water transport

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(Allen 1982; Hardie 1985; Faber et al. 1991; Ruiz-Lazano and Azcon 1995). Ectomycorrhizal fungi can also improve soil water absorption, hydraulic conductivity, and transfer of water to their host (Brownlee et al. 1983; Smith and Read 1997; Landhäusser et al. 2002; Muhsin and Zwiazek 2002).

The symbiotic relationship between higher plants and fungi has been shown to have many effects on the host plant, including increased rates of growth, increased seed production, changes in hormone levels, and changes in root:shoot allocation (Allen and Allen 1990; Nelson and Allen 1993). Because of these physiological changes and because plant species occur as a continuum from nonmycorrhizal to obligate mycorrhizal, it has been suggested that arbuscular mycorrhizae can change the competitive balance between plants (Fitter 1977; Hall 1978; Hetrick et al. 1988; Hartnett et al. 1993; Hetrick et al. 1994). It has been suggested that arbuscular mycorrhizal infection will alter the degree of "aggressivity" in favor of an already aggressive plant (West 1996) and increase species diversity by increasing intraspecific suppression and decreasing the interspecific suppression of small plants by large neighbors (Moora and Zobel 1996). The mechanisms by which the arbuscular mycorrhizae alter the competitive balance appear to be by changing the availability of soil resources (Allen and Allen 1986; Hodge 2003), or arbuscular mycorrhizae could promote the growth of one species while inhibiting a second species (Allen et al. 1989). Some evidence suggests that if a species is obligately mycorrhizal, the absence of arbuscular mycorrhizae reduces the species growth and therefore competitive ability (Hartnett et al. 1993; Hetrick et al. 1994). Less is known about the role of ectomycorrhizae in competition; however, there is a suggestion that they do significantly influence plant–plant interactions (Perry et al. 1989), and that the interactions between plants can affect the colonization of ectomycorrhizae (Haskins and Gehring 2004).

Juniperus woodlands occur on more than 30 million ha in the western United States, on 20 million ha in Texas, on escarpments throughout the Great Plains, and in scattered areas of shallow limestone soils in the eastern United States (Wells 1965; Gould 1969; Baskin and Baskin 1986; Miller and Wigand 1994; also see Chapter 1, this volume). Various species of *Quercus* are associated with *Juniperus* in many of these woodlands, especially in Texas (Van Auken et al. 1981; Van Auken 1993). In spite of the vast areas of the United States covered by species of *Juniperus* and *Quercus*, there are few comprehensive studies of their competitive ability, and fewer still of the role mycorrhizae have in their competitive ability.

Photographic evidence illustrates the growth promotion of *J. osteosperma* seedlings by mycorrhizae (Salisbury and Ross 1992), and *Glomus fasiculatum* has been identified as the native arbuscular mycorrhizal symbiont (Reinsvold and Reeves 1986). *Juniperus oxycedrus*, a species of the Mediterranean, and *J. chinensis*, a species native to China, showed increased growth when inoculated with *Glomus* spp. (Roncadori 1982; Alguacil et al. 2006). The response of other *Juniperus* species to fungal symbiosis is less certain. Arbuscular mycorrhizal infection did not increase *J. horizontalis* dry mass (Maronek et al. 1980).

Quercus spp. are usually considered to be ectomycorrhizal (Grand 1969; Rothwell et al. 1983; Mitchell et al. 1984; Daughtridge et al. 1986; Watson et al.

1990; Newton and Pigott 1991; Bakker et al. 2000; Bergero et al. 2000; Dickie et al. 2001; Egerton-Warburton and Allen 2001; Gilman 2001; Maestre et al. 2002). Although the majority of vascular plants have either ecto- or arbuscular mycorrhizae, the two types occasionally co-occur within the root as co-dominants or successional mycorrhizal associations (Molina and Trappe 1992; Allen et al. 2003). *Quercus* is one genus in which several of its members are known to have both. *Quercus rubra* (Watson et al. 1990; Dickie et al. 2001), *Q. falcata* (Grand 1969), *Q. imbricaria* (Rothwell et al. 1983), and *Q. palustris* (Watson et al. 1990) have both arbuscular- and ectomycorrhizae. Other species of *Quercus*, such as *Q. robur* (Mitchell et al. 1984) and *Q. alba* (Watson et al. 1990), are exclusively ectomycorrhizal. It has been demonstrated that arbuscular mycorrhizae do not increase nutrient uptake or growth of *Q. rubra* seedlings early in development (Dickie et al. 2001). Ectomycorrhizae have been shown to be beneficial for *Q. velutina* (Daughtridge et al. 1986); however, ectomycorrhizae were not beneficial for *Q. virginiana* growth (Gilman 2001). When inoculated with either arbuscular mycorrhizae, ectomycorrhizae, or both arbuscular mycorrhizae and ectomycorrhizae, *Q. agrifolia* seedlings benefited most when either arbuscular mycorrhizae or ectomycorrhizae were present, and were most negatively affected when inoculated with both arbuscular mycorrhizae and ectomycorrhizae (Egerton-Warburton and Allen 2001).

In this study, the effects of mycorrhizae on the growth of and competition between *Juniperus ashei* and *Quercus virginiana* (=*Q. fusiformis*) (Hatch et al. 1990), two dominant woody species of the Edwards Plateau Region of central Texas, are evaluated. Before European settlement, much of the upper part of the Plateau of central Texas was described as a savanna or grassland with mottes of *Q. virginiana. Juniperus ashei* was thought to be restricted to steep slopes and drainages (Bray 1904; Buechner 1944; Wells 1965). Today, *J. ashei* dominates much of the former grassland, in some cases forming dense thickets (Van Auken 1993; Smeins et al. 1994). The purpose of this study was to examine the role of mycorrhizae and soil nutrients on the growth, arbuscular mycorrhizal infection, and competition between *Juniperus ashei* and *Quercus virginiana* seedlings.

Materials and Methods

Fruits of *Juniperus ashei* Buchholz (Ashe juniper) and *Quercus virginiana* Small (live oak) were collected from trees located in northwestern Bexar County, Texas (29°37′ N, 98°36′ W). The pulp from *J. ashei* fruit was removed, and seeds were placed on wet paper toweling in 10-cm-deep plastic trays. Trays were covered with aluminum foil and kept in the greenhouse at temperatures from 26° to 38°C. Deionized water was added as needed to keep the toweling moist. When the radicles were 1 to 2 cm in length, they were transplanted to pots containing native soil. Fruits of *Q. virginiana* were planted directly in pots containing 1400 g of the same soil. The soil, collected from the southern edge of the Edwards Plateau, was a

Patrick series clayey-over-sandy, carbonatic-thermic, Typic Calciustoll, with the A horizon varying in depth from 25 to 41 cm (Taylor et al. 1966). The soil was air dried and sieved (6.4-mm mesh) before placement into pots lined with plastic bags (to prevent nutrient and water loss). Soil analysis indicated 5–10 g/kg carbon, 11.6 g/kg calcium, 1.3 g/kg magnesium, 1.0 mg/kg total nitrogen, 12 mg/kg phosphorus, 138 mg/kg potassium, and 196 mg/kg sulfur.

A fiberglass greenhouse was used for plant growth with photosynthetically active photon flux density (PPFD, 400–700 nm) at 37% ± 12% of the outside mean PPFD (1891 ± 129 μmol/m^2/s ± SD averaged over the experiment). Light intensity was measured with a LI-COR LI-188 integrating quantum sensor.

The experiment was a three-factor, completely factorial experiment. The effects of soil sterilization (two levels), soil nutrients (two levels), and competition (two levels) on *J. ashei* and *Q. virginiana* dry mass, root:shoot ratios, and percent arbuscular mycorrhizal infection were examined. Soil was either native soil or native soil sterilized for 60 min at 121°C and 103 kPa. Two levels of nutrients included native soil or native soil supplemented with 0.2 g N as NH_4NO_3, 0.15 g P as Na_2PO_4, 0.1 g K as KCl, and 0.04 g S as $MgSO_4$ per pot (Tiedemann and Klemmedson 1986). Competition was evaluated by comparing each species grown alone (density = 2 plants/pot) or in mixture (density = 1 *J. ashei* + 1 *Q. virginiana* plants/pot). There were five replications of each treatment.

Two growing seasons after initiation of the experiment, plant tops were harvested by clipping at the soil surface, separating by species, and determining dry mass by drying at 100°C to a constant mass. Ash-free belowground dry mass (AFDM; Böhm 1979) was measured by carefully washing the soil from the roots, separating by species, drying to a constant mass at 100°C, weighing, ashing at 650°C for 3 h, reweighing, and subtracting inorganic components. Mean dry mass per plant was used to compare growth in mixture and monoculture.

After washing and before drying, 1 g wet weight root sample was removed from each monoculture treatment for electron microscopy and arbuscular mycorrhizal staining. Root samples from mixture treatments were not harvested because the species could not be separated. For electron microscopy, root samples were fixed in 3.5% glutaraldehyde, mixed in 0.1 M cacodylate buffer (pH 7.0) for 2 h, and rinsed twice in buffer. The tissue was then dehydrated in a graded ethanol series to 100%, critical-point dried, mounted on stubs, and sputter-coated with Hummer-X to 10 nm (Birnbaum et al. 1989). Samples for mycorrhizal observation were stained using 0.05% trypan blue (Phillips and Hayman 1970). Percent vesicular-arbuscular mycorrhizal infection was determined using a variation of the gridline/intersect method (Newman 1966; Giovannetti and Mosse 1980). If any arbuscule or vesicle was found at an intersection of gridlines, that intersection was considered infected. One hundred intersections were examined for each sample, and the infection was presented as a percent. Although ectomycorrhizae are more commonly associated with woody plants (Harley and Smith 1983), we were interested in the role or effect of the arbuscule mycorrhizae on the competition of these two species because of the evidence that at least some *Juniperus* species are obligately dependent on arbuscular mycorrhizae (Salisbury and Ross 1992). In addition, by soil sterilization, we can assume that both arbuscular- and ectomycorrhizal spores were killed, although the level of ectomycorrhizae was not quantified. Some have criticized the use of soil sterilization as a means to remove fungal propagules because of the effects sterilization has on other soil microorganisms; however, results are equivocal (Hetrick et al. 1988). We did not evaluate the effects of sterilization on other soil microorganisms.

Analyses of variance were performed separately for each species to test the effects of nutrient level, soil sterilization, and competition on aboveground, belowground, and total dry mass and root:shoot ratios. Main effects and first-order and second-order interactions were entered into the model. Percent infection was arcsine transformed before performing analysis of variance. Analyses of variance of percent infection were performed separately for each species to test the effects of nutrient level and soil sterilization on percent infection. Included in the model were main effects and the first-order interaction.

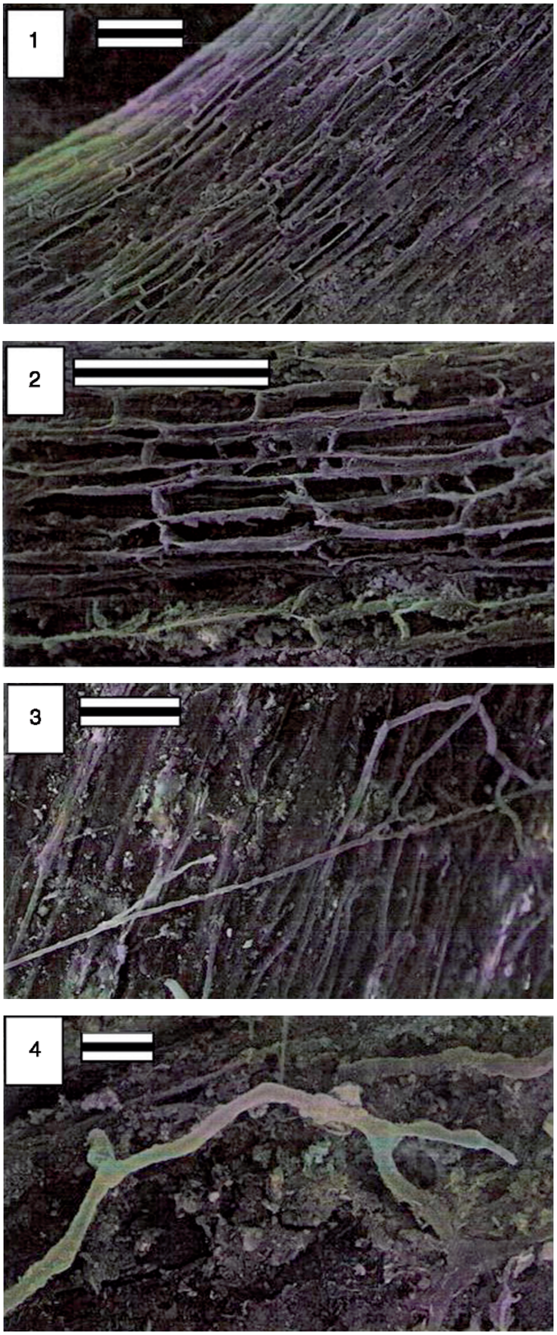
Results

Scanning electron micrographs of the surface of *Juniperus ashei* roots from plants grown in sterile soil revealed epidermal cell walls but no associated soil fungi (Figures 1, 2). When the surface of *J. ashei* roots from plants grown in nonsterile soil was examined, the cell walls of epidermal cells were visible, as well as numerous fungal hyphae (Figures 3, 4). Examination of the surface of *Quercus virginiana* roots from plants grown in sterile soil demonstrated a lack of soil fungi, but root hairs from surface epidermal cells were easily found (Figures 5, 6). When the surfaces of *Q. virginiana* roots from plants grown in nonsterile soil were examined, the roots were covered by a mantle of soil fungi (Figures 7, 8). The fungal layer was so thick in some cases that it was difficult to separate the roots of *Q. virginiana* from the fungus. The fungus, although unidentified, had branched hyphae that appeared to be septate.

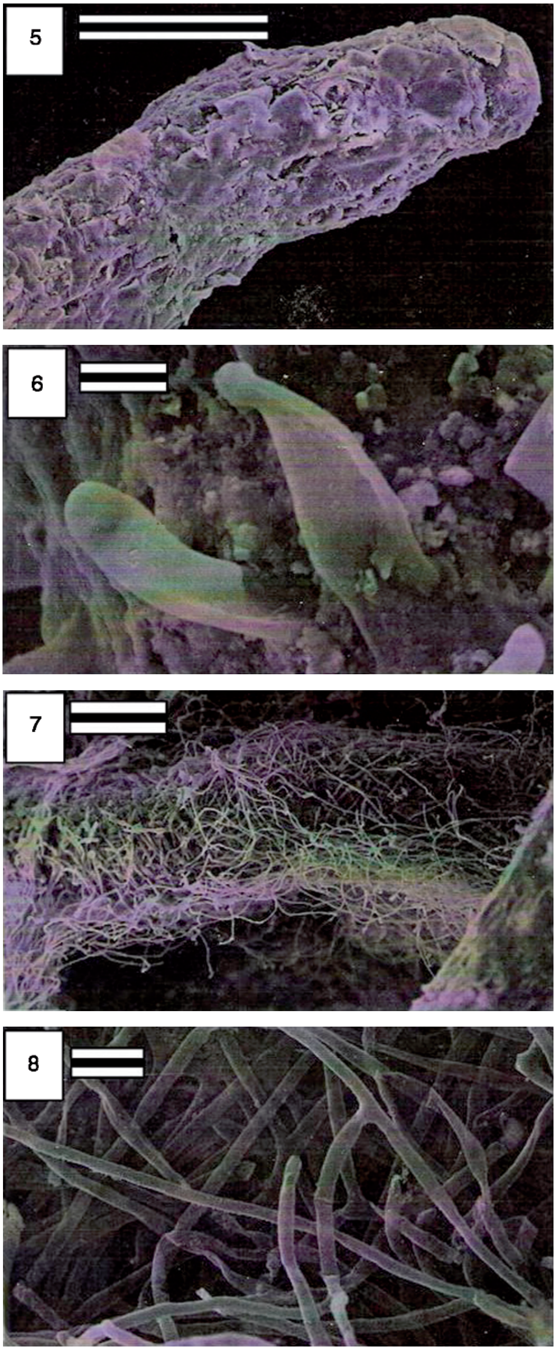
Analyses of variance indicated that soil sterilization had a significant effect on *J. ashei* aboveground, belowground, and total dry mass (Table 1). Total dry mass was significantly greater in nonsterile soil compared to sterile soil (Figure 9A). Nutrient addition and competition had no effect on aboveground, belowground, and total dry mass (see Table 1, Figure 9B,C).

For *Q. virginiana* belowground and total dry mass, soil sterilization had a significant effect (see Table 1). Total dry mass was significantly greater in the nonsterile soil treatment compared to the sterile soil (Figure 10A). Analyses of variance indicated that soil nutrient level had a significant effect on above-, belowground, and total dry mass, whereas competition had no effect (see Table 1). Total dry mass increased 1.65 times with the addition of nutrients (Figure 10B). Total dry mass in mixture and monoculture was not significantly different (Figure 10C).

Dry mass of *J. ashei* was reduced (94%–98%) in sterile soil, regardless of the nutrient level or type of competition (monoculture or mixture) (Figure 11A,B). *Juniperus ashei* did not respond to increased levels of soil nutrients when grown



Figures 1–8 Scanning electron micrographs of the root surface epidermis and associated fungi of *Juniperus ashei* (**1–4**) and *Quercus virginiana* (**5–8**). **1, 2** Roots of *J. ashei* plants grown in sterile soil without soil fungi. **3, 4** Roots of *J. ashei* plants grown in nonsterile soil with soil fungi. **5** Root tip of *Q. virginiana* plant grown in sterile soil without soil fungi. **6** Surface of root of *Q. virginiana* grown in sterile soil without fungi showing two root hairs. **7** Surface of root of



Figures 1–8 (continued) *Q. virginiana* grown in nonsterile soil covered with mantle of soil fungi. **8** Surface of root of *Q. virginiana* grown in nonsterile soil covered with a thick layer of soil fungi. Fungi are branched and appear to be septate. *Bars* **1, 2, 5, 7** 100 µm; **3** 50 µm; **4, 6, 8** 10 µm

Table 1 Sum of squares from analyses of variance of aboveground, belowground, and total dry mass, and root:shoot ratios of *Juniperus ashei* and *Quercus virginiana*, including the source of variation (sterilization, nutrients, and competition) and degrees of freedom (df)

		Juniperus ashei				*Quercus virginiana*			
Source	df	Above	Below	Total	Ratio	Above	Below	Total	Ratio
Sterilization (S)	1	108.59****	2.25****	115.67****	0.58*	5.21	14.57**	40.80**	0.45
Nutrients (N)	1	0.57	0.05	0.03	0.00	43.18****	42.69****	171.83****	0.61
Competition (C)	1	0.45	0.01	0.44	0.07	0.08	1.93	1.64	0.21
S*N	1	0.62	0.03	0.01	0.01	1.16	10.25	8.47	3.79**
N*C	1	4.81	0.03	5.87	0.01	0.78	2.83	4.46	0.13
S*C	1	0.52	0.02	0.50	0.09	0.21	0.00	0.00	0.01
C*S*N	1	4.89	0.04	6.05	0.00	0.04	0.04	0.03	0.21
Error	28	38.02	1.74	38.81	3.36	37.41	41.07	110.18	11.53
Total	35	159.23****	4.14	165.83****	4.11	92.40***	112.66**	337.71***	17.75

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.

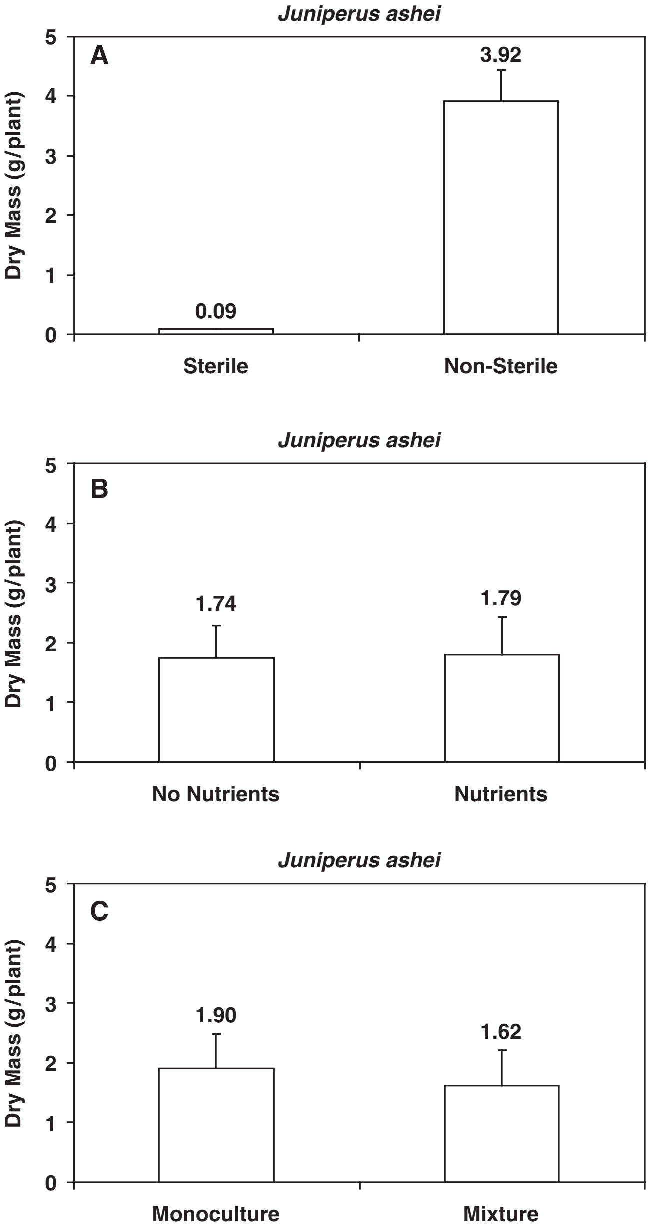


Figure 9 *Juniperus ashei* total dry mass per plant for main effects: soil sterilization (**A**), nutrients (**B**), and competition (**C**). *Numbers above bars* are the mean values; *bars* are 1 SE

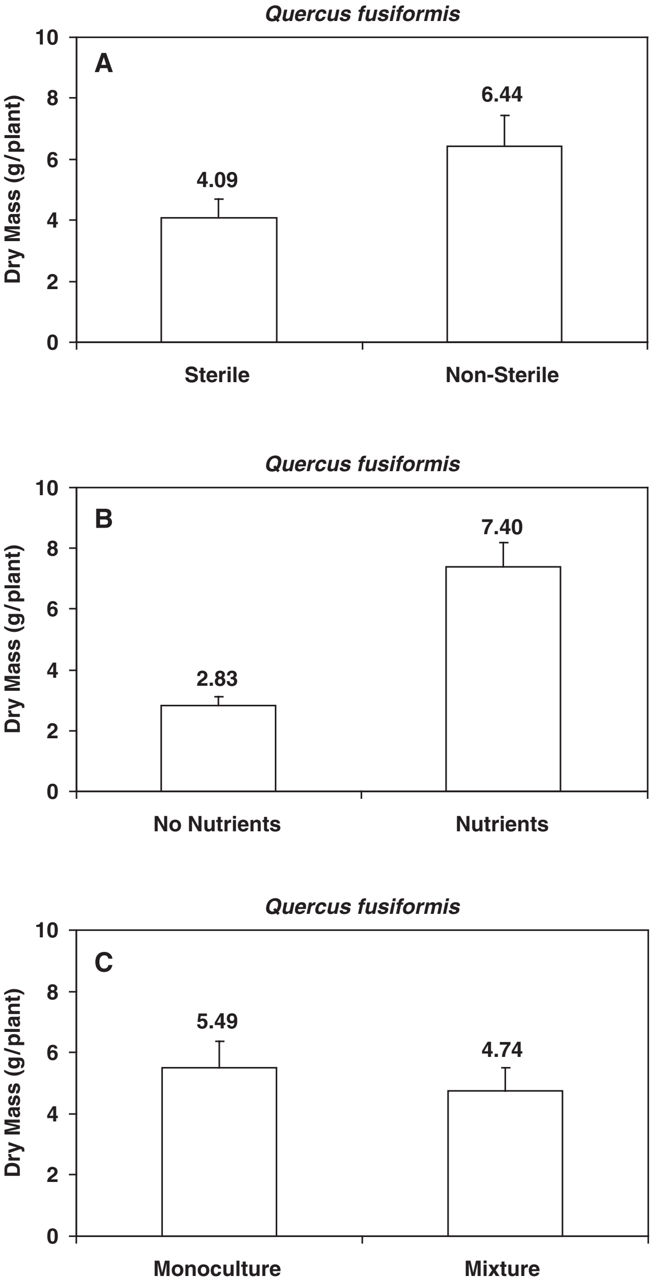


Figure 10 *Quercus virginiana* total dry mass means per plant for main effects: soil sterilization (**A**), nutrients (**B**), and competition (**C**). *Numbers above bars* are the mean values; *bars* are 1 SE

alone or in mixture with *Q. virginiana* (Figure 11C). There was no significant interaction between soil nutrients and soil sterilization for the total dry mass of *Q. virginiana*, which increased with increasing soil nutrients, regardless of soil sterilization treatment (Figure 11D). In addition, there was no significant interaction between competition and soil sterilization, although dry mass measurements were slightly higher in monoculture when compared to mixture (Figure 11E). Competition was not altered by soil nutrients; dry mass measurements were greater in monoculture than in mixture when nutrients were added, but the differences were not significant (Figure 11F).

Analyses of root:shoot ratios for *J. ashei* indicated that soil sterilization was the only significant factor (see Table 1). For *J. ashei*, root:shoot ratios were higher in sterile soil compared to nonsterile soil, indicating a shift in biomass allocation with more biomass in roots in the sterile soil compared to the nonsterile soil. There were no significant differences in root:shoot ratios for *J. ashei* between soil nutrient treatments or between types of competition. There were no significant interactions between any of the main effects. For *Q. virginiana* root:shoot ratios, the main effects (soil sterilization, soil nutrients, and competition) were not significant; however, the interaction between soil sterilization and nutrients was a significant factor (see Table 1). The significant interaction for *Q. virginiana* indicates that the root: shoot ratio response to soil sterilization was dependent on the soil nutrient level. The root:shoot ratio increased from 0.82 in sterilized soil to 1.32 in nonsterile soil. However, without nutrients, the root:shoot ratio decreased from 1.84 in sterilized soil to 0.90 in nonsterile soil. Root:shoot ratios were not significantly different in mixture and monoculture, regardless of soil sterilization or nutrient level.

Analyses of variance of percent arbuscular mycorrhizal infection in both *J. ashei* and *Q. virginiana* indicated that nutrient addition, soil sterilization, and their interaction were significant (Table 2). This result indicates that the levels of infection are dependent on the nutrient treatment for both species. For *J. ashei*, soil sterilization reduced percent infection to 0% regardless of the nutrient addition (Figure 12A). In nonsterile soil, percent infection was 48% without nutrients but only 19% with added nutrients. For *Q. virginiana* in sterilized soil, infection was 14% without nutrients and 12% when nutrients were added. However, in nonsterilized soil, percent infection was 51% without nutrient additions and 0% with nutrients (Figure 12B).

The relationship between dry mass and percent arbuscular infection is dramatic, with *J. ashei* producing almost no dry mass in sterilized soil (see Figure 9A) when the percent arbuscular mycorrhizal infection was zero (see Figure 12A). For *Q. virginiana*, the effect was not so dramatic. Total dry mass of *Q. virginiana* was reduced in sterile soil when compared to nonsterile soil; however, within the sterile soil treatment, the addition of nutrients increased total dry mass (see Figure 11D). On the other hand, percent arbuscular infection of *Q. virginiana* within the sterile soils was the same in both soil nutrient treatments (see Figure 12B), suggesting that arbuscular infection has less influence on dry mass than nutrient addition.

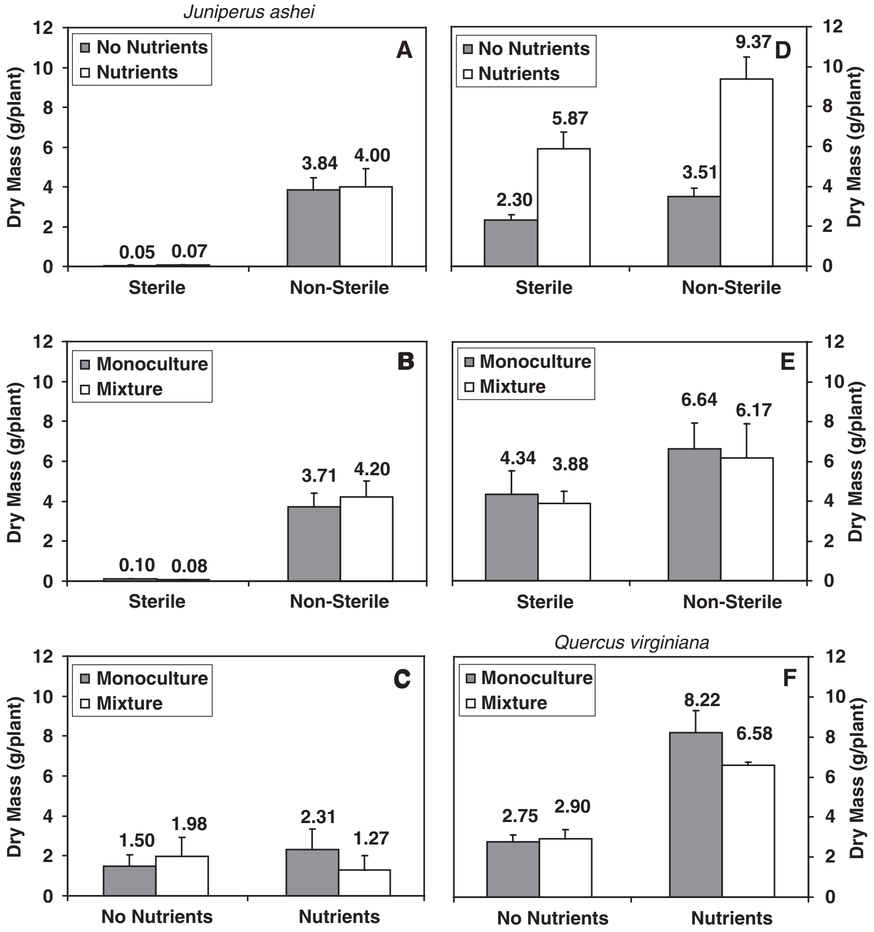


Figure 11 Interaction plots for *Juniperus ashei* and *Quercus virginiana* mean total dry mass per plant: interaction plots of soil nutrients × soil sterilization (**A, D**), competition × soil sterilization (**B, E**), and competition and soil nutrients (**C, F**). *Numbers above bars* are the mean values; *bars* are 1 SE

Table 2 Sum of squares from analyses of variance of percent infection of *Juniperus ashei* and *Quercus virginiana*, including the source of variation (sterilization and nutrients) and degrees of freedom (df)

		Juniperus ashei	*Quercus virginiana*
Source	df	Percent infection	Percent infection
Sterilization (S)	1	0.36****	0.06****
Nutrients (N)	1	0.07****	0.23****
S*N	1	0.07****	0.20****
Error	8	0.00	0.00
Total	11	0.51****	0.50****

****$P < 0.0001$.

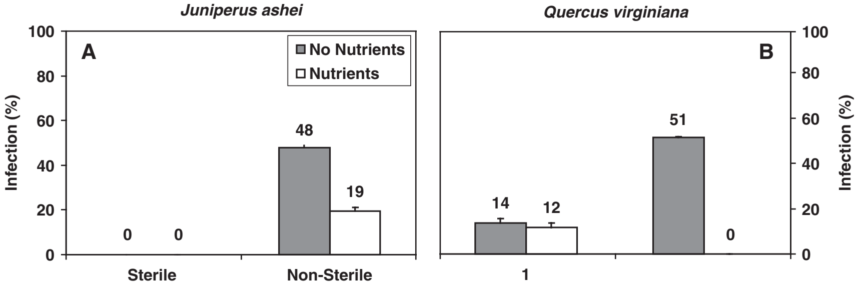


Figure 12 Results of analysis of variance (ANOVA) and interaction plots of percent vesicular-arbuscular infection of (**A**) *Juniperus ashei* and (**B**) *Quercus virginiana* for interactions of soil nutrients × soil sterilization. *Numbers above bars* are the mean values; *bars* are 1 SE

Discussion

Data from this experiment and nonquantitative photographic evidence (Salisbury and Ross 1992) indicate that at least some species of *Juniperus* are obligate mycotrophs. In addition, the results presented here suggest that the dependency on arbuscular mycorrhizae may influence distribution and establishment of *Juniperus* seedlings, possibly not by altering the competitive ability but rather by limiting their establishment in soils where the fungi are reduced or absent. Although other species of *Juniperus* have been shown to have increased growth with arbuscular mycorrhizae (Roncadori 1982; Cuenca and Lovera 1991), the obligate nature of the symbiosis has not been previously quantified.

Data presented here suggest that *Q. virginiana* seedlings have a low dependency on arbuscular mycorrhizae. Similar findings have been shown for *Q. rubra* (Dickie et al. 2001); however, at least one species, *Q. agrifolia*, has been shown to benefit from the presence of arbuscular mycorrhizae (Egerton-Warburton and Allen 2001). The dependency of *Q. virginiana* on ectomycorrhizae is uncertain because ectomycorrhizae were not quantified in this study. The growth in sterilized and nonsterilized soil was the same, so if endo- and ectomycorrhizae were killed by sterilizing of the soil, it could be inferred that the *Q. virginiana* is not dependent on endo- and ectomycorrhizae based on dry mass measurements. Ectomycorrhizae have been shown to be beneficial for some species of *Quercus* (Daughtridge et al. 1986; Egerton-Warburton and Allen 2001), but not beneficial to others (Gilman 2001).

However, drawing conclusions concerning the dependency of ectomycorrhizae from the current study should be done with caution for a number of reasons. First, there is some evidence that at least some contamination of fungi occurred in the *Quercus* treatments because the sterilized soil had higher than expected arbuscular mycorrhizal infection; this may have been caused by spores or propagules on the fruit, which were not surface sterilized. Second, contamination in greenhouses by ectomycorrhizae, even after sterilization, is common because they have small airborne spores (Trappe 1977). However, it has been shown that ectomycorrhizae are less frequent in arid hot climates (Allen et al. 1995) suggesting that contamination by ectomycorrhizae is less likely in this study. Finally, it is possible that in the nonsterile soil there was a dual arbuscular-ectomycorrhizae association or succession from arbuscular- to ectomycorrhizae, as has been shown in other *Quercus* species (Trappe 1977; Molina and Trappe 1992; Allen et al. 2003). It has been demonstrated that if both mycorrhizal types were present on *Q. agrifolia* seedlings, they may have been a carbon cost, and in turn, be less beneficial to the seedlings during the first year. In the second year, a shift to ectomycorrhizae colonization on *Q. agrifolia* occurred indicating a positive mycorrhizal effect (Egerton-Warburton and Allen 2001). The present study did not consider ectomycorrhizae or temporal changes in arbuscular mycorrhizae. If there was a shift from negative to positive effects by mycorrhizae, it would not have been detected, because measurements of growth were only taken at the end of the two years. Nevertheless, over the course of the experiment, based on dry mass measurements, mycorrhizae did not show a positive or negative effect on *Q. virginiana*.

The nonsterile, high-nutrient treatment had the highest *Q. virginiana* aboveground, belowground, and total dry mass; and also had the lowest arbuscular mycorrhizae infection. This reduced infection may suggest some mechanisms for control of mycorrhizae infection by the plant. Plants deficient in tissue P and growing in soils deficient of P are more readily colonized by arbuscular mycorrhizae than those of high-P status (Sanders 1975; Menge et al. 1978). High P in roots may regulate the rate of exchange of carbon to the fungus and perhaps reduces fungal infection. This effect may be mediated by decreasing root exudates and changing the phospholipid membrane composition, which in turn reduces membrane permeability (Graham et al. 1981). A strong correlation between arbuscular mycorrhizae colonization and mycorrhizal dependency of plants grown in P-deficient soil has been previously demonstrated (Graham et al. 1991), supporting the hypothesis that species that have root systems less dependent on mycorrhizae have evolved mechanisms to regulate mycorrhizal colonization. Mechanisms to regulate fungal colonization may have been functioning for *Q. virginiana* in this experiment. When nutrients were supplied, dry mass was highest and root P levels can be inferred to have been high, and arbuscular mycorrhizae infection was 0%. Although ectomycorrhizae were not measured, it may be inferred that their levels were also reduced.

Based on the response of these two species to soil nutrients, it seems they have different nutrient requirements and that they may establish in different areas. Data suggest that *J. ashei* may be able to grow equally well on fertile and infertile soils. This response is similar to that of *J. occidentalis*, which did not respond to nitrate and ammonium fertilization (Miller et al. 1991). Several species of *Juniperus* have been shown to colonize on nutrient-poor, disturbed sites, including *J. ashei, J. occidentalis, J. osteosperma*, and *J. virginiana* (Klopatek 1987; Miller et al. 1991; Smeins et al. 1994), suggesting that these species can tolerate low levels of soil nutrients.

Quercus virginiana is more likely to establish in areas where soil nutrients are not limiting. Several species of *Quercus* are stimulated by increased levels of soil nitrogen (Beckjord et al. 1985; Baskin and Baskin 1986). Addition of nitrogen increased the dry mass of *Q. alba* and *Q. rubra* seedlings; however, there were species-specific responses to nitrogen and carbon allocation (Beckjord et al. 1983). *Quercus alba* and *Q. rubra* total dry mass was greatest at N levels greater than 100 mg/kg, whereas the response to a phosphate gradient was species specific (Beckjord et al. 1985).

There was no indication that soil nutrient level and mycorrhizae infection were important in the competition between *J. ashei* and *Q. virginiana* seedlings. No studies have been identified that evaluate interference of woody neighbors on either *J. ashei* or *Q. virginiana*; however, competitive effects of grasses on closely related species have been found. The grass *Bouteloua gracilis* suppressed *J. pinchotii* seedlings (Smith et al. 1975), although the variation in growth of adult *J. pinchotii* could not be explained by competition from neighboring shrubs (McPherson and Wright 1989). The growth of *Q. douglasii* seedlings was negatively affected by competing annuals, but the degree of interference was dependent on the species and density of the annual (Gordon and Rice 1993). Other evidence indicates that adult *Q. douglasii* vary in root system morphology, therefore altering the level of interference imposed by neighboring species (Callaway et al. 1991).

Although soil nutrients and mycorrhizae did not affect the competition between *J. ashei* and *Q. virginiana*, there is some evidence that water limitation may be an important factor in competition between *Q. virginiana* and *J. ashei* (Fonteyn et al. 1985). Although the potential rate of photosynthesis of *Q. virginiana* is four times higher than *J. ashei* when water is available, the rates are similar when water is limiting (Owens and Knight 1992). In addition, *J. ashei* has much higher water use efficiency than *Q. virginiana* (Owens and Knight 1992). The low potential photosynthetic rates of *J. ashei* have been suggested to make it less competitive on sites with ample moisture or nutrients (Smeins et al. 1994). On sites that are drier, the low photosynthetic rate and high water use efficiency of *J. ashei* should favor it over *Q. virginiana*. Competition for water or the role that mycorrhizae might play for water uptake in these two species may be very important, especially because they differ in their mycorrhizal dependency.

The response to nutrients and soil sterilization was species specific, suggesting that seedlings of these two species respond to environmental factors rather than interference from a neighbor, at least under the experimental conditions tested. Although many species of *Juniperus* co-occur with species of *Quercus*, data presented here and elsewhere suggest that perhaps growth and establishment of *Juniperus* species are controlled more by dependency on arbuscular mycorrhizae, rather than by soil nutrients or competition from establishing or established *Quercus* species.

Summary

Approximately 95% of all terrestrial plant families have species that have mycorrhizal associations, with most of these involving a mutualistic relationship. Mycorrhizal fungi have been shown to benefit the host plant by increasing nutrient uptake and improving the water status. In many areas in North America, species of

Juniperus and *Quercus* co-occur. Several species of *Juniperus* are obligate arbuscular mycorrhizal whereas many species of *Quercus* are facultative ectomycorrhizal. Because plants occur as a continuum from nonmycorrhizal to obligate mycorrhizal, it has been suggested that mycorrhizae can change the competitive balance between plants. *Juniperus ashei* and *Q. virginiana* co-occur in the Edward's Plateau region of central Texas. The response of *J. ashei* and *Q. virginiana* to soil sterilization and soil nutrient addition seems to be a more important growth determinant than competition between the two species under the environmental conditions imposed. Growth of *J. ashei* seedlings seems to be mostly determined by the presence of mycorrhizae, whereas seedlings of *Q. virginiana* respond to increased levels of soil nutrients. Although many species of *Juniperus* co-occur with species of *Quercus*, data presented here and elsewhere suggest that growth and establishment of *Juniperus* seedlings are controlled more by dependency on arbuscular mycorrhizae, rather than by soil nutrients or competition from establishing *Quercus* seedlings.

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References

Alguacil, M., Caravaca, F., Díaz-Vivancos, P., Hernández, J., and Roldán, A. 2006. Effect of arbuscular mycorrhizae and induced drought stress on antioxidant enzyme and nitrate reductase activities in *Juniperus oxycedrus* L. grown in a composted sewage sludge-amended semi-arid soil. Plant Soil 279:209–218.

Allen, E.B., and Allen, M.F. 1986. Water relationships of xeric grasses in the field: interactions of mycorrhizas and competition. New Phytol. 104:559–571.

Allen, E.B., and Allen, M.F. 1990. The mediation of competition by mycorrhizae in successional and patchy environments. In: Perspectives on plant competition, eds. J.B. Grace and D. Tilman, pp 367–389. New York: Academic Press.

Allen, E.B., Allen, M.F., Helm, D.J., Trappe, J.M., Molina, R., and Rincon, E. 1995. Patterns and regulation of mycorrhizal plant and fungal diversity. In: The significance and regulation of soil diversity, eds. G.P. Robertson and M.J. Klug, pp 47–62. Amsterdam: Kluwer.

Allen, M.F. 1982. Influence of vesicular arbuscular mycorrhizae on water movement through *Bouteloua gracilis*. New Phytol. 91:191–196.

Allen, M.F. 1991. The ecology of mycorrhizae. Cambridge: Cambridge University Press.

Allen, M.F., Allen, E.B., and Friese, C.F. 1989. Responses of the non mycotrophic plant *Salsola kali* to invasion by vesicular-arbuscular mycorrhizal fungi. New Phytol. 111:45–49.

Allen, M.F., Swenson, W., Querejeta, J.I., Egerton-Warburton, L.M., and Treseder, K.K. 2003. Ecology of mycorrhizae: a conceptual framework for complex interactions among plants and fungi. Annu. Rev. Phytopathol. 41:271–303.

Andersen, C.P., Markhart, A.H., Dixon, R.K., and Sucoff, E.I. 1988. Root hydraulic conductivity of vesicular-arbuscular mycorrhizal green ash seedlings. New Phytol. 109:465–471.

Auge, R.M. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. Mycorrhiza 11:3–42.

Bakker, M.R., Garbaye, J., and Nys, C. 2000. Effect of liming on the ecotymycorrhizal status of oak. For. Ecol. Manag. 126:121–131.

Baskin, J.M., and Baskin, C.C. 1986. Distribution and geographical/evolutionary relationship of cedar glade endemics in southeastern United States. Assoc. Southeast. Biol. Bull. 33:138–154.

Beckjord, P.R., Melhuish, J.H., Jr., McIntosh, M.S., and Hacskaylo, E. 1983. Effects of nitrogen fertilization on growth and ectomycorrhizal formation of *Quercus alba, Q. rubra, Q. falcata*, and *Q. falcata* var. *pagodifolia*. Can. J.Bot. 61:2507–2514.

Beckjord, P.R., Melhuish, J.H., Jr., and McIntosh, M.S. 1985. Effects of nitrogen and phosphorus fertilization on growth and formation of ectomycorrhizae of *Quercus alba* and *Q. rubra* seedlings by *Pisolithus tinctorius* and *Scleroderma auranteum*. Can. J.Bot. 63:1677–1680.

Bergero, R., Perotto, S., Girlanda, M., Vidano, G., and Luppi, A.M. 2000. Ericoid mycorrhizal fungi are common root associates of a Mediterranean ectomycorrhizal plant (*Quercus ilex*). Mol. Ecol. 9:1639–1649.

Birnbaum, S.J., Borowski, F., and J.W. Wireman. 1989. Silica precipitation induced by the sulfate reducing bacterium *Desulfovibrio desulfuricans*: effects upon cell morphology and implications for preservation. In: Origin, evolution, and modern aspects of biomineralization in plants and animals, ed. R.W. Crick, pp 507–516. New York: Plenum.

Böhm, W. 1979. Methods of studying root systems. In: Ecological studies, vol.33, eds. W.D. Billings, F. Golley, O.L. Lange, and J.S. Olson, pp 1–188. New York: Springer-Verlag.

Bray, W.L. 1904. The timber of the Edwards Plateau of Texas: its relation to climate, water supply, and soil. Bulletin 47. Washington, DC: United States Department of Agriculture, Bureau of Foresty.

Brownlee, C., Duddrige, J.A., Mailbari, A., and Read, D.J. 1983. The structure and function of mycelial systems of ectomycorrhizal roots with special reference to their role in assimilate and water transport. Plant Soil 71:433–443.

Buechner, G.K. 1944. The range vegetation of Kerr County, Texas, in relation to livestock and white-tailed deer. Am. Midl. Nat. 31:697–743.

Callaway, R.M., Nadkarni, J.M., and Mahall, B.E. 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in central California. Ecology 72:1484–1499.

Clark, R.B., and Zeto, S.K. 2000. Mineral acquisition by arbuscular mycorrhizal plants. J.Plant Nutr. 23:867–902.

Cress, W.A., Throneberry, G.D., and Lindsey, D.L. 1979. Kinetics of phosphorous absorption by mycorrhizal and nonmycorrhizal tomato roots. Plant Physiol. 64:484–487.

Cuenca, G., and Lovera, M. 1991. Vesicular-arbuscular mycorrhizae in disturbed and revegetated sites from La Gran Saban, Venezuela. Can. J.Bot. 70:73–79.

Cui, M., and Nobel, P.S. 1992. Nutrient status, water uptake and gas exchange for three desert succulents infected with mycorrhizal fungi. New Phytol. 122:643–649.

Daughtridge, A.T., Pallardy, S.G., Garrett, H.G., and Sander, I.L. 1986. Growth analysis of mycorrhizal and nonmycorrhizal black oak (*Quercus velutina* Lam.) seedlings. New Phytol. 103:473–480.

Davies, F.T.J., Potter, J.R., and Linderman, R.G. 1992. Mycorrhiza and repeated drought exposure affect drought resistance and extraradical hyphae development of pepper plants independent of plant size and nutrient content. J.Plant Physiol. 139:289–294.

Dickie, I.A., Koide, R.T., and Fayish, A.C. 2001. Vesicular-arbuscular mycorrhizal infection of *Quercus rubra* seedlings. New Phytol. 151:257–264.

Egerton-Warburton, L., and Allen, M. 2001. Endo- and ectomycorrhizas in *Quercus agrifolia* Nee. (Fagaceae): patterns of root colonization and effects on seedling growth. Mycorrhiza 11:283–290.

Egerton-Warburton, L.M., Graham, R.C., and Hubbert, K.R. 2003. Spatial variability and water availability in a soil-weathered bedrock profile. Plant Soil 249:331–342.

Faber, B.A., Zasoski, R.J.Z., and Munns, D.N. 1991. A method for measuring hyphal nutrient and water uptake in mycorrhizal plants. Can. J. Bot. 69:87–94.

Fitter, A.H. 1977. Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. New Phytol. 79:119–125.

Fonteyn, P.J., McClean, T.M., and Akridge, R.E. 1985. Xylem pressure potentials of three dominant trees of the Edwards Plateau of Texas. Southwest. Nat. 30:141–146.

Gilman, E.F. 2001. Effect of nursery production method, irrigation, and inoculation with mycorrhizae-forming fungi on establishment of *Quercus virginiana*. J.Arbor. 27:30–39.

Giovannetti, M., and Mosse, B. 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New Phytol. 84:489–500.

Gordon, D.R., and Rice, K.J. 1993. Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. Ecology 74:68–82.

Gould, F.W. 1969. Texas plants: a checklist and ecological summary. Bulletin MP-585. College Station: Texas Agricultural Experiment Station.

Graham, J.H., Leonard, R.T., and Menge, J.A. 1981. Membrane-mediated decrease in root exudation responsible for phosphorus inhibition of vesicular-arbuscular mycorrhiza formation. Plant Physiol. 68:548–552.

Graham, J.H., Eissenstat, D.M., and Drouillard, D.L. 1991. On the relationship between a plant's mycorrhizal dependency and rate of vesicular-arbuscular mycorrhizal colonization. Funct. Ecol. 5:773–779.

Grand, L.F. 1969. A beaded endotrophic mycorrhiza of northern and southern red oak. Mycologia 61:408–109.

Hall, I.R. 1978. Effects of endomycorrhizas on the competitive ability of white clover. N.Z.J. Agric. Res. 21:509–515.

Hardie, K. 1985. The effect of removal of extraradical hyphae on water uptake by vesicular-arbuscular mycorrhizal fungi. New Phytol. 153:335–344.

Harley, J.L., and Smith, S.E. 1983. Mycorrhizal symbiosis. New York: Academic Press.

Hartnett, D.C., Hetrick, B.A.D., Wilson, G.W.T., and Gibson, D.J. 1993. Mycorrhizal influence on intra- and interspecific neighbor interactions among co-occurring prairie grasses. J.Ecol. 81:787–795.

Haskins, K.E., and Gehring, C.A. 2004. Long-term effects of burning slash on plant communities and arbuscular mycorrhizae in a semi-arid woodland. J. Appl. Ecol. 41:379–388.

Hatch, S.L., Gandi, K.N., and Brown, L.E. 1990. Checklist of the vascular plants of Texas. Publication MP-1655. College Station, TX: Texas A & M University System, Texas Agricultural Experiment Station.

Hetrick, B.A.D., Wilson, G.T., Kitt, D.G.K., and Schwab, A.P. 1988. Effects of soil microorganisms on mycorrhizal contribution to growth of big bluestem grass in non-sterile soil. Soil Biol. Biochem. 20:501–507.

Hetrick, B.A.D., Hartnett, D.C., Wilson, G.W.T., and Gibson, D.J. 1994. Effects of mycorrhizae, phosphorus availability, and plant density on yield relationships among competing tallgrass prairie species. Can. J.Bot. 72:168–176.

Hodge, A. 2003. Plant nitrogen capture from organic matter as affected by spatial dispersion, interspecific competition and mycorrhizal colonization. New Phytol. 157:303–314.

Ibrahim, M.A., Campbell, W.F.C., Rupp, L.A., and Allen, E.B. 1990. Effects of mycorrhizae on sorghum growth, photosynthesis, and stomatal conductance under drought conditions. Arid Soil Res. Rehabil. 4:99–107.

Klopatek, J.M. 1987. Nitrogen mineralization and nitrification in mineral soils of pinyon-juniper ecosystems. Soil Sci. Soc. Am. J.51:453–457.

Kothari, S.K., Marschner, H., and George, E. 1990. Effect of VA mycorrhizal fungi and rhizosphere microorganisms on root and shoot morphology, growth and water relations in maize. New Phytol. 116:303–311.

Landhäusser, S.M., Muhsin, T.M., and Zwiazek, J.J. 2002. The effect of ectomycorrhizae on water relations in aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) at low soil temperatures. Can. J.Bot. 80:684–689.

Liu, A., Hamel, C., Hamiliton, R.I., Ma, B.L., and Smith, D.L. 2000. Acquisition of Cu, Zn, Mn, and Fe by mycorrhizal maize (*Zea mays* L.) grown in soil at different P and micronutrient levels. Mycorrhiza 9:331–336.

Maestre, F.T., Bautista, S., Cortina, J., Diaz, G., Honrubia, M., and Vallejo, R. 2002. Microsite and mycorrhizal inoculum effects on the establishment of *Quercus coccifera* in a semi-arid degraded steppe. Ecol. Eng. 19:289–295.

Maronek, D.N., Hendrix, J.W.H., and Kiernan, J.1980. Differential growth response to the mycorrhizal fungus *Glomus fasiculatum* of Southern magnolia and Bar Harbor juniper grown in containers in composed hardwood bark-shale. J. Am. Soc. Hortic. Sci. 105:206–208.

Marschner, H., and Dell, B. 1994. Nutrient uptake in mycorrhizal symbiosis. Plant Soil 159:89–102.

Marulanda, A., Azcon, R., and Ruiz-Lozano, J.M. 2003. Contribution of six arbuscular mycorrhizal fungal isolates to water uptake by *Lactuca* sativa plants under drought stress. Physiol. Plant. 119:526–533.

McPherson, G.R., and Wright, H.A. 1989. Direct effects of competition on individual juniper plants: a field study. J. Appl. Ecol. 26:979–988.

Menge, J.A., Steirle, D., Bagyaraj, D.J., Johnson, E.L.V., and Leonard, R.T. 1978. Phosphorus concentrations in plants responsible for inhibition of mycorrhizal infection. New Phytol. 80:575–578.

Michelsen, A., and Rosendahl, S. 1990. The effect of VA mycorrhizal fungi, phosphorus and drought stress on the growth of *Acacia nilotica* and *Leucaena leucocephala* seedlings. Plant Soil 124:7–13.

Miller, P.M., Eddleman, L.W., and Miller, J.M. 1991. The response of juvenile and small adult western juniper (*Juniperus occidentalis*) to nitrate and ammonium fertilization. Can. J.Bot. 69:2344–2352.

Miller, R.F., and Wigand, P.W. 1994. Holocene changes in semiarid pinyon-juniper woodlands. BioScience 44:465–474.

Mitchell, J., Cox, S., Dixon, K., Garrett, E., and Sander, L. 1984. Inoculation of three *Quercus* spcies with eleven isolates of ectomycorrhizal fungi. II. Foliar nutrient content and isolate effectiveness. For. Sci. 30:563–572.

Molina, R., and Trappe, J.M. 1992. Specificity phenomena in mycorrhizal symbiosis: community-ecological consequences and practical implications. In: Mycorrhizal functioning: an integrative plant-fungal process, ed. M. Allen, pp 357–423. New York: Chapman & Hall.

Moora, M., and Zobel, M. 1996. Effect of arbuscular mycorrhiza on inter- and intraspecific competition of two grassland species. Oecologia (Berl.) 108:79–84.

Muhsin, T.M., and Zwiazek, J.J. 2002. Ectomycorrhizas increase apoplastic water transport and root hydraulic conductivity in *Ulmus americana* seedlings. New Phytol. 153:153–158.

Nelson, L.L., and Allen, M.F. 1993. Restoration of *Stipa pulchra* grasslands: effects of mycorrhizae and competition from *Avena barbata*. Restor. Ecol. 1:40–50.

Newman, E.I. 1966. A method of estimating the total length of root in a sample. J. Appl. Ecol. 3:139–145.

Newton, A.C., and Pigott, C.D. 1991. Mineral nutrition and mycorrhizal infection of seedling oak and birch. I. Nutrient uptake and the development of mycorrhizal infection during seedling establishment. New Phytol. 117:37–44.

Owens, M.K., and Knight, R.W. 1992. Water use on rangelands. In: Water for south Texas. CPR 5043-5046. College Station: Texas Agricultural Experiment Station.

Perry, D.A., Margolis, H., Choquette, C., Molina, R., and Trappe, J.M. 1989. Ectomycorrhizal mediation of competition between coniferous tree species. New Phytol. 112:501–511.

Phillips, J.M., and Hayman, D.S. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Br. Mycol. Soc. 55:158–161.

Reinsvold, R.J., and Reeves, F.B. 1986. The mycorrhizae of *Juniperus osteosperma*: identity of the vesicular-arbuscular mycorrhizal symbiont, and resynthesis of VA mycorrhizae. Mycologia 78:108–113.

Roncadori, R.W. 1982. Growth of *Juniperus chinensis* var. *sargentii* as influenced by vesicular-arbuscular mycorrhizae and soil fertility. HortScience 17:917–918.

Rothwell, F., Hacskaylo, E., and Fisher, D. 1983. Ecto- and endomycorrhizal fungus associations with *Quercus imbricaria* L. Plant Soil 71:309.

Ruiz-Lazano, J.M., and Azcon, R. 1995. Hyphal contributions to water uptake in mycorrhizal plants as affected by the fungal species and water stress. Physiol. Plant. 95:472–478.

Salisbury, F.B., and Ross, C.W. 1992. Plant physiology. Belmont, CA: Wadsworth.

Sanders, F.E. 1975. The effect of foliar applied phosphate on mycorrhizal infections on onion roots. In: Endomyorrhizas, eds. F.E. Sanders, B. Moss, and P.B. Tinker, pp 261–277. London: Academic Press.

Schwarzott, D., Walker, C., and Schussler, A. 2001. *Glomus*, the largest genus of arbuscular mycorrhizal fungi (Glomales), is nonmonophyletic. Mol. Phylogenet. Evol. 21:190–197.

Smeins, F.E., Owens, M.K., and Fuhlendorf, S.D. 1994. Biology and ecology of Ashe (blueberry) juniper. In: Juniper symposium, 1994, pp 9–24. Sonora, TX: Texas Agricultural Experiment Research Station.

Smith, M.A., Wright, H.A., and Schuster, J.L. 1975. Reproductive characteristics of redberry juniper. J.Range Manag. 35:126–128.

Smith, S.E., and Read, D.J. 1997. Mycorrhizal symbiosis. London: Cambridge University Press.

Taylor, F.B., Hailey, R.B., and Richmond, D.L. 1966. Soil survey of Bexar County, Texas. Washington, DC: United States Department of Agriculture, Soil Conservation Service.

Tiedemann, A.R., and Klemmedson, J.O. 1986. Long term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. Soil Sci. Soc. Am. J.50:472–475.

Trappe, J.M. 1977. Selection of fungi for ectomycorrhizal inoculation in nurseries. Annu. Rev. Phytopathol. 15:203–222.

Trappe, J.M. 1987. Phylogenetic and ecologic aspects of mycotrophy in the Angiosperms from an evolutionary standpoint. In: Ecophysiology of VA mycorrhizal plants, ed. G.R. Safir, pp 5–25. Boca Raton: CRC Press.

Van Auken, O.W. 1993. Size distribution patterns and potential population change of some dominant woody species of the Edwards Plateau Region of Texas. Tex. J.Sci. 45:199–210.

Van Auken, O.W., Ford, A.L., and Allen, J.L. 1981. An ecological comparison of upland deciduous and evergreen forests of central Texas. Am. J.Bot. 68:1249–1256.

Wallander, H. 2004. A new hypothesis to explain allocation of dry matter between mycorrhizal fungi and pine seedlings in relation to nutrient supply. Plant Soil 243:168–169.

Watson, G.W., von der Heide-Spavka, K.G., and Howe, V.K. 1990. Ecological significance of endo-/ectomycorrhiza in the oak sub-genus *Erthrovalanus*. Arbor. J.14:107–116.

Wells, P.V. 1965. Scarp woodlands, transported grassland soils, and concept of grassland climate in the Great Plains Region. Science 148:246–249.

West, H.M. 1996. Influence of arbuscular mycorrhizal infection on competition between *Holucus lanatus* and *Dactylis glomerata*. J.Ecol. 84:429–438.

Section 2

Encroachment: Community Changes

7

Ecological Impacts of Ashe Juniper on Subtropical Savanna Parklands and Woodlands

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Introduction

Savannas are inherently patchy systems where the distribution and abundance of the two dominant plant growth forms (woody plants and grasses) varies greatly over space and time in response to grazing, browsing, fire, drought, and topographic/edaphic factors (Huntley and Walker 1982; Scholes and Archer 1997). In recent times, the balance between woody plants and grasses has been disrupted in many savannas around the world as woody plants have increased in abundance at the expense of herbaceous cover and production (Van Auken 2000; Archer 2005). This woody plant proliferation is thought to be driven primarily by intensification of livestock grazing and reduced fire frequency (Archer et al. 1995), although other factors (e.g., elevated atmospheric CO_2 concentration and increased atmospheric nitrogen deposition) may also contribute (Polley et al. 1996; Köchy and Wilson 2001). Regardless of the cause, this vegetation change has the potential to alter a number of fundamental ecosystem properties, including productivity, biological diversity, biogeochemistry, and energy exchange, which can influence ecosystem processes at regional (Archer et al. 2001; Jackson et al. 2002; Huxman et al. 2005) and global scales (Schlesinger et al. 1990; Goodale and Davidson 2002).

Although woody plant encroachment is a general phenomenon of many contemporary savannas, not all woody species present in savannas show this increase and, indeed, some appear to be stable or declining in abundance (Allen-Diaz et al. 1999; Van de Vijver et al. 1999; Weltzin and McPherson 1999). A case in point is the Edwards Plateau of Texas, USA. The Edwards Plateau is a major natural region that covers about 93,000 km^2 in the west-central part of Texas (Figure 1, inset). At present, much of the vegetation of this region is classified as live oak–Ashe juniper savanna (parkland + woodland; McMahan et al. 1984). Plateau live oak (*Quercus virginiana* P. Miller var. *fusiformis* (J.K. Small) C. Sargent) is a sprouting, fire-resistant species (Muller 1951) that is thought to have been common in upland savanna parklands of the Edwards Plateau for centuries (Olmstead 1857; Buechner 1944). Populations of Plateau live oak appear to have remained static or declined in recent times (Russell and Fowler 1999), and in some cases may be displaced by Ashe juniper (Owens 1996; Smeins and Fuhlendorf 1997; Wu et al. 2001).

O.W. Van Auken (ed.), *Western North American Juniperus Communities: A Dynamic Vegetation Type.*

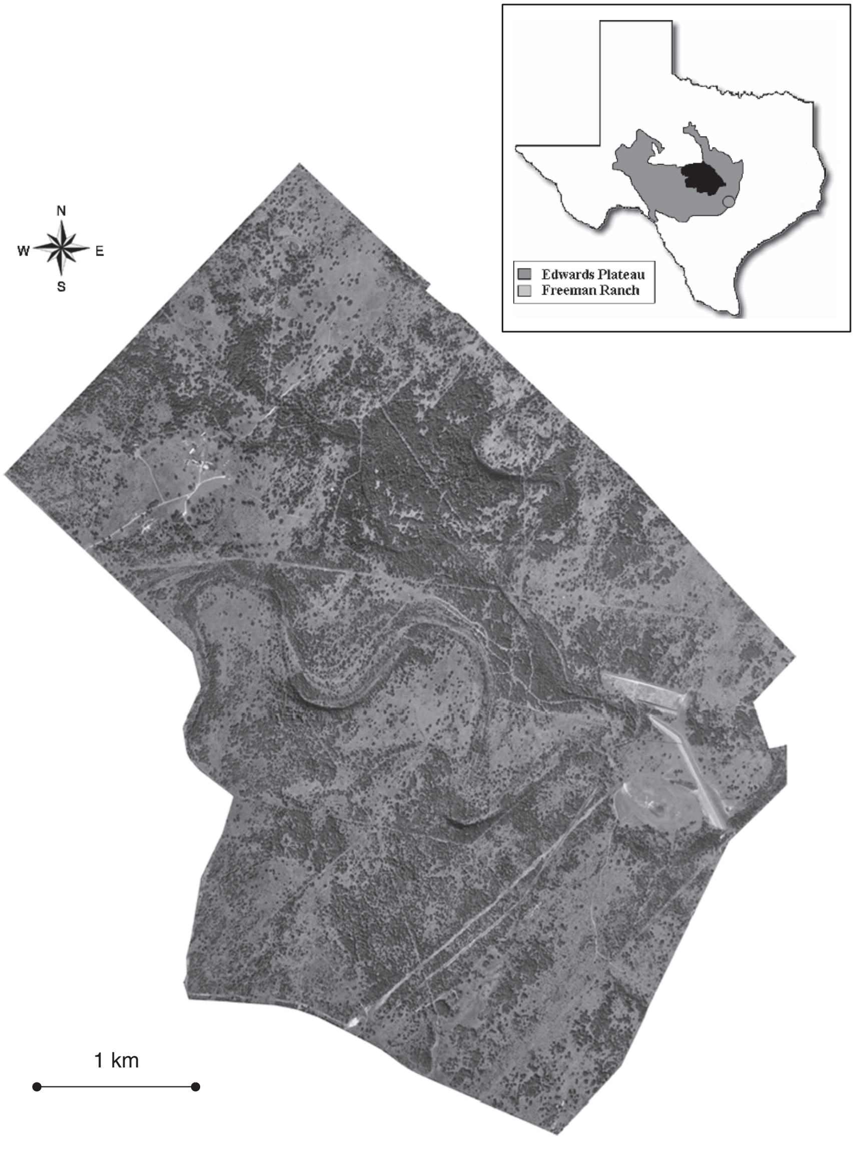

Figure 1 Aerial photograph of the Texas State University Freeman Ranch and location of the Freeman Ranch on the eastern edge of the Edwards Plateau of Texas (*inset*). Darkened area within the Edwards Plateau (*shaded area*) is the Llano Uplift. Data are from images taken in January 1995

In contrast, Ashe juniper (*Juniperus ashei* J. Buchholz) is a nonsprouting, fire-sensitive species (Fonteyn et al. 1988; Fuhlendorf et al. 1996), which is thought to have been restricted to fire-protected refugia (e.g., rocky outcrops, steep cliffs, or drainages) in the past (Foster 1917; Smeins 1980; Diamond et al. 1995; Terletzky and

Van Auken 1996). Following Anglo-European settlement and suppression of fire (ca. 150 years B.P.), this species has apparently increased in abundance in these savannas, where it often forms dense, nearly monospecific thickets (Van Auken et al. 1981; Smeins and Merrill 1988; Blomquist 1990; Fuhlendorf and Smeins 1997; Wu et al. 2001; see Van Auken and McKinley, Chapter 2, this volume).

The degree and extent of Ashe juniper increase on the Edwards Plateau, especially in the eastern part of this region, however, remains controversial (see Diamond and True, Chapter 3, this volume; Van Auken and Smeins, Chapter 1, this volume). Consequently, it is unknown what the balance of woody and herbaceous vegetation was in these savannas before settlement, and this leads to uncertainty in efforts aimed at restoring these savannas to historic conditions. Also, while considerable attention has been given to understanding the impacts of junipers, including Ashe juniper, on grassland production and diversity, biogeochemistry, and hydrology (McPherson and Wright 1990; Dye et al. 1995; Fuhlendorf et al. 1997; Wu et al. 2001; Hoch et al. 2002; see Engle et al., Chapter 14; McKinley et al., Chapter 9; Knapp et al., Chapter 8; Owens, Chapter 10; Wilcox, Chapter 11, this volume), less is known about how these effects compare to those of other woody species, such as the noninvasive Plateau live oak. This lack of understanding is particularly relevant for the Edwards Plateau where Ashe juniper is but one of many woody species that occur in these savannas.

In this chapter, we summarize research conducted over the past decade that has examined various aspects of the ecology of Ashe juniper in the subtropical savannas of the eastern Edwards Plateau. The site where this research was conducted is considered typical of many areas of the central and western United States where various species of *Juniperus* are increasing in density in adjacent communities. Our goal has been to place the ecological impacts of the invasive Ashe juniper in some historical perspective and in relation to other woody species, especially Plateau live oak. Specifically, we here (1) characterize the contemporary woody vegetation in relation to soils and topography, to better understand factors influencing the current distribution and abundance of Ashe juniper and other woody species and to gauge the potential for additional juniper/woody plant increase in the future; (2) examine historical changes in woody patches that are currently dominated by Ashe juniper and Plateau live oaks to clarify the long-term stability and persistence of these prominent woody elements; (3) determine effects of Ashe juniper and Plateau live oak on soils and seed banks; and (4) experimentally test whether established Ashe junipers compete with Plateau live oaks during grassland-to-woodland succession. We conclude with a brief discussion of some of the implications of these impacts for savanna restoration and long-term vegetation change in this region.

Study Site

Studies were conducted at the 1700-ha Texas State University Freeman Ranch, Hays County, Texas (29°56′ N, 98° W) located within the Balcones Canyonlands subregion of the eastern Edwards Plateau of central Texas, USA (see Figure 1).

The climate of this location is classified as subtropical–subhumid with mean annual temperature and precipitation of 19.4°C and 857 mm, respectively (Dixon 2000). The majority of soils at the Freeman Ranch have been classified in the Rumple-Comfort association and the Comfort-Rock outcrop complex (Batte 1984). These soils are shallow (typically 30 cm or less), clay-rich (mean clay content of near-surface soil = 40%; Jessup 2001), well-drained Argiustolls that have developed over indurated limestone. Topographically, the majority of the ranch consists of level to undulating terrain [elevation, 204–274 m above sea level (asl)], but steep north- and south-facing slopes and escarpments do occur along intermittent drainages (see Figure 1). Therefore, a diversity of habitats that differ in soils, exposure, and microclimate exist on the ranch, supporting a mixture of vegetation types ranging from relatively open parklands in uplands to near closed canopy woodlands on slopes and along drainages. Although long-term records are incomplete, it is thought that the Freeman Ranch has experienced moderate to heavy grazing pressure by domestic livestock since the mid-1800s. At present, grazing pressure is less than in the past, although much of the property continues to be grazed by cattle, sheep, and goats.

Contemporary Vegetation Patterns

Classification of broad vegetative cover types (woody versus herbaceous = grassy) using digital color infrared (IR) aerial images indicates that, for the Freeman Ranch as a whole, the aerial cover of herbaceous and woody-dominated patches is approximately equal (grass = 48.4%; woody = 49.3%) at present. Across this landscape, grasses and woody plants occur on all soil types and terrains, yet the relative abundance of these cover types differs in relation to topography and soils (Figure 2). In particular, woody plants tend to dominate the shallower Comfort-Rock soils, whereas grasses dominate the deeper Rumple-Comfort soils, in both uplands and lowlands. In addition, grasslands generally are more abundant on level, undulating terrain, whereas woodlands dominate the steeper slopes (>5°). This woody dominance is greater on the cooler, shaded north-facing slopes than the more exposed south-facing slopes.

Although woody plants occupy a diversity of habitats on the Freeman Ranch, there are distinct differences in the composition and structure of woody plant communities in these habitats (Figure 3; Table 1). In the uplands, most woody plants are highly aggregated in discrete tree/shrub clusters (locally referred to as "mottes"; Knight et al. 1984), scattered among grasslands in a relatively open parkland setting. In many cases, these woody clusters contain one or several central Plateau live oak trees with a dense growth of shrubs in the understory (Figure 3A). As many as 20 different shrub species can be found in these live oak clusters, but typically only 5 to 11 species occur in any given cluster (Phillips and Barnes 2003). Ashe juniper is the dominant species in the understory and, overall, is the co-dominant with the overstory Plateau live oak in these clusters (see Table 1). In general, the live oaks in these uplands parklands tend to be larger than in the other woody communities,

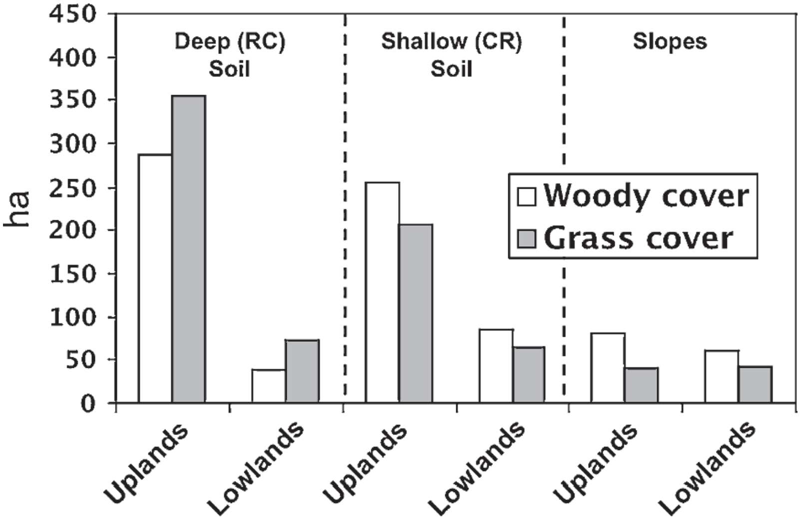

Figure 2 Land surface area of the Freeman Ranch covered by woody and herbaceous (grass) vegetation in relation to soils and topography. Shallow (*CR*) and deep (*RC*) soils refer to Comfort-Rock (thin, rocky soils) and Rumple-Comfort (slightly deeper, less rocky soils) soils, respectively. Uplands and lowlands were delineated based on elevation (uplands, 232–287 m above sea level; lowlands, 204–232 m above sea level; using USGS digital elevation models, 30-m resolution). Slope habitats were defined as areas where slope inclinations exceeded 5°. Soil data were obtained from digitized maps of Batte (1984). These soil and topographic features were then integrated using ARC/VIEW GIS software to produce different topoedaphic habitats. Classification of cover was based on the 1-m resolution DOQQ aerial color infrared image using MultiSpec image analysis software and ground-based sampling in mixed-species grasslands (5 × 5 m quadrats) and monospecific stands of Plateau live oaks and Ashe juniper (10 × 10 m quadrats) at selected geo-referenced locations. Approximately 2% of the landscape consisted of nonvegetated surfaces (e.g., roads, buildings, and exposed rock or caliche)

and individual live oak trees in these clusters commonly have a basal diameter exceeding 80 cm (Figure 4B).

In contrast to the relatively open parklands, woody plants occur in higher densities (see Table 1) and form near closed canopy woodlands on slopes and along drainages. The most extensive woodland type at the Freeman Ranch is a mixed evergreen woodland that occurs on gentle upland slopes where soils are shallow and rocky (see Figure 3B). Ashe juniper currently dominates both the overstory and understory strata in these evergreen woodlands (see Table 1; Barnes et al. 2000). Texas persimmon (*Diospyros texana*), a facultative evergreen small tree/shrub (Nelson et al. 2002), is an important understory species in this community. Although Plateau live oak is common in these evergreen woodlands, its relative abundance is considerably less here than in the parklands. Woody species richness in this community is similar to that in the other woody habitats, but woody plant density is less here than in the deciduous woodlands (Table 1). In general, these evergreen woodlands at the Freeman Ranch appear similar in species composition

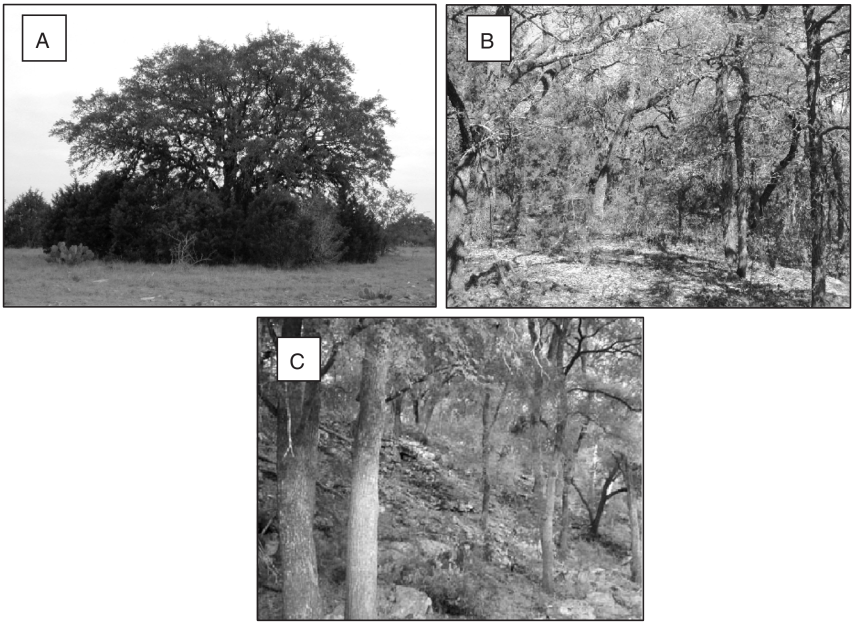

Figure 3 Examples of the three major woody plant communities at the Texas State University Freeman Ranch. Savanna parklands occur in uplands and consist of grasslands and discrete live oak clusters (**A**) that typically possess a central Plateau live oak tree and a mixed-species woody understory dominated by Ashe juniper. Mixed evergreen woodlands (**B**) occur in uplands and on dry, gentle slopes, whereas deciduous woodlands (**C**) are restricted to shaded, north-facing slopes along intermittent drainages and in narrow canyons

and dominance to the evergreen woodlands/scrub forests of the southeastern Edwards Plateau previously described by Van Auken et al. (1981) and Van Auken (1988).

Deciduous woodlands are restricted to north-facing slopes associated with intermittent drainages, narrow canyons, and escarpments (see Figure 3C). In a strict sense, these woodlands are composed of a mixture of deciduous and evergreen woody species (see Table 1). However, there is (or at least has been historically) a stronger deciduous element in these mesic deciduous woodlands than in the drier evergreen woodlands, and there are certain deciduous species (*Cercis canadensis, Morus microphylla, Ungnadia speciosa*, and others) that are restricted to these deciduous woodlands (Table 1). Aspects of this community are often evident as narrow strips of deciduous woods/forests that occur in association with spring seeps and steep canyon walls (Van Auken et al. 1981). These deciduous forests have strong floristic affinities with more eastern deciduous forests (Van Auken et al. 1981) and are distinct in species composition from the drier evergreen woodlands (Gelbach 1988; Van Auken 1988). Here, we use the term "deciduous woodlands" in a general sense to describe all woody vegetation on north-facing slopes; this

Table 1 Relative ranks of common woody plant species in different communities at the Texas State University Freeman Ranch

		Woody community type		
Species	Growth form	Live oak clusters	Evergreen woodland	Deciduous woodland
Quercus virginiana var. *fusiformis*	Evergreen tree	1	5	6
Juniperus ashei	Evergreen tree/shrub	2	1	1
Diospyros texana	Evergreen tree/shrub	3	2	2
Celtis spp.	Deciduous tree	4	7	5
Forestiera pubescens	Deciduous shrub	5	4	Present
Ulmus crassifolia	Deciduous tree	6	3	3
Berberis trifoliata	Evergreen shrub	7	6	Present
Sideroxylon lanuginosum	Evergreen shrub	8	Present	9
Ilex decidua	Deciduous shrub	9	9	Present
Prosopis glandulosa	Deciduous tree	10	Absent	Absent
Quercus buckleyi	Deciduous tree	Present	8	8
Eysenhardtia texana	Deciduous shrub	Absent	10	Absent
Sophora secundiflora	Evergreen shrub	Present	Present	4
Ilex vomitoria	Evergreen shrub	Present	Present	7
Garrya ovata	Evergreen shrub	Absent	Absent	10
Number of woody species		21	19	20
Woody plant density (number/ha)		900	3100	4200

Only the ranks of the top 10 species are shown. If a species occurs within a community but is ranked below 10, it is indicated as "present." Species not encountered in sampling are indicated as "absent." Data are for combined overstory and understory strata and are based on importance values that include measures of canopy cover and frequency (clusters), basal cover and density (evergreen woodlands), and basal cover, density, and frequency (deciduous woodland). Live oak cluster data are from 20 discrete clusters in upland savanna parklands (Phillips 1999). Evergreen woodland data are from point-centered quarter sampling (192 points; Barnes et al. 2000). Deciduous woodland data are from ten 10 × 10 m quadrats (Elliott 2004). Species richness data are from Barnes et al. (2000), Ramirez (2002), Phillips and Barnes (2003) and Elliott (2004). Density data are from Elliott (2004), where data for live oak clusters are for the entire parkland habitat (grassland + woody clusters). Nomenclature follows Jones et al. (1997).

encompasses the narrow strip deciduous forests as well as the surrounding woodlands.

At present, the deciduous woodlands at the Freeman Ranch are dominated by Ashe juniper, Texas persimmon, and cedar elm (*Ulmus crassifolia*; see Table 1). Plateau live oak is less abundant here than in the evergreen woodlands. The deciduous Texas oak (*Q. buckleyi*) is often considered a characteristic overstory species of these deciduous woodlands (Van Auken et al. 1981), but our data indicate that this species is presently not a dominant in these habitats at the Freeman Ranch. Similarly, other deciduous tree species, such as black cherry (*Prunus serotina*),

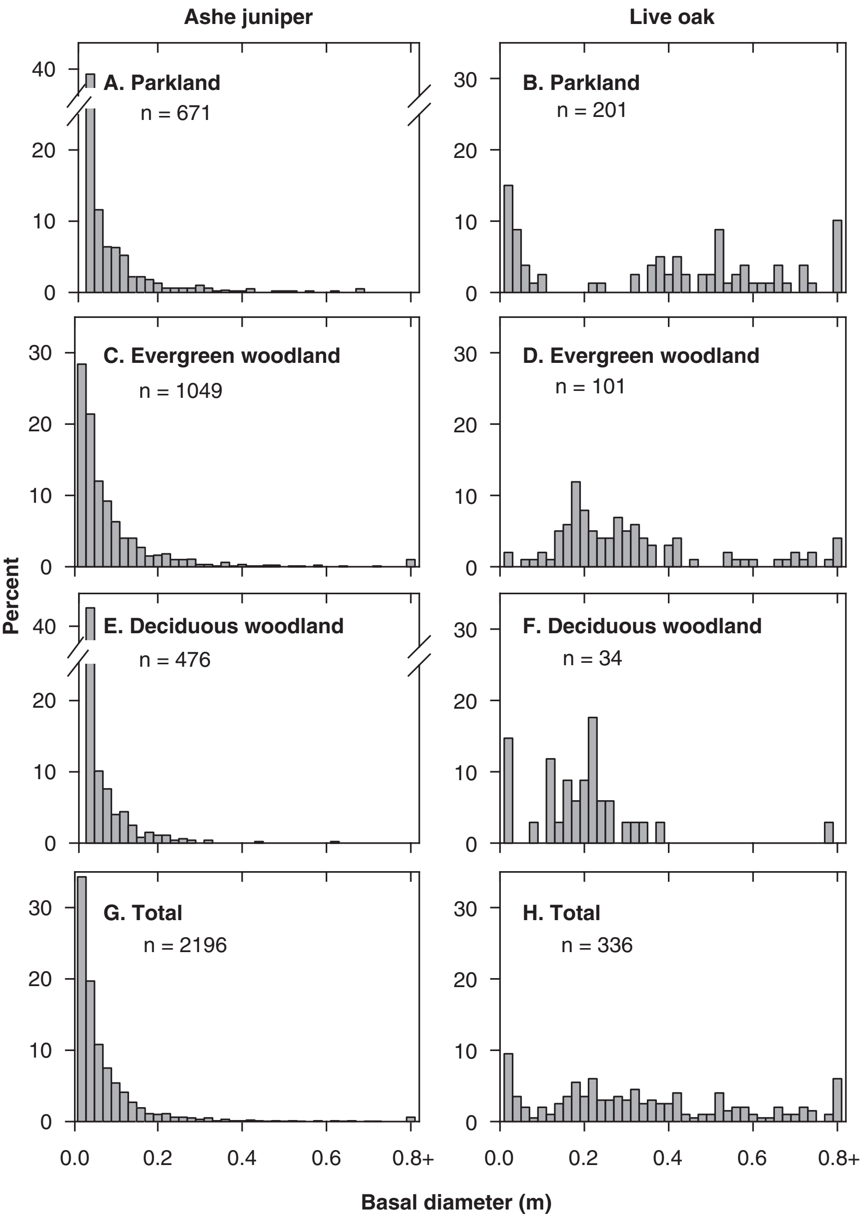

Figure 4 Frequency distributions of stem basal diameters for Ashe juniper and Plateau live oak in three woody plant communities at the Texas State University Freeman Ranch. Data for parklands are from 20 individual live oak clusters (Phillips 1999) and ten 10 × 10 m quadrats (Elliott 2004). Data for the other communities are from 20 (evergreen woodland) and 10 (deciduous woodland) 10 × 10 m quadrats (Elliott 2004)

Texas ash (*Fraxinus texensis*), and black walnut (*Juglans nigra*), which have previously been reported to be common in the deciduous forests of north-facing slopes on the eastern Edwards Plateau (Van Auken et al. 1981; Van Auken 1988), are notably absent or rare in these habitats on the Freeman Ranch. Demographic studies suggest that adult recruitment is not occurring in these hardwoods at a number of locations in this region (Van Auken 1993; Russell and Fowler 2002). It is unknown whether these species were historically more abundant in the deciduous woodlands at the Freeman Ranch than they are today.

Our vegetation sampling therefore indicates that, at present, Ashe juniper dominates or co-dominates each of the three major woody communities (live oak clusters, evergreen woodlands, and deciduous woodlands) at the Freeman Ranch. Size distributions of this species are similar in the three communities, and all show a strong bias toward the smallest size-classes (Figure 4). Few junipers with basal stem diameters exceeding 20 cm are found in any habitat. Similar size distributions for this species have previously been reported by Van Auken (1993). These demographic features are suggestive of rapidly expanding populations in all habitats at the Freeman Ranch. In contrast, populations of Plateau live oak possess fewer small individuals, and there is a dearth of intermediate- (Figure 4B) and large-sized plants (Figure 4F) in certain habitats. For this species, most of the smallest size-classes consist of vegetative root sprouts and not true seedlings or saplings. Even many mature live oaks consist of multiple, clonal stems. Thus, it is difficult to evaluate size–age relationships and sexual regeneration in this species. Nonetheless, it appears that this species exhibits demographic attributes associated with static or declining populations (Russell and Fowler 2002).

Historical Changes in Woody Patches

As already indicated, historical accounts and analyses (Olmstead 1857; Krueger 1976; Weniger 1988; Goyne 1991; Taylor and Smeins 1994; Van Auken and Smeins, Chapter 1, this volume) suggest that the current vegetation of this region has been greatly altered from its pre-settlement condition by Anglo-Europeans who arrived 150 to 200 years ago. However, this is somewhat controversial, and there are other opinions (see Diamond and True, Chapter 3, this volume). In general, the native grasslands are thought to have experienced decreases in C_4 tall- and midgrasses, while experiencing increases in C_4 shortgrasses, C_3 grasses, and C_3 forbs in response to chronic or intense grazing by domestic livestock (Smeins and Merrill 1988). Associated with these changes in the grasslands has been an increase in some but not all woody (C_3) plants (Van Auken 1993; Fuhlendorf and Smeins 1997). Evidence for the historical distribution and abundance of the two most prominent woody plant types (i.e., Plateau live oaks and Ashe juniper) is, however, largely anecdotal and therefore often biased, imprecise, and sometimes even contradictory (Smeins 1980; Smeins and Fuhlendorf 1997; Diamond and True, Chapter 3; Van Auken and Smeins, Chapter 1, this volume).

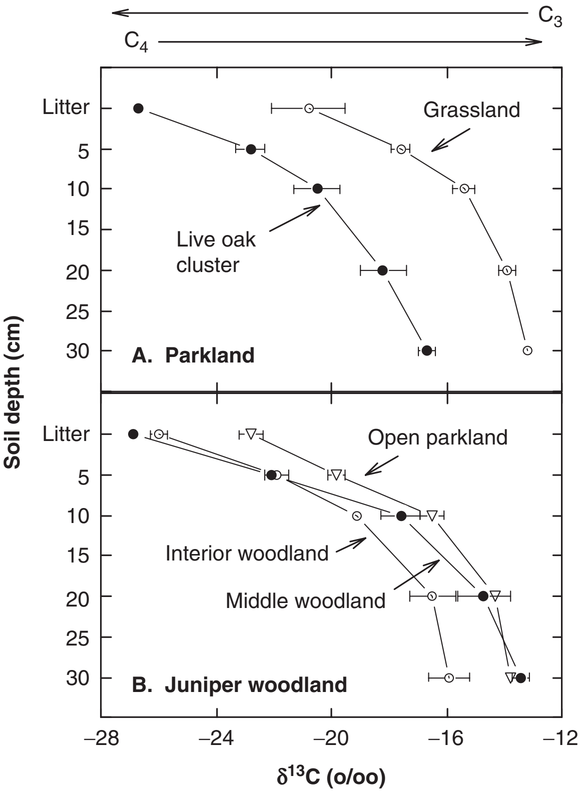

Figure 5 Depth profiles of $\delta^{13}C$ from surface litter and soil organic matter in upland savanna parklands (**A**) and mature Ashe juniper woodlands (**B**) at the Texas State University Freeman Ranch. The interior woodland site was 20 m from the edge of a prominent escarpment; the middle woodland site was 60 m from the interior woodland; and the open parkland site was ~160 m from the interior woodland. Data are means (±SE), $n = 6$ (grasslands and live oak clusters) and $n = 3$ (juniper woodlands). (Redrawn with permission from Jessup et al. 2003)

In an effort to clarify historical vegetation changes and woody patch dynamics (specifically the temporal and spatial changes in C_3/C_4 vegetation composition), we examined stable isotopes of organic carbon from soils and vegetation in grasslands, Plateau live oak clusters, and Ashe juniper woodlands (Jessup et al. 2003). Because of fundamental differences in stable carbon isotope ratios ($\delta^{13}C$) between C_3 plants (almost all woody species, many forbs, and cool season grasses; mean $\delta^{13}C$ about −28‰) and C_4 plants (warm season grasses; mean $\delta^{13}C$ about −14‰; Jessup et al. 2003), isotopic signatures of soil organic carbon have been widely used to infer vegetation change in mixed C_3/C_4 ecosystems (Boutton 1996), including the encroachment of woody C_3 plants into C_4-dominated grasslands (McPherson et al. 1993; Schwartz et al. 1996; Boutton et al. 1998). For our study, we sampled in upland savanna parklands and an Ashe juniper woodland that occurred at the edge of a steep escarpment associated with a major intermittent drainage (Sink Creek). In the parkland habitat, we sampled from open grasslands and the understories of large Plateau live oak clusters (mean diameter at breast height of central live oak tree = 1.3 m). In the Ashe juniper woodland, we sampled along transects that ran out from the cliff edge (interior woodland; dense woody cover) into an adjacent parkland (sparse woody cover).

In the grasslands and live oak clusters, we found that soil $\delta^{13}C$ increased significantly with depth (Figure 5A), indicating that the relative productivity of C_4 species (largely C_4 grasses) has declined in modern times in both habitats. However, at the deepest soil increment sampled (20–30 cm), the $\delta^{13}C$ in the live oak clusters showed a much stronger C_3 isotopic signature (or a more negative value) than the nearby grasslands. The precise age of the central live oak trees in our sampled clusters is not known and cannot be readily determined from growth ring analysis (Russell and Fowler 1999). Harlow et al. (1996) indicate that individuals of *Q. virginiana* can attain ages of at least 300 years of age. Radiocarbon dating of similar soils near this region show mean residence times of 200 to 500 years at 15 to 30 cm for bulk soil organic carbon (Boutton et al. 1998). Thus, our findings are consistent with the view that upland live oaks have been long-term components of these savannas and that their establishment in these habitats likely predates Anglo-European settlement.

The enrichment in soil $\delta^{13}C$ with depth (less negative value) in the grasslands is consistent with the hypothesis that continuous grazing of this site has resulted in the replacement of highly palatable and productive C_4 tall- and midgrasses (e.g., *Andropogon gerardii, Sorghastrum nutans, Schizachyrium scoparium*, and *Bouteloua curtipendula*) by less-productive, grazing-tolerant C_4 and C_3 grasses (e.g., *Bouteloua rigidiseta* and *Nasella leucotricha = Stipa leucotricha*) and C_3 forbs (e.g., *Croton monanthygynus* and *Gutierrezia texana*), which currently dominate these grasslands (Barnes et al. 2000). In the live oak clusters, the changes in $\delta^{13}C$ with depth may reflect C_3–C_4 compositional shifts that occurred during the development and expansion of these tree/shrub clusters (e.g., the growth of the live oak and understory shrubs progressively contributed more C_3 biomass while simultaneously reducing C_4 biomass by shading out grasses), as occurs in other subtropical savannas (Archer et al. 1988). The development of these mixed-species clusters may well have been enhanced by the suppression of fire since settlement (Fonteyn et al. 1988). It is also possible that these tree/shrub clusters are relatively recent features in these savannas and that historical parkland landscapes may have consisted of scattered live oaks embedded within a relatively continuous herbaceous understory. Indeed, one can occasionally find individuals of late-successional C_4 grasses (e.g., *Schizachyrium scoparium* and *Andropogon gerardii*) in these wooded understories.

Soil samples taken from varying distances away from the cliff edge in the Ashe juniper woodland also showed enrichment in $\delta^{13}C$ with depth (see Figure 5B). However, at the middle woodland location (and other exterior woodland sites; Jessup et al. 2003) the $\delta^{13}C$ signature at depth converged with that in adjacent grassland/parkland areas. The isotopic signature at depth for the most interior sampling location was unique and more C_3 like. These findings, together with the general characteristics of the inner woodland (i.e., widely spaced and large Ashe juniper trees with basal diameters >1 m), suggest that Ashe juniper was already present at this site before Anglo-European settlement. However, the boundary of this juniper woodland has not been stable over the past 100 to 200 years but has encroached into surrounding grassland. This scenario is consistent with the notion that at times in the past, when fires set by lighting strikes and/or Native Americans were common, Ashe juniper was restricted to relatively cool and moist sites (e.g., near steep cliffs or drainages) similar to those of the innermost portion of this woodland (Foster 1917; Smeins 1980; Diamond et al. 1995; Fuhlendorf et al. 1996; Terletzky and Van Auken 1996).

Effects of Live Oaks and Junipers on Soils

When woody plants occupy grasslands, they typically modify the microclimate and soils in their immediate surroundings (Jackson et al. 1990; McPherson 1997; Gass and Barnes 1998; Hibbard et al. 2001; see Breshears, Chapter 4, this volume), and this is the case for the live oaks and junipers in these savannas. In our studies, we found that surface soils associated with the Plateau live oak clusters and mature Ashe juniper woodlands had higher fractions (g kg^{-1}; not shown, but see Jessup et al. 2003) and densities (g m^{-2}; Figure 6) of soil organic C than did the soils of nearby grassland patches. However, although both soil organic C and total N were higher in the live oak clusters than the juniper woodlands, soil N densities were comparable between juniper woodlands and grasslands. These findings indicate that, although Plateau live oaks have been a long-term component of the Edwards Plateau region, these live oak clusters represent sites where soil organic C and N stores have apparently increased in the past several hundred years. Also, where mechanical clearing or fire has been absent, the expansion of Ashe juniper woodlands into grazed grasslands has been accompanied by increases in soil organic C, with little or no change to soil N stores.

In addition to their effects on soil biogeochemistry, live oaks and junipers also alter soil seed banks, but they do so in different ways. For these studies, surface soil samples (0–5 cm) were collected seasonally (May, September, December, and March) from open grasslands, live oak-dominated woodlands, and young juniper stands (estimated to be 20–40 years old based on juniper sizes; Smeins and Fuhlendorf 1997) from six different pastures at the Freeman Ranch (Ruiseco 1998). Samples were placed in a glasshouse, and emergent seedlings were identified and regularly censused over 8 to 14 months. Results indicate that this "germinable" seed bank beneath relatively young Ashe junipers was distinct in a number of ways from seed banks in grazed grasslands and under live oaks (Figure 7). In all three habitats, annual species, especially annual forbs, dominated the seed

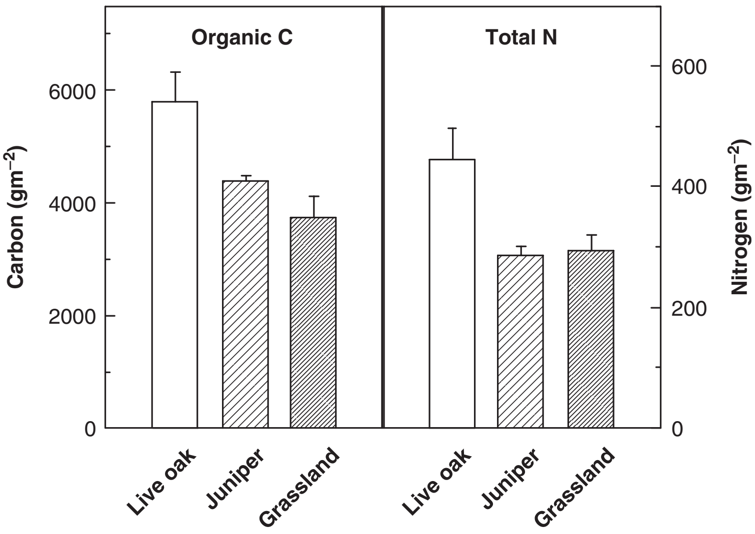

Figure 6 Organic carbon and total nitrogen densities of surface (0–10 cm) soils beneath live oak clusters, Ashe juniper woodlands (interior woodland site), and grasslands (savanna parklands) at the Texas State University Freeman Ranch. Data are means ± 1 SE; *n* = 5 for live oak clusters and grasslands, *n* = 3 for the Ashe juniper woodland. (Redrawn with permission from Jessup et al. 2003)

banks, and late-successional species were largely absent. Seed banks associated with junipers showed the highest species richness but were intermediate in species diversity (Figure 7A,C). Total seedling densities of seed banks associated with junipers were higher than in live oak seed banks but were statistically comparable with grasslands (Figure 7B). Over all habitats, 116 species were recorded and 18 species were common to all habitats. Four species were unique to grasslands, 6 species were found only in the juniper seed banks, and 3 species were restricted to live oak habitats. Notably, there were characteristic early- to mid-successional grassland species (e.g., *Hordeum pusillum, Hilaria belangeri*, and *Aristida oligantha*) that were absent from both juniper and live oak seed banks. Woody species were absent from grassland seed banks, and no seedlings of Ashe juniper were found in the germinable seed banks of any habitat. Thus, occupation of grasslands by Ashe juniper quickly alters the soil seed bank but does so in ways that are distinct from live oaks, likely as a result of juniper-induced alterations in seed rain and modification of understory vegetation. The lack of a persistent seed bank for Ashe juniper implies that seedling recruitment for this species requires frequent dispersal of seeds into these habitats. However, at least in wooded habitats, Ashe juniper seedlings may survive in the understory for several years and thus provide a "seedling" bank should the canopy be lost (Jackson and Van Auken 1997).

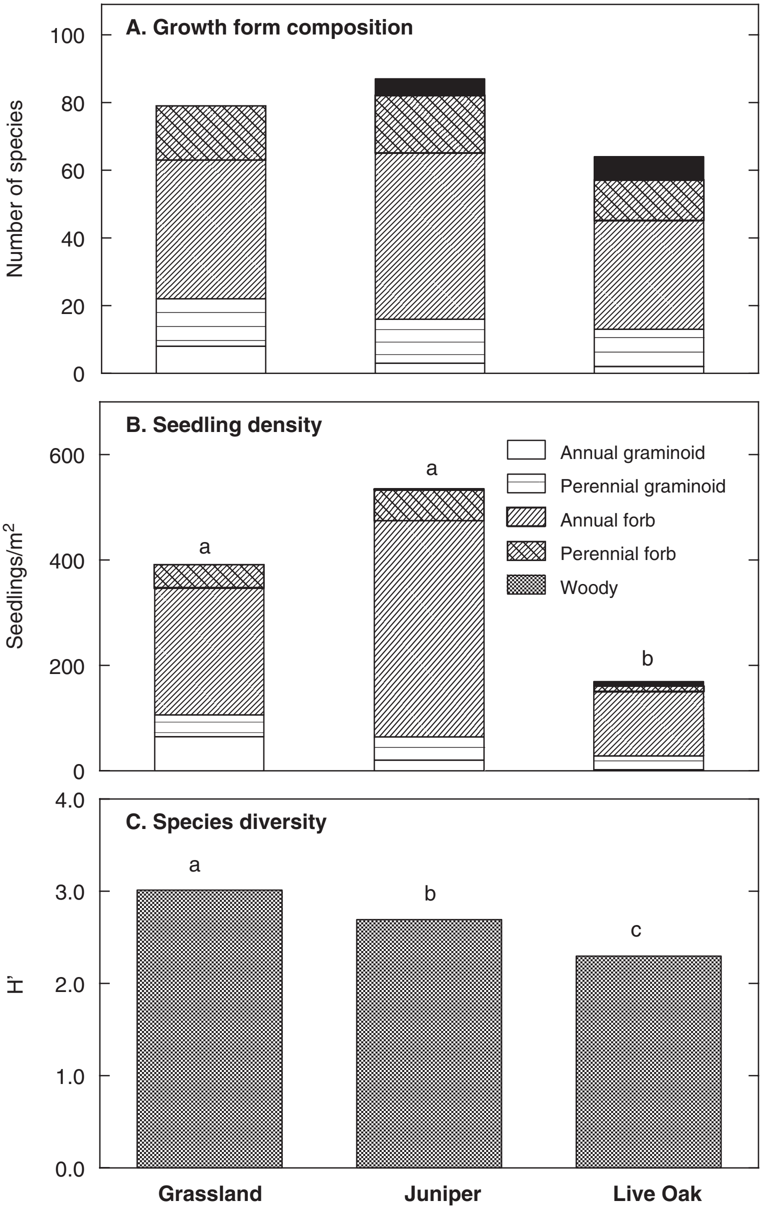

Figure 7 Growth form richness (**A**), density (seedlings m^{-2}) (**B**), and species diversity (**C**) of germinable seed banks from soil beneath grasslands, young Ashe junipers, and mature live oaks at the Texas State University Freeman Ranch. Data are means (n = 6 pastures) pooled across season. Seedling density means and Shannon–Weiner diversity indices (H') with *different letters* are significantly different at $P < 0.05$ as determined by Tukey's HSD (honestly significantly different) test. (From Ruiseco 1998)

Live Oak–Juniper Interactions

The encroachment of many woody plants into grasslands often involves an initial facilitation phase whereby an established woody species serves as a “nurse plant” for other species that then colonize in its understory (Archer et al. 1988). Over time, these discrete tree/shrub clusters increase in size and complexity and, depending on site conditions, may eventually coalesce to form continuous canopy woodlands. Previous studies on the Edwards Plateau have shown that Ashe junipers are more frequently associated with trees such as live oaks than in open grasslands (Fowler 1988; Fonteyn et al. 1988). Thus, it has been suggested that Plateau live oaks function as nurse plants for Ashe junipers, thereby facilitating their establishment and/or growth. The precise nature of this facilitation is not yet understood, but likely involves enhancement of seed dispersal, as well as modification of microclimate and soils (Chavez-Ramirez and Slack 1993; Anderson et al. 2001; Phillips and Barnes 2003).

How long this overstory facilitation of junipers persists beyond the seedling establishment phase is unknown at present. In some nurse plant associations, facilitation gives way, in time, to competition as the understory increases in size and resource demands (Callaway 1995). In some cases, the original nurse plant may be competitively excluded by the understory (Yeaton 1978; McAuliffe 1984). It is possible, however, that overstory facilitation continues beyond the seedling establishment phase (Barnes and Archer 1999). In addition, some degree of resource partitioning could occur between overstory and understory, which would then minimize competitive effects of the understory. If this occurs, overstory–understory coexistence could be possible.

Historically, increases in Ashe juniper have often been associated with decreases in Plateau live oak abundance on parts of the Edwards Plateau (Smeins and Merrill 1988), and some have suggested that established Ashe junipers are strong competitors with live oaks (Owens 1996). The implication is that Ashe junipers are competitively displacing live oaks in certain habitats. As an experimental test for understory Ashe juniper competition against the overstory Plateau live oak, we conducted a replicated ($n = 10$), selective removal study at the Freeman Ranch. For this study, the juniper-dominated understory was mechanically cleared from some upland live oak clusters (understory removal treatment) while in others the live oak overstory and the shrub understory were left intact (controls). Physiological (leaf gas exchange and water potential) and growth (leaf/twig biomass and leaf litter) responses of the live oak trees in these two treatments were then monitored periodically over a 2-year period (Ramirez 2002).

When averaged over two growing seasons, we found that removal of the juniper-dominated woody understory significantly increased leaf CO_2 and H_2O exchange but had no effect on shoot water potential in live oaks (Table 2). This enhancement of leaf gas exchange in live oaks, however, did not translate into detectable increases in growth or litter production. It is possible that effects on

Table 2 Response of Plateau live oaks (*Quercus virginiana* var. *fusiformis*) in upland clusters to removal of the Ashe juniper (*Juniperus ashei*)-dominated woody understory

Response variable	Control	Understory removal	*P*
Shoot water potential (MPa)	−1.79 ± 0.08	−1.70 ± 0.07	0.50
Net CO_2 uptake (µmol m^{-2} s^{-1})	17.0 ± 0.8	18.3 ± 0.7	0.04
Stomatal conductance (mmol m^{-2} s^{-1})	338.7 ± 1.2	383.2 ± 1.3	0.02
Shoot dry mass (g)	1.91 ± 0.29	2.04 ± 0.20	0.50
Shoot length (cm)	12.1 ± 1.8	12.8 ± 1.6	0.67
Litter production (g m^{-2})	80.2 ± 9.5	95.6 ± 7.8	0.22

Controls = intact woody understory. Data are from Ramirez (2002) and are means ± SE ($n = 10$) averaged over a 2-year period. Water potential data are from predawn and midday measurements, net CO_2 uptake data are from midday measurements, and stomatal conductance are from morning and midday measurements. Shoot dry mass (leaf + stem) and shoot length data are from four terminal shoots/tree. Litter data are total leaf litter collected from three litter traps/tree over an 8-week period before leaf abscission. For all variables except leaf litter, *P* values are from univariate repeated measures analysis of variance for a completely randomized design, where individual clusters were the experimental units. Litter data were analyzed as a univariate analysis of covariance, with leaf area index of individual clusters (estimated with a plant canopy analyzer; LiCor, Lincoln, NE, USA) as the covariate. *P* values are for main effects (removal treatment) only. Not shown are *P* values for time (significant at $P < 0.001$ for all variables tested) and treatment × time interactions (not significant at $P > 0.05$ for all variables).

live oak growth may become evident over longer time frames, although over the time period of this study (2 years), we saw no indication that treatment effects were increasing with time [i.e., treatment × time interactions were generally not significant; $P > 0.05$, repeated-measures analysis of variance (ANOVA); Ramirez 2002]. Thus, although we observed some degree of competition between the juniper-dominated understory and the overstory live oak, it is unclear if these effects are of sufficient magnitude for juniper to eventually replace the live oaks. We should note that these studies were conducted on large live oaks that occupied relatively deep soils (e.g., Figure 3A), and it seems unlikely that overtopping of live oaks by junipers would occur. Live oaks are known to be more deeply rooting than Ashe juniper (Jackson et al. 1999). Also, seasonal comparisons of predawn plant water potentials, which are indicators of physiological rooting depths, suggest that some degree of belowground resource partitioning occurs between these species: live oaks appear to utilize stable deeply stored soil moisture whereas junipers rely more on surface moisture that is seasonally variable (Figure 8). These differences in soil moisture utilization could minimize belowground competition and thus contribute to overstory and understory coexistence, at least in these habitats. It is possible that the competitive effect of junipers on live oaks would be greater on drier sites or shallower soils (such as the evergreen woodlands) where live oaks are less robust and there is less opportunity for belowground resource partitioning.

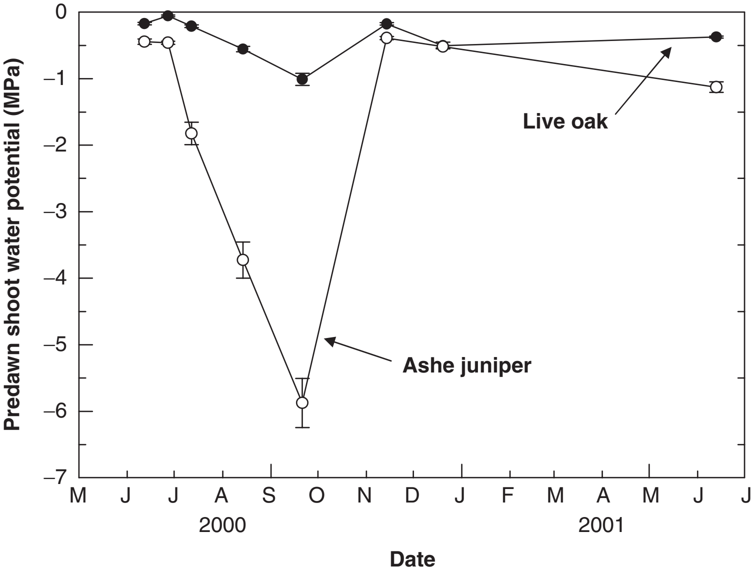

Figure 8 Seasonal predawn shoot water potentials of Plateau live oaks (*closed circles*) and Ashe junipers (*open circles*) in live oak clusters in upland savanna parklands at the Texas State University Freeman Ranch. Data are means ± SE ($n = 6$ clusters); error bars within the size of the symbol are not shown. (From Ramirez 2002)

Summary

The contemporary vegetation of the Texas State University Freeman Ranch is a mosaic of woody and grassland vegetation and is thus representative of subtropical savannas on the eastern Edwards Plateau of Texas. At present, woody plants cover about 50% of the landscape and occupy all major habitats; however, the relative abundance of woody and herbaceous cover varies with soil types and topography. In general, grass (herbaceous) cover dominates sites with relative deep soils and minimal slope, whereas woody plants dominate shallow soils of steeper slopes (see also Diamond and True, Chapter 3, this volume). Our findings suggest that not all "suitable" sites are currently occupied by woody plants. If this is the case, there is the potential for additional woody plant increase in the future. On the other hand, there are still habitats with significant, albeit degraded, herbaceous cover, which are likely governed by grassland successional processes (Archer 1995). For example, at the Freeman Ranch, fire-induced mortality of Ashe juniper is high in open parklands but minimal in dense woodlands, even following hot summer fires (Elliott 2004). Thus, reductions in grazing coupled with frequent controlled fire may be adequate to reinvigorate and even reestablish grasslands in some, but not all, habitats.

Ashe juniper is but 1 of about 40 species of woody plants identified at the Freeman Ranch, although it is the dominant, or at least the co-dominant, species in all woody plant communities studied (i.e., Plateau live oak clusters, evergreen woodlands, and deciduous woodlands). Size distributions in all habitats show a strong bias toward the smallest size-classes and relatively few large individuals. Thus, the potential exists for increase in Ashe juniper abundance, not only in parklands but also in both evergreen and deciduous woodlands. By comparison, size distributions of Plateau live oak are more strongly biased toward the larger (and presumably older) individuals, and, in some habitats, there is little evidence of adult recruitment by this species. Similar findings have been reported for other hardwood species in this region (Van Auken 1993; Russell and Fowler 1999, 2002). Factors contributing to the lack of adult recruitment in these trees are not fully understood, but high levels of herbivory by whitetail deer (*Odocoileus virginianus*) may be important (Russell et al. 2001; Russell and Fowler 2004). Plateau live oaks are also susceptible to oak wilt disease, caused by the fungus *Ceratocystis fagacearum*, and in some cases may be negatively affected by increases in the abundance of Ashe junipers and other woody species in their understories (but see above). Thus, a number of factors may be contributing to the apparent demographic decline of live oaks and other hardwood species in these woodlands. In any case, it does appear that, in a broad sense, both evergreen and deciduous woodlands at the Freeman Ranch are currently dominated by Ashe juniper and other shrubs rather than hardwood trees.

Our findings from stable carbon isotope analyses of soil organic matter indicate that both Ashe juniper and Plateau live oak have been long-term woody components in these savannas. However, it is clear that Ashe junipers have recently expanded into grassland habitats from their more restrictive distribution in the past. Field observations indicate that mature Ashe juniper woodlands, such as the one we sampled, are rare at this site and in the region (Smeins and Fuhlendorf 1997), which is likely the result of historical logging of these woodlands and the indiscriminant clearing of junipers for rangeland management purposes in recent times (Foster 1917; Krueger 1976; Smeins and Fuhlendorf 1997). These mature juniper woodlands are, however, distinctly different in structure and composition than the juniper "thickets" created by recently established junipers. Old growth juniper woodlands also provide critical habitat for endangered species, such as the golden-cheeked warbler (*Dendroica chrysoparia*). Therefore, it is important that the historical distribution of Ashe juniper be delineated and that the remaining mature juniper woodlands be given high priority for preservation (Diamond et al. 1997).

Both Ashe junipers and Plateau live oaks alter soils relative to grasslands, but there are important species differences that have consequences for restoration and land management. Because soil organic carbon was higher in juniper woodlands than in grasslands, it is possible that juniper increase could increase soil carbon storage in these systems. However, this would likely occur without any changes in soil nitrogen stores. On the other hand, because soil organic C and total N were lower in the mature juniper woodland than in the live oak clusters, if live oaks are replaced by Ashe junipers, soil C and N stores would likely be reduced. Thus, depending on habitat, juniper increase could either increase or decrease soil C and N storage. A quantitative assessment of landscape- and regional-level carbon and nitrogen sequestration associated with woody plant increase in this and other dryland ecosystems (Scholes and Noble 2001) therefore requires an understanding of the temporal and spatial dynamics of the specific types of woody plants involved in this vegetation change.

In addition to effects on soil biogeochemistry, Ashe juniper occupation of grazed grasslands rapidly alters soil seed banks in ways that could impact efforts in restoration. In particular, a number of early- and mid-successional grassland species are absent from the seed banks associated with young junipers. Chronic grazing also alters the seed banks of these grasslands (Kunican and Smeins 1992). Thus, the herbaceous community that develops on heavily grazed sites following juniper removal (either by fire or mechanical clearing) will likely be very different than that following disturbance of ungrazed or lightly grazed late-successional grasslands. Different successional trajectories may therefore exist in grasslands and recently cleared juniper sites. The fact that perennial mid- and tallgrasses were absent from all seed banks indicates that reestablishment of late-successional grasslands will depend on the input of propagules from outside the site. Habitats (such as road ditches, fence lines, rocky outcrops, and isolated shrub patches) that currently provide refugia for these grazing-sensitive species will likely play critical roles as seed sources for grassland restoration.

Ashe junipers and Plateau live oaks appear to interact in both positive and negative ways that influence vegetation change in these savannas. Although findings from our relatively short-term (2 years) removal study challenge the widely held belief that Ashe junipers are strong competitors against live oaks, experimental studies such as this one are notably lacking. Additional long-term experimental studies conducted in different habitats (parklands and woodlands) are needed to fully evaluate the hypothesis that Ashe junipers are competitively replacing Plateau live oaks (and other woody species) from these savannas. In this respect, we know very little about the mechanisms or the temporal and spatial dynamics of facilitation and competition between junipers and live oaks. Consequently, it is difficult to precisely predict how, in the absence of intervention, this vegetation will change in the future. Nonetheless, if trends continue it seems likely that the open live oak parklands and diverse woodlands, which were apparently common on these landscapes before Anglo-European settlement, may continue to experience an increase in abundance and dominance of Ashe juniper and other unpalatable woody species (e.g., Texas persimmon). This vegetation change has had, and will continue to have, significant impacts on the structure and function of these ecosystems. Whether these Edwards Plateau landscapes and vegetation can ever be restored to pre-Anglo-European settlement conditions remains an open question.

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References

Allen-Diaz, B., Bartolome, J.W., and McClaran, M.P. 1999. California oak savanna. In: Savannas, barrens, and rock outcrop plant communities of North America, ed. R.C. Anderson, J.S. Fralish, and J.M. Baskin, pp 322–339. Cambridge: Cambridge University Press.

Anderson, L.J., Brumbaugh, M.S., and Jackson, R.B. 2001. Water and tree-understory interactions: a natural experiment in a savanna with oak wilt. Ecology 82:33–49.

Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience 2:83–99.

Archer, S. 2005. Proliferation of woody plants in grasslands and savannas: a bibliography. University of Arizona: http://ag.arizona.edu/research/archer/.

Archer, S., Scifres, C., Bassham, C.R., and Maggio, R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecol. Monogr. 58:111–127.

Archer, S.R., Schimel, D.S., and Holland, E.A. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2? Clim. Change 29:91–99.

Archer, S., Boutton, T.W., and Hibbard, K.A. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Global biogeochemical cycles in the climate system, eds. E.-D. Schulze, S.P. Harrison, M. Heimann, E.A. Holland, J. Lloyd, I.C. Prentice, and D. Schimel, pp 115–137. San Diego: Academic Press.

Barnes, P.W., and Archer, S. 1999. Tree-shrub interactions in a subtropical savanna parkland: competition or facilitation? J. Veg. Sci. 10:525–536.

Barnes, P.W., Liang, S.-Y., Jessup, K.E., Ruiseco, L.E., Phillips, P.L., and Reagan, S.J. 2000. Soils, topography and vegetation of the Freeman Ranch. Freeman Ranch Publication Series No. 1-2000. San Marcos: Southwest Texas State University Press.

Batte, C.D. 1984. Soil survey of Comal and Hays Counties, Texas. Washington, DC: USDA Soil Conservation Service.

Blomquist, K.W. 1990. Selected life history and synecological characteristics of Ashe juniper on the Edwards Plateau of Texas. M.S. thesis. College Station: Texas A&M University.

Boutton, T.W. 1996. Stable carbon isotope ratios of soil organic matter and their use as indicators of vegetation and climate change. In: Mass spectrometry of soils, eds. T.W. Boutton, and S.I. Yamasaki, pp 47–82. New York: Dekker.

Boutton, T.W., Archer, S.R., Midwood, A.J., Zitzer, S.F., and Bol, R. 1998. $\delta^{13}C$ values of soil organic carbon and their use in documenting vegetation change in a subtropical savanna ecosystem. Geoderma 82:5–41.

Buechner, H.K. 1944. The range vegetation of Kerr County, Texas, in relation to livestock and white-tailed deer. Am. Midl. Nat. 31:697–743.

Callaway, R.M. 1995. Positive interactions among plants. Bot. Rev. 61:306–349.

Chavez-Ramirez, F., and Slack, R.D. 1993. Carnivore fruit-use and seed dispersal of two selected plant species of the Edwards Plateau, Texas. Southwest. Nat. 38:141–145.

Diamond, D.D., Rowell, G.A., and Keddy-Hector, D.P. 1995. Conservation of Ashe juniper (*Juniperus ashei* Buchholz) woodlands of the Central Texas Hill Country. Nat. Areas J. 15:189–202.

Diamond, D.D., True, C.D., and He, K. 1997. Regional priorities for conservation of rare species in Texas. Southwest. Nat. 42:400–408.

Dixon, R. 2000. Climatology of the Freeman Ranch, Hays County, Texas. Freeman Ranch Publication Series No. 3-2000. San Marcos: Southwest Texas State University.

Dye, K.L., Ueckert, D.N., and Whisenant, S.G. 1995. Redberry juniper-herbaceous understory interactions. J. Range Manag. 48:100–107.

Elliott, K.G. 2004. Wildfire-induced mortality of woody plants in a central Texas savanna. M.S. thesis. San Marcos: Texas State University.

Fonteyn, P.J., Stone, M.W., Yancy, M.A., Baccus, J.T. and Nadkarni, N.M. 1988. Determination of community structure by fire. In: Edwards Plateau vegetation: plant ecological studies in Central Texas, eds. B.B. Amos, and F.R. Gehlbach, pp 91–100. Waco, TX: Baylor University Press.

Foster, J.H. 1917. The spread of timbered areas in Central Texas. J. For. 15:442–445.

Fowler, N.L. 1988. Grasslands, nurse trees, and co-existence. In: Edwards Plateau vegetation: plant ecological studies in Central Texas, eds. B.B. Amos, and F.R. Gehlbach, pp 91–100. Waco, TX: Baylor University Press.

Fuhlendorf, S.D., and Smeins, F.E. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus–Quercus* savanna. J. Veg. Sci. 8:819–828.

Fuhlendorf, S.D., Smeins, F.E., and Grant, W.E. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecol. Model. 90:245–255.

Fuhlendorf, S.D, Smeins, F.E., and Taylor, C.E. 1997. Browsing and tree size influences on Ashe juniper understory. J. Range. Manag. 50:507–512.

Gass, L., and Barnes, P.W. 1998. Microclimate and understory structure of live oak (*Quercus fusiformis*) clusters in central Texas, USA. Southwest. Nat. 43:183–194.

Gelbach, F.R. 1988. Forests and woodlands of the northeastern Balcones escarpment. In: Edwards Plateau vegetation: plant ecological studies in Central Texas, eds. B.B. Amos, and F.R. Gelbach, pp 57–77. Waco, TX: Baylor University Press.

Goodale, C.L., and Davidson, E.A. 2002. Carbon cycle: uncertain sinks in the shrubs. Nature (Lond.) 418:593–594.

Goyne, M.A. 1991. A life among the Texas flora: Ferdinand Lindheimer's letters to George Engelmann. College Station, TX: Texas A&M University Press.

Harlow, W.M., Harrar, E.S., Hardin, J.W., and White, F.M. 1996. Textbook of dendrology. New York: McGraw-Hill.

Hibbard, K.A., Archer, S., Schimel, D.S., and Valentine, D.W. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. Ecology 82:1999–2011.

Hoch, G.A., Briggs, J.M., and Johnson, L.C. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578–586

Huntley, B.J., and Walker, B.H. (eds.) 1982. Ecology of tropical savannas. Berlin: Springer-Verlag.

Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Snyder, K.A., Small, E.E., Hultine, K., Pockman, W.T., and Jackson, R.B. 2005. Ecohydrological implications of woody plant encroachment. Ecology 86:308–319.

Jackson, J.T., and Van Auken, O.W. 1997. Seedling survival, growth and mortality of *Juniperus ashei* (Cupressaceae) in the Edwards Plateau region of central Texas. Tex. J. Sci. 49:267–278.

Jackson, L.E., Strauss, R.B., Firestone, M.K., and Bartolome, J.W. 1990. Influence of tree canopies on grassland productivity and nitrogen dynamics in deciduous oak savanna. Agric. Ecosyst. Environ. 32:89–105.

Jackson, R.B., Moore, L.A., Hoffmann, W.A., Pockman, W.T., and Linder, C.R. 1999. Ecosystem rooting depth determined with caves and DNA. Proc. Natl. Acad. Sci. U.S.A. 96:11387–11392.

Jackson, R.B., Banner, J.L., Jobbágy, E.G., Pockman, W.T., and Wall, D.H. 2002. Ecosystem carbon loss with woody plant increase of grasslands. Nature (Lond.) 418:623–626.

Jessup, K.E. 2001. Vegetation dynamics of a live oak-juniper savanna: an isotopic assessment. M.S. thesis. San Marcos: Texas State University.

Jessup, K.E., Barnes, P.W., and Boutton, T.W. 2003. Vegetation dynamics in a *Quercus–Juniperus* savanna: an isotopic assessment. J. Veg. Sci. 14:841–852.

Jones, S.D., Wipff, J.K., and Montgomery, P.M. 1997. Vascular plants of Texas. Austin, TX: University of Texas Press.

Knight, R.W., Blackburn, W.H., and Merrill, L.B. 1984. Characteristics of oak mottes, Edwards Plateau, Texas. J. Range Manag. 37:534–537.

Köchy, M., and Wilson, S.D. 2001. Nitrogen deposition and forest expansion in the northern Great Plains. J. Ecol. 89:807–817.

Kunican, R.J., and Smeins, F.E. 1992. Soil seed bank of a semiarid Texas grassland under tree long-term (36 years) grazing regimes. Am. Midl. Nat. 128:11–21.

Krueger, M.A.P. 1976. Second fatherland: the life and fortunes of a German immigrant. College Station, TX: Texas A&M University Press.

McAuliffe, J.R. 1984. Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. Oecologia (Berl.) 64:319–321.

McMahan, C.A., Frye, R.G., and Brown, K.L. 1984. The vegetation types of Texas. Texas parks and wildlife. Available at http://www.tpwd.state.tx.us/frames/admin/veg.

McPherson, G.R. 1997. Ecology and management of North American savannas. Tucson: University of Arizona Press.

McPherson, G.R., and Wright, H.A. 1990. Effects of cattle grazing and *Juniperus pinchotii* canopy cover on herb cover and production in western Texas. Am. Midl. Nat. 123:144–151.

McPherson, G.R., Boutton, T.W., and Midwood, A.J. 1993. Stable carbon isotope analysis of soil organic matter illustrates vegetation change at the grassland/woodland boundary in southeastern Arizona, USA. Oecologia (Berl.) 93:95–101.

Muller, C.H. 1951. The significance of vegetative reproduction in *Quercus*. Madrono 11:129–137.

Nelson, J.A., Barnes, P.W., and Archer, S. 2002. Leaf demography and growth responses to altered resource availability in woody plants of contrasting leaf habit in a subtropical savanna. Plant Ecol. 160:193–205.

Olmstead, F.L. 1857. A journey through Texas. New York: Dix, Edwards.

Owens, M.K. 1996. The role of leaf and canopy-level gas exchange in the replacement of *Quercus virginiana* (Fagaceae) by *Juniperus ashei* (Cupressaceae) in semiarid savannas. Am. J. Bot. 83:617–623.

Phillips, P.L. 1999. Composition of the woody plant understory of Plateau live oak (*Quercus virginiana* var. *fusiformis*) clusters in a central Texas savanna. M.S. thesis. San Marcos: Texas State University.

Phillips, P.L., and Barnes, P.W. 2003. Spatial asymmetry in tree-shrub clusters in a subtropical savanna. Am. Midl. Nat. 149:59–70.

Polley, H.W., Johnson, H.B., Mayeux, H.S., and Tischler, C.R. 1996. Are some of the recent changes in grassland communities a response to rising CO_2 concentrations? In: Carbon dioxide, populations, and communities, eds. C. Körner and F.A. Bazzaz, pp 177–195. San Diego: Academic Press.

Ramirez, P.A. 2002. Live oak (*Quercus virginiana* var. *fusiformis*) – Ashe juniper (*Juniperus ashei*) interactions in a central Texas savanna. M.S. thesis. San Marcos: Texas State University.

Ruiseco, L.E. 1998. Woody plant effects on soil seed banks in a central Texas savanna. M.S. thesis. San Marcos: Texas State University.

Russell, F.L., and Fowler, N.L. 1999. Rarity of oak saplings in savannas and woodlands of the eastern Edwards Plateau, Texas. Southwest. Nat. 44:31–41.

Russell, F.L., and Fowler, N.L. 2002. Failure of adult recruitment in *Quercus buckleyi* populations on the eastern Edwards Plateau, Texas. Am. Midl. Nat. 148:201–217.

Russell, F.L., and Fowler, N.L. 2004. Effects of white-tailed deer on the population dynamics of acorns, seedlings and small saplings of *Quercus buckleyi*. Plant Ecol. 173:59–72.

Russell, F.L., Zippin, D.B., and Fowler, N.L. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. Am. Midl. Nat. 146:1–26.

Scholes, R.J., and Archer, S.R. 1997. Tree–grass interactions in savannas. Annu. Rev. Ecol. Syst. 28:517–544.

Scholes, R.J., and Noble, I.R. 2001. Storing carbon on land. Science 294:1012–1013.

Schlesinger W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., and Whitford, W.J. 1990. Biological feedbacks in global desertification. Science 247:1043–1048.

Schwartz, D., de Foresta, H., Mariotti, A., Balesdent, J., Massimba, J.P., and Girardin, C. 1996. Present dynamics of the savanna-forest boundary in the Congolese Mayombe: a pedological, botanical, and isotopic (^{13}C and ^{14}C) study. Oecologia (Berl.) 106:516–524.

Smeins, F.E. 1980. Natural role of fire on the Edwards Plateau. In: Prescribed burning on the Edwards Plateau of Texas, ed. L.D. White, pp 4–16. College Station, TX: Texas Agricultural Extension Service.

Smeins, F.E., and Fuhlendorf, S.D. 1997. Biology and ecology of Ashe juniper. In: Juniper symposium, ed. C.A. Taylor, pp 33–47. Technical report 97-1. College Station, TX: Texas A&M Research and Extension Center.

Smeins, F.E., and Merrill, L.B. 1988. Long-term change in a semi-arid grassland. In: Edwards Plateau vegetation: plant ecological studies in Central Texas, eds. B.B. Amos, and F.R. Gehlbach, pp 101–114. Waco, TX: Baylor University Press.

Taylor, C.A., Jr., and Smeins, F.E. 1994. A history of land use of the Edwards Plateau and its effect on the native vegetation. In Juniper symposium, pp 1–8. Technical report 94-2. College Station, TX: Texas Agricultural Experiment Station.

Terletzky, P.A., and Van Auken, O.W. 1996. Comparison of cedar glades and associated woodlands of the southern Edwards Plateau. Tex. J. Sci. 48:55–67.

Van Auken, O.W. 1988. Woody vegetation of the southeastern escarpment and plateau. In: Edwards Plateau vegetation: plant ecological studies in central Texas, eds. B.B. Amos and F.R. Gelbach, pp 43–55. Waco, TX: Baylor University Press.

Van Auken, O.W. 1993. Size distribution patterns and potential change of some dominant woody species of the Edwards Plateau region of Texas. Tex. J. Sci. 45:199–210.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–215.

Van Auken, O.W., Ford, A.L., and Allen, J.L. 1981. An ecological comparison of upland deciduous and evergreen forests of central Texas. Am. J. Bot. 68:1249–1256.

Van de Vijver, C.A.D.M., Foley, C.A., and Olff, H. 1999. Changes in the woody component of an East African savanna during 25 years. J. Trop. Ecol. 15:545–564.

Weniger, D. 1988. Vegetation before 1860. In: Edwards plateau vegetation: plant ecological studies in Central Texas, eds. B.B. Amos and F.R. Gehlbach, pp 17–23. Waco, TX: Baylor University Press.

Weltzin, J.F., and McPherson, G.R. 1999. Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. Ecol. Monogr. 69:513–534.

Wu, X.B., Redeker, E.J., and Thurow, T.L. 2001. Vegetation and water yield dynamics in an Edwards Plateau watershed. J. Range Manag. 54:98–105.

Yeaton, R.I. 1978. A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan desert. J. Ecol. 66:651–656.

8

Ecological Consequences of the Replacement of Native Grassland by *Juniperus virginiana* and Other Woody Plants

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Introduction

Although grasslands have been altered by humans for thousands of years (Wedel 1961; Bond et al. 2003), the loss of grassland as a result of anthropogenic activities has increased dramatically over the past 150 years. When Europeans first settled the Midwest and Great Plains, the greatest threat to native grasslands was the conversion of the most highly productive of these ecosystems to row-crop agriculture (Samson and Knopf 1994). Later, with improvements in soil moisture management and irrigation technology, even low-productivity grasslands were plowed. Today, those remnants of the most productive grasslands that escaped the plow are threatened, as are most of Earth's ecosystems, by a variety of global change phenomena (Vitousek et al. 1997), with the invasion and expansion of woody species into grasslands one of the greatest of these threats. The replacement of grasslands by shrubland, woodland, and forest is a concern not only in the United States but worldwide (Archer et al. 1988; Van Auken 2000; Roques et al. 2001; Silva et al. 2001). Species of woody plants that invade grasslands may include both native plants which previously existed as more minor components of the ecosystem as well as alien species (Bragg and Hulbert 1976; Harcombe et al. 1993).

In the mesic grasslands of the central United States, the last remaining extensive tracts of tallgrass prairie in Kansas, Oklahoma, and Texas are at risk from both shrub expansion from within and forest encroachment from the edges. Alteration in land management (grazing regimens) and the loss of an essential natural driver in the system (fire) associated with human population growth are two causal mechanisms often cited for the increase in shrubs and trees in northeast Kansas tallgrass prairies (Figure 1;Knight et al. 1994; Hoch et al. 2002; Briggs et al. 2002; Heisler et al. 2003). Shrub patches or "islands" that rapidly expand with reduced fire frequencies may be key focal sites for the establishment of many forest species in this and similar grasslands (Petranka and McPherson 1979; Gehring and Bragg 1992; Lett and Knapp 2005). Ultimately, however, closed-canopy *Juniperus virginiana* forest can completely displace the native grassland ecosystem in many sites (Hoch et al. 2002). A similar replacement of grassland by this and other *Juniperus* species has occurred in Texas and Oklahoma (see other chapters in this volume).

O.W. Van Auken (ed.), *Western North American Juniperus Communities: A Dynamic Vegetation Type.*

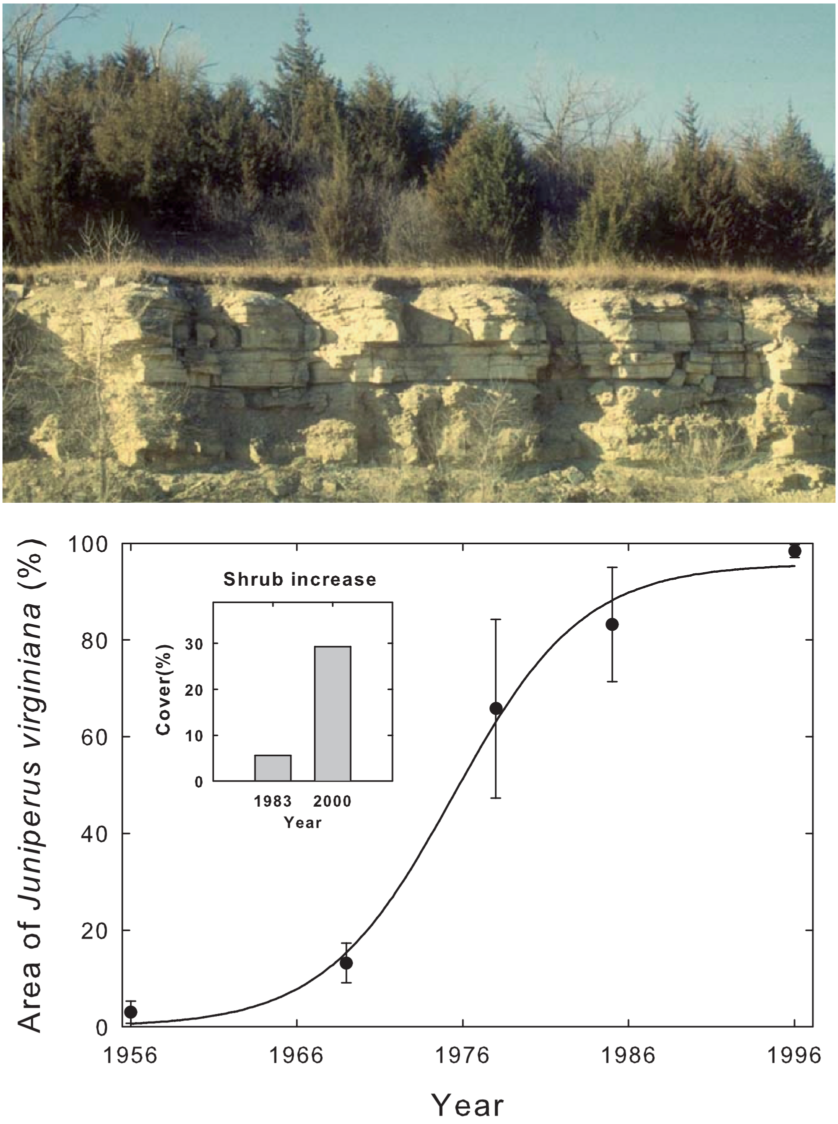

Figure 1 *Top: Juniperus virginiana* displacing a native C_4-dominated tallgrass prairie on a shallow upland soil in northeast Kansas. In contrast to riparian forests that expand into grassland from lowland topographic positions where soils are deep, *J.virginiana* is capable of invading grasslands in lowlands and uplands and seemingly without regard to soil type or depth. *Bottom*: Increase in area of *Juniperus virginiana* forest in northeast Kansas over a 40-year period. *Inset*: Increase in cover of shrubs (all species) along permanent transects in an infrequently burned watershed on the Konza Prairie Biological Station over a 17-year period. *Error bars* for *J.virginiana* represent ±1 SE of the mean based on five sites. (Modified from Hoch et al. 2002; Heisler et al. 2003)

Table 1 Shifts in ecological attributes with the replacement of native C_4 grassland by *Cornus drummondii* shrub islands and then *Juniperus virginiana* forest

Attribute	C_4 grassland	*Cornus* islands	*Juniperus* forest
Dominant growth form	Graminoid	Shrubs	Tree
Biomass allocation	More belowground	?	More aboveground
Annual aboveground NPP[a]	356 ± 28 g/m^2	1035 ± 83 g/m^2	725–1044 g/m^2
Standing aboveground biomass[b]	850 ± 46 g/m^2	4201 ± 835 g/m^2	14860 ± 3123 g/m^2
Dominant photosynthetic pathway	C_4	C_3	C_3
Leaf phenology	Deciduous	Deciduous	Evergreen
Root system[c]	Fibrous, shallow	?	Tap root, deep
Sensitivity to drought[d]	Sensitive	Moderate	Drought tolerant
Response to fire[e]	Positive	Intermediate	Negative
Species richness[f]	High (21.4 ± 1.1)	Intermediate (14.0 ± 1.0)	Low (1.2 ± 0.3)

Values are means with SE or ranges.

NPP, net primary productivity.

[a] Briggs and Knapp 1995; Lett et al. 2004; Norris et al. 2001a.

[b] Abrams et al. 1986 (unburned grassland); Lett et al. 2004; Norris et al. 2001a.

[c] Weaver 1958; Ormsbee et al. 1976.

[d] Axmann and Knapp 1993; McCarron and Knapp 2001; Ormsbee et al. 1976.

[e] Knapp and Seastedt 1986; Briggs et al. 2002; McCarron and Knapp 2003; Hoch et al. 2002.

[f] Lett and Knapp 2005; Hoch et al. 2002; values are based on 1 m^2 for the grassland and shrub islands and 10 m^2 plots for the forest.

The ecological consequences of the replacement of C_4-dominated grassland by C_3 shrubs and trees can be varied and substantial (Table 1). The most striking of these consequences include alterations in aboveground biomass and the shift in foliage phenology from deciduous, warm season activity in grasses and shrubs to evergreen in *Juniperus* forest. However, there are many more subtle consequences that may be of equal or greater importance. The objectives of this chapter are to (1) review the general ecological consequences of the replacement of grassland dominated by the C_4 grass *Andropogon gerardii* by shrubs and then forest dominated by *J. virginiana*, (2) present new data on important temporal shifts in photosynthetic activity and the climatic controls on C uptake resulting from this grassland-to-forest conversion, and (3) forecast how global change factors will differentially impact these two ecosystem types.

Study Site

Research was conducted at and within 20 km of the Konza Prairie Biological Station (KPBS) in northeast Kansas (39°05′ N, 96°35′ W). KPBS is a 3487-ha native mesic grassland (tallgrass prairie) dominated by warm season C_4 grasses (primarily *A. gerardii* and *Sorghastrum nutans*), but with a species-rich pool of herbaceous C_3 forbs (Freeman

1998). KPBS experiences a temperate midcontinental climate of cold dry winters and warm wet summers, with the majority of the average annual precipitation (30-year mean = 835 mm) occurring between April and September (Figure 2). Although *J. virginiana* has increased significantly in the region during the past 20 years (Hoch et al. 2002), closed-canopy forests are thus far absent from the site. Thus, to assess the ecological consequences of complete conversion of grassland to forest, sites near KPBS have been the focus of several studies (Norris et al. 2001a,b; Hoch et al. 2002).

For the *J. virginiana* photosynthetic gas-exchange studies reported here, we selected a site (~15 km N of KBPS on state-owned land that is protected from fire) with trees about 4 to 5 m in height where canopy closure has not yet occurred.

Patterns and Controls of Photosynthesis

During a 30-month period (October 1997–February 2000), we measured leaf-level gas exchange on randomly selected shoots on the south side of eight *J. virginiana* individuals. Measurements were made at midday (1100–1400) at 2-week intervals during the months of April–October and at monthly intervals in the winter months. Only days mostly free of clouds (direct photon flux density >1500 mmol m^{-2} s^{-1}) were sampled, and in the winter, we avoided sampling on days when air temperatures were less than −5°C (assuming that physiological activity would be nil on such days). Our goal was to document the potential maximum gas-exchange capacity of this species throughout a replicated annual cycle.

To compare the annual course of photosynthetic activity in the dominant grass with *J. virginiana*, we also measured midday gas exchange in *A. gerardii* under similar conditions at KPBS. Photosynthesis was measured over a similar 30-month time period (although no winter measurements were made because of senescence). We measured this grass in annually burned and intermittently and long-term unburned sites on KPBS representative of the suite of management practices in adjacent grasslands. These data were combined to provide a representative level of physiological activity.

In both *A. gerardii* and *J. virginiana*, gas exchange was measured in situ with a field portable gas-exchange system (LI-COR 6200; LI-COR, Lincoln, NE, USA) in the closed-flow mode. Terminal portions of shoots of *J. virginiana* or two or three grass leaves were sealed in a clear cuvette for 15- to 30-s measurement periods during which CO_2 depletion was measured. Leaf area enclosed in the cuvette was determined by measuring the rectangular dimensions of enclosed leaves for *A. gerardii* and from the projected leaf area of shoots of *J. virginiana*. Projected leaf area was measured in the laboratory by transporting measured shoots to a video leaf area meter.

Annual patterns of gas exchange in both species were averaged by month for the 30-month sampling periods, and environmental correlates of these patterns were assessed. Precipitation and air temperature were obtained from weather stations at KPBS and the Tuttle Creek Dam weather station 5 km N of Manhattan KS (operated by the U.S. Army Corps of Engineers with data available from the Kansas State University Weather Data Library). Climatic data were similar from both sites; thus,

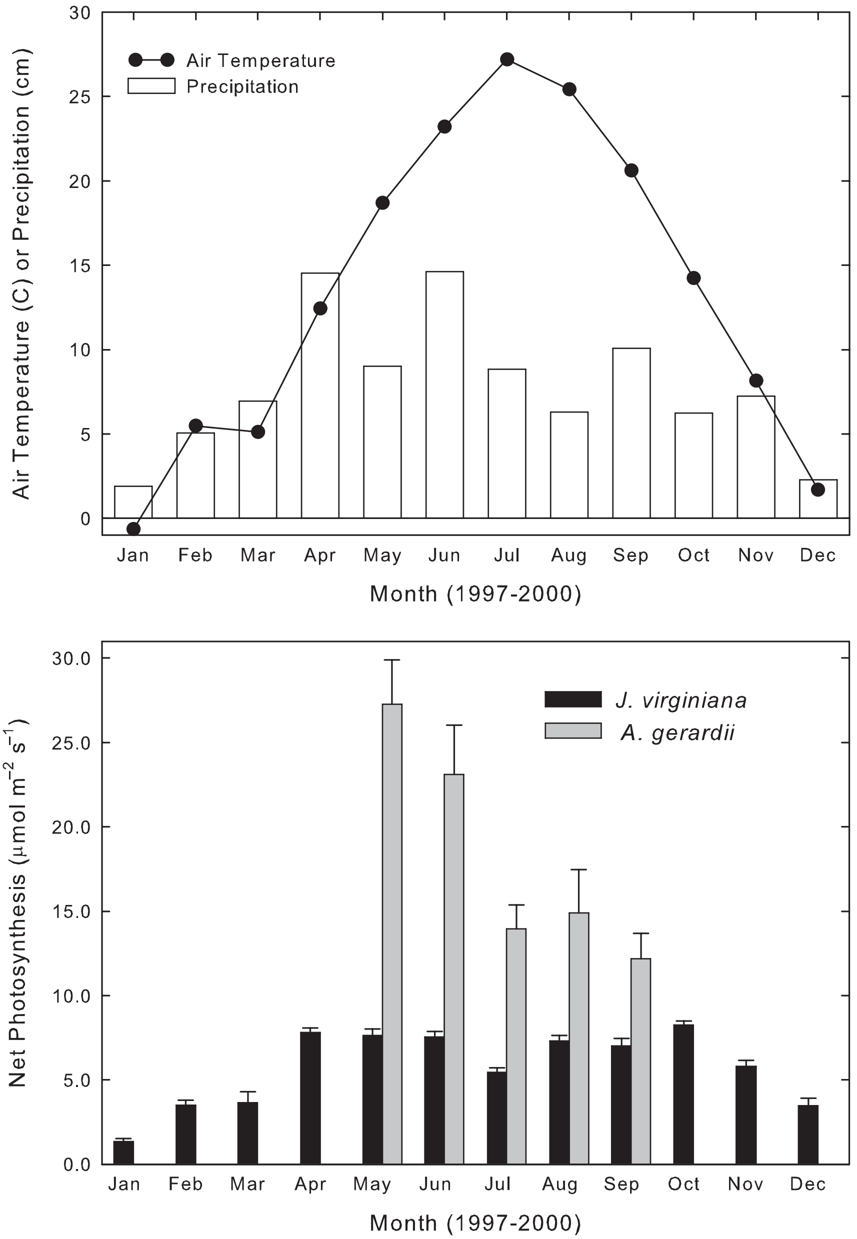

Figure 2 *Top*: Monthly mean air temperature and precipitation from the Konza Prairie Biological Station weather station for the period during which photosynthetic measurements were made. *Bottom*: Monthly mean net photosynthesis rates (instantaneous) for *J.virginiana* trees (4–5 m in height) growing in tallgrass prairie and *Andropogon gerardii*, the dominant C_4 grass in this mesic grassland. Measurements were made over a 30-month period from sites that were protected from fire for *J.virginiana* and from sites both exposed and protected from fire for *A. gerardii*. *Error bars* represent 1 SE of the mean

analyses of KPBS data are presented. Soil moisture data at a depth of 50 cm were available for KPBS only. Simple and multiple regressions analyses (ordinary least square and nonlinear) were performed to evaluate relationships between these abiotic factors and temporal patterns of photosynthetic activity.

Patterns and Controls of Photosynthetic Activity

Juniperus virginiana forest cover has increased rapidly in this region (see Figure 1) with a concurrent loss of C_4 grassland. There were dramatic differences in both the seasonal dynamics and the magnitude of photosynthetic rates of the dominant vegetation when forest and grasslands were compared (see Figure 2). As expected, when photosynthetic rates of a C_4 grass are compared to C_3 shrubs or forest species (Figure 3), seasonal mean photosynthetic rate of foliage differed as much as threefold. This alteration in photosynthetic physiology was accompanied by a change in phenological activity from a 5-month period for *A. gerardii* to 12 months for the evergreen leaves of *J. virginiana* (see Table 1, Figure 2). The long-term average air temperature is above 0°C in every month of the year in northeast Kansas (Hayden 1998) and was also during this study period, with the exception of January (see Figure 2). Consequently, on virtually all sunny days, positive net photosynthesis was measured for *J. virginiana* throughout the winter (Figure 2). Although seasonal rates of photosynthesis in *A. gerardii* (5-month season) were much higher than in *J. virginiana* (see Figure 3), if calculated on a 12-month basis, annual rates were similar in the dominant grass and tree species.

The environmental factors controlling seasonal patterns of C gain in grassland versus forest also differed. Photosynthetic rates in *A. gerardii* were best correlated

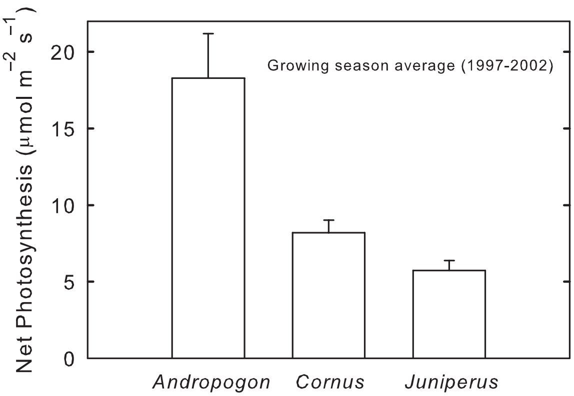

Figure 3 Comparison of seasonally averaged leaf-level net photosynthetic rates for the C_4 dominant grass, *Andropogon gerardii*, the most common C_3 shrub that displaces native grassland at Konza Prairie, *Cornus drummondii*, and the C_3 forest tree, *Juniperus virginiana*. Data for all species are from three growing seasons: 1997–2000 for *A. gerardii* and *J. virginiana* and 2000–2002 for *C. drummondii*. *Error bars* represent 1 SE of the mean

seasonally to soil moisture levels at 50-cm depth (Figure 4). Indeed, the seasonal decline in net photosynthesis coincided with the two driest and warmest months during the growing season (see Figure 2). In contrast, leaf-level photosynthesis in *J. virginiana* was not related to general patterns of seasonal soil moisture variation for KPBS, precipitation, or any climatic variable directly related to water availability. Instead, air temperature was the best predictor of photosynthetic rates, particularly in the winter months (see Figure 4). In the summer months, no climatic factor correlated with photosynthetic rates in *J. virginiana*, perhaps reflecting the relatively constant level of photosynthetic activity from April to October (see Figure 2).

General Ecological Consequences

Juniperus virginiana cover has increased at a rate of 2.3% per year during the past 40 years in areas adjacent to KPBS, with shrubs on KPBS (including *Cornus drummondii* and *Rhus glabra*) increasing at a similar rate (see Figure 1; Hoch et al. 2002; Heisler et al. 2003). This increase in woody plant cover represents a dramatic shift in many ecological attributes compared to native mesic grassland (see Table 1). The most important of these shifts, from the perspective of ecosystem productivity, are the dramatic increase in aboveground biomass in shrub islands and forest and the temporal shift in C uptake from occurring only during the warmest months of the year in grassland to a 12-month pattern more typical of other evergreen species in the region (Maragni et al. 2000; see Figure 2). Although consequences for plant community structure have not been a major focus of research, the loss of plant species richness with woody plant invasion (from both shrubs and trees; Figure 5) is clearly another important consequence from the biodiversity and biogeochemical perspective. Indeed, the virtual loss of all the dominant grassland species from the understory of *J. virginiana* forests (Kaul and Keeler 1983; Gehring and Bragg 1992; Hoch et al. 2002) may represent an irreversible change in ecosystem structure and an alternative stable state. Even in the relatively young *Cornus drummondii* shrub islands that displace grasslands in Kansas, a 45% loss in species richness has been measured, with the herbaceous flora dominated by C_3 forbs and sedges rather than C_4 grasses (Lett and Knapp, 2005). Thus, any increase in woody plants in these grasslands has the potential to dramatically alter plant community structure and those ecosystem attributes that are influenced by plant characteristics (decomposition, N cycling, soil C, etc.; Norris et al. 2001a,b; Smith and Johnson 2003).

Patterns and Controls of C Uptake

The decrease in rates of photosynthesis with the replacement of *A. gerardii* by the shrub *C. drummondii* and then *J. virginiana*, and the extension of the seasonal pattern of C uptake (see Figures 2, 3), were not unexpected consequences of the replacement of C_4 grassland by C_3 forest. However, the difference in the primary environmental control of C uptake for *A. gerardii* versus *J. virginiana*, water versus temperature,

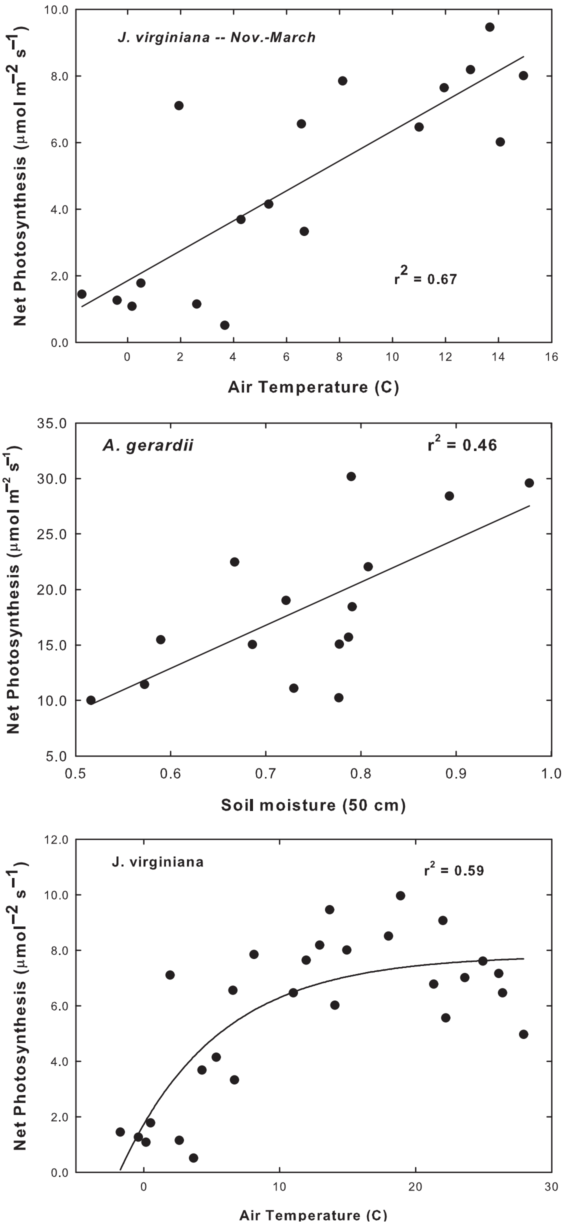

Figure 4 *Top*: Relationship between leaf-level net photosynthetic rates (A) and soil moisture at 50 cm (SWC) for *A. gerardii* from 1997–2000. Regression equation: A = −10.4 + 38.3 (SWC). Photosynthetic data are monthly means from Figure 2; soil moisture data (% field capacity) are mean monthly neutron probe measurements from the Konza Prairie LTER program (http://climate.konza.ksu.edu/). *Middle*: Relationship between leaf-level instantaneous net photosynthetic rates (A) and air temperature (T) for *J. virginiana* from 1997–2000. Nonlinear rectangular hyperbola regression: A = Ao + a(T)/(b + (T)). Photosynthetic data are monthly means from Figure 2; temperature data (at 2 m aboveground) are from the Konza Prairie LTER weather station. *Bottom*: Relationship between net photosynthetic rates and air temperature for *J. virginiana* for only the winter months (November through March). Regression equation: A = 1.8 + 0.45(T). All relationships were significant at $P < 0.05$ level

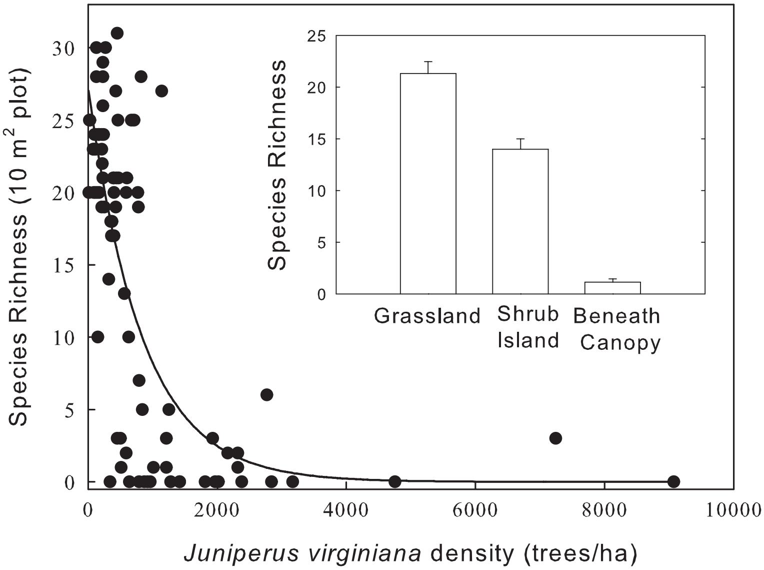

Figure 5 The reduction in plant species richness (herbaceous understory) with an increase in woody species in mesic grassland. Relationship between *J. virginiana* and richness is based on five forest sites in northeast Kansas. *Inset*: Comparison of herbaceous species richness in grassland, beneath shrub islands (dominated by *Cornus drummondii*), and beneath the canopy of *J. virginiana* forest (*inset*) are from sites near and on the Konza Prairie Biological Station. Note richness values are based on 1 m^2 for the grassland and shrub islands and 10 m^2 plots for the forest. *Error bars* represent 1 SE of the mean. (Data modified from Hoch et al. 2002; Lett and Knapp, 2005)

respectively, may represent a fundamental shift in the regulation of energy flow through these ecosystems. Productivity in temperate grasslands across the United States has been repeatedly characterized as strongly water limited (Sala et al. 1988; Epstein et al. 1997a; Paruelo et al. 1997), and the mesic grasslands of northeast Kansas are no exception (Briggs and Knapp 1995; Knapp et al. 2001). Although the degree to which water limits biotic activity may be less in mesic grasslands such as the tallgrass prairie relative to other systems (e.g., deserts; Briggs and Knapp 1995; Huxman et al. 2004), the importance of temperature as an abiotic variable explaining patterns of productivity in central United States grasslands is typically only manifest at large regional scales (Epstein et al. 1997b). Thus, the strong regulation of C uptake in *J. virginiana* by temperature, with precipitation (or soil water) perhaps of secondary importance, represents an important alteration in the abiotic control of ecosystem functioning.

This lack of a relationship between patterns of C uptake and precipitation in *J. virginiana* is consistent with the seasonal gas-exchange characteristics of *J. ashei* in south-central Texas (Owens and Schreiber 1992). In this semiarid region, photosynthesis in *J. ashei* occurred in all winter months and was unrelated to seasonal variations in precipitation. Similarly, within the summer growing season, both the photosynthetic and water relationships of *A. gerardii* were much more sensitive to changes in water availability than in the shrub *C. drummondii* or

J. virginiana (Axmann and Knapp 1993; McCarron and Knapp 2001). Combined, these data and results from other studies (Ormsbee et al. 1976) suggest that both *C. drummondii* and *J. virginiana* are less affected by water availability, and are likely more drought tolerant, than the mesic grasses they are displacing (see Table 1).

Plant–water relationships affect and are affected by photosynthetic activity, and *Juniperus* invasion likely has dramatic impacts on ecosystem water use, given the shift from negligible annual C uptake occurring outside the summer growing season (in grassland) to up to 40% (*Juniperus* forest) occurring when temperatures are much cooler (see Figure 2). This temporal shift also will minimize the expected advantage in water use efficiency of the C_4 grasses because a significant fraction of gas exchange in *J. virginiana* occurs during periods of low evaporative demand.

How Will Global Change Affect C_4 Grasslands Versus Juniper Forest?

Alterations in the dominant growth form (tree versus grass) and associated photosynthetic physiology and phenology, differences in drought tolerance, and shifts in the environmental controls over C gain will certainly alter ecosystem responses to global changes forecast for the central United States (Table 2). Widely accepted forecast global changes include increased temperatures, atmospheric CO_2 concentrations, and N inputs (Shaw et al. 2000; IPCC 2001; Norby and Luo 2004). Further, an increase in extreme climatic events, including droughts and reduced soil moisture caused by temperature-driven increases in evapotranspiration, reduced precipitation, or both, may be particularly important for the central United States (Easterling et al. 2000; Knapp et al. 2002). Changes in land management and use will likely result in a decrease in fire frequency with population growth and important interactions with livestock grazing that will increase woody plant success (Valone and Kelt 1999; Hoch et al. 2002).

The predicted responses listed in Table 2 are coarse approximations of comparative responses of C_4 grassland versus C_3 forest to these global change factors, with many contingencies implicit. For example, warmer summer temperatures could

Table 2 Predicted responses of native C_4-dominated mesic grassland and *Juniperus virginiana* forest to forecast global changes in the central United States

Factor	C_4 grassland	*Juniperus* forest
Increased temperature		
Summer	+,−	−
Winter	0	++
Decreased precipitation	—	0,−
Increased CO_2	0,+	++
Increased N deposition	−	+

See text for rationale and studies on which these predictions are based. Sufficient data are not available for predicting responses of shrubs.

benefit C_4-dominated grassland if the growing season was lengthened, but might have a direct negative effect if only extreme midsummer temperatures were affected or an indirect negative effect as a result of greater evaporative demand. Similarly, decreased precipitation might not be expected to affect *J. virginiana* as compared to the less drought tolerant *A. gerardii*, given the lack of a relationship between C uptake and precipitation for this or other *Juniperus* species (Owens and Schreiber 1992). However, extreme reductions in rainfall and prolonged drought would negatively affect all plant species, including *Juniperus*.

Conversely, we can be more confident in predicted responses to some forecast changes to some factors; warmer winter temperatures will likely have strong positive effects on *J. virginiana* C gain (see Figure 4). Increased N is likely to benefit *Juniperus* forest because C_4 plants have lower N requirements than C_3 plants, and previous studies have shown that N addition to C_4-dominated grassland results in rapid conversion to C_3 dominance (Wedin and Tilman 1993). Finally, although elevated CO_2 has been shown to indirectly benefit this C_4 grassland through improved soil–and plant–water relationships (Knapp et al. 1993; Owensby et al. 1997), both direct and indirect benefits should be manifest in a C_3 forest. Rather than attempt to quantify responses to individual factors, we advocate a comparative approach for interpreting the predictions in Table 2. Combining these leads to the conclusion that, relative to *A. gerardii*-dominated grassland, *J. virginiana* forest will benefit more (or be less negatively impacted) by forecast global change factors than the native C_4 grassland, thus increasing the likelihood for its expansion and the replacement of tallgrass prairie in the future.

Conclusions

Alterations in ecosystem structure and function linked to anthropogenic activities are numerous (Vitousek et al. 1997; Shaw et al. 2000; Parmesan and Yohe 2003), but the most extreme impacts are likely to occur when one dominant species is replaced by another that differs in growth form, such as shrubs or evergreen forest species displacing grassland. Numerous and diverse ecological consequences are the result, ranging from the readily apparent (increased aboveground biomass), to surprising shifts in abiotic controls of C uptake patterns (water in grassland versus temperature in forest), to those that are likely to have long-term consequences for ecosystem services (altered species abundance and loss; Smith and Knapp 2003). With regard to *J. virginiana* replacement of mesic grassland (tallgrass prairie), the importance of this phenomenon is magnified by the present-day rarity of this formerly widespread grassland type (Samson and Knopf 1994). A number of issues are still to be resolved, including (1) the need to understand how grasslands being invaded by shrubs and *Juniperus* species can be managed to arrest this increase or even reduce woody plant abundance; (2) how the long-term stability of these shrublands or forests compares to native grassland, particularly with regard to fire, extreme drought, and C storage; and (3) how or if closed-canopy *Juniperus* forest represents an alternative stable state or can be readily restored to grassland after catastrophic events such as fire.

Summary

The invasion of grasslands by woody species is a phenomenon of concern worldwide. In the mesic grasslands of the Central United States, the last extensive tracts of mesic productive grassland are threatened by both shrub expansion and forest encroachment (primarily *Juniperus virginiana*). Alteration in land management (primarily fire suppression interacting with livestock grazing) is one mechanism for the increase in woody plant abundance in these productive grasslands. In some sites, closed-canopy *J. virginiana* forest has completely replaced native grassland, resulting in a wide array of ecological consequences. These changes include shifts in photosynthetic physiology of the dominant species (from C_4 grasses with high photosynthetic potential to C_3 trees with much lower rates of C uptake), concurrent shifts in environmental controls over patterns of growth (from water availability in grassland to temperature in forest), large increases in aboveground productivity and biomass in forest, and reductions in plant species richness during the transition from grassland to forest. These shifts in ecological attributes today will alter future responses to a range of global changes forecast for this region.

References

Abrams, M.D., Knapp, A.K., and Hulbert, L.C. 1986. A ten-year record of aboveground biomass in a Kansas tallgrass prairie: effects of fire and topographic position. Am. J. Bot. 73:1509–1515.

Archer, S., Scifres, C., Bassham, C.R., and Maggio, R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecol. Monogr. 58:111–127.

Axmann, B.D., and Knapp, A.K. 1993. Water relations of *Juniperus virginiana* and *Andropogon gerardii* in an unburned tallgrass prairie watershed. Southwest. Nat. 38:325–330.

Bond, W.J., Midgley, G.F., and Woodward, F.I. 2003. What controls South African vegetation—climate or fire? S. Afr. J. Bot. 69:79–91.

Bragg, T.B., and Hulbert, L.C. 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range Manag. 29:19–24.

Briggs, J.M., and Knapp, A.K. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position and fire as determinants of aboveground biomass. Am. J. Bot. 82:1024–1030.

Briggs, J.M., Knapp, A.K., and Brock, B.L. 2002. Expansion of woody plants in tallgrass prairie: a 15 year study of fire and fire-grazing interactions. Am. Midl. Nat. 147:287–294.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., and Mearns, L.O. 2000. Climate extremes: observations, modeling, and impacts. Science 289:2068–2074.

Epstein, H.E., Lauenroth, W.K., Burke, I.C., and Coffin, D.P. 1997a. Productivity patterns of C3 and C4 functional types in the U.S. Great Plains. Ecology 78:722–731.

Epstein, H.E., Lauenroth, W.K., and Burke, I.C. 1997b. Effects of temperature and soil texture on ANPP in the U.S. Great Plains. Ecology 78:2628–2631.

Freeman, C.C. 1998. The flora of Konza Prairie: a historical review and contemporary patterns. In: Grassland dynamics: long-term ecological research in tallgrass prairie, eds. A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins, pp 69–80. New York: Oxford University Press.

Gehring, J.L., and Bragg, T.B. 1992. Changes in prairie vegetation under eastern red cedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie. Am. Midl. Nat. 128:209–217.

Harcombe, P.A., Cameron, G.N., and Glumac, E.G. 1993. Above-ground net primary productivity in adjacent grassland and woodland on the coastal prairie of Texas, USA. J. Veg. Sci. 4:521–530.

Hayden, B.P. 1988. Regional climate and the distribution of tallgrass prairie. In: Grassland dynamics: long-term ecological research in tallgrass prairie, eds. A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins, pp 19–34. New York: Oxford University Press.

Heisler, J.L., Briggs, J.M., and Knapp, A.K. 2003. Long-term patterns of shrub expansion in a C_4-dominated grassland: fire frequency and the dynamics of shrub cover and abundance. Am. J. Bot. 90:423–428.

Hoch, G.A, Briggs, J.M., and Johnson, L.C. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578–586.

Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E., Smith, S.D., Tissue, D.T., Zak, J.C., Weltzin, J.F., Pockman, W.T., Sala, O.E., Haddad, B.M., Harte, J., Koch, G.W., Schwinning, S., Small, E.E., and Williams, D.G. 2004. Convergence across biomes to a common rain-use efficiency. Nature (Lond.) 429:651–654.

IPCC. 2001. Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change, eds. J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, and C.A. Johnson. Cambridge: Cambridge University Press.

Kaul, R.P., and Keeler, K.H. 1983. Effects of grazing and juniper-canopy closure on the prairie flora in Nebraska High-Plains canyons. In: Proceedings of the eighth North American prairie conference, ed. R. Brewer, pp 95–105. Kalamazoo, MI: Western Michigan University.

Knapp, A.K., and Seastedt, T.R. 1986. Detritus accumulation limits productivity in tallgrass prairie. BioScience 36:662–668.

Knapp, A.K., Hamerlynck, E.P., and Owensby, C.E. 1993. Photosynthetic and water relations responses to elevated CO_2 in the C_4 grass *Andropogon gerardii*. Int. J. Plant Sci. 154:459–466.

Knapp A.K., Briggs, J.M., and Koelliker, J.K. 2001. Frequency and extent of water limitation to primary production in a mesic temperate grassland. Ecosystems 4:19–28.

Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S., and McCarron, J.K. 2002. Rainfall variability, carbon cycling and plant species diversity in a mesic grassland. Science 298:2202–2205.

Knight, C.L., Briggs, J.M., and Nellis, M.D. 1994. Expansion of gallery forest on Konza Prairie Research Natural Area, Kansas, USA. Landsc. Ecol. 9:117–125.

Lett, M.S., and Knapp, A.K. 2005. Woody plant encroachment and removal in mesic grassland: production and composition responses of herbaceous vegetation. Am. Midl. Nat., 153:217–231.

Lett, M.S., Knapp, A.K., Briggs, J.M., and Blair, J.M. 2004. Influence of shrub encroachment on aboveground net primary productivity and carbon and nitrogen pools in a mesic grassland. Can. J. Bot. 82:1363–1370.

Maragni, L.A., Knapp, A.K., and McAllister, C.A. 2000. Patterns and determinants of potential carbon gain in the C_3 evergreen, *Yucca glauca* (Liliaceae), in a C_4 grassland. Am. J. Bot. 87:230–236.

McCarron, J.K., and Knapp, A.K. 2001. C_3 woody plant expansion in a C_4 grassland: are grasses and shrubs functionally distinct? Am. J. Bot. 88:1818–1823.

McCarron, J.K., and Knapp, A.K. 2003. C_3 shrub expansion in a C_4 grassland: positive post-fire responses in resources and shoot growth. Am. J. Bot. 90:1496–1501.

Norby, R.J., and Luo, Y. 2004. Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world. New Phytol. 162:281–293.

Norris, M.D., Blair, J.M., Johnson, L.C., and McKane, R.B. 2001a. Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. Can. J. For. Res. 31:1940–1946.

Norris, M.D., Blair, J.M., and Johnson, L.C. 2001b. Land cover change in eastern Kansas: litter dynamics of closed-canopy eastern redcedar forests in tallgrass prairie. Can. J. Bot. 79:214–222.

Ormsbee, P., Bazzaz, F.A., and Boggess, W.R. 1976. Physiological ecology of *Juniperus virginiana* in old fields. Oecologia (Berl.) 23:75–82.

Owens, M.K., and Schreiber, M.C. 1992. Seasonal gas exchange characteristics of two evergreen trees in a semiarid environment. Photosynthetica 26:389–398.

Owensby, C.E., Ham, J.M., Knapp, A.K., Bremer, D., and Auen, L.M. 1997. Water vapour fluxes and their impact under elevated CO_2 in a C_4-tallgrass prairie. Global Change Biol. 3:189–195.

Parmesan, C., and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature (Lond.) 421:37–42.

Paruelo, J.M., Epstein, H.E., Lauenroth, W.K., and Burke, I.C. 1997. ANPP estimates from NDVI for the central grassland region of the United States. Ecology 78:953–958.

Petranka, J.W., and McPherson, J.K. 1979. The role of *Rhus copallina* in the dynamics of the forest-prairie ecotone in north-central Oklahoma. Ecology 60:956–965.

Roques, K.G., O'Connor, T.G., and Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. J. Appl. Ecol. 38:268–280.

Sala, O.E., Parton, W.J., Joyce, L.A., and Lauenroth, W.K. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.

Samson, F., and Knopf, F. 1994. Prairie conservation in North America. BioScience 44:418–421.

Shaw, M.R., Zavaleta, E.S., Chiariello, N.R., Cleland, E.E., Mooney, H.A., and Field, C.B. 2000. Grassland responses to global environmental changes suppressed by elevated CO_2. Science 298:1987–1990.

Silva, J.F., Zambrano, A., and Fariñas, M.R. 2001. Increase in the woody component of seasonal savannas under different fire regimes in Calabozo, Venezuela. J. Biogeogr. 28:977–983.

Smith, D.L., and Johnson, L.C. 2003. Expansion of *Juniperus* in the Great Plains: changes in soil organic carbon dynamics. Global Biogeochem. Cycles 17:13-1–13-12.

Smith, M.D., and Knapp, A.K. 2003. Dominant species maintain ecosystem function with non-random species loss. Ecol. Lett. 6:509–517.

Valone, T.J., and Kelt, D.A. 1999. Fire and grazing in a shrub-invaded arid grassland community: independent or interactive ecological effects? J. Arid Environ. 42:15–28.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–215.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., and Melillo, J.M. 1997. Human domination of earth's ecosystems. Science 277:494–499.

Weaver, J.E. 1958. Summary and interpretation of underground development in natural grassland communities. Ecol. Monogr. 28:55–78.

Wedel, W.R. 1961. Prehistoric man on the Great Plains. Norman, OK: University of Oklahoma Press.

Wedin, D.A., and Tilman, D. 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Ecol. Monogr. 63:199–229.

9

Altered Ecosystem Processes as a Consequence of *Juniperus virginiana* L. Encroachment into North American Tallgrass Prairie

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Introduction

Expanding cover and abundance of woody plants in grasslands and savannas (afforestation) is a worldwide phenomenon with the potential to alter ecosystem structure and function in a variety of important ways (Van Auken 2000; Archer et al. 2001). Increases in woody plant cover, or conversion of grasslands to woodlands, may alter ecosystem processes such as nutrient cycling and availability, which influence primary productivity, resource competition, species richness, and composition, as well as the interactions between plants, animals, and microorganisms (Vitousek 2004). Nutrient cycling dynamics and the long-term stability of carbon (C) and nitrogen (N) pools may also change as a result of a shift in the allocation of plant biomass and ecosystem C and N stocks from largely belowground in grasslands to aboveground in woodlands. These ecosystem changes may, in turn, alter regional terrestrial and atmospheric biogeochemistry if newly established woodlands act as a sink for C and N (Moiser 2001).

An important form of woody plant expansion in grasslands of the U.S. Central Plains is an increase in the cover and abundance of *Juniperus virginiana*, or eastern redcedar. *Juniperus virginiana* L. (hereafter redcedar) is the most widely distributed *Juniperus* species in the continental United States, occurring in every state east of the 100th meridian (Fowells 1965). In the eastern Great Plains and other areas, redcedar has encroached into adjacent grasslands at an unprecedented rate, affecting approximately 7 million hectares (ha) in western portions of its range (Schmidt and Leatherberry 1995; Briggs et al. 2002). Redcedar, similar to most other *Juniperus* species in North America, forms both dispersed community associations, or often, very dense (130–3500 trees/ha), nearly monospecific stands (Norris et al. 2001b; Briggs et al. 2002; Rhoades et al. 2004; McKinley 2006). Redcedar is typically found in more mesic areas than most western *Juniperus* species, and in a very broad range of soils across the eastern United States.

Juniperus expansion in North America began in the late 1800s as European settlement and associated land management practices and other anthropogenic activity became more extensive (Smeins 1983; see chapters 1 and 14, this volume). Historically, because of their sensitivity to fire, *Juniperus* trees mainly grew in areas that were sheltered from intense fire, such as rocky outcrops or areas with shallow soils. Fire suppression and reduced fuel

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loads resulting from grazing by domestic ungulates have been widely implicated in promoting the rapid expansion of these native trees beyond their historical distribution (Van Auken 2000; Archer et al. 2001; Briggs et al. 2002). The ecosystem consequences of conversion from grassland to woodland are often significant (Archer et al. 1988; Archer 1990; Belsky 1994; Hester 1996; Van Auken 2000; Archer et al. 2001; Norris et al. 2001b; Jackson et al. 2002; Smith and Johnson 2003, 2004; Briggs et al. 2005; McKinley 2006; Norris et al. 2007), and the encroachment of *Juniperus* into areas of native grassland might be expected to cause substantial changes in key ecosystem properties and processes, given the change in dominant plant life form from C_4 grasses to a C_3 coniferous tree species. Here we summarize results from a variety of studies, mostly conducted in the Central Plains, which have assessed potential changes in ecosystem C and N pools and fluxes as redcedar expands into native grasslands.

Site Description

The majority of studies reviewed here utilized native tallgrass prairie sites paired with adjacent redcedar stands developed in areas that until recently were grassland. These studies (Norris et al. 2001a,b; Briggs et al. 2002; Smith and Johnson 2003, 2004; McKinley 2006; Norris et al. 2007) were conducted in the Flint Hills region of northeastern Kansas in close proximity (<25 km) to the Konza Prairie Biological Station (KPBS) (39°05′ N, 96°35′ W). Proximity to the KPBS, the primary location of the Konza Prairie Long-Term Ecological Research (LTER) program, allows the use of a variety of baseline data on ecological processes in native tallgrass prairie. Average monthly temperature ranges from a January low of −2.7°C to a July high of 26.6°C (NOAA 2004). Average annual total precipitation is 835 mm with 75% falling during the growing season (Bark 1987). Soils in this region are highly variable, but generally consist of cherty, silty clay loams or silt loams overlaying limestone bedrock. These soils commonly have low inorganic N and available P but are relatively high in organic matter (2.3%–5.0%). Topographic relief divides the landscape into upland plateaus with mostly shallow soils, slopes with outcrops of limestone, and lowlands with deeper alluvial and colluvial soils (Oviatt 1998). Redcedar stands are especially prominent in relatively shallow soil upland sites, and those sites were used in the studies reported here.

The dominant native vegetation in the northern Flint Hills is tallgrass prairie, dominated by a matrix of perennial, warm season C_4 grasses including big bluestem (*Andropogon gerardii* Vit.), little bluestem (*Schizachyrium scoparium* Michx.), indiangrass (*Sorghastrum nutans* Nash) (Anderson et al. 2001), and switchgrass (*Panicum virgatum* L.) (Kuchler 1967; Freeman and Hulbert 1985). These C_4 grasses contribute the majority of annual net primary productivity (ANPP) (Knapp et al. 1998a). However, a highly diverse mixture of less abundant species, including C_3 grasses and sedges and a diverse array of forbs, contributes to the high floristic diversity of these grasslands (Freeman and Hulbert 1985). The native tallgrass prairie flora also includes a smaller number of native woody plants, such as buckbrush

(*Symphoricarpos orbiculatus* Moench.), New Jersey tea (*Caenothus herbaceous* Raf.), smooth sumac (*Rhus glabra* L.) and rough-leaved dogwood (*Cornus drummondii* CA May), which can be locally abundant, especially in prairie that is infrequently burned (Briggs et al. 2005).

Assessing the effects of grassland conversion to redcedar forests was done using multiple paired sites consisting of native tallgrass prairie that was burned frequently (1- to 3-year fire return intervals) and either recently grazed by cattle (Norris et al. 2001a,b; Smith and Johnson 2003, 2004; Norris et al. 2007) or not grazed in the recent past (McKinley 2006). Each tallgrass prairie site was paired with an adjacent redcedar stand that had developed on an area that was historically grassland and which shared similar soil type, slope, position, and aspect. Historical aerial photographs and analysis of soil organic carbon (SOC) isotopic composition confirmed that these stands of redcedar, which utilize a C_3 photosynthetic pathway (creating organic carbon more depleted in $\delta^{13}C$ organic carbon), were recently established on areas historically dominated by C_4 grasslands (with accumulated SOC relatively more enriched in ^{13}C) (Smith and Johnson 2003; McKinley 2006). Each redcedar stand was at least $0.5\,ha^{-1}$ and consisted of relatively mature trees (~30–80 years) creating dense (680–1900 trees ha^{-1}) stands with complete or nearly complete canopy cover.

Potential Drivers of Altered Ecosystem Processes

Microclimate

Juniperus trees modify the microclimate beneath their canopies relative to grasslands (Breashears et al. 1997, 1998; Smith and Johnson 2004). Soil temperatures were consistently higher, sometimes by as much as 8°C, in grasslands than in comparable redcedar sites (Figure 1) (McKinley 2006), which may contribute to changes in soil processes. For example, Smith and Johnson (2004) found a 38% reduction in soil respiration in redcedar soils compared to adjacent grassland sites and concluded that soil temperatures, rather than soil moisture, explained most of the variability in soil respiration. An estimated Q_{10} value for soil respiration, which represents the sensitivity of soil respiration (a measure of microbial activity) to temperature, was slightly less in redcedar soils (2.2) compared to grassland soils (2.4) (Smith and Johnson 2004). Differences in soil moisture in redcedar stands and grasslands may result from differences in soil temperatures, as well as canopy interception and evapotranspiration. However, periodic measurements indicated that soil water content tended to only be slightly greater in grassland soils on a mean seasonal basis (Figure 2), and soil water content explained much less of the measured variance in soil respiration than did temperature (Smith and Johnson 2004). Therefore, differences in soil temperatures, and the microbial response to temperatures, appear to be a major driver in the alteration of some key ecosystem processes, such as soil CO_2 flux, following redcedar encroachment into grasslands.

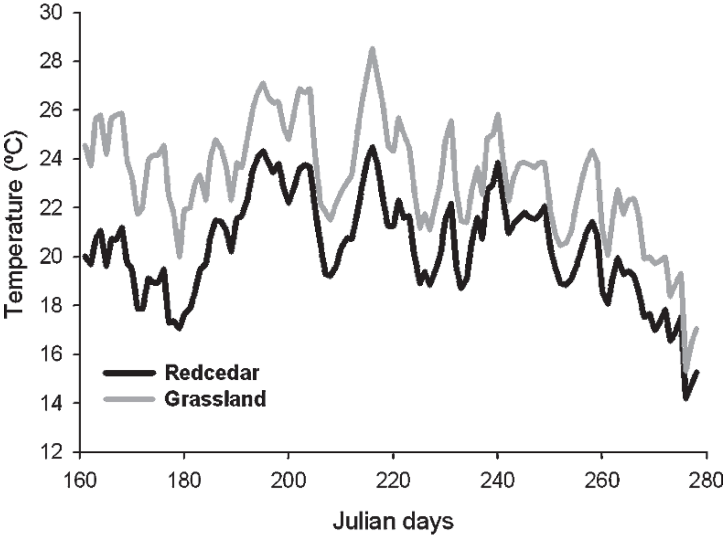

Figure 1 Hourly averages of mineral soil temperatures at 5-cm depth in redcedar and grassland soils measured from mid-June through mid-October (McKinley 2006). Measurements were made simultaneously at four sites, with four thermocouples per vegetation type. Grassland soil temperatures were greater at nearly all times compared to redcedar stands, with the differences reaching 8°C. Temperatures tended to converge in nighttime and after significant rainfall events

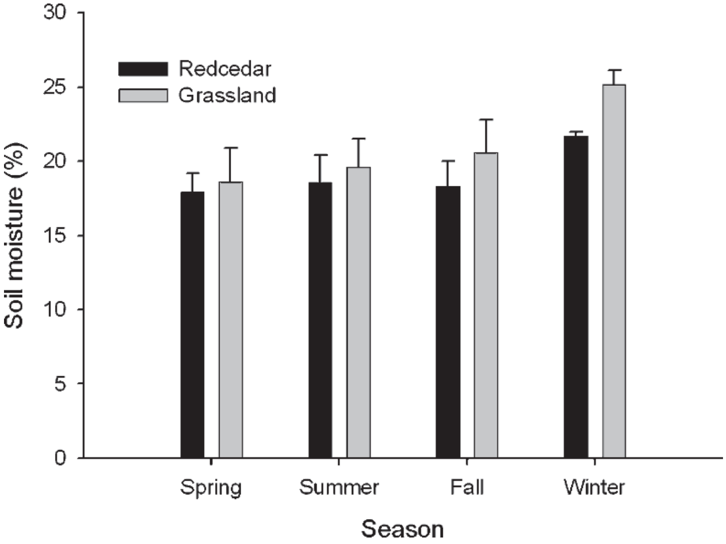

Figure 2 Seasonal patterns of gravimetric soil moisture (mean ± SE) averaged over a 2-year period at four sites from multiple measurements per season (McKinley 2006). Mean seasonal soil moisture was not significantly different in any season ($P > 0.05$), although grassland soils tended to be greater

Ecosystem Productivity and Biomass Accumulation

Species with inherently fast growth rates such as redcedar can exhaust soil nutrients by sequestering essential nutrients in plant biomass and create feedback loops that exacerbate soil nutrient limitations (Chapin 1980; Vitousek 1982, 2004). Aboveground biomass in redcedar stands in two different studies in the northern Flint Hills ranged from 114,120 to 210,952 kg ha^{-1} in sites that were 35 to 80 years old (Norris et al. 2001b) and 94,620 to 150,001 kg ha^{-1} in sites that were 35 to 55 years old (McKinley 2006). These aboveground biomass accumulations were much greater than peak biomass of grasslands in similar topographic positions (20-year mean peak from KPBS = 3,690 kg ha^{-1}, range = 1,780–5,700 kg ha^{-1}; see Knapp et al. 1998a) and occurred over a relatively short period of time. Greater ANPP in redcedar stands (7,250–10,440 kg ha^{-1} $year^{-1}$) compared to annually burned upland grasslands (3,690 kg ha^{-1} $year^{-1}$) (Norris et al. 2001b; Norris et al. 2007), coupled with the elimination of fire in redcedar communities, has allowed for this rapid accumulation of biomass. Differences in productivity of these communities, and presumably changes in litter quality or quantity, may alter nutrient cycles and soil nutrient availability, affecting further community changes.

Litter Inputs

Litter chemistry influences decomposition rates and, consequently, C and N mineralization and N availability, which may be especially important in N-limited soils such as those characteristic of tallgrass prairie (Blair et al. 1998). The quantity and quality of plant litter inputs also control the accumulation and storage of C and N as soil organic matter (SOM). Thus, changes in the quantity, quality, and location (aboveground versus belowground) of plant litter inputs as redcedar encroaches into grasslands may be an important driver of altered ecosystem processes such as C mineralization and N cycling, and these processes can, in turn, influence higher plant growth and subsequent nutrient feedback loops.

Foliar litter inputs, and root inputs from either exudates or root turnover, are the main sources of soil C and N (McClaugherty et al. 1982). Carbon-to-nitrogen ratios, percent (%) lignin, lignin-to-N ratios, and other indices of litter quality have been shown to strongly influence decomposition and the release of N from decomposing litter. Although the majority of redcedar biomass (bolewood) is of low quality (i.e., C:N > 250:1), greater allocation of biomass N to foliage and roots may make these tissues, and the fine litter produced from them, relatively high quality (low C:N) (Norris et al. 2001a). For example, foliage of both redcedar and mixed-bulk grassland vegetation had relatively low C:N ratios in midgrowing season (July), 37:1 and 56:1, respectively (McKinley 2006). However, both redcedar and *A. gerardii* resorb significant amounts of leaf N before senescence, resulting in higher C:N ratios in foliar litter of both redcedar (~52:1) and *A. gerardii* (~70:1)

(Norris et al. 2001a). Reports of C:N ratios of redcedar and *A. gerardii* fine roots (≤2-mm diameter) vary, with Norris et al. (2001b) reporting values of ~101:1 for redcedar roots (1–2 mm diameter) and ~70:1 for *A. gerardii* roots, whereas McKinley (2006) found that the C:N ratios of fine (< 2 mm diameter) redcedar roots were significantly lower (~70:1) compared to mixed-species roots excavated from an adjacent annually burned, ungrazed prairie (~90:1). Although redcedar may provide comparable or better quality fine litter input as indexed by C:N ratios, lignin content, which can also strongly influence decomposition, was three times greater in litter of redcedar foliage and twice that in root biomass compared to the foliar litter and roots of the dominant grasses (Norris et al. 2001b).

Norris et al. (2001a) found that litterfall in redcedar stands averaged about 500 g m^{-2} $year^{-1}$, which was an order of magnitude greater than litterfall (52 g m^{-2} $year^{-1}$) in annually burned grasslands (Seastedt 1988). Redcedar litterfall contributed approximately 4 g N m^{-2} $year^{-1}$ to the O-horizon, and a total litter N accumulation of 25–56 g N m^{-2} in redcedar stands (Norris et al. 2001a; McKinley 2006). However, the net release of N from decomposing redcedar litter is slow. In a 2-year litter decomposition study, Norris et al. (2001a) detected no net release of N. In another study, field incubations of soil cores with and without the presence of an intact O-horizon indicated no detectable contributions of the O-horizon to inorganic N production during the 30-day incubations (McKinley 2006). Despite potentially large surface litter inputs and accumulations of organic N, surface litter decomposition appears to contribute little to inorganic N in the mineral soil in short-term assays. The eventual release of inorganic N from surface redcedar litter may require long periods of time due to differences in litter chemistry relative to grassland species (Murphy et al. 1998; Norris et al. 2001a). However, foliar litter inputs may contribute to the size of the SOM pool in the surface mineral soil, as evidenced by replacement of grass-derived soil organic carbon (SOC) with redcedar-derived SOC in the shallow mineral soil horizons of redcedar stands (Smith and Johnson 2004, McKinley 2006).

The turnover of redcedar root biomass may also provide significant quantities of organic matter to the mineral soil, but this input has not been quantified, and we know of no comparative studies of fine root productivity or turnover in grassland and redcedar sites. However, there are comparative studies that address fine root biomass in redcedar stands and grasslands and the decomposition dynamics of redcedar fine root litter. Redcedar root biomass including both fine/small roots (< 2 mm diameter) and coarse roots (≥ 2 mm diameter) in excavated soil monoliths (25 × 25 × 10 cm) was more than double the root biomass found in adjacent grasslands (McKinley 2006). Root biomass may become concentrated in upper soil horizons in shallow soils where these redcedar communities typically develop, and this may allow greater concentrations of root inputs per unit soil volume, ultimately altering soil processes. In addition to large accumulations of redcedar roots, there were greater concentrations of N in redcedar fine roots (0.74%), measured in the late growing season compared to roots of mixed species in adjacent grasslands (0.51%) (McKinley 2006). In contrast, Norris et al. (2001a) reported that redcedar roots had lower concentrations of N than did roots of *A. gerardii*. The apparent discrepancy between these studies may reflect seasonal and site-specific differences in root tissue N, as well as differences in comparing roots of a single grass species (*A. gerardii*; see Norris et al. 2001a) with roots of a mixture of grassland species (McKinley 2006), or the inclusion of smaller redcedar roots (≤1-mm diameter) in tissue analyzed by McKinley. Norris et al. (2001a) also found that redcedar root decay rates were 35% less than *A. gerardii* roots, suggesting the potential for root litter to contribute to greater soil organic matter accumulations in redcedar stands. The contribution of root inputs in *Juniperus* stands has been largely overlooked, but given the large amount of root biomass and differences in root chemistry of redcedar and the dominant grasses they replace, belowground litter inputs may be very important in influencing soil processes, such as N cycling, in newly established redcedar stands.

Altered Ecosystem Processes

Carbon Storage and Flux

Changes in carbon allocation patterns following redcedar encroachment into grasslands are so profound that the bulk of the ecosystem C storage shifts from belowground in grasslands (~96%) to aboveground (~52%) in redcedar stands (Norris et al. 2001b; McKinley 2006). The top 10 cm of mineral soils in redcedar stands has 12% greater soil organic carbon (SOC) per square meter compared to adjacent grassland soils (McKinley 2006). Increased total SOC pools have been observed in other comparisons of soils under the canopies of *Juniperus* relative to adjacent grasslands or intercanopy patches (Bates et al. 2002; Smith and Johnson 2003; Miller et al. 2005). Increased organic C storage in the soil and potential changes in SOM composition may be especially important factors affecting nutrient availability in redcedar stands.

Smith and Johnson (2003) took advantage of the differences in photosynthetic pathways of redcedar, a C_3 plant, and the C_4 grasses that historically dominated these grasslands, and utilized a stable isotope technique to determine the proportion of SOC in new redcedar stands that was derived from recent forest litter inputs. They found that a significant portion (~20%) of the SOC in the top 25 cm of the mineral soil originated from forest inputs, with the greatest replacement (~40%) in the shallow mineral soil horizons (0–2.5 cm) (Figure 3a). Smith and Johnson (2003) also found that the proportion of SOC of redcedar origin decreased rapidly and predictably with depth to less than 11% below 10 cm (Figure 3b). Analysis of $\delta^{13}C\text{-}CO_2$ produced from soil respiration in laboratory incubations of the top 10 cm of mineral soil from redcedar stands revealed consistently more depleted (negative) $\delta^{13}C$ values than those of the corresponding bulk SOC (Smith 2001). These values when used in a mixing model indicated that ~65% of soil C respired was of forest origin, which indicated greater microbial utilization of new forest C, suggesting that this pool was more labile

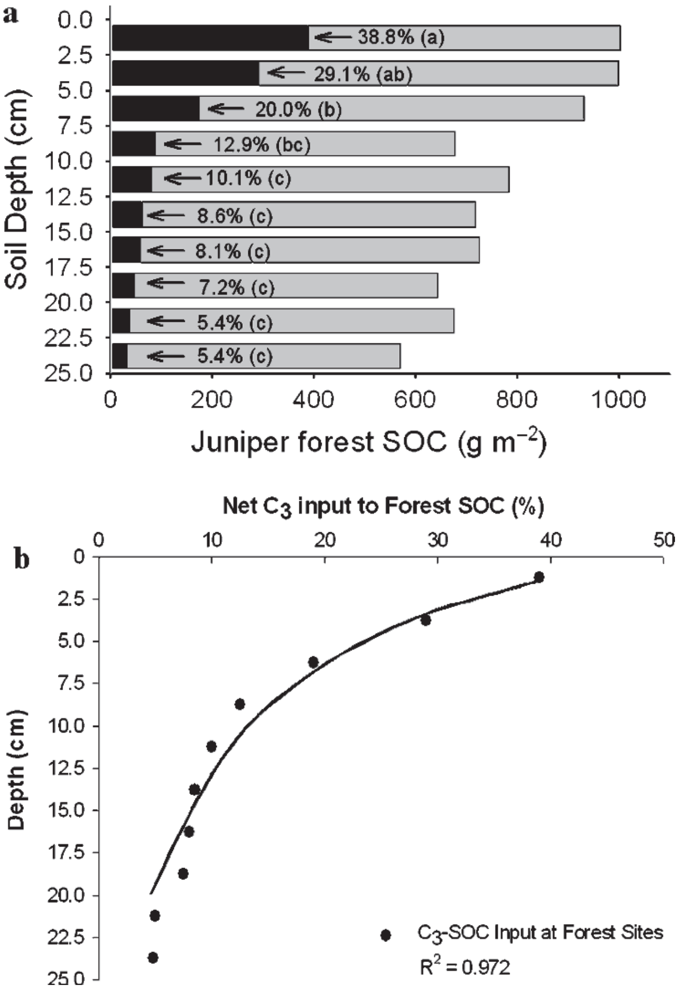

Figure 3 **a** Amounts and percentages of C_3 forest-derived and C_4 prairie-derived C in soil organic carbon (SOC) profiles in redcedar forest. *Dark bars*, SOC derived from forest; *gray bars*, SOC derived from residual prairie carbon. A mixing model (Balesdent et al. 1988; Arrouays et al. 1995) used to calculate net C_3-SOC input into redcedar forest soils over 40–60 years. The *solid portion* of each bar is new C_3-SOC; the *shaded portion* is prairie carbon composing the remainder of SOC. *Numbers to the right of an arrow* indicate the percent C_3 input at each soil depth. *Different letters* indicate statistically significant differences among depths in the forest profile. **b** Regression performed on the C_3-C% input data points indicating an exponential decrease of net C input with increasing depth. (From Smith and Johnson 2004; reproduced by permission of American Geophysical Union)

than the total soil C pool. These results indicate the important role of new forest organic inputs in soil processes such as CO_2 flux via microbial respiration.

Laboratory soil incubations performed under optimal temperature and moisture conditions can reveal differences in substrate quality or quantity, but the results ignore differences in potential abiotic drivers that may be important under field conditions. Laboratory soil incubation assays done by McKinley (2006) corroborated the finding of reduced soil respiration (38%) in soils of redcedar stands by Smith and Johnson (2004), indicating slight but nonsignificant reductions (~5%–13%) in mineralizable C in redcedar stands compared to adjacent grasslands. In contrast, mineralizable N, although not significantly different, was two- to threefold greater in soils of redcedar stands compared to adjacent grassland soils (McKinley 2006). As a result, C mineralization to net N mineralization (Cmin:Nmin) ratios were significantly lower in redcedar soils. Lower Cmin:Nmin ratios, interpreted as an index of substrate quality, suggest that the organic matter pools of redcedar soils may have a higher substrate quality compared to adjacent grasslands (McKinley 2006).

Nitrogen Accumulation and Availability

Frequent fires are common in highly productive grasslands such as tallgrass prairie, and volatilization of N during fire is the major avenue of N loss from ungrazed tallgrass prairie (Blair et al. 1998). In contrast, redcedar stands only develop in the absence of fire (Briggs et al. 2002), and this has a significant effect on ecosystem-level N loss and retention. Both Norris et al. (2001b) and McKinley (2006) reported substantially greater accumulation of total ecosystem N in redcedar stands compared to adjacent grasslands. While biomass nitrogen allocation has largely shifted to aboveground in redcedar stands, at least 85% of total ecosystem N storage remains belowground as a result of large litter and SOM pools (Smith and Johnson 2003; McKinley 2006). Especially important are changes in soil organic N, found to be 21% greater in redcedar soils than in comparable grasslands, which may contribute to greater N availability (McKinley 2006). Reduced ecosystem N losses in redcedar stands resulting from the elimination of N volatilization during fire probably plays a major role in observed increases (~50%) in ecosystem N storage (including aboveground biomass, organic and mineral soil to 10 cm) in redcedar stands relative to the grasslands they replaced (McKinley 2006). Depending on the amount of accumulated plant litter, grasslands lose substantial amounts of N (1–4 g N m^{-2} $year^{-1}$) when burned (Blair 1997). In contrast, the absence of fire in redcedar stands allows a substantial accrual of both C and N in aboveground biomass and surface litter (Norris et al. 2001a,b; McKinley 2006).

Elimination of fire may be a significant contributor to N accumulation in redcedar stands, but altered N inputs may also be important as *Juniperus* species are not known N fixers. The complex redcedar plant architecture and year-round photosynthetic capacity may allow greater potential uptake of atmospheric N from wet and dry deposition. Large increases in ecosystem N in the center as well as the edges of contiguous redcedar stands, suggest that N translocation directly from adjacent grasslands, although possible, is not substantial (McKinley 2006). However, N translocation from deeper portions of the soil profile or through geologic substrates is possible, but has not been investigated. Other exogenous sources of N input into *Juniperus* stands, such as animal inputs or N fixation from lichens (Foreman and Dowden 1977) are possible, but these probably do not contribute enough to account for the size and rate of accrual in current ecosystem N pools. Mechanisms of N accretion in these Juniperus communities are still a matter of conjecture and are in need of investigation.

Concentrations of KCl-extractable inorganic N in soils of redcedar stands and grasslands are small; measured concentrations of ammonium (NH_4^+) and nitrate (NO_3^-) combined usually did not exceed 6 µg N g^{-1} soil (Figure 4a), and NH_4^+ was the dominant form. Mean seasonal concentrations of extractable inorganic N in redcedar stands and grasslands were usually not significantly different, with the exception of winter, when significantly greater concentrations of extractable N occurred in grasslands [one-way analysis of variance (ANOVA), $F = 13.39$, $P = 0.02$], a trend that started in the late fall and continued into early spring (Figure 4a). Differences in wintertime extractable soil N of redcedar and grassland soils were likely caused by differences in seasonal patterns of plant uptake, as redcedar may continue to utilize inorganic soil N in late fall through early spring when the grasses are dormant.

Low concentrations of extractable inorganic N suggest strong N limitations on plant growth. Extractable N pools in grasslands typically reach a maximum in the early spring that coincides with grassland “greenup” (Figure 4a). This increase in extractable N may alleviate N limitations in the beginning of the growing season in grassland soils when plant demand for N begins to rapidly increase in response to plant growth. This overwinter accumulation of extractable N in grasslands appears to be a result of reduced (or eliminated) plant uptake, because measured net N mineralization during the winter was small or negative (Figure 4b). Consistently low concentrations of extractable N in redcedar stands suggest sustained N limitations throughout most of the year. Small NO_3^- pools found in both ecosystems are of particular interest, because small NO_3^- pools reduce the potential for N losses through soil leaching or denitrification that could exacerbate N limitations on plant growth.

Net N mineralization exhibited strong seasonal patterns in both redcedar and grassland soils, with the highest rates in the spring and summer months (>2 µg N g soil^{-1} day^{-1}), intermediate rates in the fall, and low or negative rates in winter months (Figure 4b). Although net N mineralization rates tended to be greater in redcedar stands compared to grassland, there were no significant differences with any average seasonal rate ($P \leq 0.05$). However, when cumulative N mineralization rates were calculated on an annual basis, redcedar soils had significantly greater annual net N mineralization rates (11.52 ± 0.38 µg N g^{-1} soil year^{-1}) compared to grassland soils (7.90 ± 0.26 µg N g^{-1} soil year^{-1}) (one-way ANOVA, $F = 60.67$, $P = 0.02$). Greater N mineralization rates, yet similar or lower concentrations of extractable

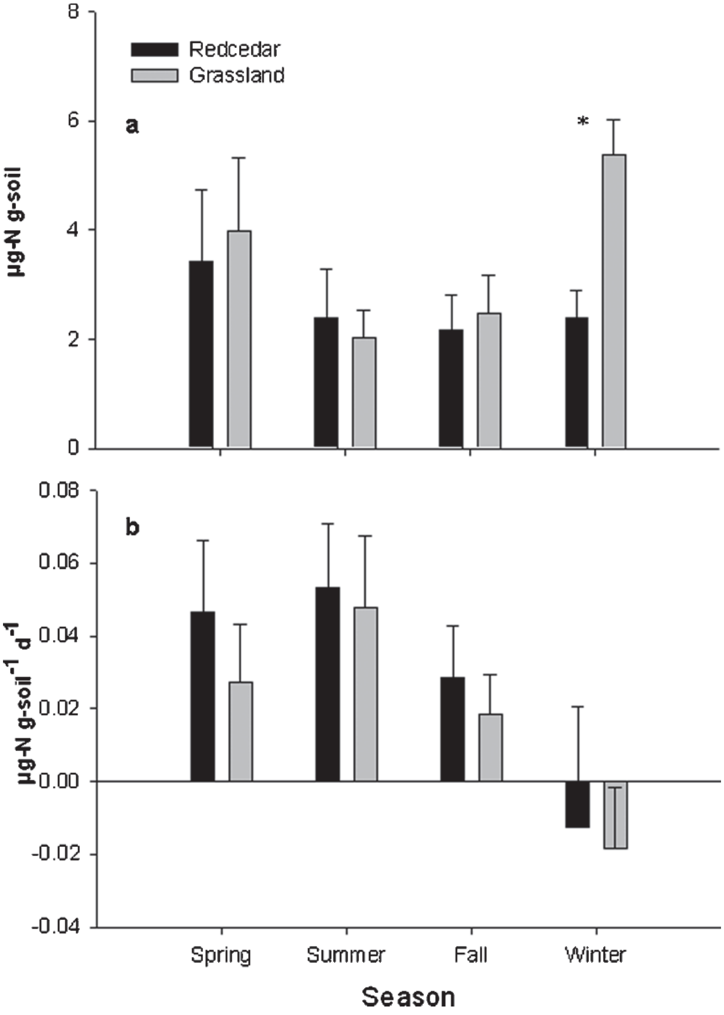

Figure 4 Seasonal patterns of extractable soil inorganic nitrogen (**a**) and net N mineralization (**b**) (mean ± SE) averaged over a 2-year period across four paired sites. Extractable N pools were relatively small in both redcedar and grassland soils over all seasons. There were few differences in soil-extractable N pools in most seasons, with the exception of winter, when grassland soils had significantly greater concentrations [one-way analysis of variance (ANOVA), $F = 13.39$, $P = 0.02$]. Soil net N mineralization was not significantly different between redcedar and grassland soils; however, there was a consistent trend of greater N mineralization rates in redcedar soils. *Asterisks* represent significant differences between vegetation types (redcedar and grassland) for that specific time ($\alpha = 0.05$)

soil N in redcedar stands compared to grassland soils, suggest substantial utilization of available inorganic N by redcedar most of the year (Figure 4 a,b). There are other reports of soil nitrogen availability under redcedar and other *Juniperus* canopies and adjacent grassland communities, measured as either net N mineralization or extractable inorganic N (Charley and West 1977; Klopatek 1987; Klopatek et al. 1990; Miller et al. 1991; Padien and Lajtha 1992; Klopatek and Klopatek 1997; Klemmedson and Tiedemann 2000; Robert and Jones 2000; Bates 2002; Stark et al. 2002; Svejcar and Miller 2002; Stubbs and Pyke 2005; McKinley 2006; Norris et al. 2007), and most of these studies support greater N availability under *Juniperus* canopies relative to either adjacent ungrazed grasslands or intercanopy spaces in a variety of ecosystems.

Nitrogen availability in grasslands can change dramatically with differences in land management, particularly with fire and grazing regimes (Schimel et al. 1991; Blair et al. 1998; Knapp et al. 1998b; Johnson and Marchett 2001; Briggs et al. 2001). For example, annually burned grasslands typically have lower extractable N pools and lower net N mineralization rates compared to less frequently burned sites (Blair et al. 1998). Norris et al. (2007) measured extractable N and net N mineralization over a 2-year period, comparing redcedar stands with adjacent frequently burned cattle-grazed grasslands. Norris et al. (2007) found only small differences in extractable N and net N mineralization (with the grasslands sites having slightly greater N availability). Although Norris et al. (2007) reported similar rates of annual N mineralization in redcedar soils, 14.4 μg N g^{-1} soil $year^{-1}$ compared to 11.5 μg N g^{-1} soil $year^{-1}$ in a later study (McKinley 2006), net N mineralization rates were much greater in recently grazed grassland soils (~17 μg g^{-1} soil $year^{-1}$) compared to long-term ungrazed grasslands (~8 μg N g^{-1} soil $year^{-1}$) in a comparable study (McKinley 2006). The presence of cattle can increase net N mineralization by concentrating highly labile N inputs, affecting plant tissue quality and soil feedback loops by decreasing N immobilization potential (Schimel et al. 1991). Thus, the relative changes in soil N availability resulting from redcedar encroachment may depend, in part, on other land management practices, such as fire and grazing, that have strong effects on N availability in native grasslands (Johnson and Marchett 2001).

Altered Plant Resource Use

Leaf-level photosynthetic nitrogen use efficiency (PNUE) is defined as the maximum carbon assimilation rate (A_{max}) relative to the amount of total nitrogen in the leaf (Lambers et al. 1998). Plants with high PNUE are able to achieve high photosynthetic rates with relatively small amounts of nitrogen. There are typically differences in PNUE between C_3 and C_4 species, with C_4 species generally being more efficient (Sage and Pearcy 1987). In evergreens, A_{max} and consequently PNUE may be further constrained by thick cell walls that limit gas exchange, or leaf N may be allocated to maintaining leaf longevity rather than invested in photosynthetic enzymes (Field and Mooney 1983). In redcedar, PNUE ranged between 0.5 and 1.1 μmol CO_2 g^{-1} N s^{-1} over the course of a year. The highest values were observed in early fall and were caused by higher photosynthetic rates, as leaf N concentrations varied little throughout the year (McKinley 2006). *Andropogon gerardii*, a dominant C_4 species in the paired grassland sites, had much greater PNUE values, which ranged between 17.8 and 29.8 μmol CO_2 g^{-1} N s^{-1} (McKinley 2006).

Although instantaneous metrics of PNUE are much lower in redcedar stands relative to grasses they replace, leaf longevity, greater leaf area, and the ability to assimilate CO_2 year round, particularly when grasses are senescent, may allow greater annual ecosystem-level nitrogen use efficiency (NUE) and primary productivity (Field and Mooney 1983; Miller et al. 1987; Escudero and Mediavilla 2003). Ecosystem-level nitrogen use efficiency (NUE), defined as the ratio of ANPP to litterfall N, provides an index of the amount of aboveground biomass produced per unit of N lost (Chapin 1980; Vitousek 1982). Norris et al. (2007) calculated an ecosystem NUE of 223 for redcedar and 93 for adjacent grassland, which indicated that redcedar was about 2.5 times more efficient in producing biomass per unit N lost in senesced plant tissue. Greater NUE in redcedar stands compared to grasslands is a result of differences in plant phenology that allow more conservative N use, attributable in part to longer leaf lifespan and potential to photosynthesize year round, as well as stand development in consistently low soil N availability (Chapin 1980; Vitousek 1982).

Conclusions

Redcedar encroachment into native grasslands can lead to significant changes in C and N cycling, which also alters the accumulation and patterns of the storage of these elements compared to the grasslands they replace. Redcedar canopies cause substantial reductions in soil temperature, which influence soil processes such as C mineralization. Despite alterations in abiotic conditions that reduce soil respiration, there appears to be slightly enhanced N availability in redcedar stands compared to adjacent annually burned ungrazed prairie, but this was detectable only with long-term measurements. Soil temperatures appear to drive differences in C mineralization, whereas substrate quality may drive differences in N mineralization between ecosystem types. Nitrogen availability in both redcedar and grassland communities is characterized by low concentrations of inorganic nitrogen and relatively low rates of net N mineralization. Changes in soil processes resulting from grassland to redcedar conversion appear to allow soil C accretion through reduced soil CO_2 flux, while simultaneously allowing greater soil N availability to support greater ANPP in redcedar communities.

Redcedar encroachment creates localized patches of increased resource availability, specifically N, but also in some other macronutrients (e.g., Ca and Mg) (McKinley 2006). Increases in resource availability are commonly found with shrub/woodland encroachment in arid and semiarid regions (Schlesinger et al. 1990; Scholes and Archer 1997; Kieft et al. 1998; Hibbard et al. 2001). Intrinsic properties of *Juniperus* stands lead to more conservative N cycling and conditions that may relieve N constraints, which allow greater maintained productivity, at least until other factors (i.e., light or perhaps other nutrients) become more limiting as the forest matures. Reduced N losses caused by the elimination of fire probably play a considerable role in observed increased ecosystem N storage and mitigation against the occurrence of more severe N constraints in most *Juniperus* communities. Also, very similar to the grasslands these redcedar stands replace, very small soil extractable NO_3^- indicates minimal potential for nutrient losses and low contributions to terrestrial and atmospheric loss pathways (Vermes and Myrold 1991; Sotomayor and Rice 1996).

Enhanced soil N availability and greater NUE of redcedar communities may favor redcedar expansion into adjacent grassland communities. Although PNUE, an instantaneous measurement of NUE at the leaf level, indicates that redcedar are comparatively inefficient compared to the C_4 grasses (i.e., *Andropogon gerardii* Vitman) they replace, the ability to consistently photosynthesize year round allows redcedar to have much greater overall stand-level NUE. The combination of greater N availability, more efficient use of N, and year-round photosynthetic capacity allows much greater ANPP and biomass accumulation than in grasslands. Eventually, redcedar plants obtain sufficient size to reduce available photosynthetically active radiation to grasses beneath the canopy, thus potentially altering the competitive balance between these life forms (Schimel et al. 1991).

Many researchers have suggested that expansion of forest ecosystems may be part of the "missing" carbon sink, which may play a role in the mitigation of increasing greenhouse gases (Myneni et al. 2001). In redcedar, there is almost a fourfold difference in total ecosystem C storage relative to grasslands (including root estimates), which amounts to more than 100 Mg C ha^{-1} of additional C (Norris et al. 2001a; McKinley 2006). Redcedar-dominated ecosystems act as strong C and N sinks in these converted mesic grasslands. However, these ecosystems cannot maintain significant rates of C accumulation indefinitely; as redcedar communities mature, their potential role in further C sequestration becomes limited, as seen in older western juniper communities (Miller et al. 1990; Tiedemann and Klemmedson 2000). Also, given that the bulk of the new C and N allocation is aboveground, these pools are very vulnerable to significant and rapid losses, primarily through fire (Klopatek et al. 1990). In addition, long-term ecosystem stores of C and N in the soil may be lost through soil erosion (Davenport 1998) because of reduced or absent plant cover under the redcedar canopies (Briggs et al. 2002). Also, redcedar communities exposed to future increases in anthropogenic N deposition may vary in rates of C and N accumulation, but the potential effects are currently unknown.

Expansion by redcedar and other *Juniperus* species will likely continue in the near future, having substantial consequences on the biogeochemistry, productivity, and species diversity of a variety of ecosystems (Norris et al. 2001a,b; Briggs et al. 2002; Smith and Johnson 2003, 2004; McKinley 2006; Norris et al. 2007). The ultimate end state of these altered ecosystems in terms of structure and function, as well as the role of redcedar in community succession and ecosystem stability of redcedar communities, is unclear, but seems certain to be significant. Management of redcedar must be carefully considered because of the pronounced effects of different management regimes on the expansion of existing redcedar communities and the potential for community alterations with redcedar encroachment into grasslands. *Juniperus* has a unique niche in North American grassland ecosystems, as this unprecedented recent expansion will probably continue to play a large role in changing ecosystem structure and function in many communities.

Summary

Juniperus virginiana, an important woody plant invader in the Central Plains of the United States, has increased dramatically in density and cover in large areas previously dominated by highly diverse prairie communities. This change in plant cover has the potential to significantly alter key ecosystem properties and processes. Results from a variety of studies, mostly conducted in the Central Plains, that have assessed potential changes in ecosystem C and N pools and fluxes as *J. virginiana* expands into native grasslands were summarized. Differences in plant growth form, biomass, and phenology of *J. virginiana* forests, relative to grasslands, alter the soil microclimate as well as litter quality and quantity, which influence soil microbial activity and key soil processes. Changes induced by the shift from grasslands to *J. virginiana* forests include increased aboveground net primary productivity and litterfall, increased organic carbon (C) accrual in surface litter and soil, reductions in soil respiration, and replacement of C_4 grass-derived soil C with new C from *J. virginiana* trees. These aggrading forests also exhibit significant total ecosystem N accumulation and a trend for increased soil N availability compared to grasslands. Although leaf-level instantaneous photosynthetic nitrogen use efficiency (NUE) was more than a magnitude higher in the dominant grass, *Andropogon gerardii*, ecosystem-level NUE (the ratio of ANPP to litterfall N) was about 2.5 times greater in *J. virginiana* forests. This high ecosystem-level NUE and greater soil N availability may contribute to the rapid accrual of C in newly established *J. virginiana* forests. Although *J. virginiana* forests may provide strong regional carbon sinks, these sinks are vulnerable to significant losses through volatilization in fire, as well as losses through soil erosion caused by reduced herbaceous cover in these forests.

References

Anderson, L.J., Brumbaugh, S.M., and Jackson, R.B. 2001. Water and tree-understory interactions: a natural experiment in a savanna with oak wilt. Ecology 82:33–39.

Archer, S. 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. J. Biogeogr. 17:453–462.

Archer, S., Boutton, T.W., and Hibbard, K.A. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Global Biogeochemical Cycles in the Climate system, eds. E.D. Schulze, M. Heimann, S. Harrison, E. Holland, J. Lloyd, I Prentice, d. Schimel, pp 115–138. San Diego, Academic Press.

Archer, S., Scifres, C., and Bassham, C.R. 1988. Autogenic succession in a subtropical savanna, conversion of grassland to thorn woodland. Ecol. Monogr. 58:111–127.

Arrouays, D., Balesdent, J.B., Mariotti, A., and Girardin, C. 1995. Modeling organic carbon turnover in cleared temperate forest soils coveted to maize cropping by using ^{13}C natural abundance measurements. Plant Soil 173:191–196.

Balesdent, J.B., Wagner, G.H., and Mariotti, A. 1988. Soil organic matter turnover in long-term field experiments as revealed by carbon-13 natural abundance. Soil Sci. Am. J. 52:118–124.

Bark, D. 1987. Konza Prairie Research Natural Area, Kansas *In* The Climates of the Long-term Ecological Research Sites. In: *Institute of Artic and Alpine Research, Occasional Paper Number 44* ed. Greenland D, pp 45–50. University of Colorado, Colorado.

Bates, J.D., Svejcar, T.J., and Miller, R.F. 2002. Effects of juniper cutting on nitrogen mineralization. J. Arid Environ. 51:221–234.

Belsky, A.J. 1994. Influences of trees on savanna productivity, tests of shade, nutrients, and tree-grass competition. Ecology 75:922–932.

Blair, J.M. 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. Ecology 78:2359–2368.

Blair, J.M., Seastedt, T.R., Rice, C.W., and Ramundo, R.A. 1998. Terrestrial nutrient cycling in tallgrass prairie. In: Grassland dynamics: long-term ecological research in tallgrass prairie, eds. A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins, pp 222–243. New York: Oxford University Press.

Breashears, D.D., Rich, P.M., Barnes, F.J., and Campbell, K. 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecol. Appl. 7:1201–1215.

Breashears, D.D., Nyhan, J.W., Heil, C.E., and Wilcox, B.P. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and inter-canopy patches. Int. J. Plant Sci. 159:1010–1017.

Briggs, J.M., Knapp, A.K., and Brock, B.L. 2001. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. Am. Midl. Nat. 147:287–294.

Briggs, J.M., Hoch, G.A., and Johnson, L.C. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578–586.

Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S., and McCarron, J.K. 2005. An ecosystem in transition: woody plant expansion into mesic grassland. Bioscience 55:2245–2257.

Chapin, F.S. 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst. 11:233–260.

Charley, J.L., and West, N.E. 1977. Micro-patterns of nitrogen mineralization activity in soils of some shrub dominated semi-arid ecosystems of Utah. Soil Biol. Biochem. 9:357–365.

Davenport, D.W. 1998. Viewpoint: Sustainability of pinyon-juniper ecosystems: a unifying perspective of soil erosion thresholds. J. Range Manag. 51:231–240.

Escudero, A., and Mediavilla, S. 2003. Decline in photosynthetic nitrogen use efficiency with leaf age and nitrogen resorption as determinants of leaf life span. J. Ecol. 91:880–889.

Field, F., and Mooney, H.A. 1983. The photosynthesis-nitrogen relationship in wild plants. In: On the economy of plant form and function: Proceedings of the sixth Maria Moors Cabot symposium evolutionary constraints on primary productivity, adaptive patterns of energy capture in plants, ed. T.J. Givnish, pp 25–55. Harvard: Cambridge University Press.

Foreman, R.T.T., and Dowden, D.L. 1977. Nitrogen fixing lichen roles from desert to alpine in the Sangre de Cristo mountains, New Mexico. Bryologist 80:561–570.

Fowells, H.A. 1965. Silvics of forest trees of the United States. Handbook 271. Washington, DC: U.S. Department of Agriculture.

Freeman, C.C., and Hulbert, L.C. 1985. An annotated list of the vascular flora of Konza Prairie Research Natural Area, Kansas. Trans. Kans. Acad. Sci. 88:84–115.

Hester, J.W. 1996. Influence of woody dominated rangelands on site hydrology and herbaceous production. M.S. thesis. College Station: Texas A&M University.

Hibbard, K.A., Archer, S., Schimel, D.S., Valentine, D.W. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. Ecology 82:1999–2011.

Jackson, R.B., Banner, J.L., Jobbagy, E.G., Pockman, W.T., and Wall, D.H. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature (Lond.) 418:623–626.

Johnson, L.C., and Matchett, J.R. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. Ecology 82:3377–3389.

Kieft, T.L., White, C.S., Loftin, S.R., Aguilar, R., Craig, J.A., and Skaar, D.A. 1998. Temporal dynamics in soil carbon and nitrogen resources at a grassland-shrubland ecotone. Ecology 79:671–683.

Klemmedson, J.O., and Tiedemann, A.R. 2000. Influence of western juniper development on distribution of soil and organic layer nutrients. Northwest Sci. 74:1–11.

Klopatek, C.C., and Klopatek, J.M. 1997. Nitrifiers and mycorrhizae in pristine and grazed pinyon-juniper ecosystems. Arid Res. Rehabil. 11:331–342.

Klopatek, J.M. 1987. Nitrogen mineralization and nitrification in mineral soils of pinyon-juniper ecosystems. Soil Sci. Am. J. 51:453–457.

Klopatek, J.M., Klopatek, C.C., and DeBano, L.F. 1990. Potential variation of nitrogen transformations in pinyon-juniper ecosystems resulting from burning. Biol. Fertil. Soils 10:35–44.

Knapp, A.K., Briggs, J.M., Blair, J.M., and Turner, C.L. 1998a. Patterns and controls of aboveground net primary production in tallgrass prairie. In: Grassland dynamics: long-term ecological research in tallgrass prairie, eds. A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins, pp 193–221. New York: Oxford University Press.

Knapp, A.K., Conrad, S.L., and Blair, J.M. 1998b. Determinants of soil CO_2 flux from a subhumid grassland: effect of fire and fire history. Ecol. Appl. 8:760–770.

Kuchler A.W. 1967. Some geographic features of the Kansas Prairie. Trans. Kanras Acd. sci. 70:388–401.

Lambers, H., Chapin, F.S., and Pons, T.L. 1998. Photosynthesis respiration and long-distance transport. In: Plant physiological ecology, pp 56–58. New York: Springer-Verlag.

McClaugherty, C., Aber, J.D., and Melillo, J. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63:1481–1490.

McKinley, D.C. 2006. Consequences of conversion of native mesic grassland to coniferous forest on soil processes and ecosystem C and N storage. Ph.D. dissertation. Manhattan, KS: Kansas State University (available http://hdl.handle.net/2097/253).

Miller, P.M., Eddleman, L.E., and Kramer, P.J. 1990. Allocation patterns of carbon and minerals in juvenile and small-adult *Juniperus occidentalis*. For. Sci. 36:734–746.

Miller, P.M., Eddleman, L.E., and Miller, J.M. 1991. The response of juvenile and small-adult western juniper (*Juniperus occidentalis*) to nitrate and ammonium fertilization. Can. J. Bot. 69:2344–2352.

Miller, R.F., Eddleman, L.E., and Angell, R.F. 1987. Relationship of western juniper stem conducting tissue and basal circumference to leaf area and biomass. Great Basin Nat. 47:349–354.

Miller, R.F., Bates, J.D., Svejcar, T.J., Peirson, F.B., and Eddleman, L.E. 2005. Biology, ecology, and management of western juniper (*Juniperus occidentalis*). Technical bulletin 152. Corvallis: Oregon State University, Agricultural Experiment Station.

Moiser, A.R. 2001. Exchange of gaseous nitrogen compounds between agricultural systems and the atmosphere. Plant Soil 228:17–27.

Murphy, K.L., Klopatek, J.M., and Klopatek, C.C. 1998. The effects of litter quality and climate on decomposition along an elevational gradient. Ecol. Appl. 8:1061–1071.

Myneni, R.B., Dong, J., Tucker, C.J., Kaufmann, R.K., Kauppi, P.E., Liski, J., Zhou, L., Alexeyev, V., and Hughes, M.K. 2001. A large carbon sink in the woody biomass of Northern forest. Proc. Natl. Acad. Sci. U.S.A. 98:14784–14789.

National Oceanic and Atmospheric Administration (NOAA). 2004. National Climate Center, Ashville, NC.

Norris, M.D., Blair, J.M., and Johnson, L.C. 2001a. Land cover change in eastern Kansas: litter dynamics of closed-canopy eastern redcedar forests in tallgrass prairie. Can. J. Bot. 79:214–222.

Norris, M.D., Blair, J.M., Johnson, L.C., and McKane, R.B. 2001b. Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. Can. J. For. Res. 31:1940–1946.

Norris, M.D., Blair, J.M., and Johnson, L.C. 2007. Altered ecosystem nitrogen dynamics as a consequence of land cover change in tallgrass prairie. Am. Midl. Nat. 158:

Oviatt, C.G. 1998. Geomorphology of Konza Prairie. In: Grassland dynamics: long-term ecological research in tallgrass prairie, eds. A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins, pp 35–47. New York: Oxford University Press.

Padien, D.J., and Lajtha, K. 1992. Plant spatial patterns and nutrient distribution in pinyon-juniper woodlands along an elevational gradient in northern New Mexico. Int. J. Plant Sci. 153:425–433.

Rhoades, C.C., Miller, S.P., and Shea, M.M. 2004. Soil properties and soil nitrogen dynamics of prairie-like forest openings and surrounding forest in Kentucky's Knobs region. Am. Midl. Nat. 152:1–11.

Roberts, C., and Jones, J.A. 2000. Soil patchiness in juniper-sagebrush-grass communities of central Oregon. Plant and Soil 223:45–61.

Sage, R.F., and Pearcy, R.W. 1987. The nitrogen use efficiency of C_3 and C_4 plants. Plant Physiol. 84:959–963.

Schimel, D.S., Kittel, T.G.F., Knapp, A.K., Seastedt, T.R., Parton, W.J., and Brown, V.B. 1991. Physiological interactions along resource gradients in a tallgrass prairie. Ecology 72:672–684.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., and Whitford, W.G. 1990. Biological feedbacks in global desertification. Science 247:1043–1048.

Schmidt, T.L., and Leatherberry, E.C. 1995. Expansion of eastern juniper in the lower Midwest. Natl. J. Am. For. 12:180–183.

Scholes, R.J., and Archer, S. 1997. Tree-grass interactions in savannas. Annu. Rev. Ecol. Syst. 28:517–544.

Seastedt, T.R. 1988. Mass, nitrogen, and phosphorus dynamics in foliage and root detritus of tallgrass prairie. Ecology 69:59–65.

Smeins, F.E. 1983. Origin of the brush problem: a geographical and ecological perspective of contemporary distributions. Brush Manag. Symp. 5–16.

Smith, D. 2001. Changes in soil carbon dynamics during juniper expansion into tallgrass prairie. Ph.D. dissertation. Manhattan, KS: Kansas State University.

Smith, D., and Johnson, L.C. 2004. Vegetation-mediated changes in microclimate reduce soil respiration as woodlands expand into grasslands. Ecology 85:3348–3361.

Smith, D.L., and Johnson, L.C. 2003. Expansion of *Juniperus virginiana* L. in the Great Plains: changes in soil organic carbon dynamics. Global Biogeochem. Cycles 17:1–12.

Sotomayor, D., and Rice, C.W. 1996. Denitrification in soil profiles beneath grassland and cultivated soils. Soil Sci. Am. J. 60:1822–1828.

Stark, J.M., Smart, D.R., Hart, S.C., and Haubensak, K.A. 2002. Regulation of nitric oxide emissions from forest and rangeland soils of western North America. Ecology 83:2278–2292.

Stubbs, M.M., and Pyke, D.A. 2005. Available nitrogen: a time-based study of manipulated resource islands. Plant Soil 270:123–133.

Tiedemann, A.R., and Klemmedson, J.O. 2000. Biomass and nutrient distribution and system nutrient budget for western juniper in central Oregon. Northwest Sci. 74:12–24.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–215.

Vermes, J.F., and Myrold, D.D. 1991. Denitrification in forest soils of Oregon. Can. J. For. Rest. 22:504–512.

Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. Am. Nat. 119:553–572.

Vitousek, P.M. 2004. Nutrient Cycling and Limitation: Hawai'i as a Model System. Princeton: Princeton University Press.

10
Juniper Tree Impacts on Local Water Budgets

M. Keith Owens

Introduction

In semiarid and arid ecosystems, available water is undoubtedly the most limiting resource. Woody plant encroachment has changed semiarid ecosystems from grasslands to woodlands and has subsequently altered the water balance of these plant communities. In many regions of the western United States, juniper trees are the primary woody species encroaching on rangelands (Archer 1994; Van Auken 2000; Ansley et al. 2001). Juniper trees are adapted over a wide range of environmental conditions, as evidenced by their widespread distribution in North America (see Chapter 1, this volume). They have successfully established in grasslands of the Great Plains (Gehring and Bragg 1992) and on harsh, dry sites in semiarid rangelands (Miller and Rose 1995; Soule and Knapp 2000). In central Texas, the density and aerial cover of Ashe juniper (*Juniperus ashei* Buchholz) has increased over the past 200 years. Originally limited to rocky outcrops or areas of low fuel availability, Ashe juniper has invaded almost 2.7 million hectares (ha) on the Edwards Plateau. Typical characteristics of invasive species often include high photosynthetic rates, distinct seasonal patterns of photosynthesis and growth, flexible resource allocation, and life history strategies that allow rapid dispersal. Life history traits, susceptibility to fires, grazing management, and hydrological characteristics of juniper communities and other factors are addressed in other chapters of this book. This chapter focuses on the physical and physiological impact of juniper trees on the local water budget.

The physical impact of a tree on rainfall is through the redistribution via canopy interception, evaporation, and stemflow. Through these processes, precipitation is redirected and the fate of the water is changed. Ignoring the amount of precipitation intercepted by tree canopies, or lumping it with evapotranspiration, can cause large errors in estimating other parts of the hydrological budget (Savenije 2004). If interception is ignored, water captured by the tree canopy would be lumped with the soil water pool and consequently lead to overestimation of transpiration. Interception and evaporation can be a significant portion of the total evapotranspiration. For instance, Guevara-Escobar et al. (2000) reported that total evapotranspiration from a poplar (*Populus deltoides* Bart. ex March) forest in New Zealand averaged

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2.7 to 3.0 mm day^{-1} during the spring growing period and of that 1.4 mm day^{-1} was lost as canopy interception. Not accounting for interception could have led to a dramatic overestimation of transpiration. The morphology of juniper trees (*Juniperus* sp.) is ideally suited for intercepting and retaining precipitation. The scale-like leaf structure and the large leaf area combine to hold a significant amount of water in the canopy. This water can then be either evaporated back to the atmosphere or redistributed to the area immediately adjacent to the bole of the tree via stemflow and then be available for transpirational water use.

The physiological impact is through transpiration by both juvenile and mature trees (Owens 1996; Moore and Owens 2006). The redistribution of water (physical impact) directly affects the amount of water available to the trees and can ultimately affect transpiration.

Physical Impact

The fate of precipitation within a tree community can be divided into canopy interception and evaporation, throughfall, stemflow, litter interception, and soil recharge. Canopy interception is the portion of ambient rainfall that is retained by the leaves and bark and generally has a negative effect on the horizontal distribution of water by retaining small pulses of precipitation in the canopy (Loik et al. 2004; Owens et al. 2006), thus preventing water from reaching the ground surface. Throughfall is the portion of ambient rainfall that either falls through the canopy without being deflected or may be intercepted by a branch and temporarily redirected but ultimately falls to the ground surface. Stemflow is the portion of the rainfall that flows on the outside of the stem during a storm; it can particularly affect the vertical distribution of water by funneling water to the base of the tree where it can infiltrate rapidly (Devitt and Smith 2002) or be redistributed less rapidly through diffusion or hydraulic redistribution (Schwinning and Sala 2004). Litter interception is the amount of rainfall held in the upper layer of coarse organic matter and is generally unavailable for plant use. Through these avenues, the vertical and horizontal spatial heterogeneity of water within a woody plant community can be drastically altered by the physical presence of trees.

Precipitation is redistributed horizontally by running off bare interspaces and into vegetated patches where infiltration might be greater (Dunkerley 1997; Reid et al. 1999). Rainfall can also be redistributed by funneling water from the outer portion of the canopy toward the base of the plant (Herwitz 1986; Martinez-Meza and Whitford 1996; Devitt and Smith 2002). The increased soil water near the base of the tree has been shown to increase the moisture available to individual plants (Martinez-Meza and Whitford 1996). The amount of rainfall intercepted by tree canopies and lost to evaporation is species specific and may be a function of rainfall intensity (Schowalter 1999; Silva and Rodriguez 2001) and leaf morphology (Hester 1996; Carlyle-Moses 2004). Shrubs in semiarid systems have been reported to intercept from 13% to 40% of bulk rainfall, deciduous trees from 9% to 20%, and coniferous trees from 20% to 48% (Carlyle-Moses 2004). When growing in the same environment, conifers typically exhibit a higher interception than broadleaf plants (Moreno et al. 1993; Silva and Rodriguez 2001).

A 3-year study was conducted in Ashe juniper communities in the Edwards Plateau to investigate rainfall partitioning in tree canopies (Owens et al. 2006). More than 2700 individual rainfall events were recorded at 10 study sites. Averaged over all storms, about 61% ± 3% (mean ± SE) of the bulk rainfall reached the soil surface beneath juniper trees, while the remaining 39% ± 3% was intercepted by either the canopy or the coarse litter and then lost to evaporation. The high canopy interception and evaporation were mainly the result of the large number of small storms that experienced total, or nearly total, interception. Most of the precipitation from storms less than 2.54 mm was either intercepted by the canopy (96%) or the litter layer (2%), leaving only 2% of the bulk rainfall to reach the soil surface beneath the juniper trees (Figure 1). The low-intensity storms, although numerous, contribute little moisture to the soil surface.

As storm size increased, the proportionate amount of water intercepted by the canopy and lost to evaporation decreased. Approximately 50% direct throughfall did not occur until at least 11 mm rain occurred. At this time, about 43% of the rain was intercepted by the canopy, 5.6% was intercepted by the litter, and 2% occurred as stemflow. The remaining 50% directly reached the soil surface. At the highest rainfall levels, more than 80% of the rain directly reached the soil surface as throughfall, nearly 5.6% was intercepted by the litter layer, 4% occurred as stemflow and 10% was intercepted by the canopy. Interception by the litter layer peaked quickly and remained constant after saturation.

A thorough review of woody plants by Carlyle-Moses (2004) shows an average of 8.2% of precipitation reaches the soil as stemflow, although there is great variability between plant species. This average is slightly greater than the 5% observed for Ashe juniper (see Figure 1), but the branching pattern and shaggy bark of Ashe juniper can cause stemflow to be deposited as redirected throughfall before the water reaches the main trunk of the tree. The redirection of precipitation via stemflow can result in a concentration of water from 5 (Slaughter 1997) to 30 (Bellot and Escarre 1998) times greater near the stem than ambient rainfall. If we assume that the stemflow would impact an area of 0.5 m^2 around the base of the tree, our study indicates that the funneling of stemflow water results in a 21:1 ratio of concentration of rainfall near the trunk when compared to ambient rainfall. For example, during a 100-mm rainfall, this 0.5 m^2 area would receive 10.5 l rainfall rather than the 0.51 that a similar-sized area would receive just from rainfall. The higher recorded infiltration rates under juniper trees would allow this water to remain on the site beneath the tree rather than being lost as overland flow (Thurow and Hester 1997). This additional water could be used to increase the competitive effectiveness of the plant (Ndawula-Senyimba et al. 1971) or it could quickly pass by the root system and enter the deeper portions of the soil profile (Martinez-Meza and Whitford 1996). Given the current density of Ashe juniper trees on the Edwards Plateau, the funneling effect of stemflow could have a large impact on local and regional water budgets.

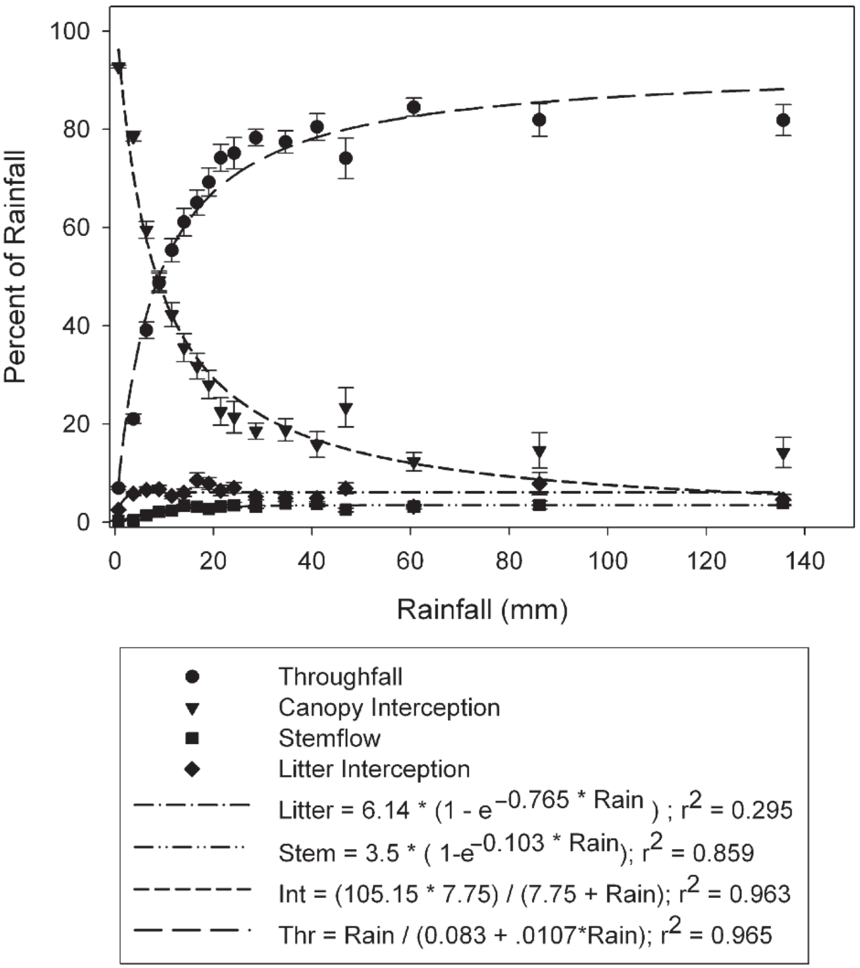

Figure 1 Rainfall partitioning into canopy interception, throughfall, stemflow, and litter interception for Ashe juniper trees in the Edwards Plateau of Texas. (Reprinted from Owens et al. 2006, with permission from Wiley)

Physiological Impacts

Leaf Scale

Leaf-level measurements are particularly useful when evaluating how a plant species reacts to environmental stress or microsite conditions, or when comparing how co-occurring species react to the same environment. For instance, in an open woodland and under similar environmental conditions, live oak (*Quercus virginiana* var. *fusiformis*) maintained a significantly greater rate of leaf-level photosynthesis and transpiration than Ashe juniper (Owens and Schreiber 1992). This relationship also held in a closed woodland (Bendevis 2006), where photosynthesis was twice as great for live oak than for Ashe juniper (13.12 vs. 6.47 µmol m^{-2} s^{-1}, respectively). The primary physical factors affecting leaf-level gas exchange are where the leaf occurs in the canopy of the tree and where the tree grows in relationship to other trees.

Canopy Location

The location of an individual leaf within the canopy of a tree can affect gas-exchange rates and water use. In open woodland, gas exchange within a juniper canopy was controlled by a combination of cardinal direction, height in the canopy, time of day, and month of observation (Owens and Schreiber 1992). Leaves in the upper one-third of the canopy had gas exchange rates about 20% greater than leaves in the lower portions of the canopy. Leaves on the southeast side of the tree had higher rates in the morning than in the afternoon, and the opposite was true for leaves on the northwest side of the tree. Only in months with low precipitation (<2.5 cm) was there no difference in gas exchange between any of the canopy locations.

This observation is in contrast to a closed woodland where there were no differences in gas exchange based on canopy location (Bendevis 2006). In closed woodland, the canopy structure was much thinner, with all leaves concentrated near the top of the tree; in fact, mean leaf area index per tree was only 0.91 compared with a leaf area index of 5.2 for trees in the open woodland. Light was able to diffuse throughout the canopy, and transpiration was similar for sun and shade leaves. Only environmental effects such as precipitation and temperature affected gas-exchange rates.

Microsite

The effect of the microsite location on transpiration and carbon uptake was examined over a 2-year period at three sites across Texas (Moore and Owens 2006). At each site, juvenile trees (trees showing no signs of seed production) were selected either in an open area or with a mature juniper overstory. One-half of the trees with a juniper overstory then had that mature plant cut down and removed, resulting in small trees either (1) in the open, (2) with a mature overstory, or (3) released from competition. This treatment scenario would allow the effects of light versus water competition to be separated.

Combining data from all measurement dates and times resulted in combined rates of carbon uptake and transpiration that were significantly greater in released plants compared to those grown under an adult canopy. Values for carbon uptake were also significantly greater in released plants than the rates observed for plants grown in the open at one site. Average carbon uptake of released plants was

94% to 162% greater than that of plants beneath an adult canopy and 22% to 44% greater than open-grown plants. In the same individuals, average transpiration of released plants was 22% to 72% greater than that of plants beneath an adult canopy and 13% to 22% greater than open-grown plants. The observed differences in gas exchange among treatments persisted for at least 21 months. Further, gas exchange was particularly elevated in released plants compared to open-grown or plants beneath the canopy when plants were under water stress (daily average water potential, less than −1 MPa).

The differences in gas exchange observed among juvenile Ashe juniper treatments provide insights into the relative importance of light and microsite conditions for leaf-level physiology. The microsite under a mature tree may be more ideal either because of preexisting factors (e.g., deeper soil or fractured bedrock) or because of factors created by the adult itself (e.g., deeper litter layer, more soil nutrients, greater soil water-holding capacity). If light is the limiting factor, then gas-exchange rates of juveniles beneath the canopy should be lower than the rates of juveniles grown in the open. If competition from adults for other resources is the primary limiting factor for juvenile trees, then gas exchange of open-grown juveniles should be comparable to those juveniles whose overstory had been removed. If both light and microsite are important factors then the juveniles with the canopy overstory removed should have the greatest gas-exchange rates. In fact, gas-exchange rates were greatest for juveniles when the canopy overstory was removed. Juveniles growing beneath an adult canopy most likely experienced suppressed carbon uptake because of light limitations resulting from shading. Average light levels of beneath-canopy plants were only about half as much as the levels for plants growing in the open (average of 439 ± 14 vs. 625 ± 20 μmol m^{-2} s^{-1}). Net assimilation beneath the canopy was only half that of released plants, but transpiration was only 18% to 42% lower, suggesting that photosynthesis was light limited. Juveniles growing in released microsites also had greater gas-exchange rates than juveniles grown in the open, also suggesting that water was a limiting factor.

Canopy Scale

Scaling from leaf-level measurements to canopy-level estimates must be undertaken with great care. Most leaf-level measurements are made to compare how species react to environmental conditions, stresses, and competition. Therefore, the samples are typically taken on sunny days during active growth periods. Modeling to the canopy level can be complex when sun position, total leaf area, leaf distribution within the canopy, and neighboring plants are considered. Previous models have been rather simplistic to allow direct comparisons between co-occurring species (Owens 1996). These estimates have been extrapolated to estimate total water use from a plant community, but the combined errors from all the estimates may be large.

Recent technological developments allow a more integrated estimate of water use by estimating total sapflux throughout extended periods of time. The primary techniques use heat balance, heat pulse, or heat dissipation methodology. The heat balance technique is best suited for small or round stems and may not be effective for the convoluted shape of mature juniper trees. On individual branches, however, this technique is very effective. It is a short-term (<3 weeks) measurement so it does not integrate over a growing season, but diurnal patterns of transpiration can be measured. The heat pulse technique supplies a very small pulse of heat and then measures the time required to reach a distant point in the sapwood. This technique can also be very effective, but low sapflux rates can be problematical. The heat dissipation technique supplies a constant heat source and measures the difference in temperature between a heated and an unheated sensor in the sapwood. All three techniques can be used with Ashe juniper, depending on the objectives of the study.

Importance of Stemflow

Funneling rainfall to the base of the tree occurs in almost every storm. As demonstrated above, the funneling ratio for juniper trees is about 21 to 1, meaning that the base of the tree receives more than 20 times as much rainfall as a similar-sized area away from a tree. The ecological significance of this funneling effect can be investigated using canopy-level or branch-level transpiration. If the stemflow water is used by the tree, then transpiration should increase following precipitation. If the water is being funneled past the rooting zone, then transpiration should not increase.

We investigated these hypotheses using two different techniques. First, we instrumented branches with heat balance gauges (DynaMax, Houston, TX, USA) and added either 19 or 381 water as stemflow. When 191 stemflow was added, there was no net increase in transpiration (Figure 2, upper panel), but transpiration increased by 72% to 89% when 381 stemflow was added (Figure 2, lower panel). This observation suggests that small rainfall events do not add sufficient stemflow to increase transpiration, but that rainfall redirected as stemflow can be used by the plant. In a second investigation, heat pulse needles were placed in trees at three different sites. One-half the trees at each site had stemflow collected, measured, and removed while the other trees received normal stemflow. These trees were monitored for 2 months encompassing a rainy period. All transpiration rates were converted to a typical 30-cm basal diameter tree for comparisons. Over the 55-day period, transpiration was significantly greater for trees with stemflow compared to trees without stemflow (Figure 3). Trees with stemflow received about 1021 additional water near the base of the tree, and increased transpiration accounted for about 451 of that additional rainfall. This trial suggests that stemflow water may be used by the tree but that some of the additional water may also be bypassing the root system via conduit flow, resulting in deeper recharge.

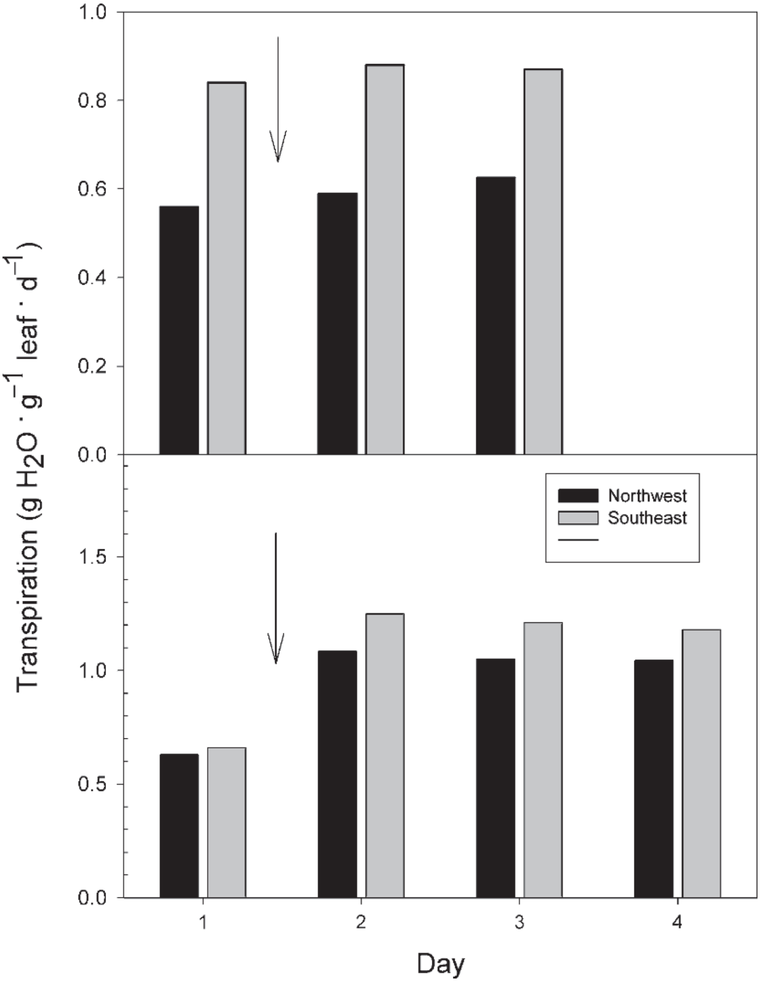

Figure 2 Transpirational water loss after 191 (*upper panel*) or 381 (*lower panel*) water was added as stemflow to Ashe juniper trees. *Arrows* show the timing of the water application

Responses to Rainfall Events

In semiarid rangelands, precipitation is the driving variable for many ecosystem processes (Loik et al. 2004; Schwinning et al. 2004), but it is not evenly distributed throughout the year. The size and frequency of precipitation pulses can be critical for plant growth and survival. In subhumid regions, precipitation pulses are larger but may be less significant because of greater annual precipitation. The importance of pulse events for juniper transpiration can be determined by measuring sapflux before, during, and after a rainfall event.

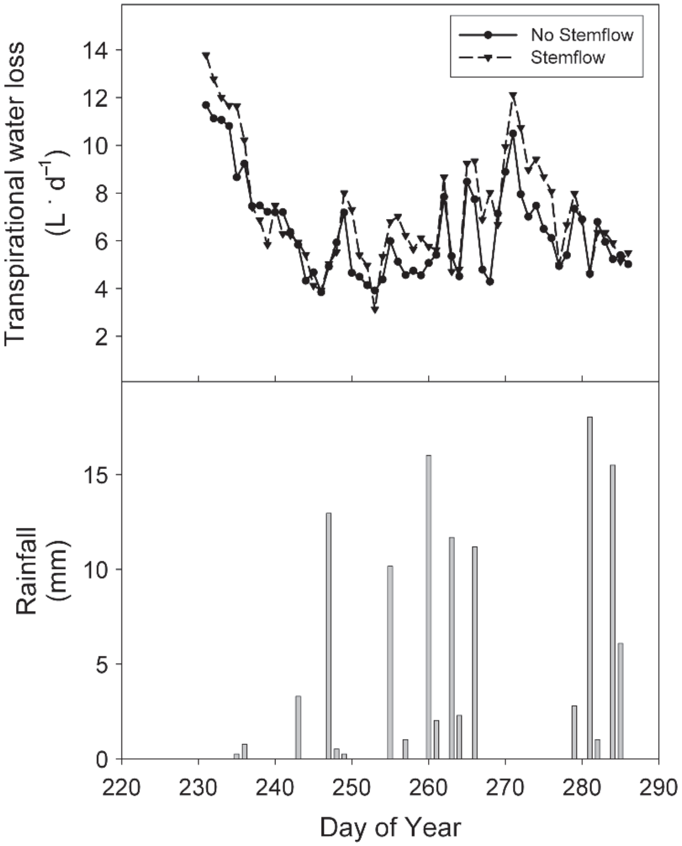

Figure 3 Transpirational water loss from Ashe juniper trees with stemflow and without stemflow over a 55-day period (*upper panel*). *Lower panel* shows the ambient precipitation during the study

Approximately 40% of the ambient rainfall is intercepted by the juniper canopy and is presumably lost to evaporation. During the time required for the water to evaporate, the tree is not transpiring and therefore may be conserving water. The difference between evaporative loss from the canopy and gain from a lack of transpiration is the real measure of water lost during and immediately after rainfall. A preliminary study using heat balance gauges on juniper branches on trees under a rainfall simulator and on unwatered trees showed that transpiration decreased soon after the rainfall simulation began (Figure 4). The tree maintained a low transpiration rate throughout the simulated rainfall and had rates similar to unwatered trees about 90 min after rainfall stopped. A second rainfall simulation and the onset of nightfall precluded monitoring the trees longer.

In a separate study, juniper and live oak trees were instrumented with heat dissipation sensors and monitored over a 2-year period to record transpiration after natural rainfall. Storms were divided into small (<25 mm), medium (25–60 mm),

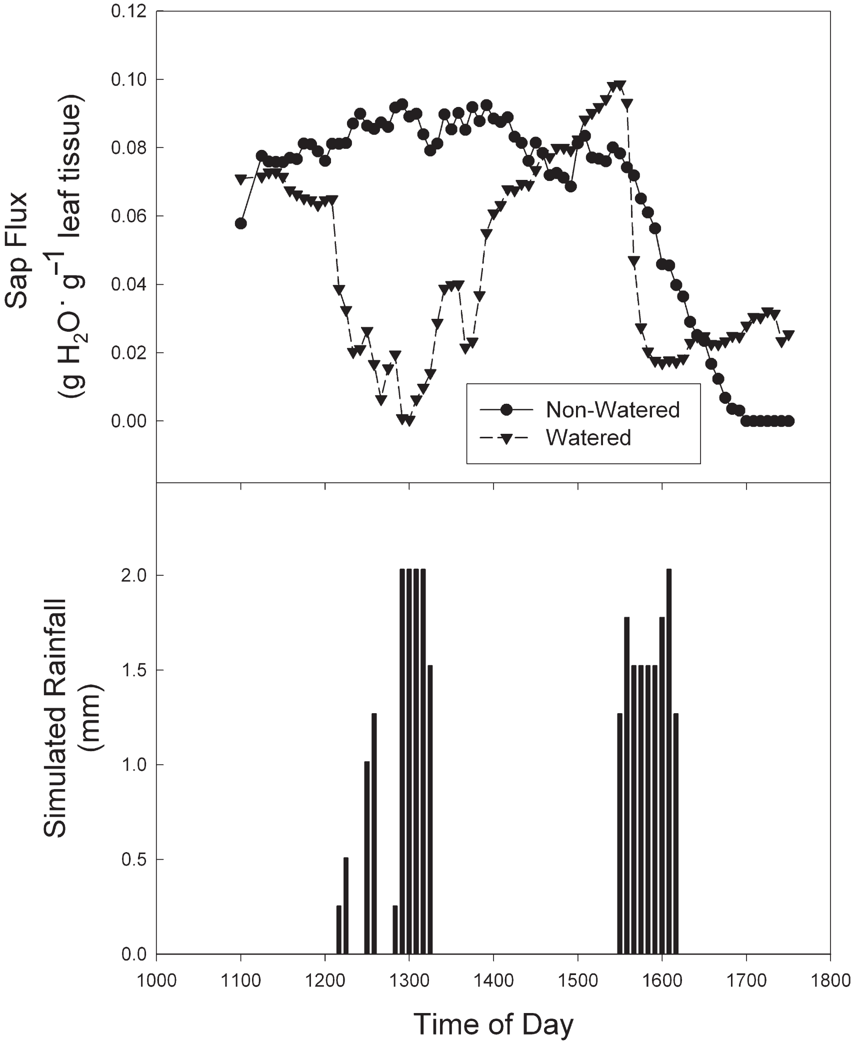

Figure 4 Sap flux (*upper panel*) of Ashe juniper branches during two rainfall simulations (*lower panel*) at the Sonora Research Station in west-central Texas

and large (>60 mm) categories over the study period. Sapflux was averaged for the 3 days before the storm and for the 3 days after the storm to determine the net percentage increase in transpiration. Juniper trees were largely unresponsive to precipitation and demonstrated very small, statistically nonsignificant, changes in transpiration (Figure 5). Live oak trees, on the other hand, were very responsive and increased transpiration by nearly 100% after large storms. The lack of response following small storms is not surprising given that a large portion of small storms is intercepted by the canopy and never reaches the ground surface

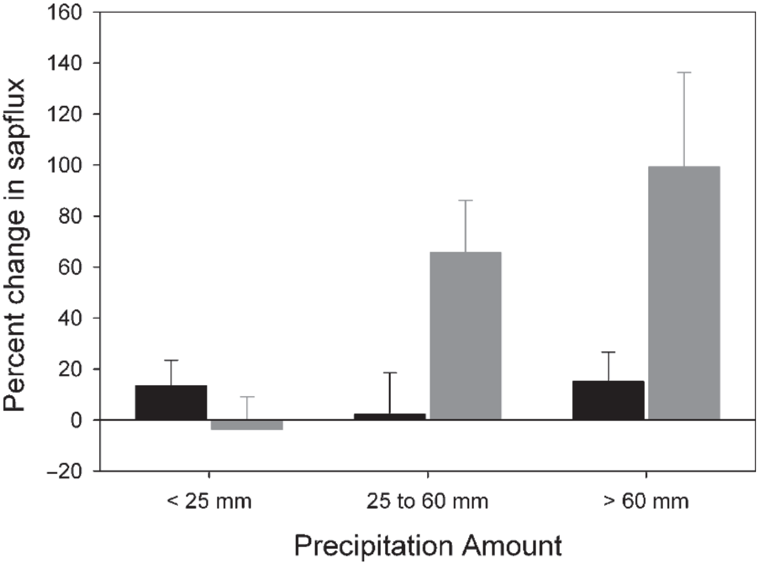

Figure 5 Percent increase in sapflux of Ashe juniper (*left bar* in pair) and live oak (*right bar* in pair) following storms of three different sizes at the Freeman Ranch site in central Texas

(Owens et al. 2006). The ability of oak trees to respond to precipitation has been reported on the leaf level (Owens and Schreiber 1992) but not on the canopy level. The responsiveness might be related to the specific hydraulic capacity, or the potential to transport water, of both species. McElrone et al. (2004) reported the mean conduit diameter of Ashe juniper was less than one-third of the conduit diameter of live oak. Specific hydraulic conductivity of live oak was 12 (stems) to 25 (deep roots) greater than that of juniper. Therefore, the basic ability to transport water is much greater in live oak, and it is able to increase water flow when it is available.

Community Level

Modeling gas exchange from the leaf level, or even the tree level, to the community level can be problematical. In addition to the canopy-level processes already discussed, the number of trees in savanna settings, the number in closed woodlands, and the number of different canopy sizes must be considered. Each of these measurements has a degree of error associated with the estimation, and these errors are often multiplicative rather than additive. Even when the modeling is complete, the purpose of the model must be clearly stated as determining how juniper trees affect local water budgets, not as how much water can be gained from removing juniper trees. When trees are removed, other vegetation will grow in their place and transpire water. Those new plants must be considered when estimating water yield.

Early estimates of water use were about 125 l water transpired per day for a mature Ashe juniper tree (Owens 1996). The estimate falls within other reported values for daily water use for woody plants (mean = 189 l; Wullschleger et al. 1998) but is greater than estimates for Ashe juniper based on Bowen ratio estimates (32.7 l/day; Dugas et al. 1998) and for other juniper species (21 l/day (Angell and Miller 1994). The estimate of 125 l/day was derived for trees growing in an open savanna with full canopies. Leaf area index (LAI) averaged greater than 5.2, with a total leaf area of 142 m^2 in each tree. A recent study in a closed-canopy woodland resulted in much lower estimates of water use. Bendevis (2006) reported canopy-level water use as 92 mmol s^{-1} during the most active periods and 20.8 mmol s^{-1} during low growth, or water-stressed, periods. These observations convert to 71.5 and 16.2 l/day based on a 12-h day. The rates of gas exchange per unit leaf area observed by Bendevis (2006) were similar to the rates observed earlier (Owens and Schrieber 1992; Owens 1996). The difference in daily totals can be attributed to the canopy structure. Trees in the closed woodland had less that 20% of the canopy found in the open-grown trees (LAI, 0.91 vs. 5.2, respectively). Clearly, the estimates of leaf area are critical in extrapolating data from the leaf to the tree scale.

To model water use, an estimate of the number of trees in a juniper community is needed. The estimate must be subdivided into canopy size-classes and into open-grown versus closed-woodland trees. Recent samples collected at the Freeman Ranch in central Texas demonstrate the different community structures. The closed woodland averaged 1904 trees ha^{-1} (± 152, SE) and the open savanna averaged 699 trees ha^{-1} (± 70, SE). The woodland was composed mostly of trees less than 2 m in canopy diameter (56%) with only 16% of the trees larger than 5 m in canopy diameter. The open savanna had fewer small trees (27%) with mostly larger, mature trees (38%). This combination of tree sizes and the leaf area indices presented earlier results in over twice as much leaf area per hectare in the savanna compared to the woodland (3634 vs. 1732, respectively).

Summary

Combining the information on the physical and the physiological impact of juniper trees on local water budgets demonstrates that trees growing in open savannas have a larger impact on water budgets than do individual trees in the closed woodlands. The greater leaf area of the savanna trees captures more water via rainfall interception and loses more water via transpiration. The greater number of trees in the woodlands partially offsets the tree-level differences so that water use on a hectare basis is just slightly greater for the savanna than for the closed woodland. These results need to be verified by comparing the leaf-level extrapolations with heat dissipation estimates of sapflux at the tree level and with eddy covariance estimates at the community level.

References

Angell, R.F., and Miller, R.F. 1994. Simulation of leaf conductance and transpiration in *Juniperus occidentalis*. For. Sci. 40:5–17.

Ansley, R.J., Wu, X.B., and Kramp, B.A. 2001. Observation: long-term increases in mesquite canopy cover in a North Texas savanna. J. Range Manag. 54:171–176.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: Ecological implications of livestock herbivory in the West, M. Vavra, M.A. Laycock, and R.D. Pieper, pp 13–68. Denver: Society for Range Management.

Bellot, J., and Escarre, A. 1998. Stemflow and throughfall determination in a resprouted Mediterranean holm-oak forest. Ann. Sci. For. 55:847–865.

Bendevis, M. A. 2006. Comparison of photosynthetic responses of ashe juniper and live oak on the Edwards Plateau, Texas. M.S. thesis. College Station: Texas A&M University.

Carlyle-Moses, D.E. 2004. Throughfall, stemflow, and canopy interception loss fluxes in a semi-arid Sierra Madre Oriental matorral community. J. Arid Environ. 58:180–201.

Devitt, D.A., and Smith, S.D. 2002. Root channel macrospores enhance downward movement of water in a Mojave Desert ecosystem. J. Arid Environ. 50:99–108.

Dugas, W.A., Hicks, R.A., and Wright, P. 1998. Effect of removal of Juniperus ashei on evapotranspiration and runoff in the Seco Creek watershed. Water Resources Research 34:1499–1506.

Dunkerley, D.L. 1997. Banded vegetation: survival under drought and grazing pressure based on a simple cellular automaton model. J. Arid Environ. 35:419–428.

Gehring, J.L., and Bragg, T.B. 1992. Changes in prairie vegetation under eastern red cedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie. Am. Midl. Nat. 128:209–217.

Guevara-Escobar, A., Edwards, W.R.N., Morton, R.H., Kemp, P.D., and MacKay, A.D. 2000. Tree water use and rainfall partitioning in a mature poplar-pasture system. Tree Physiol. 20:97–106.

Herwitz, S.R. 1986. Infiltration-excess caused by stemflow in a cyclone-prone tropical rainforest. Earth Sur. Proc. Landf. 11:401–412.

Hester, J.W. 1996. Influence of woody dominated rangelands on site hydrology and herbaceous production, Edwards Plateau, Texas. MS Thesis. Texas A&M University, College Station, TX. 112p.

Loik, M.E., Breshears, D.D., Lauenroth, W.K., and Belnap, J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Oecologia (Berl.) 141:269–281.

Martinez-Meza, E., and Whitford, W. 1996. Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. J. Arid Environ. 32:271–287.

McElrone, A.J., Pockman, W.T., Martinez-Vilalta, J., and Jackson, R.B. 2004. Variation in xylem structure and function in stems and roots of trees to 20 m depth. New Phytol. 163:507–517.

Miller, R.F., and Rose, J.A. 1995. Historic expansion of *Juniperus occidentalis* (Western Juniper) in southeastern Oregon. Great Basin Nat. 55:37–45.

Moore, G.W., and Owens, M.K. 2006. Removing adult overstory trees stimulates growth and transpiration of conspecific juvenile trees. Range. Ecol. Manag. 59:416–421.

Moreno, G., Gallardo, J.F., and Ingelmo, F. 1993. Effects on rainfall gradient on tree water consumption and soil fertility on *Quercus pyrenaica* forests in the Sierra de Gata (Spain). Acta Geol. Hisp. 29:119–129.

Ndawula-Senyimba, M.S., Brink, V.C., and McLean, A. 1971. Moisture interception as a factor in the competitive ability of bluebunch wheatgrass. J. Range. Manag. 24:198–200.

Owens, M.K. 1996. The role of leaf and canopy-level gas exchange in the replacement of *Quercus virginiana* (*Fagaceae*) by *Juniperus ashei* (Cupressaceae) in semiarid savannas. Am. J. Bot. 83:617–623.

Owens, M.K., and Schreiber, M.C. 1992. Seasonal gas exchange characteristices of two evergreen trees in a semiarid environment. Photosynthetica 26:389–398.

Owens, M.K., Lyons, R.K., and Alejandro, C.J. 2006. Rainfall partitioning within semiarid juniper communities: effects of event size and canopy cover. Hydrol. Process. 20:3179–3189.

Reid, K.D., Wilcox, B.P., Breshears, D.D., and MacDonald, L. 1999. Runoff and erosion in a pinon-juniper woodland: influence of vegetation patches. Soil Sci. Soc. Am. J. 63:1869–1879.

Savenije, H.H.G. 2004. The importance of interception and why we should delete the term evapotranspiration from our vocabulary. Hydrol. Process. 18:1507–1511.

Schowalter, T.D. 1999. Throughfall volume and chemistry as affected by precipitation volume, sapling size, and defoliation intensity. Great Basin Nat. 59:79–84.

Schwinning, S., and Sala, O.E. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia (Berl.) 141:211–220.

Schwinning, S., Sala, O.E., Loik, M.E., and Ehleringer, J.R. 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. Oecologia (Berl.) 141:191–193.

Silva, I.C., and Rodriguez, H.G. 2001. Interception loss, throughfall and stemflow chemistry in pine and oak forests in northeastern Mexico. Tree Physiol. 21:1009–1013.

Slaughter, J.D.J. 1997. Throughfall, stemflow, and infiltration rates of *Juniperus ashi* on the Edwards Plateau, Texas. M.S. thesis. Austin: University of Texas.

Soule, P.T., and Knapp, P.A. 2000. *Juniperus occidentalis* (Western juniper) establishment history on two minimally disturbed research natural areas in central Oregon. West. N. Am. Nat. 60:26–33.

Thurow, T.L., and Hester, J.W. 1997. Hydrologic characteristics. In: Juniper symposium, ed. C.A. Taylor, pp 9–22. San Angelo, TX: Texas A&M University.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–215.

Wullschleger, S.D., Meinzer, F.C., and Vertessy, R.A. 1998. A review of whole-plant water use studies in trees. Tree Physiol. 18:499–512.

11

Juniperus Woodlands and the Water Cycle on Karst Rangelands

Bradford P. Wilcox

Introduction

Semiarid woodlands are expanding their ranges, both within the United States and across the globe (Archer et al. 2001). Particularly striking in the United States has been the spread of juniper, numerous species of which have been expanding in extent and density. This spread has been documented in the Northwest (Miller and Wigand 1994; Miller and Rose 1995, 1999), the Southwest (Swetnam et al. 1999; Brockway et al. 2002), Texas (Ansley et al. 1995; Smeins et al. 1997; Yager and Smeins 1999), and even the Great Plains (Briggs et al. 2002; Heisler et al. 2003; Lett and Knapp 2003; McCarron and Knapp 2003). The reasons for woody plant encroachment are complex, but two underlying and related factors are clearly identifiable: (1) overgrazing on grasslands and rangelands, which, by reducing the amount of fine fuel, has led to (2) a decrease in the frequency of natural fires (Archer 1994; Van Auken 2000), no doubt caused in part by fire suppression.

Two logical and important questions being asked are these: "What hydrological changes occur as juniper density and extent change?" and "At what scale are these changes manifested?" Although the answers are not yet clear, it is certain that they will differ from region to region. The question of hydrological linkages with changes in juniper cover has been investigated for different types of juniper woodlands, more in depth for some than for others. For example, considerably more research, and longer-term research, has focused on the hydrology of piñon-juniper woodlands (Wilcox and Breshears 1995; Davenport et al. 1998; Reid et al. 1999; Wilcox et al. 2003) than on that of the juniper woodlands in the Northwest and Great Plains. In Texas, most of the work, although it is not very much, has been done on Ashe juniper woodlands on the Edwards Plateau, whereas practically nothing is known about the hydrology of redberry juniper woodlands.

In this chapter, I review the state of our knowledge concerning how Ashe juniper may be affecting the hydrology of the Edwards Plateau, an extensive karst formation in central Texas. It is this region in which recharge and streamflow may be the most sensitive to changes in woody plant cover. Even though the scientific jury is still out concerning this issue, there is a great deal of political will and strong public support for using tax dollars to attempt to increase water yield by reducing shrub cover.

O.W. Van Auken (ed.), *Western North American Juniperus Communities: A Dynamic Vegetation Type.*

To evaluate the feasibility of such ventures, I present an analysis based on a review of the literature (peer-reviewed as well as “gray”), anecdotal observations, and preliminary analyses of recently collected data. Owing to the complexity of the Edwards Plateau and the paucity of information, both the conceptual model and the conclusions drawn are partly speculative (based on my own interpretation of the limited information available).

One reason for the persistent confusion and controversy regarding the effects of juniper on the water budget is that the scale for which information is desired is usually different from the scale at which data are collected. It is the largest scale—the landscape scale—in which society is most interested when considering whether trees may be modifying the hydrology of a region. Unfortunately, this is also at this scale that we have the least information and poorest understanding of how vegetation may affect streamflow and recharge. Most of the information available has been collected at the tree or small-plot scale; we have had, therefore, no choice but to extrapolate information from small scales to larger scales. Such extrapolation is risky when the scale of interest is very large; it must be done cautiously and with a good understanding of how processes may change as scale increases. One way of raising the level of confidence in extrapolation is, where possible, to compare estimates made at multiple scales.

In this chapter, I explicitly define the spatial scale at which data have been collected, or observations made, and then attempt to summarize our understanding at the following scales of interest: (1) tree (small-plot) scale; (2) hillslope scale; (3) small-catchment scale; and (4) landscape scale. The tree scale is the amount of space taken by an individual tree. The hillslope scale is large enough to encompass many trees and thereby to manifest important hillslope processes such as overland flow, depression storage, and deposition of sediment. Small catchments are large enough to manifest channel and groundwater flow processes.

Setting

The Edwards Plateau region of central Texas is a remarkable and dynamic landscape. It is one of the major geographic features of Texas, “extending across thousands of square miles of diverse landscape between the Southern High Plains and the Balcones Escarpment” (Woodruff 2003; see other chapters in this volume). Physiographically, the region is made up of the Edwards Plateau uplands and the Hill Country. The Edwards Plateau proper is “a high-standing, flat-surfaced limestone bench which is now bordered by a steep, southeastern fault face known as the Balcones Escarpment” (Spearing 1991). The Hill Country is a heavily dissected region between the Plateau uplands and the Balcones Escarpment.

An important characteristic of the region, particularly toward the east and the south, is that both surface water and groundwater are relatively abundant, considering that the climate is semiarid. The Edwards Aquifer, a highly productive aquifer, is one of many aquifers in the region (Mace et al. 2004). Their presence is largely the result of the nature of the geological parent material, a karst limestone that allows rapid infiltration and subsurface movement of water (Maclay 1995). The perennially flowing rivers, many of which feed the Edwards Aquifer, typically originate at the margin of the Edwards Plateau uplands and the Hill Country. Major river systems in the region include the Nueces, Frio, Medina, Guadalupe, Pedernales, and Llano. However, these water resources are coming under increasing pressure from a growing population, especially in the urban areas that fringe the Balcones Escarpment. Another distinctive feature of the Plateau is its predominantly woodland character. The vegetation is mostly juniper and oak, with Ashe juniper (*Juniperus ashei*) a species of major importance. Although the exact mechanisms and extent of transformation are not clearly documented, the consensus is that woody plants—Ashe juniper in particular—cover more of the region now than 150 years ago, during pre-settlement times. Most experts attribute the shift in vegetation cover to increased grazing and decreased frequency of fire.

Influence of Ashe Juniper on Water

Tree Scale

Trees and shrubs exert a strong influence on the movement of water in their immediate vicinity through a variety of mechanisms, including (1) changing the infiltration characteristics of the soil, (2) capturing water by interception, and (3) using water in the process of transpiration.

Soil Infiltration Characteristics

Windblown sediments and tree litter accumulate beneath shrubs, thus increasing the porosity, organic matter content, and infiltration capacity of the soils directly below these layers (Dunkerley 2000). Higher infiltration rates beneath shrub canopies than in adjacent intercanopy areas has been broadly demonstrated for many vegetation types (Lyford and Qashu 1969; Seyfried 1991; Joffre and Rambal 1993; Bergkamp 1998; Schlesinger et al. 1999). As demonstrated by Hester et al. (1997), infiltration capacities under Ashe juniper are typically very high (Figure 1).

Interestingly, the impression is widespread that greater juniper density will reduce infiltration, leading to increased surface runoff and erosion. Thurow and Hester (1997) suggest that this is indeed often the case, because juniper encroachment means less available forage; thus, if the same numbers of livestock are present, the result will be overgrazing of the intercanopy areas.

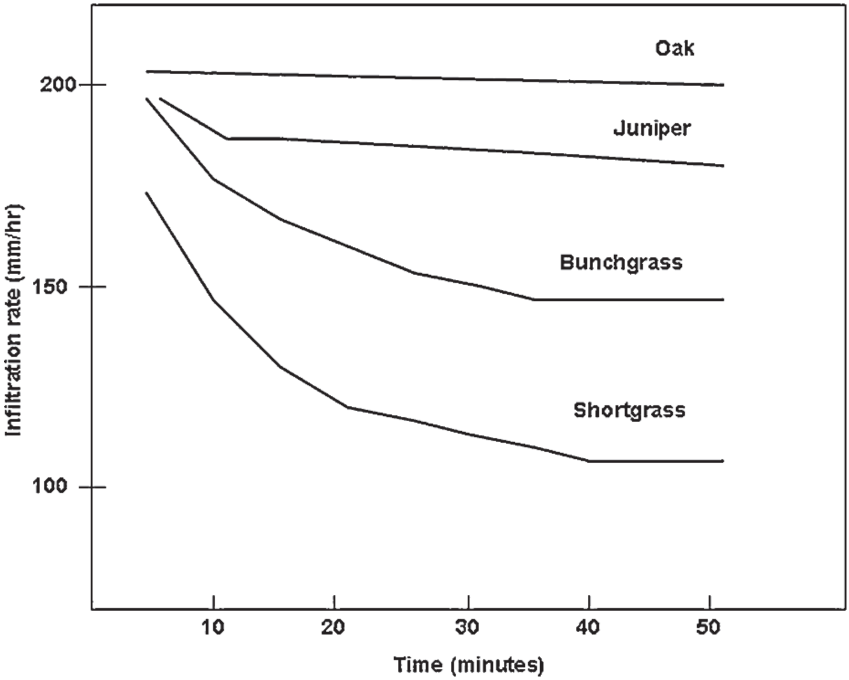

Figure 1 Infiltration rates for several vegetation types on the Edwards Plateau during 50 min of simulated rainfall application. (Figure redrawn from Hester et al. 1997)

Interception and Transpiration

If woody plants have the potential to decrease water yield, it is by increasing the total amount of evapotranspiration, either by capturing water before it reaches the soil (interception) or by consuming water from the soil (transpiration).

Evergreen shrubs, such as juniper, have a particularly large capacity for capturing precipitation, both because they retain their leaves year round and because of the large surface area of their leaves. Interception by the underlying litter layer may be considerable as well. Thurow and Hester (1997) estimated that water losses from the combined interception of juniper canopies and underlying litter layers approached 70% to 80%. However, in a more recent and comprehensive study of interception by Ashe juniper, Owens and Lyons (2003) estimate that interception from the canopy and litter layer is about 47% of precipitation. They calculate that for a densely covered juniper woodland (80% cover) about 250 mm would be intercepted annually. An additional important finding of their work is that interception differs dramatically between small storms and larger storms: virtually 100% of small-storm rainfall is captured by interception, whereas a much smaller percentage (around 20%) is intercepted during large storms.

Transpiration under Ashe juniper cover should be greater than that under herbaceous cover because Ashe juniper transpires throughout the year and also can access water at greater depth. In a cave survey, Jackson et al. (1999) found Ashe juniper roots to a depth of 7 m. In this same study, they report oak (*Quercus fusiformis*) roots to a depth of 22 m. Owens and Ansley (1997), on the basis of direct measurement of Ashe juniper transpiration rates, concluded that a mature Ashe juniper is capable of transpiring about 125 L of water per day. They estimate that, on the landscape scale, this would be equivalent to between 300 and 425 mm water per year, depending on the density of trees.

In summary, as demonstrated by Owens and collaborators, dense stands of juniper intercept or transpire very large quantities of water. Thus, in semiarid regions where juniper cover is extensive and dense, most of the precipitation would be used by the trees. At the same time, obviously, the numbers arrived at need to be interpreted with caution. Were juniper not present, other vegetation would transpire and intercept water; therefore, to assume that removal of juniper would make all or most of the water inputs to the system available for recharge and/or streamflow would be an oversimplification.

Hillslope Scale

Here, the "hillslope" is defined as an area large enough to manifest hillslope runoff processes (overland flow) but not so large as to include stream channels. At this scale, two principal kinds of data have been collected: direct measures of evapotranspiration using Bowen ratio technology and preliminary data on runoff from hillslope-scale rainfall simulation experiments.

Evapotranspiration

Some of the most intriguing and important work on the water cycle of the Edwards Plateau was done by Dugas et al. (1998). This study, presented in a peer-reviewed publication, is important from at least two perspectives: (1) it is one of the few that explicitly examine the effect of juniper control on the water budget (by evaluating changes in evapotranspiration after removal of juniper) at a scale larger than that of a single tree or small plot; and (2) it uses an alternative method of estimating recharge rates on the Plateau.

Dugas et al. (1998) estimated evapotranspiration at a community level using the Bowen ratio–energy balance method, which enables integrated evapotranspiration to be calculated over a large area (in this case, the scale of observation was 250 × 600 m). They found that, over the entire period of the study, shrub removal had little effect on community-level evapotranspiration (evapotranspiration was slightly lower following shrub removal, but not to a statistically significant degree). In other words, daily evapotranspiration was about the same whether or not juniper were present. The cumulative data, on the other hand, suggest that there was some effect for the initial period following treatment; during the first 3 years, total water savings was estimated at around 120 mm.

A less-emphasized but equally important result of the study was an independent estimate of recharge for the Edwards Plateau. As calculated by the Bowen ratio method, average annual evapotranspiration accounts for only about 65% of the water budget; in other words, the remaining 35% of the water is available for streamflow and/or deep recharge. This result contrasts with most earlier estimates of evapotranspiration on the Edwards Plateau, arrived at via the water budget method (whereby evapotranspiration is assumed to be equal to the difference between average precipitation and streamflow). According to earlier estimates, evapotranspiration accounts for 85% to 90% of the water budget (Maclay 1995).

The 1998 study by Dugas et al. was conducted within the Seco Creek watershed, which is instrumented with a streamflow-monitoring USGS gauge, enabling evapotranspiration estimates using the water budget method to be compared with those yielded by the Bowen ratio measurements. According to the USGS measurements for the same years as the Dugas et al. 1998 study, Seco Creek streamflow makes up some 20% of the water budget; therefore, on the basis of the water budget difference method, evapotranspiration would constitute around 80% (Table 1), a figure some 15% higher than that arrived at by Dugas et al. (1998). These differences are intriguing and suggest that recharge in the Edwards Plateau may be significantly higher than previously suspected. Obviously, more work needs to be done using direct measurements of evapotranspiration to confirm the results from the Dugas et al. (1998) experiments.

Table 1 A comparison of evapotranspiration (ET) estimated from Seco Creek for 1991–1995 using the water budget method and direct measurements from the Bowen ratio towers in the Dugas et al. (1998) study

Year	P (mm)	Q (mm)	ET (mm)	ET (%)
Water budget method				
1991	1161	256	904	78
1992	1242	500	741	59
1993	639	99	539	84
1994	822	39	782	95
1995	860	81	778	79
Average	944	195	748	79
Bowen ratio ET method				
1991	1161	545	47	
1992	1242	670	54	
1993	639	536	84	
1994	822	526	64	
1995	860	627	73	
Average	944	580	64	

In the water budget method, ET is estimated as the difference between precipitation (P) and streamflow (Q). Precipitation (P) values were taken from Dugas et al. (1998). Streamflow (Q) was measured by the USGS.

Runoff

Large-scale rainfall simulation studies are currently being conducted on the Edwards Plateau, enabling us to collect data on another important process at the hillslope scale: runoff. We are using simulated rainfall on areas having a range of slope lengths from 12 to 20 m. At the downslope end of each area, we typically install a trench 2 to 3 m deep for measurement of subsurface flow and detailed mapping of soils (Figure 2).

Figure 2 Photograph of a trench at the downslope end of an experimental hillslope receiving simulated rainfall. The trench is designed for capturing and measuring shallow subsurface flow as well as monitoring soil moisture at various depths

Although these studies are just getting underway, we have already made several significant observations: First, little if any surface runoff has come from areas having thick juniper canopies (runoff was measured for two such areas), even with rainfall as heavy as 380 mm in 90 min. Infiltration rates under these canopies are obviously very high, consistent with those measured at the small-plot scale (Hester et al. 1997). A second and very interesting observation is that shallow subsurface flow, or interflow, is an important runoff mechanism on these landscapes. It has been documented at every location but seems to be most important on juniper-covered hillslopes in the wake of large rainfall events (under these conditions, it accounts for a significant portion of the water budget; Sorenson 2004). In other words, these studies suggest that for large rainfall events much of the water that infiltrates into these soils is rapidly routed offsite via subsurface flow.

Small Catchment Scale

Small Catchments with Springs

Springs all across Texas have dried up in the past 150 years as pumping of groundwater has accelerated (Brune 2002). Some declines in spring flow may be related to increases in woody plant cover; there certainly are many anecdotal accounts of springs drying up after the encroachment of woody plants and of spring flow being revived after woody plant cover was reduced. These accounts are consistent and numerous enough that they have to be taken seriously, but unfortunately there is little documented evidence to substantiate them. One study has actually documented an increase in spring flow following juniper removal: Wright (1996), working on a 3.2-ha catchment in the Seco Creek Watershed, reported that spring flow increased from 3.11 to 3.78 gal/min following removal of Ashe juniper. (This increase in flow is equivalent to about 40 mm on an annual basis.) Although this study is commonly cited as proof that shrub control leads to increases in water yield, a limitation of the report is that the methodologies, calculations, and assumptions used are not well documented.

Small Catchments Without Springs

A handful of studies have considered the effect of juniper removal on small catchments where no springs are present. Richardson et al. (1979) compared runoff from two small catchments (around 4 ha each) for a 10-year period. Juniper was removed from one of the catchments the fifth year by root plowing, which led to a decrease in surface runoff of about 20% (evidently the root plowing enhanced surface storage). In another paired catchment study, Dugas et al. (1998) found that removing juniper cover by hand had little influence on surface runoff from small catchments (5.5 and 3.6 ha) in the Seco Creek watershed.

The most comprehensive evaluation of the influence of juniper removal on runoff from small catchments in the Edwards Plateau region has been on the Annandale Ranch in Uvalde County (Wilcox et al. 2005). In that study, streamflow from nine small catchments, ranging in size from about 4 to 6 ha, was monitored over a 13-year period. Following a 2-year observation period, juniper was partially or entirely removed from six of the catchments; this removal had no significant measurable influence on streamflow from these catchments. Recharge was not evaluated, so we could not determine whether changes in tree cover influenced recharge.

Landscape Scale

It is at the landscape scale—and larger scales—that there is the most interest in using juniper control as a means for increasing water supply (recharge, streamflow, or both). Shrub control is viewed as a viable strategy for increasing water yield in many parts of Texas (TWDB 2002), despite the fact that no studies have ever demonstrated landscape-scale effects. To be sure, even if there is a linkage between shrub cover and streamflow or recharge, this may be impossible to detect at larger scales. For this reason, indirect methods—such as analysis of historic streamflow trends and use of hydrological models—must be employed to evaluate the potential effect of shrub cover modifications on larger-scale hydrology.

Analysis of Streamflow

Streamflow data going back to the early 1900s are available for many of the major rivers on the Edwards Plateau. On the Llano River, for example, streamflow gauging began around 1915. These long-term data are essential if we are to understand the nature and variability of streamflow on the Edwards Plateau and their relationship to climate. In addition, such records may shed light on the sensitivity of streamflow to landscape changes. For example, if woody cover on the Edwards Plateau changed dramatically during the last century, and if—as some modeling exercises predict—streamflow responds dramatically to changes in woody plant cover, then the streamflow record should reflect those changes. To date, only a few attempts at such analysis have been made, the most comprehensive being an examination by the Lower Colorado River Authority of historical trends on the Pedernales River (LCRA 2000). In that study, the LCRA found no evidence of changes in streamflow during the period of record, which began in 1939. In other words, woody plant cover either has not changed appreciably since 1939 or has changed without affecting streamflow. We have conducted similar, although less comprehensive, analyses for other rivers on the Edwards Plateau. So far, the only detectable changes in streamflow are those clearly related to climate. This type of analysis is very preliminary, but I believe that it holds promise for determining whether changes in vegetation cover may alter streamflow at the landscape scale. A complete analysis would require records of changes in streamflow and land cover during the same period.

Modeling Studies

The influence of shrub cover on streamflow and recharge in the Edwards Plateau region has been investigated via a suite of modeling studies. Each of these has predicted that water yield would increase following a decrease in shrub cover. Using the SWAT model, Bednarz et al. (2001) provide an optimistic assessment of increased flow in the Pedernales River following removal of shrubs from about 200,000 acres of this 800,000-acre catchment (Figure 3). They calculate that the average annual flow of the Pedernales would increase by about 35%, which is equivalent to an increase in water yield of about 130 mm per treated area (from 95 to 228 mm/year). Similarly, Afinowicz et al. (2005), also using the SWAT model, predicted an increase in streamflow following brush control on the Edwards Plateau. However, this analysis was for a smaller stream, the North Fork of the Upper Guadalupe River. They predicted a water yield increase of 47 mm/year per treated area.

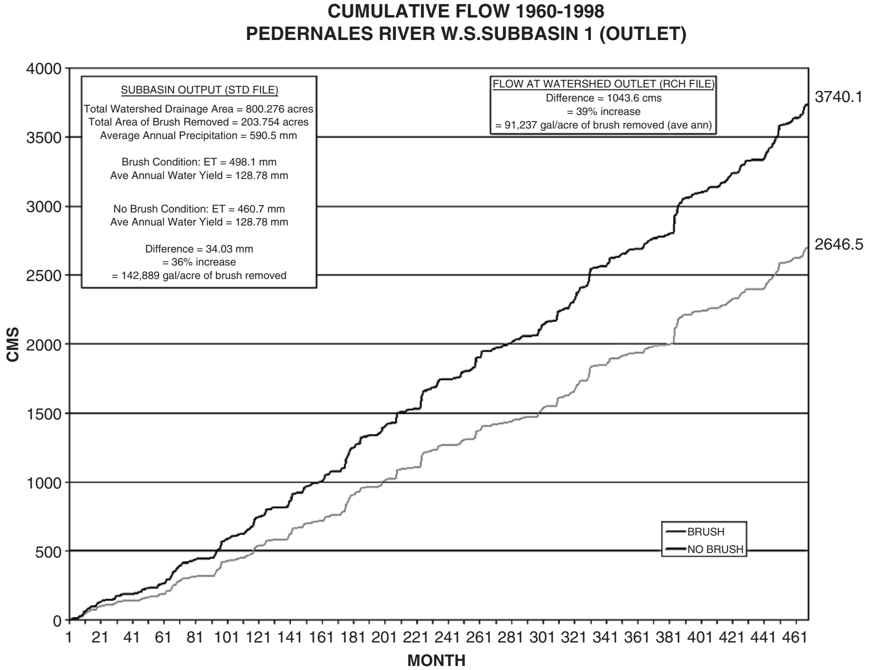

Figure 3 Cumulative monthly streamflow (m^3/s) of the Pedernales River as simulated by the SWAT model for two conditions: (1) with brush cover at current levels and (2) with 81,000 ha of shrubs removed. (Figure from Bednarz et al. 2001)

Wu et al. (2001), working in the Cusenberry Draw in the western portion of the Edwards Plateau, used the SPUR model to estimate that water yield in areas with no juniper could be as high as 15% of the water budget (80 mm in an average year) but would drop to almost zero if woody plant cover increased to 20%.

To summarize, all the modeling studies on the Edwards Plateau have predicted that reducing shrub cover will increase streamflow and/or recharge, but the magnitude of the predicted increases differs by at least threefold. Obviously, model predictions depend on both the model that is used and the assumptions made in running the model.

Role of Large Events

An additional factor that is pertinent to understanding the interactions of woody plants and water at the landscape scale is the role of large events or floods. Floods occur frequently in Central Texas, and although they can be devastating from a social and economic perspective, they are essential and even dominant players in the regional hydrological cycle. Simply put, without flooding or very large runoff events, the surface reservoirs and subsurface aquifers would not fill. An extreme example is the Edwards Plateau flood of July 2002. Rains began on June 30, 2002, and by July 7 as much as 900 mm rain had fallen in some parts of the Plateau. The flooding that ensued was enormous. The Frio River at Uvalde, which normally has little if any flow during the summer months, peaked at more than 5097 cms (180,000 cfs). Groundwater responses were equally dramatic: the Edwards Aquifer—which had fallen to such critical levels that the Edwards Aquifer Authority had issued a drought management alert—rose in just 1 week by more than 12 m (as measured in the J17 well), almost a record level. Thus, in a very short time a single large flood brought the Edwards Aquifer from critically low levels to nearly full.

Hydrological response to such large events is little affected by the extent of woody plant cover. If woody plants have any effect, it should be on the slower recharge processes and smaller events, those operating at the same temporal scales as transpiration and interception and infiltration. What is not known is the relative importance of *fast-flow* (large-event) processes versus *slow-flow* processes. It may be that recharge and streamflow are so completely dominated and controlled by fast-flow events that slow flow is relatively unimportant. Or, it may be that slow flow is critical for sustaining aquifers and streams. More detailed analysis is needed to resolve these issues.

Summary

When we review what we know, or think we know, concerning the linkages between Ashe juniper and the water cycle on karst rangelands, it is obvious that scale matters. The influence of juniper on the water cycle changes dramatically as the scale of observation increases from the tree scale to the landscape scale. For example, at the tree scale as much as 250 mm/year of water can be intercepted and more than 400 mm/year can be transpired—an amount nearly equal to the total annual average rainfall for much of the Edwards Plateau. However, at the hillslope and small-catchment scales, the most additional spring flow or recharge resulting from juniper removal that has been measured is around 40 mm/year (less than 5% of the annual water budget). This finding means that most of the water savings from reducing interception and transpiration by juniper are not directly transferred to recharge or streamflow. Instead, water is either intercepted or transpired by the remaining vegetation. At still larger scales, we have yet to detect changes in either recharge or streamflow, which means that either there is no effect at these scales or, if there is one, it has been too difficult to detect. On the basis of available field data, the most optimistic assessment is that we may be able to increase "water yield" (streamflow and/or recharge) by about 5% of the annual water budget. These results are consistent with some modeling work (Afinowicz et al. 2005).

Using our current knowledge, we can make the following generalizations.

At the small-catchment scale, if spring flow is present the effect of shrub removal should be measurable, whereas if spring flow is not present, changes in woody plant cover have little influence on streamflow. However, streamflow can be affected if surface conditions are dramatically altered; for example, mechanical removal of shrubs that disturbs surface soils actually decreases runoff by increasing depression storage. Studies of evapotranspiration at the small-catchment scale as well as anecdotal observation do suggest that reducing woody plant cover, by reducing evapotranspiration, is likely to lead to higher flow from these small catchments. Clearly, however, small watershed studies need to be designed and implemented so that we can better estimate the response of small-catchment streamflow to juniper removal.

At the largest scales, visible effects seem to completely disappear, or at least there are no documented effects. Many people are surprised and dismayed to hear that there is actually not a single documented case of streamflow changing as a result of reduced woody plant cover, but that is indeed the case. However, the reason for this is that the type of study that could demonstrate such an effect requires a long-term commitment and considerable investment. In the absence of such studies, our next best option is analysis of long-term streamflow records and land use records. At present, we simply have no evidence that Edwards Plateau rivers are behaving any differently than they have over at least the last hundred years.

References

Afinowicz, J.D., Munster, C.L., and Wilcox, B.P. 2005. Modeling the effects of brush management for increasing water yield on the Edwards Plateau, Texas. J. Am. Water Res. Assoc., 41:181–193.

Ansley, R.J., Pinchak, W.E., and Ueckert, D.N. 1995. Changes in redberry juniper distributions in northwest Texas. Rangelands 17:49–53.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: Ecological implications of livestock herbivory in the

West, eds. M. Vavra, W.A. Laycock, and R.D. Pieper, pp 13–68. Denver, CO: Society for Range Management.

Archer, S., Boutton, T.W., and Hibbard, K.A. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Global biogeochemical cycles in the climate system, pp 115–138. Durham, NC: Academic Press.

Bednarz, S.T., Dybala, T., Muttiah, R.S., Rosenthal, W., and Dugas, W.A. 2001. Brush/water yield feasibility studies. Temple, TX: Blackland Research Center.

Bergkamp, G. 1998. A hierarchical view of the interactions of runoff and infiltration with vegetation and microtopography in semiarid shrublands. Catena 33:201–220.

Briggs, J.M., Knapp, A. K., and Brock, B.L. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. Am. Midl. Nat. 147:287–294.

Brockway, D.G., Gatewood, R.G., and Paris, R.B. 2002. Restoring grassland savannas from degraded pinyon-juniper woodlands: effects of mechanical overstory reduction and slash treatment alternatives. J. Environ. Manag. 64:179–197.

Brune, G.M. 2002. Springs of Texas. College Station, TX: Texas A&M University Press.

Davenport, D.W., Breshears, D.D., Wilcox, B.P., and Allen, C.D. 1998. Viewpoint: Sustainability of piñon-juniper ecosystems. A unifying perspective of soil erosion thresholds. J. Range. Manag. 51:231–240.

Dugas, W.A., Hicks, R.A., and Wright, P. 1998. Effect of removal of *Juniperus ashei* on evapotranspiration and runoff in the Seco Creek Watershed. Water Resour. Res. 34:1499–1506.

Dunkerley, D.L. 2000. Assessing the influence of shrubs and their interspaces on enhancing infiltration in an arid Australian shrubland. Range. J. 22:58–71.

Heisler, J.L., Briggs, J.M., and Knapp, A.K. 2003. Long-term patterns of shrub expansion in a C-4-dominated grassland: fire frequency and the dynamics of shrub cover and abundance. Am. J. Bot. 90:423–428.

Hester, J.W., Thurow, T.L., and Taylor, C.A. 1997. Hydrologic characteristics of vegetation types as affected by prescribed burning. J. Range. Manag. 50:199–204.

Jackson, R.B., Moore, L.A., Hoffmann, W.A., Pockman, W.T., and Linder, C.R. 1999. Ecosystem rooting depth determined with caves and DNA. Proc. Natl. Acad. Sci. U.S.A. 96:11387–11392.

Joffre, R., and Rambal, S. 1993. How tree cover influences the water balance of Mediterranean rangelands. Ecology 74:570–582.

LCRA. 2000. Pedernales River Watershed: brush control assessment and feasibility study. Austin, TX: Lower Colorado River Authority.

Lett, M.S., and Knapp, A.K. 2003. Consequences of shrub expansion in mesic grassland: resource alterations and graminoid responses. J. Veg. Sci. 14:487–496.

Lyford, F., and Qashu, H.K. 1969. Infiltration rates as affected by desert vegetation. Water Resour. Res. 5:1373–1377.

Mace, R.E., Angle, E.S., and Mullican, W.F. 2004. Aquifers of the Edwards Plateau. Austin, TX: Texas Water Development Board.

Maclay, R.W. 1995. Geology and hydrology of the Edwards Aquifer in the San Antonio area, Texas. Water-Resources Investigations Report 95-4186. Austin, TX: United States Geological Survey.

McCarron, J.K., and Knapp, A.K. 2003. C-3 shrub expansion in a C-4 grassland: positive post-fire responses in resources and shoot growth. Am. J. Bot. 90:1496–1501.

Miller, R.F., and Rose, J.A. 1995. Historic expansion of *Juniperus occidentalis* (western juniper) in southeastern Oregon. Great Basin Nat. 55:37–45.

Miller, R.F., and Rose, J.A. 1999. Fire history and western juniper encroachment in sagebrush steppe. J. Range. Manag. 52:550–559.

Miller, R.F., and Wigand, P.E. 1994. Holocene changes in semiarid pinyon-juniper woodlands. BioScience 44:465–474.

Owens, K.W., and Ansley, J. 1997. Ecophysiology and growth of Ashe and redberry juniper. In: Juniper symposium, ed. C.A. Taylor, pp 19–31. San Angelo, TX: Texas A&M University.

Owens, K.W., and Lyons, R.K. 2003. Evaporation and interception water loss from juniper communities on the Edwards Aquifer Recharge area. Uvalde, TX: Texas Agricultural Experiment Station.

Reid, K.D., Wilcox, B.P., Breshears, D.D., and MacDonald, L. 1999. Runoff and erosion in a pinon-juniper woodland: influence of vegetation patches. Soil Sci. Soc. Am. J. 63:1869–1879.

Richardson, C.W., Burnett, E., and Bovey, R.W. 1979. Hydrologic effects of brush control on Texas rangelands. Trans. Am. Soc. Agric. Eng. 22:315–319.

Schlesinger, W.H., Abrahams, A.D., Parsons, A.J., and Wainwright, J. 1999. Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico. I. Rainfall simulation experiments. Biogeochemistry 45:21–34.

Seyfried, M.S. 1991. Infiltration patterns from simulated rainfall on a semiarid rangeland soil. Soil Sci. Soc. Am. J. 55:1726–1734.

Smeins, F.E., Fuhlendorf, S.D., and Taylor, C.A. 1997. Environmental and land use changes: a long-term perspective. In: Juniper symposium, ed. C.A. Taylor, pp 3–21. San Angelo, TX: Texas A&M University.

Sorenson, J.R. 2004. The use of large plot rainfall simulation to investigate runoff generation on the Edwards Plateau, Texas. M.S. thesis. College Station: Texas A&M University.

Spearing, D. 1991. Roadside geology of Texas. Missoula, MT: Mountain Press.

Swetnam, T.W., Allen, C.D., and Betancourt, J.L. 1999. Applied historical ecology: using the past to manage for the future. Ecol. Appl. 9:1189–1206.

Thurow, T.L., and Hester, J.W. 1997. How an increase or a reduction in juniper cover alters rangeland hydrology. In: Juniper symposium, ed. C.A. Taylor, pp 9–22. San Angelo, TX: Texas A&M University.

TWDB. 2002. Water for Texas. Austin, TX: Texas Water Development Board.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–215.

Wilcox, B.P., and Breshears, D.D. 1995. Hydrology and ecology of pinyon-juniper woodlands: conceptual framework and field studies. In: Desired future conditions for pinyon-juniper ecosystems, pp 109–119. Flagstaff, AZ: United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Wilcox, B.P., Breshears, D.D., and Allen, C.D. 2003. Ecohydrology of a resource-conserving semiarid woodland: effects of scale and disturbance. Ecol. Monogr. 73:223–239.

Wilcox, B.P., Owens, K.W., Knight, R.W., and Lyons, R. 2005. Do woody plants affect streamflow on semiarid karst rangelands? Ecol. Appl., 15:127–136.

Woodruff, C.M. 2003. Lost landscapes of the Edwards Plateau. In: Time, land, and Barton Creek: an excursion to Shield Ranch, Travis and Hays Counties, Texas, eds. C.M. Woodruff and E. W. Collins, pp 25–30. Austin, TX: Austin Geological Society.

Wright, P.N. 1996. Spring enhancement in the Seco Creek water quality demonstration project. Annual project report. Hondo, TX: Seco Creek Water Quality Demonstration Project.

Wu, X.B., Redeker, E.J., and Thurow, T.L. 2001. Vegetation and water yield dynamics in an Edwards Plateau watershed. J. Range Mgmt. 54:98–105.

Yager, L.Y., and Smeins, F.E. 1999. Ashe juniper (*Juniperus ashe*: Cupressaceae): canopy and litter effects on understory vegetation in a juniper-oak savanna. Southwest. Nat. 44:6–16.

Section 3

Management

12
The Combined Influence of Grazing, Fire, and Herbaceous Productivity on Tree–Grass Interactions

Samuel D. Fuhlendorf, Steven A. Archer, Fred E. Smeins, David M. Engle, and Charles A. Taylor, Jr.

Introduction

Although *Juniperus* communities are native to most regions of North America, they have proliferated in many areas of the Great Basin and Great Plains that historically supported grasslands, shrublands, and savannas. Explanations for the observed increases in *Juniperus* dominance, as well as other woody plant communities, are the subject of ongoing debate. The balance between herbaceous and woody vegetation is regulated by complex interactions between climate (e.g., amount and seasonality of rainfall), soils (e.g., soil texture and depth), and disturbance regimes (e.g., fire, gazing, browsing) (Walker 1987; Scholes and Archer 1997; Higgins et al. 2000). Changes in one or more of these factors can potentially elicit a change in the ratio of woody to herbaceous plants. Accordingly, climate change, intensification of grazing, elimination of fire and browsing (Hastings and Turner 1965; Grover and Musick 1990; Archer 1994; Fuhlendorf et al. 1996), atmospheric CO_2 enrichment (Idso 1992; Johnson et al. 1993), and nitrogen deposition (Köchy and Wilson 2001) have all been invoked as potential reasons for woody plant proliferation over the past century (see reviews by Archer 1994; Van Auken 2000). However, because these factors are correlative and interact across multiple spatiotemporal scales, it is neither feasible nor realistic to assess their relative importance using traditional, short-term factorial experiments. Field studies based on space-for-time substitutions and comparisons of landscapes with differing management histories have been used to assess long-term changes, but results from such studies are difficult to replicate, interpolate, or extrapolate and do not explicitly test causality. As a result, there is still considerable debate as to the relative importance of grazing, climate, and fire influences on community dynamics in drylands (O'Connor 1995; Fernandez-Gimenez and Allen-Diaz 1999; Illius and O'Connor 1999; Fuhlendorf et al. 2001). Dynamic simulation modeling is an underutilized tool that can be used to evaluate how climate or climate–disturbance interactions potentially affect tree–grass ratios and to test competing hypotheses attempting to account for woody plant increases over the past century.

Grazing, fire, and climate strongly interact to influence woody plant abundance via effects on herbaceous production and composition. High rainfall can promote

O.W. Van Auken (ed.), *Western North American Juniperus Communities: A Dynamic Vegetation Type.*

woody plant establishment, but greater herbaceous production in high rainfall years generates fine fuels and makes the system more prone to fire in subsequent dry periods (Swetnam 1988; Swetnam and Betancourt 1990; Harrington 1991). However, grazing can reduce the frequency and intensity of fire directly, by removing fine fuels and amplifying the heterogeneity of fuel continuity, and indirectly by causing a shift in plant community composition to less-productive and more-ephemeral species. Furthermore, growth of woody plants may be enhanced on grazed sites, thus enabling them to more quickly attain sizes at which they are more resistant to fire (Archer 1989, 1995). Accordingly, woody plant encroachment has been associated with grazing-induced reductions in fire frequency (Madany and West 1983; Swetnam 1988; Baisan and Swetnam 1990; Savage and Swetnam 1990). Our ability to predict the specific conditions under which woody plant encroachment might occur and the rates and dynamics of woody plant community development thus requires an integrated assessment of climate–fire–grazing interaction effects on herbaceous composition and production and woody plant growth rates.

Woody plant encroachment is a threat to sustainable livestock production in commercial enterprises and pastoral societies because of its adverse effects on herbaceous production (Scholes and Archer 1997). Habitat alterations resulting from woody plant encroachment also affect wildlife populations (Ben-Shaher 1991; Coppedge et al. 2001; Fuhlendorf et al. 2002). Prescribed burning is an important tool for maintaining grasslands and savannas (Wright and Bailey 1982); but to be effectively used, livestock grazing pressure must often be relaxed to allow fine fuels to accumulate, which requires a sacrifice of short-term revenues. Because relaxation of grazing is a cost, land managers are interested in knowing the minimum frequency with which a given management unit might need to be burned to maintain herbaceous production at a socioeconomically viable level. A knowledge of minimum prescribed fire frequencies is also of interest from the perspective of mitigating their undesirable effects on air quality. Estimating the minimum fire frequencies needed to maintain grasslands and savanna landscapes requires an integrated assessment of climate–fire–grazing interactions at decadal time scales.

Juniperus spp. (Cupressaceae) have been encroaching into grasslands and savannas in the central and western United States over the past century (Owensby et al. 1973; Bragg and Hulbert 1976; Bidwell et al. 2000; Archer et al. 2004; also see Chapter 8, this volume). Fuhlendorf et al. (1996) developed a model to examine fire frequency/intensity effects on growth and stand development of this arborescent evergreen tree. We elaborated that model to include grazing and climate influences on herbaceous composition and production and used it to address the following questions for *Juniperus* spp. in the southern Great Plains of North America: (1) What is the rate of transformation of grasslands and savannas to *Juniperus* woodlands? (2) How does the fire frequency required to maintain a savanna physiognomy change with increasing grazing pressure? (3) How do fire, grazing from domestic herbivores, and weather interact across sites with variable productivity? (4) Are shifts from grass to *Juniperus* dominance gradual, and linear; or nonlinear and characterized by abrupt thresholds? and (5) What are management options to limit the encroachment of *Juniperus* plants into Southern Great Plains grasslands and savannas?

Study Sites

The model was parameterized for sites of contrasting productivity in the Southern Great Plains of the United States. A low-productivity site [mean annual precipitation (MAP) = 600 mm] was represented using data from the Texas Agricultural Experiment Station on the Edwards Plateau (Amos and Gehlbach 1988) near Sonora, Texas (31° N, 100° W; Smeins and Merrill 1988). A high-productivity site (MAP = 850 mm), representing tallgrass prairie landscapes, was parameterized with data from the Oklahoma State University Research Range near Stillwater (36°22′ N, 99°04′ W) (Ewing and Engle 1988). Landscapes at both sites were gently sloping (2%–4%) and heterogeneous with respect to soil depth. Both sites were historically grassland-dominated landscapes interspersed with patches of *Quercus* species, and both sites have recently experienced marked increases in *Juniperus* spp. [*J. ashei* at the Edwards Plateau site (Smeins and Merrill 1988) and *J. virginiana* at the tallgrass prairie site (Owensby et al. 1973; Bragg and Hulbert 1976; Bidwell et al. 2000)].

Model Overview

The following section briefly describes a previously developed landscape-level model that simulated the influence of fire frequency and intensity on the density and size of *J.* ashei, an evergreen, nonsprouting, arborescent, woody plant at the low-productivity site. A conceptual diagram of the model and the input and output factors are presented in Figure1. Subsequent sections then describe how that model was elaborated to examine changes in woody plant abundance under fire regimes altered by livestock (cattle) grazing on sites with contrasting aboveground primary production potentials.

Fire and Woody Plant Abundance

The STELLA (High Perfomance Systems, Inc. Hanover 1994) modeling environment was used to simulate the landscape-level influence of fire on woody plant dominance on a topoedaphically homogenous landscape over 150 years with an annual time step (Fuhlendorf et al. 1996) (see Figure 1). State variables represented the density of *J.* ashei (plants/ha). *Juniperus* plants established from seed and subsequently grew into canopy diameter size-classes (Table 1) based on known

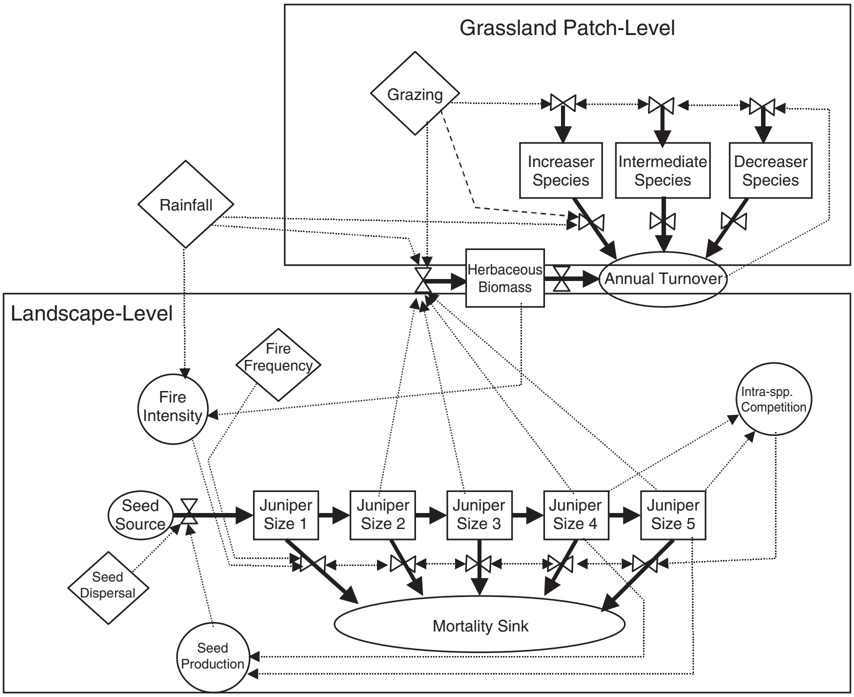

Figure 1 Multilevel conceptual model of the interactive effects of climate, grazing, and fire on tree–grass interactions. The abundance of a fire-sensitive woody plant (*Juniperus* spp.) is affected by fire intensity. Livestock grazing, rainfall, and woody plant abundance influence the composition and aboveground biomass of the herbaceous vegetation, which affects fire intensity. The model was used to ascertain what frequency of prescribed burning would be required to maintain a grassland or savanna physiognomy on high (850 mm) and low (600 mm) annual rainfall sites with contrasting livestock grazing regimes. *Solid lines* represent information transfer; *dotted lines* represent influence. (From Fuhlendorf et al. 1996)

Table 1 Mortality (%) assigned to *Juniperus* size-classes experiencing different fire intensities[a]

		Fire intensity		
Size-class	Canopy diameter (m)	Low	Medium	High
1	<0.75	20	70	99
2	0.76–1.50	20	60	99
3	1.51–3.00	10	50	80
4	3.01–6.0	0	5	30
5	>6.0	0	1	5

Fire intensity is a function of herbaceous biomass expressed relative to the maximum production under conditions of no livestock grazing (see text for explanation).

[a] See Fuhlendorf et al. (1996).

size–age relationships (Fuhlendorf 1992; Fuhlendorf et al. 1997). Trees reached seed-bearing size in diameter Class 3 and were considered mature in Class 5. Seedling establishment was a function of seed dispersal from offsite sources and onsite seed production. Seed dispersal into the area by birds and mammals (Chavez-Ramirez and Slack 1994) was simulated as stochastic events. Onsite seed production was dependent on the density of *Juniperus* plants in the three largest canopy classes. Seedling establishment was stochastic and constrained by environmental conditions (see Fuhlendorf et al. 1996).

Juniperus mortality was density dependent and varied with tree size. *Juniperus* mortality from fire was dependent on tree size and the frequency and intensity of burning. Fire intensity, in turn, was influenced by herbaceous biomass and season (summer versus winter). As trees increased in size and density, they became more resistant to fire-induced mortality and caused a reduction in herbaceous biomass (Fuhlendorf et al. 1997), resulting in a feedback that decreased fire intensity and subsequent fire mortality. Fire-induced mortality altered tree size and density, resulting in a feedback to intraspecific tree competition. Climatic variability was not included in the *Juniperus* growth/mortality model, except as a random affect on seedling establishment.

Grazing and Fire

The *Juniperus* stand development model reviewed in the previous section was elaborated to include livestock (cattle) grazing influences on the fire regime. Livestock grazing changes both the herbaceous composition and productivity, thus altering fire frequency/intensity to potentially affect woody plant mortality. Grazing reduces herbaceous biomass both directly (through the process of forage consumption) and indirectly by causing the replacement of productive species by less productive species. State variables in the grazing submodel included total herbaceous biomass and the relative composition of three herbaceous species functional groups (S_i): those that *increase* in importance with grazing (hereafter referred to as "increasers"), those that *decrease* in importance with grazing (= "decreasers"), and an *intermediate* category representing species whose abundance peaks under moderate levels of grazing (= "intermediates") (Dyksterhuis 1949). The relative contribution to aboveground net primary production (ANPP) varies among these three functional groups as grazing increases (decreasers > intermediate > increasers) (Dyksterhuis 1949; Fuhlendorf and Smeins 1997). In our model, annual ANPP was represented as a proportion of the maximum expected to occur under no livestock grazing and favorable climatic conditions: 3500 kg/ha at the low rainfall site (Wiedenfeld and McAndrew 1968; Bryant et al. 1979; Taylor 1983; Robinson 1990; Kothmann 1968) and 6500 kg/ha at the high-productivity site (Engle et al. 1987; Gillen et al. 1998; McCollum et al. 1999). Direct effects of grazing on herbaceous biomass occurred through defoliation of grasses and was dependent on grazing intensity (heavy, moderate, or ungrazed).

Parameterization

In the original model, fire intensity was dependent on herbaceous biomass (high or low) and season of fire (winter or summer) (Fuhlendorf et al. 1996). In this study, the model was parameterized only for winter (cool season) fires, where intensity was dependent on herbaceous biomass. Summer fires were not considered because of the lack of quantitative data on herbaceous production. For the low-productivity site, fire intensities were "high" when herbaceous biomass was more than 60% of maximum potential, "medium" when herbaceous biomass was 30% to 60% of maximum, and "low" when herbaceous biomass was less than 30% of maximum. Fire intensity classes for the high-productivity site were set at greater than 40% (= high), 20% to 40% (= medium), and less than 20% (= low) of maximum herbaceous production potential. Fire-induced tree mortality was a function of tree size and fire intensity (see Table 1). Fire frequency (no fire, or fire every 2, 5, 7, 10, or 15 years) was a driving variable in the modeling experiment.

Juniperus virginiana and *J. ashei* were the woody species of interest at the high- and low-productivity sites, respectively. Time spent in the canopy diameter size-classes in Table 1 was 10, 10, 10, and 25 years, respectively, for *J. ashei* (Fuhlendorf 1992; Blomquist 1990; Fuhlendorf et al. 1996), and 8, 8, 8, and 20 years, respectively, for *J. virginiana* (Engle and Kulbeth 1992). The growth rate of *J. virginiana* at the high-productivity site was approximately 20% greater than

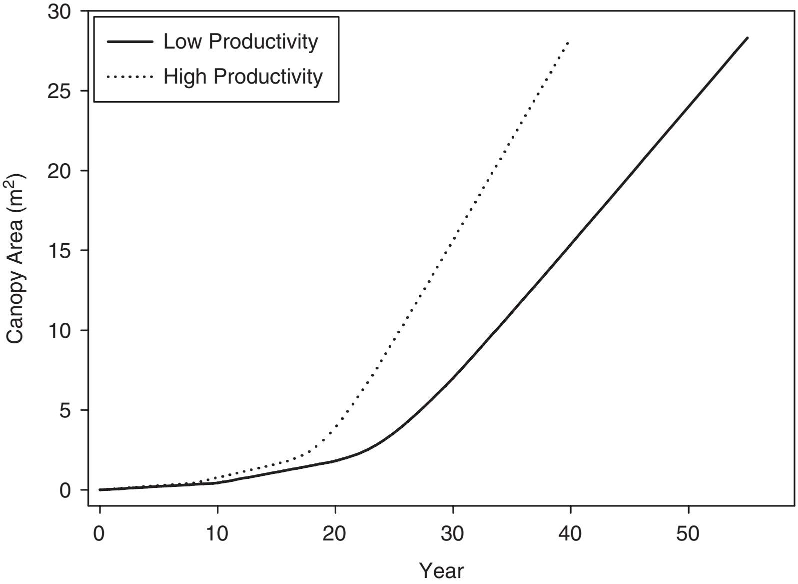

Figure 2 Rates of *Juniperus* canopy area (m^2) expansion without fire on the low productivity site [*J. ashei*; mean annual precipitation (MAP), 600 mm; Fuhlendorf 1992] and the high productivity site (*J. virginiana*; MAP, 850 mm; Engle and Kulbeth 1992)

that of *J. ashei* at the low-productivity site without fire (Figure 2). Fire–grazing interactions were evaluated with 10-replicate, 150-year simulations (annual time steps).

Juniperus species are unpalatable evergreens that generally experience little herbivory (Pritz et al. 1997; Riddle et al. 1999), so it is reasonable that the influence of livestock herbivory is confined to the herbaceous component. The long-term influence of grazing on herbaceous vegetation at the low-productivity site has been well documented (see Fuhlendorf and Smeins 1997, 1998). Short-term studies at the high-productivity site indicate similar grazing influences on herbaceous productivity and composition (Cassels et al. 1995; Gillen et al. 1998). Grazing effects on floristic composition and production at both sites are reasonably described by the Dyksterhuis (1949) conceptual model. The same grazing submodel was therefore used for both sites, with variables scaled to represent relative production and composition. The model was initialized as an open savanna with herbaceous functional group (S_i; $i = 1$–3) composition representing a plant community ungrazed by livestock: increasers (S_1) = 10%, intermediates (S_2) = 20%, and decreasers (S_3) = 70%. Livestock grazing was a driving variable set as heavy continuous, moderate continuous, or ungrazed. Moderate and heavy continuous grazing represented removal of 50% and 75% of annual net primary productivity, respectively. In regions with low productivity, it is common to defer livestock grazing 1 year before a prescribed fire to accumulate fine fuel. We therefore included two additional grazing regimes to simulate this practice: moderate with 1-year rest and heavy with 1-year rest. Weather variation (W) (annual precipitation and temperature extremes) was represented as a random driving multiplier ranging from 0.01 to 2.0. In an average year ($W = 1.0$), weather would have no influence on primary production.

Changes in herbaceous composition were dependent upon the formation of gaps (G) within the grassland patches. G was influenced by W and calculated as:

$$G = \sum_{i=1}^{3} S_i^{*}(W^{*}0.05) \tag{1}$$

where S_i was the relative composition of each herbaceous functional group. On average, this allowed for a 5% annual turnover in the relative abundance of increaser, decreaser, and intermediate grazing response groups and reflected an average longevity approximating that observed for dryland grasses (about 20 years; Canfield 1957). During wet years ($W = 0.01$ to 0.7) annual herbaceous turnover ranged from ~0 $[G = \sum_{i=1}^{3} S_i^{*}(0.01^{*}0.05)]$ to 10.5% $[G = \sum_{i=1}^{3} S_i^{*}(0.7^{*}0.05)]$; during dry years ($W = 1.3$ to 2.0), annual turnover ranged from 19.5. $[G = \sum_{i=1}^{3} S_i^{*}(1.3^{*}0.05)]$ to 30% $[G = \sum_{i=1}^{3} S_i^{*}(2.0^{*}0.05)]$. When gaps formed, the functional group composition then changed as dictated by grazing intensity (Table 2).

The relative composition of each grazing response group (S_i) was multiplied by a constant for each grazing treatment–species group combination (C_j; $j = 1, 9$) to

Table 2 Percentage (%) of herbaceous gaps occupied by various functional groups (increasers, decreasers, and invaders) under contrasting livestock grazing

	Grazing regime[a]		
Herbaceous Functional group	Heavy	Moderate	Ungrazed
Increasers	90	40	10
Intermediates	9	40	15
Decreasers	1	20	75

Gaps were created by climate-induced plant turnover (see Eq. 1).

[a] Regimes: heavy, 75% utilization; moderate, 50% utilization.

Source: Based on Fuhlendorf and Smeins (1997).

Table 3 Constants (C_j, $j = 1, 9$) used to estimate the relative herbaceous biomass in each functional group–livestock grazing regime combination

	Grazing regime		
Functional group (S_i; $i = 1$–3)	Heavy	Moderate	Ungrazed
Increasers	0.20	0.35	0.50
Intermediates	0.40	0.50	0.75
Decreasers	0.60	0.90	1.00

account for changes in primary production accompanying changes in herbaceous species (functional group) composition (Table 3). Heavy grazing resulted in communities dominated by less productive, early seral increasers, and intermediate species that were also more responsive to climatic variation than the more productive decreasers they replace (Fuhlendorf and Smeins 1997, 1998). Thus, weather variation was represented by multiplying the $\underset{\cdot}{C}_jS_i$ term for the increaser and intermediate species by *W*. To account for the influence of woody plant density on herbaceous biomass, the sum of the individual $\underset{\cdot}{C}_jS_i$ terms were multiplied by HB/100 (proportional reduction in herbaceous biomass for all *Juniperus* size-classes relative to the maximum that could occur in the absence of trees; Fuhlendorf et al. 1996). Herbaceous aboveground biomass (*H*, expressed as a percentage of the maximum possible), accounting for the combined influence of grazing, weather, and woody plant density, was thus calculated as

$$H = W(\underset{\cdot}{C}_jS_1 + \underset{\cdot}{C}_jS_2) + \underset{\cdot}{C}_jS_3 * (HB/100). \tag{2}$$

Results

Low-Productivity Site (600 mm MAP)

Simulated changes in herbaceous functional group composition (Figure 3) and production (Table 4) were in general agreement with field data from the central Texas low-productivity site. In the absence of livestock grazing, the initial herbaceous vegetation, dominated by the taller, more productive species in the *decreaser* functional group, maintained its dominance. Under heavy livestock grazing,

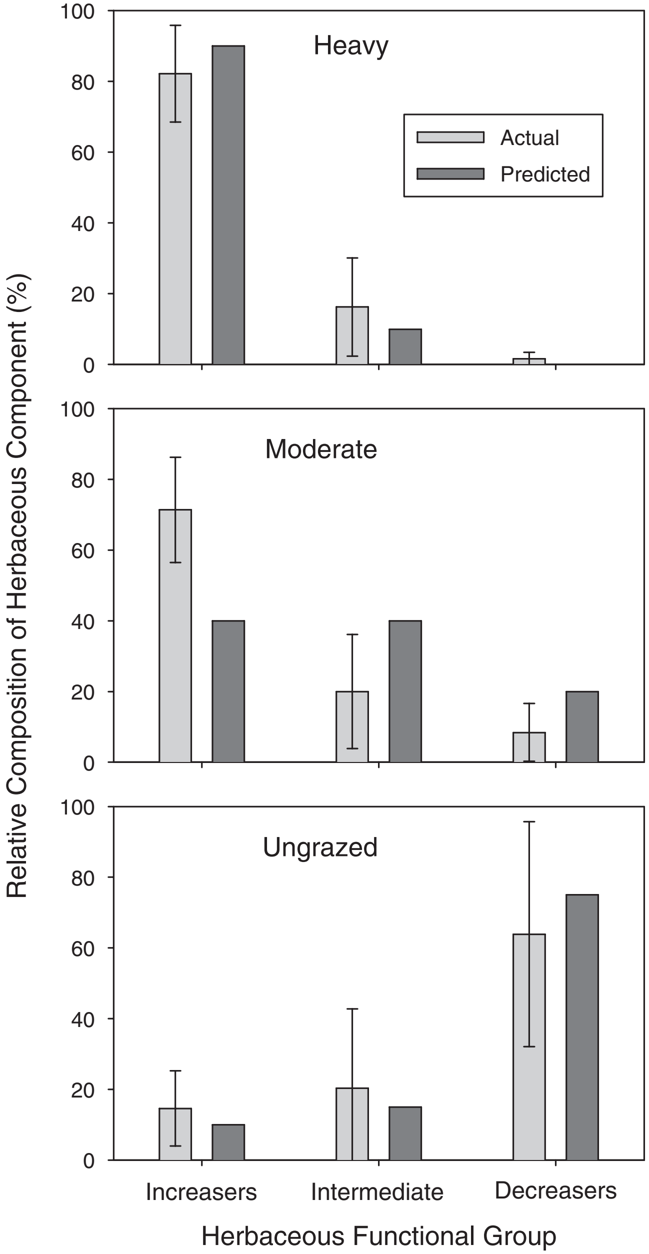

Figure 3 Mean (±SE), actual (Fuhlendorf and Smeins 1997), and predicted relative composition of herbaceous functional groups (*increasers*, *intermediates*, *decreasers*) in contrasting livestock grazing treatments (*heavy*, *moderate*, and *ungrazed*) at the low-productivity site in central Texas. For this comparison, initial conditions of the model were set to those present when livestock grazing treatments and long-term monitoring plots were installed in 1948 (heavily grazed). Results show the relative composition in 1993 (the last year of monitoring data available when this study was conducted)

Table 4 Range of predicted and actual herbaceous biomass (kg/ha) (standing biomass after grazing) on landscapes with contrasting woody cover and livestock grazing histories at the Texas A&M Sonora Research Station near Sonora, Texas

		Grazing treatment		
Woody cover (%)	Data source	Heavy	Moderate	Ungrazed
0	Model prediction	300–875 (8%–25%)	1050–2275 (30%–65%)	2800–3500
0	Bryant et al. (1979)[a]	—	1600–3200 (46%–91%)	—
20	Model Prediction	280–800 (8%–22%)	1000–2100 (29%–60%)	2600–3300 (75%–95%)
20	Kothmann (1968)	100–500 (3%–15%)	400–1100 (11%–31%)	
20	Taylor et al. (1979)	—	600–1600 (17%–45%)	—
25	Robinson (1990)	—	500–2200 (15%–63%)	
30	Model prediction	175–700 (5%–20%)	875–1575 (25%–45%)	1225–2100 (35%–60%)
30	Taylor (1983)	100–900 (3%–25%)	—	800–1600 (23%–46%)

Percent of potential maximum (3500 kg/ha) is shown in parentheses.

[a] Woody plants removed via root plowing followed by seeding with grasses.

dominance shifted to the *increaser* functional group, with species comprising the *decreaser* group becoming rare. The amount and annual variation in aboveground herbaceous biomass was influenced by grazing regime, by the density and size of *J. ashei*, and by climatic variability (Figure 4). In the absence of fire, density of the three largest *J. ashei* size-classes increased rapidly, peaking at a density of ~200 plants ha^{-1} within about 60 years (Figure 4B). At this point, density-dependent thinning occurred, causing densities to stabilize at ~100 plants ha^{-1}, regardless of grazing pressure. About 60 years into the simulation, herbaceous biomass became dynamically stable at ~10% to 40% of maximum potential on the heavily grazed and ungrazed sites, respectively (Figure 4A). With a 10-year fire frequency (and cessation of grazing for 1 year before each fire, to allow fine fuel accumulation), the herbaceous production of ungrazed and moderately grazed landscapes was maintained (Figure 4C) because fire intensity was sufficient to prevent *J. ashei* encroachment. However, on the heavily grazed site, fire intensities were reduced such that prescribed burning could not curtail *J. ashei* encroachment (Figure 4D). As a result, *Juniperus* densities increased, causing herbaceous biomass to decline (Figure 4C) to levels comparable those of the heavily grazed–no fire treatments (Figure 4A), albeit 40 to 50 years later. Temporal trends in the decline of herbaceous aboveground production accompanying grazing and *Juniperus* encroachment were nonlinear function of fire frequency mediated by rainfall (Figure 5). The variation around the mean herbaceous production values (Figure 5) and mean *J. ashei* densities (Table 5) computed from replicated simulations was typically small in herbaceous- and woody-dominated vegetation states and markedly higher in states representing transitions between these contrasting endpoints.

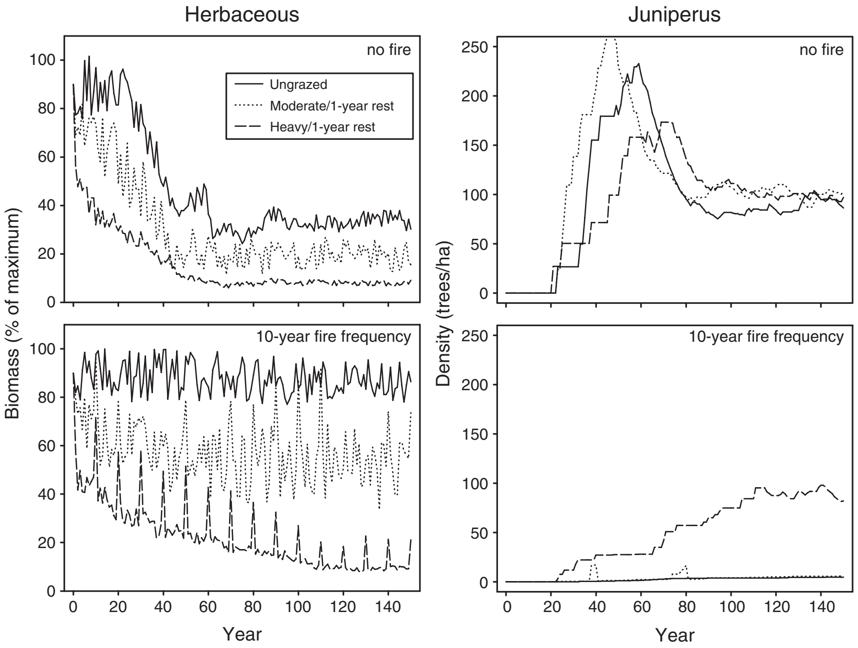

Figure 4 Simulated trends in herbaceous biomass (*left column:* top = **A**, bottom = **C**) and *Juniperus* density (*right column:* top = **B**, bottom = **D**) under three livestock grazing regimes and two fire regimes at the low rainfall site in central Texas (output representative of a single model run is shown). Herbaceous biomass is expressed as a percentage of the maximum possible; *Juniperus* density is pooled across the three largest size-classes. Annual variation in herbaceous biomass is weather related (Fuhlendorf and Smeins 1997, 1998). For burned landscapes, pastures were rested for 1 year before each fire to allow fine fuel accumulation (resulting in biomass production peaks in years with sufficient rainfall)

At the low rainfall site in central Texas, in the absence of livestock grazing (ungrazed), a fire frequency of less than 15 years was, on average, sufficient to keep *Juniperus* abundance low (<22 total trees ha^{-1}) and maintain herbaceous production at levels above 70% of maximum (see Figure 5C; see Table 5). Under moderate grazing, the critical fire return interval required to maintain grassland dominance on the low-productivity site was 5 years (see Figure 5B). With a fire frequency of 15 years, *Juniperus* woodlands consistently developed because grazing-induced reductions in fuel loads reduced fire intensity to the point where trees could consistently attain sizes resistant to fire. When grazing was curtailed the year before burning, extension of the fire return interval to 10 years enabled maintenance of a savanna physiognomy (Figure 5E).

Heavy grazing led to the formation of a closed-canopy woodland (see Table 5) with low herbaceous production (see Figure 5A). Herbaceous biomass (5%–25% of maximum) was never sufficient to carry a fire of sufficient intensity to prevent *Juniperus* establishment and growth, even in years with optimum rainfall.

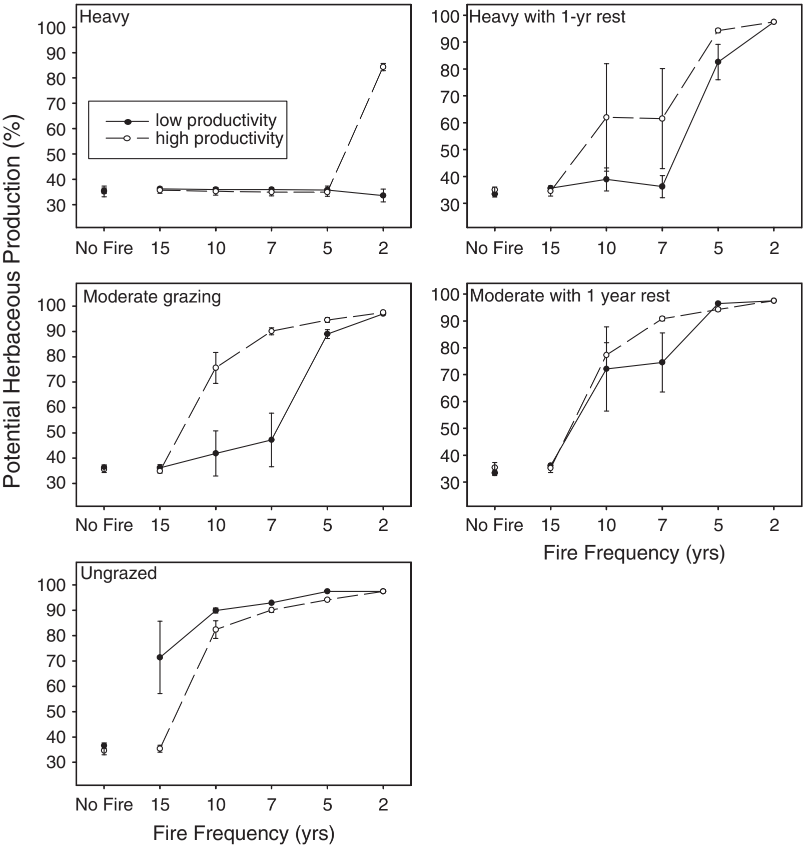

Figure 5 Potential herbaceous production at high- (MAP = 850 mm, Oklahoma) and low- (MAP = 600 mm, central Texas) productivity sites in relation to fire frequency for landscapes experiencing *Juniperus* encroachment under different livestock grazing regimes (**A** = *heavy, top left*; **B** = *moderate, middle left*; **C** = *ungrazed, bottom left*; **D** = *heavy + rest, top right*; **E** = *moderate+rest, lower right*). Potential herbaceous production is presented relative to the maximum potential in the absence of *Juniperus*. Results are means ± SD from replicated (n = 10) 150-year simulations

Table 5 Mean density (trees/ha) of large (canopy diameter >6 m) *Juniperus ashei* trees across all grazing treatments and fire frequencies for the low productivity site

	Grazing treatment				
Fire treatment	Ungrazed	Moderate with rest	Moderate	Heavy with rest	Heavy
No fire	70.6 (4.4)	70.2 (4.6)	70.0 (4.6)	71.8 (3.5)	72.7 (3.3)
15-year frequency	21.4 (84.1)	70.5 (3.5)	69.3 (3.6)	71.3 (2.7)	70.5 (2.6)
10-year frequency	6.9 (14.5)	20.5 (94.6)	59.4 (24.9)	66.8 (7.3)	70.6 (2.7)
7-year frequency	3.8 (13.16)	12.8 (88.3)	46.1 (34.3)	45.0 (3.2)	69.9 (2.7)
5-year frequency	0 (0)	0.9 (55.6)	7.6 (22.4)	3.9 (61.5)	70.6 (5.1)
2-year frequency	0 (0)	0 (0)	0.5 (60.0)	0 (0)	74.2 (7.1)

Coefficients of variation shown in parentheses.

Maintenance of grasslands was possible under heavy grazing but required both a high fire return interval (5 years) and 1 year of deferred grazing (Figure 5D).

High-Productivity Site (850 mm MAP)

Greater herbaceous production potential at the high rainfall Oklahoma grassland site meant greater fine fuel loads, hence greater fire intensity and higher tree (*J. virginiana*) mortality. However, *Juniperus* growth rates were also greater at the high rainfall site (see Figure 2). As a result, the relationship between grazing and fire return intervals necessary to maintain grassland dominance differed markedly from that observed for the low rainfall site. In the absence of livestock grazing, the critical fire frequency required to maintain a savanna physiognomy on the high-productivity site (10 years) was greater than that required on the low-productivity site (15 years) (Figure 5C; Figure 6). Moderate grazing had relatively little influence on the fire frequency needed to maintain a savanna on the high-productivity site (10 years), whereas moderate grazing dramatically altered the fire return interval needed to maintain savanna on the low-productivity site (15 years under no grazing versus 5 years under moderate grazing) (see Figure 5B). Indeed, for the ungrazed, moderately grazed, and moderately or heavily grazed with a rest before burning, the fire return interval required to maintain grasslands was fairly robust at about 10 years. Under heavy grazing, sufficient fuel could accumulate on the high-productivity site such that burning at 2-year intervals was still a management option for maintaining a savanna physiognomy, even without deferring grazing the year before burning (Figures 5A, 6).

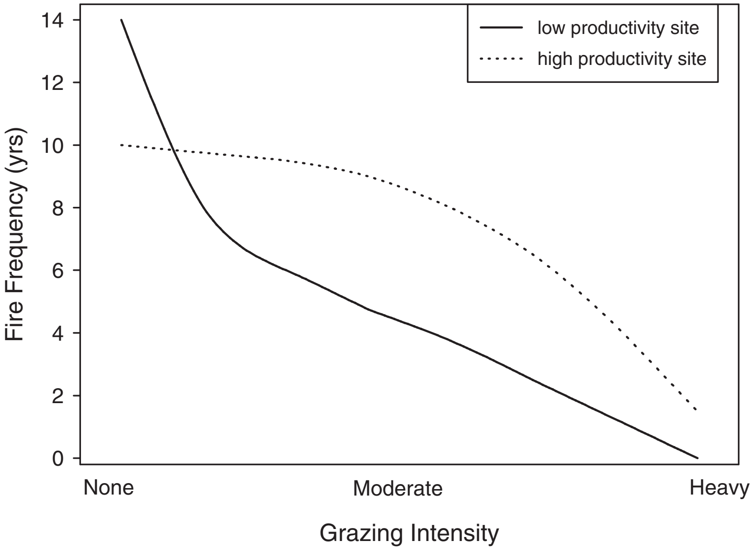

Figure 6 Theoretical presentation of fire frequency at various grazing intensities at a low-productivity site and a high-productivity site

Discussion

Long-term (45-year) analysis of permanent quadrats from the low-productivity site has documented directional trends, whereby heavy grazing resulted in short-grass-(= increasers) dominated communities of reduced productivity (Fuhlendorf and Smeins 1997, 1998). When grazing is relaxed, herbaceous composition changes and communities become dominated by more productive midheight grasses (= decreasers). Long-term directional shifts between these herbaceous states were generally linear and primarily driven by grazing; short-term dynamics embedded within the long-term changes exhibited nondirectional fluctuation associated with variability in weather and seed production. Simulated changes in species composition were representative of the long-term general patterns from the field with the assumption that fine-scaled stochasticity is removed by the large-scale nature of the model (Fuhlendorf and Smeins 1997, 1998). Predictions of relatively stable states in herbaceous composition dependent on grazing accurately depicted field data following 45 years under different grazing treatments (see Figure 3).

The balance between contrasting woody and herbaceous life forms that characterize savanna ecosystems are a function of interactions between rainfall (notably amount and seasonality), soil properties (notably texture and depth), fire, and herbivory (grazing of grasses, browsing of woody plants) (Walker 1987; Scholes and Archer 1997; Van Auken 2000). Numerous conceptual and quantitative models have attempted to addressed the nature and relative importance of these interactions (c.f. Belsky 1990; Scholes and Walker 1993; Höchberg et al. 1994; Higgins et al. 2000). These models have led to multiple hypotheses concerning the stability of grasslands and the coexistence of grasses and woody plants in savannas. Destabilization of grasslands and tree–grass interactions in savannas appears to have occurred since the mid-1800s, as evidenced by widespread reports of woody plant proliferation in these systems worldwide (see bibliography in Archer et al. 2001, 2004). As reviewed in the Introduction, causes for these changes in the life form composition of vegetation remain the subject of active debate.

In this study, we evaluated the interactive influence of fire, livestock grazing, and climatic fluctuation on the woody–herbaceous balance on sites with contrasting annual rainfall. Model predictions of changes in herbaceous aboveground production associated with grazing and *Juniperus* encroachment were accurate (see Figure 3). Pre-settlement fire frequencies are not well known in the Southern Great Plains but have been estimated at 3 to 10 years (Fuhlendorf and Engle 2001). This frequency was the combined result of natural ignitions and ignitions by First Nation peoples (Sauer 1950; Stewart 1955; Schüle 1990). Our results suggest that maintenance of pre-Anglo-European settlement grasslands and open savannas in the southern Great Plains could have been achieved with fires occurring as infrequently as 15 years. At longer fire return intervals, tree size and density increase past critical thresholds to limit potential herbaceous production to below what is needed to carry a fire that can limit *Juniperus* stand development. In the absence of fire, these grasslands can be transformed into dense, closed-canopy woodlands within 50 years without invoking directional changes in climate, atmospheric CO_2, or nitrogen deposition. The direct effect of grazing was manifested in the composition and production of the herbaceous community, which indirectly influenced tree dynamics through its effect on fuel loads and hence fire intensity. This indirect effect of grazing on tree–grass interactions was exacerbated on low-productivity sites. Weather patterns were not important to long-term changes except when the woody–herbaceous mixture was near a critical transition threshold inflection point. Under these conditions, variation in weather produced a wide range of grass–woody plant ratios, as indicated by the large variance in mean grass production (see Figure 5).

The striking differences between high-and low-productivity sites were the result of differences in the outcome of interactions between the availability of fine fuel for fires and woody plant growth rates. Fine fuel biomass required to generate fires capable of inducing mortality of 1-m-diameter, 1-m-tall *J. ashei* and *J. virginiana* trees is about 1500 kg/ha (Wink and Wright 1973; Engle and Kulbeth 1992). This amount would be equivalent to about 25% and 40% of the maximum potential herbaceous production for the high- and low-productivity sites, respectively. When livestock grazing occurred at intensities that did not reduce fuel loads below these threshold levels, it had no bearing on the relationship between fire and woody plant density (see Figure 5). When maximum potential production was inherently low as a consequence of rainfall constraints, grazing and periodic drought were more likely to combine to reduce the probability that fuel loads would be sufficient to cause fire-induced tree mortality (see Figure 4). Therefore, the advent of moderate livestock grazing had minimal influence on the grass–woody balance at the high-productivity sites but was critical in the conversion of grasslands to woodlands through its interaction with fire on low-productivity sites. Heavy grazing reduced the effectiveness of fire in maintaining grassland dominance regardless of site productivity.

It is generally assumed that the herbaceous vegetation associated with long-term grazed sites is less effective in precluding woody plant seedling establishment than the herbaceous vegetation characterizing lightly grazed sites. Similarly, it is generally assumed that heavily grazed herbaceous plants will be less effective at competitively excluding woody plant seedlings than lightly grazed or ungrazed herbaceous plants. However, numerous field experiments have not borne out these generalizations (Archer 1995; Jurena and Archer 2003). The interpretation emerging from some of these field experiments is that herbaceous vegetation has relatively little influence on woody plant seedling establishment. As a result, it has been predicted that grazing-induced changes in herbaceous composition and production should influence woody plant recruitment via alteration of the fire regime rather than via relaxation of grass competition with tree seedlings (Archer 1995). Results from our modeling experiments support this prediction and concur with field data from the low rainfall site (Smeins and Merrill 1988; Rieneke 1996; Smeins and Fuhlendorf 1997).

Our model represented climate as a random variable that primarily influenced production and composition of the herbaceous component. Climatic fluctuations were particularly noteworthy when fire frequencies were near the threshold levels required to prevent *Juniperus* stand development. Most variables in the model were parameterized as fixed, so random climatic fluctuations were responsible for most of the variation in herbaceous production means that were generated by averaging over 10 model runs. Variance about the herbaceous production means was substantially inflated when *Juniper* densities were at fire frequency threshold levels critical for maintaining grassland (see Figure 5). This result suggests that as landscapes near thresholds associated with fire return interval and grazing intensity their resistance to state-change may be enhanced under some weather patterns and compromised under others.

Model results illustrate how nonlinear rates of change in life form composition may occur when several factors are simultaneously evaluated. Effects of grazing or fire on a given plant functional group, when evaluated independent of each other, would likely produce very different dynamics. However, when interactions between fire, grazing, and plant functional groups are considered in concert, feedback mechanisms may result in dramatic threshold behaviors. Resource managers should be cognizant of these nonlinear dynamics and monitor conditions so that land use practices can be adjusted before critical thresholds are crossed. Our model affirms the critical role that fire plays in the conservation and management of grasslands and savannas. Increased stature and density of woody plants can be controlled with periodic fires, and this model indicates the fire frequency required to maintain grassland and savanna structure under various grazing regimes. Utilizing minimal fire frequencies and low intensities can reduce economic costs and hazards associated with prescribed fires. On highly productivity landscapes, fire can be readily integrated into traditional grazing practices and greatly enhance economic returns (Bernardo et al. 1988). On low-productivity sites, management of grazing becomes critical because of fuel limitations. The use of fire to maintain grassland dominance fuel loads is inherently constrained by low rainfall or shallow soils that require either more frequent fires or conducting the fires under more extreme environmental conditions, which increase the cost of conducting the fire and the probability of a fire escaping.

Conclusions

- Fire, grazing, and site productivity interact to regulate the relative abundance of woody and herbaceous vegetation. Weather influenced the nature of these interactions and may strengthen or dampen feedbacks. These weather effects may be particularly important when systems are near transition thresholds and may make systems either more or less vulnerable to state-change.
- Maintenance of savannas and grasslands requires prescribed burning.
- The frequency of fire needed to maintain grassland and open savanna was a positive function of woody plant growth rates.
- Shifts from grass to woody plant dominance were nonlinear and were characterized by fire frequency thresholds that varied as a function of livestock

grazing, which affected the fine fuel loads required to generate fires that impact woody plants.

- On low-productivity grassland sites, *Juniperus ashei* gained dominance in about 60 years without fire or grazing. A fire return interval of ~15 years was required to maintain an open grassland in the absence of grazing. Moderate grazing reduced the required fire return interval to ~5 years. With heavy grazing and fire, reductions in herbaceous biomass were such that fire could not be used to maintain an open grassland or savanna.
- On high-productivity sites, *Juniperus virginiana* gained dominance in ~45 years without fire or grazing. Under conditions of no or moderate grazing, a fire return interval of ~10 years was required to maintain an open grassland. With heavy grazing, a 2- to 3-year fire return interval was required to maintain an open grassland or savanna.
- Managers should be cognizant of fire–grazing–climate interactions and the nonlinear, threshold responses of vegetation to variations in their relative importance. This awareness, coupled with use of relatively simple models such as the one used in this study, would enable land use practices to be adjusted before undesirable transitions from grass to woody plant dominance occur.

Summary

The physiognomic transformation of grasslands and savannas to shrublands and woodlands has been widely reported in the world's drylands over the past century. Its causes, which are the subject of active debate, generally center around changes in climate, intensification of livestock grazing, and elimination of fire. Because these factors are correlative and interact across multiple spatiotemporal scales, quantifying their relative importance via field experimentation is difficult. We therefore conducted modeling experiments to evaluate the interactive effects of grazing, fire, and climate on tree–grass dynamics in low- and high-productivity southern Great Plains U.S. grasslands. Results from the multiscale modeling approach indicate that maintenance of pre-Anglo-European grasslands and open savannas in the southern Great Plains could have been achieved with fire return intervals of 15 years or less. In the absence of fire, succession to *Juniperus* woodland can occur on both high- and low-productivity sites, regardless of livestock grazing pressure. The livestock grazing regime (none, moderate, or heavy) did, however, affect the rates and dynamics of the physiognomic transformation and the eventual steady-state woody plant density. Our results offer guidelines for assessing the frequency and timing of prescribed burns that might be needed to maintain the grass–woody plant balance in grazed ecosystems.

References

Amos, B.B., and Gehlbach, F.R. (eds.) 1988. Edwards Plateau vegetation: plant ecological studies in central Texas. Waco, TX: Baylor University Press.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? Am. Nat. 134:545–561.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: Ecological implications of livestock herbivory in the West, eds. M. Vavra, W. Laycock and R. Pieper, pp 13–68. Denver, CO: Society for Range Management.

Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience 2:83–99.

Archer, S., Boutton, T.W., and Hibbard, K.A. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Global biogeochemical cycles in the climate system, eds. E.D. Schulze, M. Heimann, S. Harrison, E.A. Holland, J. Lloyd, I.C. Prentice, and D. Schimel. San Diego: Academic Press.

Archer, S, Boutton, T.W., and McMurtry, C.R. 2004. Carbon and nitrogen storage in a savanna landscape: field and modeling perspectives. In: Global environmental change in the ocean and on land, eds. H. Kawahata and H. Koizumi, pp 359–373. Dordrecht: Kluwer.

Baisan, C.H., and Swetnam, T.W. 1990. Fire history on a desert mountain range, Rincon Mountain Wilderness, Arizona, USA. Can. J. For. Res. 20:1559–1569.

Belsky, A.J. 1990. Tree/grass ratios in East African savannas: a comparison of existing models. J. Biogeogr. 17:483–489.

Ben-Shaher, R. 1991. Successional patterns of woody plants in catchment areas in a semi-arid region. Vegetatio 93:19–27.

Bernardo, D.L., Engle, D.M., and McCollum, F.T. 1988. An economic assessment of risk and returns from prescribed burning on tallgrass prairie. J. Range. Manag. 41:178–183.

Bidwell, T.G., Engle, D.M., Moseley, M.E., and Masters, R.E. 2000. Invasion of Oklahoma rangelands and forests by eastern redcedar and ashe juniper. Circular E-947. Stillwater, OK: Oklahoma State University, Cooperative Extension Service.

Blomquist, K.W. 1990. Selected life history and synecological characteristics of Ashe juniper on the Edwards Plateau of Texas. M.S. thesis. College Station: Texas A&M University.

Bragg, T.B., and Hulbert, L.C. 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range. Manag. 29:19–24.

Bryant, F.C., Kothmann, M.M., and Merril, L.B. 1979. Diets of sheep, Angora goats, Spanish goats, and white-tailed deer under excellent range conditions. J. Range. Manag. 32:412–417.

Canfield, R.H. 1957. Reproduction and life span of some perennial grasses of southern Arizona. J. Range. Manag. 10:199–203.

Cassels, D.M., Gillen, R.L., McCollum, F.T., Tate, K.W., and Hodges, M.E. 1995. Effects of grazing management on standing crop dynamics in tallgrass prairie. J. Range. Manag. 48:81–84.

Chavez-Ramirez, F., and Slack, R.D. 1994. Effects of avian foraging and post-foraging behavior on seed dispersal patterns of Ashe juniper. Oikos 71:40–46.

Coppedge, B.R., Engle, D.M., Masters, R.E., and Gregory, M.S. 2001. Avian response to landscape change in fragmented southern Great Plains grasslands. Ecol. Appl. 11:47–59.

Dyksterhuis, E.J. 1949. Condition and management of rangeland based on quantitative ecology. J. Range. Manag. 2:104–115.

Engle, D.M., and Kulbeth, J.D. 1992. Growth dynamics of crowns of eastern redcedar at three locations in Oklahoma. J. Range. Manag. 45:301–305.

Engle, D.M., Stritzke, J.F., and Claypool, P.L. 1987. Herbage standing crop around eastern redcedar trees. J. Range. Manag. 40:237–239.

Ewing, A.L., and Engle, D.M. 1988. Effects of late summer fire on tallgrass prairie microclimate and community composition. Am. Midl. Nat. 120:212–223.

Fernandez-Gimenez, J., and Allen-Diaz, B. 1999. Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. J. Appl. Ecol. 36:871–885.

Fuhlendorf, S.D. 1992. Influence of age / size and grazing history on understory relationships of Ashe juniper. M.S. thesis. College Station: Texas A&M University.

Fuhlendorf, S.D., and Engle, D.M. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience 51:625–632.

Fuhlendorf, S.D., and Smeins, F.E. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus–Quercus* savanna. J. Veg. Sci. 8:819–828.

Fuhlendorf, S.D., and Smeins, F.E. 1998. Influence of soil depth on plant species response to grazing within a semi-arid savanna. Plant Ecol. 138:89–96.

Fuhlendorf, S.D., Smeins, F.E., and Grant, W.E. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecol. Model. 90:245–255.

Fuhlendorf, S.D., Smeins, F.E., and Taylor, C.A. 1997. Influence of tree size and browse history on understory relationships of Ashe juniper. J. Range. Manag. 50:507–512.

Fuhlendorf, S.D., Briske, D.D., and Smeins, F.E. 2001. Herbaceous community structure in a semi-arid savanna: the relative contribution of grazing and climatic variability. Appl. Veg. Sci. 4:177–188.

Fuhlendorf, S.D., Woodward, A.J.W., Leslie, D.M., Jr., and Shackford, J.S. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations. Landsc. Ecol. 17:617–628.

Gillen, R.L., McCollum, F.T., III, Tate, K.W., and Hodges, M.E. 1998. Tallgrass prairie response to grazing system and stocking rate. J. Range. Manag. 51:139–146.

Grover, H.D., and Musick, H.B. 1990. Shrubland encroachment in southern New Mexico, USA: an analysis of desertification processes in the American southwest. Clim. Change 17:305–330.

Harrington, G.N. 1991. Effects of soil moisture on shrub seedling survival in a semi-arid grassland. Ecology 72:1138–1149.

Hastings, J.R., and Turner, R.L. 1965. The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semi-arid region. Tucson: University of Arizona Press.

Higgins, S.I., Bond, W.J., and Trollope, S.W. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savannna. J. Ecol. 88:213–229.

Höchberg, M.E., Menaut, J.C., and Gignoux, J. 1994. The influences of tree biology and fire in the spatial structure of a West African savannah. J. Ecol. 82:217–226.

Idso, S.B. 1992. Shrubland expansion in the American Southwest. Clim. Change 22:85–86.

Illius, A.W., and O'Connor, T.G. 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. Ecol. Appl. 9:798–813.

Johnson, H.B., Polley, H.W., and Mayeux, H.S. 1993. Increasing CO_2 and plant–plant interactions: effects on natural vegetation. Vegetatio 104–105:157–170.

Jurena, P.N., and Archer, S. 2003. Woody plant establishment and spatial heterogeneity in grasslands. Ecology 84:907–919.

Köchy, M., and Wilson, S.D. 2001. Nitrogen deposition and forest expansion in the northern Great Plains. J. Ecol. 89:807–817.

Kothmann, M.M. 1968. The botanical composition and nutrient content of the diet of sheep grazing on poor condition pasture compared to good condition pastures. Ph.D. dissertation. College Station: Texas A & M University.

Madany, M.H., and West, N.E. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology 64:661–667.

McCollum, F.T., III, Gillen, R.L., Karges, B.R., and Hodges, M.E. 1999. Stocker cattle response to grazing management in tall-grass prairie. J. Range. Manag. 52:120–126.

O'Connor, T.G. 1995. Acacia karoo invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. Oecologia (Berl.) 103:214–223.

Owensby, C.E., Blan, K.R., Eaton, B.J., and Russ, O.G. 1973. Evaluation of eastern redcedar infestations in the northern Kansas Flint Hills. J. Range. Manag. 26:256–260.

Pritz, R.K., Launchbaugh, K.L., and Taylor, C.A. 1997. Effects of breed and dietary experience on juniper consumption by goats. J. Range. Manag. 50:600–606.

Riddle, R.R., Taylor, C.A., Jr., Huston, J.E., and Kothmann, M.M. 1999. Intake of ashe juniper and liveoak by angora goats. J. Range. Manag. 52:161–165.

Reinecke, R.K. 1996. Ashe juniper seed production and germination, seedling dynamics and response of live oak/juniper mottes to summer fire. M.S. thesis. College Station: Texas A&M University.

Robinson, C.L. 1990. Botanical and chemical composition of sheep diets on two grazing systems in the Edwards Plateau. M.S. thesis. College Station: Texas A&M University.

Sauer, C. 1950. Grassland climax, fire and management. J. Range. Manag. 3:16–20.

Savage, M., and Swetnam, T.W. 1990. Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. Ecology 71:2374–2378.

Scholes, R.J., and Archer, S.R. 1997. Tree–grass interactions in savannas. Annu. Rev. Ecol. Syst. 28:517–544.

Scholes, R.J., and Walker, B.H. 1993. An African savanna: synthesis of the Nylsvley study. Cambridge: Cambridge University Press.

Schüle, W. 1990. Landscapes and climate in prehistory: interaction of wildlife, man, and fire. In: Fire in the tropical biota, ed. J.G. Goldammer, pp 273–315. New York: Springer-Verlag.

Smeins, F.E., and Fuhlendorf, S.D. 1997. Biology and ecology of Ashe juniper. In: Proceedings, 1997 juniper symposium, ed. C.A. Taylor, Jr. Technical report 97–1. San Angelo, TX: Texas A&M Research and Extension Center.

Smeins, F.E., and Merrill, L.B. 1988. Long-term change in semi-arid grassland. In: Edwards Plateau vegetation: plant ecological studies in central Texas, eds. B.B. Amos and F.R. Gehlbach, pp 101–114. Waco, TX: Baylor University Press.

Stewart, O.C. 1955. Fire as the first great force employed by man. In: Man's role in changing the face of the Earth, ed. W.L. Thomas, pp 115–133. Chicago: University of Chicago Press.

Swetnam, T.W. 1988. Fire history and climate in the southwest United States. Proceedings of effects of fire management of southwestern natural resources. General technical report RM-191. Washington, DC: United States Department of Agriculture.

Swetnam, T.R., and Betancourt, J.L. 1990. Fire–southern oscillation relations in the southwestern United States. Science 249:1017–1020.

Taylor, C.A. 1983. Foraging strategies of goats as influenced by season, vegetation and management. Ph.D. dissertation. College Station: Texas A&M University.

Van Auken, O.W. 2000. Shrub invasions of semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–216.

Walker, B.H. (ed.) 1987. Determinants of tropical savannas. Oxford: IRL Press.

Wiedenfeld, C.C., and McAndrew, J.D. 1968. Soil survey of Sutton County, Texas. Soil Conservation Service. Washington, DC: United States Government Printing Office.

Wink, R.L., and Wright, H.A. 1975. Effects of fire on a juniper community. J. Range. Manag. 26:326–329.

Wright, H.A., and Bailey, A.W. 1982. Fire ecology: United States and Southern Canada. New York: Wiley.

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Ecological Consequences of Using Prescribed Fire and Herbivory to Manage *Juniperus* Encroachment

C.A. Taylor, Jr.

Introduction

Encroachment of *Juniperus* species into what had previously been grasslands or savannas coincides with the development of the livestock industry (Archer 1994). Before European settlement and their introduction of stock-farming practices, these vegetation communities were maintained by periodic fires (Frost 1998) and the grazing/browsing habits of native wildlife (Smeins et al. 1997). These early ranchers did not have experience in semiarid regions, and consequently they did not anticipate how their introduction and management of domesticated livestock and suppression of fire would alter the rangeland structure from mostly a grassland to a woodland dominated by oak, mesquite, and juniper (Taylor and Smeins 1994; Wills 2005). The increase in these woody plants, particularly juniper, has resulted in major environmental tradeoffs that have significant implications for ranch enterprises and for the land use patterns supported by rangelands and surrounding regions, particularly in the Edwards Plateau of central Texas (Thurow et al. 1997). Many research studies report that dense stands of mature juniper cannot be managed effectively with fire alone (Ansley and Rasmussen 2005). Because the cost of traditional brush management practices (i.e., herbicides and mechanical treatments) often exceeds the economic returns that result from implementing these practices, viable options to solving the juniper problem are limited, especially once larger juniper trees are established. However, landscapes dominated by juniper, even mature juniper, can be returned to a grassland community with the use of prescribed fire and herbivory, especially by goats. The objective of this chapter is to discuss the ecological consequences of reclaiming juniper rangelands with sustainable, cost-effective management practices.

Original Vegetation and Climate

On the uplands and divide regions of the Edwards Plateau of central Texas, the pre-settlement landscape was probably open with shrubby thickets of live oak (*Quercus virginiana* Mill.) and shinoak (*Quercus* spp.) and an occasional larger

O.W. Van Auken (ed.), *Western North American Juniperus Communities: A Dynamic Vegetation Type.*

live oak and honey mesquite (*Prosopis glandulosa*). In the valleys, slopes, and shallow soils, the dominant grasses were little bluestem (*Schizachyrium scoparium* (Michx.) Nash), sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), Indian grass (*Sorghastrum nutans* L. Nash), cane bluestem (*Bothriochloa barbinodis* var. barbinodis Lag. Herter), Texas cupgrass (*Eriochloa sericea* (Scheele) Munro), common curly mesquite (*Hilaria belangeri* (Steud.) Nash), Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.), and others. Warm season perennial forbs were also abundant with a diverse mixture of woody shrubs. Kidneywood (*Eysenhardtia texana* scheele), littleleaf leadtree (*Leucaena retusa* Benth. in Gray), Carolina buckthorn (*Rhamnus caroliniana* Walt.), Texas mulberry (*Morus microphylla* Buchl.), white honeysuckle (*Lonicerna albiflora* T. & G.), plum (*Prunus* sp.), bumelia (*Bumelia lanuginose* (Michx.) Pers.), and sumacs (*Rhus* spp.) were just a few of the more desirable woody shrubs that were relatively abundant.

Primary plant growth usually occurs in late spring and early summer, then slows with hot dry weather until a secondary growth period follows the early fall moisture. The tall grasses of the pre-settlement period initiate their flowering time and seed production to correspond with fall moisture. Mid- and shortgrasses tend to flower earlier and more frequently than the tallgrasses whereas most annual forbs germinated seed in wet falls and winters and flowered in the spring.

The climate of the Edwards Plateau can be described as mesothermal, subhumid to semiarid, with potential evapotranspiration exceeding rainfall in all months. Average rainfall exceeds 76 cm on the eastern margins of the Plateau, declining gradually to 38 cm in the west. Peak rainfall usually occurs from mid-April to mid-June as general rains associated with frontal activity. A second peak usually occurs as tropical storms come inland from the Gulf of Mexico from August to October. Drought is a common process for this region. The timing and sequencing of drought and wet cycles may predispose some of these areas to woody plant encroachment. Distant events such as the El Nino/Southern Oscillation off the west coast of South America are known to have major impacts on weather at great distances. Droughts in various areas are highly correlated with these events, as are associated increased fire frequencies and other vegetation-altering disturbances.

Impact of Euro-American Settlement of the Edwards Plateau

Before the 1880s, vast areas of the Edwards Plateau of central Texas, especially the uplands and divide regions, were grasslands or savannas. These areas evolved with both migratory and nonmigratory grazing and browsing animals, floods, drought, and fire. When the weather was dry, lightning and Native Americans started fires that burned large areas. This influence of climate, fires, and grazing and browsing animals favored grasses and forbs and suppressed woody plants such as juniper. The Edwards Plateau was settled from east to west between 1840 and 1885, largely by German emigrants and Americans from the southern United States. These early pioneers came from humid farming areas or directly from European countries characterized by mild climates and deep, productive soils. The semiarid environment and shallow, rocky soils of central Texas were a new type of land for these early settlers.

European settlement of the Edwards Plateau region eventually brought about three ecologically significant changes: the introduction of large numbers of domestic livestock, yearlong grazing, and the reduction in the role of fire. These changes in management eventually resulted in a decrease in grass production and an increase in density and cover of many woody plants, in particular Ashe (blueberry) juniper (*Juniperus ashei* Buchholz) and redberry (*J. pinchotii* Sudw.) juniper.

As a consequence of many negative experiences with fire, much of the ranching industry implemented fire suppression techniques rather than prescribed fire to manage fuel loads. For example, fire guards were constructed on most large central Texas ranches. The XIT ranch began plowing guards in 1885, the first year cattle were placed on its range (Haley 1929). Within a year over a thousand miles of guards, 100 feet wide, had been plowed on the ranch. Another early method of fire suppression was the "beef drag" (Haley 1929): "When a bunch of cowboys arrived at a fire, one roped a cow, steer, heifer, etc., another shot it or cut its throat, and one side was quickly skinned from belly to back. The head was cut off so as not to be in the way and ropes were tied to a front and hind leg. With the skinned side downward and with ropes on their saddle horns, two cowboys dragged this along the line of the fire, one riding to either side of the blaze. The loose hide flopped out behind and helped extinguish the flames. Men followed on foot to beat the remaining fire out with wet tow sacks, saddle blankets, etc."

Texans even tried to legislate fire from their rangelands. The first law passed by the Texas legislature in 1848 made it illegal to fire the prairies between July 1 and February 15, except on land belonging to the person doing the firing. In 1884 a second law was passed making it a felony to set fire to grass (Haley 1929). Eventually civilization (i.e., roads, towns, cities, fields, fire departments, and overgrazing) reduced fires to a minimum. However, it is the author's opinion, along with that of many others, that the reverse should occur, and fire should be significantly increased within the state of Texas, in particular the Edwards Plateau region, and in other parts of western North America.

Dense Stands of Juniper: Area Problem

Dense stands of Ashe and redberry juniper reduce forage production and plant diversity (Smeins et al. 1997; Dye et al. 1995), interfere with handling and movement of livestock (Scifres 1980), degrade wildlife habitat (Belsky 1996), increase volatile fuel loads (Wright and Bailey 1982), and reduce the availability of water (Thurow and Hester 1997). Because of the negative consequences of juniper encroachment, many rangeland professionals as well as landowners consider juniper to be the largest economic and ecological problem facing land management in the Edwards Plateau today. In fact, juniper continues to increase in density and spread into new areas at a rapid rate (Ueckert et al. 2001). Ashe and redberry juniper contain phytochemicals that reduce their palatability to livestock and wildlife (Riddle et al. 1996; Pritz et al. 1997). Protection from herbivory through the production of phytochemicals and a prolific potential for seed production and dispersion is part of the reason these plants have extended their geographic range as well as increased in density.

Ecological Influence of Goats

Management of juniper on rangeland is usually expensive, and success can be variable for most techniques. Therefore, preventative measures and management of such lands requires an understanding of the causes of the problem as well as the implementation of cost-effective juniper control methods to meet resource goals and objectives; this requires an understanding of the life history and physiological aspects of the vegetation and how they are related to the grazing/browsing behavior and physiology of the livestock. Doing so allows for identification of a period of plant vulnerability where one can properly utilize grazing techniques to guide succession toward a desired plant community. Previous research at the Sonora, Texas, Research Station has shown that immature juniper foliage has lower concentrations of terpenoids than mature juniper foliage (Taylor and Fuhlendorf 2003). Also because of different compositions of terpenoids, mature redberry juniper is less palatable than mature Ashe juniper (Riddle et al. 1996; Pritz et al. 1997).

On the Sonora Research Station, juniper has increased from less than 1% canopy cover in 1948, when all existing juniper were removed by hand clearing, to the current level of greater than 50% in some pastures. For a 52-year period of study, the effects of different grazing treatments (i.e., stocking rate of goats) on juniper recruitment and size are summarized in Table 1. The pasture in which all livestock, goats, and fire were excluded for 53 years had the highest density of large juniper

Table 1 Density of juniper (plants/ha) by size-classes (height in meters)

Duration of treatment	Treatment[a]	0 to less than 0.5 m	0.5 to less than 1 m	1–2 m	More than 2 m	Total
1949–2002	53 years, no goats	511	116	203	815	1645
1977–2002[b]	25 years, no goats	358	225	195	487	1265
1986–2002[c]	16 years, no goats	1583	906	45	45	2579
1986–2002[c]	16 years, no goats	1410	883	89	173	2495
1949–2002	53 years, light goats	338	35	143	358	874
1949–2002	53 years, light goats	277	22	99	178	576
1949–2002	53 years, heavy goats	165	35	20	84	304

Juniper was removed (hand-cut) from all treatments in 1949.

[a] Light goats, stocking rate of 2.7 ha/goat year long; heavy goats, stocking rate of 0.9 ha/goat year long.

[b] Pasture was goated heavy from 1949 to 1977.

[c] Pasture was goated heavy from 1949 to 1986.

trees and the greatest canopy cover of juniper and other woody plants (75%). In two pastures, goats and fire were excluded for the past 16 years each. These two pastures had the greatest density of juniper plants of all treatments, but most of these plants were less than 1 m tall and had a juniper canopy cover less than 15%. The two pastures, which had light goat grazing pressure for 53 years, had significantly less juniper than the non-goat pastures, especially in the juniper size category of less than 1 m tall and a juniper canopy cover less than 10%. The pasture that was heavily browsed by goats for 53 years had the lowest juniper density of all treatments and a juniper canopy cover less than 5%.

From these data, it is readily apparent that herbivory by goats can have an effect on juniper recruitment, even though junipers are protected from browsing animals by plant compounds that render them relatively unpalatable. Research at the Sonora Station has shown that the winter diets of goats average about 10% juniper (but in some years, as much as 20%–30%) and that Spanish goats and/or Spanish × Boer cross goats consume more juniper than Angora goats (Taylor et al. 1997).

Targeting Juniper Seedlings with Goats: A Case Study

A seed germination (emergence) and seedling preference study was conducted on the Sonora Station during 1994. The objectives of this study were (1) to document the seasonal germination of redberry and Ashe juniper seeds and (2) to quantify the preference for redberry and Ashe juniper seedlings in the cotyledon growth stage by Angora goats compared to live oak and Ashe juniper with mature foliage. Mature Ashe and redberry juniper have scale leaves with fully developed glandular trichomes. Glandular trichomes containing secretory cells in the epidermal layer are the primary sites of terpenoid production and accumulation in most oil-producing species (Yamaura et al. 1992, Gershenzon et al. 1992). It was our hypothesis that juniper seedlings are more palatable because of their immature leaves and therefore more vulnerable to herbivory than juniper with mature foliage.

For the germination trial, more than 10,000 fruits or berries were collected from 40 female trees (20 trees per species) during December 1993 through January 1994. Pulp was removed from the juniper berries before planting. Two hundred 0.95-l pots were filled with soil collected from a site on the Research Station that supported equal numbers of redberry and Ashe juniper. Fifty seeds per pot were planted about 1.3 cm deep in each pot in early March 1994. Seedling emergence was recorded biweekly, and emerged seedlings were marked with 24-gauge colored telephone wire to prevent multiple counts of the same seedling. Data were composited seasonally (spring = March through April; summer = May through September; fall = October through November; and winter = December through February).

Total germination of redberry and Ashe juniper averaged 5.7% and 5.3%, respectively. Only one redberry juniper seedling emerged 22 months after the seeds were planted. This low germination is typical of these two plant species (Smeins and Fuhlendorf 1997). Based on their results from germination studies, also conducted on the Sonora Research Station, they concluded that desiccation, bacteria, and other degrading factors seemed to destroy the seeds after 18 months. In another study near Uvalde, Texas, emergence of juniper seedlings from a seed bank was 0% whereas germination of freshly collected seeds was 5% (Owens and Schliesing 1995).

For the 1994 germination study, total germination was not so important as when germination actually occurred. Percent of total germination of redberry seeds averaged 11.9%, 0%, 26.7%, and 61.3% for the spring, summer, fall, and winter, respectively. The pots were monitored for another two seasons after the winter period, but no new seedlings were observed. Percent of total germination of Ashe juniper averaged 9.4%, 0%, 18.2%, and 72.3% for the spring, summer, fall, and winter seasons, respectively. For both species, the greatest level of germination occurred approximately 12 months after seeds had been collected from the trees.

As soil moisture was readily available and fairly constant throughout the germination study, temperature must have been a major factor in determining when germination was initiated. Smeins and Fuhlendorf (1997) reported that favorable precipitation during the late spring period was responsible for germination of juniper seeds. They also reported that cold stratification of seeds with the fruit removed increased overall germination. Even though results of these germination studies still leave some uncertainty, knowledge of the level of juniper berry production along with seasonal weather conditions should elucidate optimal periods of seedling recruitment. Based on the current study as well as others, results indicate that favorable climatic conditions (mild, wet winter) provides the potential for optimal recruitment of new juniper seedlings. This knowledge allows management to respond with strategies to increase the harvest of juniper seedlings by means of the management of goats.

The germination study was concluded when no new seedlings were recorded for two successive seasons. Juniper seedlings from the germination study were then used in a cafeteria feeding trial to determine their palatability relative to other plants that would normally be found in the area. In the fall of 1992, live oak acorns were collected and planted in small styrofoam cups filled with soil from the Research Station. After these seedlings reached 1 year of age they were transplanted to 0.95–l pots (one seedling per pot). Ashe juniper plants 30.5 to 45.7 cm tall with mature foliage were randomly located on the Research Station and transplanted into 0.95–l pots in 1993. Live oak and juniper with mature foliage were included in the cafeteria trials because these plants are generally abundant where juniper seedling recruitment is taking place and we wanted a better understanding of how goats would use the vegetation when browsing. Live oak is more palatable than redberry or Ashe juniper (Taylor 1992). Although live oak also has phytochemicals (tannins) that affect palatability and intake, its tannins apparently are less aversive to domesticated herbivores than terpenoids.

Four Angora goats were selected for the cafeteria trials. A total of 16 cafeteria trials were conducted (four trials per goat). The number of pots of each species needed for the cafeteria trials were placed outside the greenhouse approximately 1 month before the feeding trials to allow plants to “harden.” For each trial, four

0.95–l pots each of redberry juniper seedlings, Ashe juniper seedlings, live oak, and Ashe juniper with mature foliage were placed into a pen. Pots were randomly arranged in a tray and the goats were allowed to browse on the plants for 5 min. Three different methods were used to quantify use on each plant species: one method recorded the bites/plant, and another method was a measure of plant disappearance by measuring pre- and postbrowsing plant length. Feeding time per plant was also recorded. Calculation of Rodgers' indices of preference were determined from the bite data. This method of determining preference is recommended for cafeteria trials where forage is not replenished as it is consumed (Krebs 1989).

Number of bites per minute averaged 21, 16, 13, 11, and 5 for the first, second, third, fourth, and fifth minutes of feeding trials, respectively. Biting rate over each 5-min trial was affected mostly by forage disappearance. As the preferred foliage was harvested, goats reduced their biting rate and spent more time searching through the remaining foliage.

Number of bites for the first minute averaged 15.4, 3.9, 1.4, and 0.4 for live oak, redberry juniper seedlings, Ashe juniper seedlings, and Ashe juniper with mature foliage, respectively. Goats generally selected live oak, removing the easily accessible foliage first, and then moved to redberry and Ashe juniper seedlings. Values calculated by using Rodgers' indices of preference were 0.87, 0.53, 0.34, and 0.24 for live oak, redberry juniper seedling, Ashe juniper seedling, and Ashe juniper with mature foliage, respectively. These values were determined from the entire 5-min cafeteria trial. Live oak was preferred over other species ($P < 0.05$), and redberry and Ashe juniper seedlings were preferred over Ashe juniper with mature foliage ($P < 0.05$).

After the cafeteria trials were completed, the plants were monitored and plant deaths were recorded. Sixteen percent of the redberry juniper seedlings were killed by goat herbivory compared to 39% for Ashe juniper seedlings. Any seedlings bitten below the cotyledon area died. The average height from mineral soil to the cotyledons was 1.8 cm for redberry juniper seedlings, which represented 18.5% of the total plant height, compared to 3.6 cm for Ashe juniper seedlings, which represented 35.7% of total plant height. Because the cotyledons were more elevated for Ashe juniper seedlings, they were more vulnerable to herbivory than redberry juniper seedlings. These findings were unexpected but may help explain why redberry and Ashe juniper are not evenly distributed over the Research Station. For example, two long-term livestock exclosures at the Sonora Research Station (exempt of livestock grazing and browsing since 1948) have an Ashe juniper to redberry juniper ratio of 95:5 (based on plant density). Pastures that have had some level of domestic herbivory since 1948 have Ashe juniper to redberry juniper ratios that range from 80:20 to 5:95.

Another trial was initiated on the Sonora Research Station in 1985 to measure the effect of artificial perch sites on juniper recruitment. A 16.2-ha pasture was chosen that had a canopy cover greater than 25% of juniper with seed bearing trees. Three different sites (149 m^2 each) within the study pasture were chosen that were free of juniper. Wire mesh panels (1.2 m tall) were used to exclude animals (protected site) from half of each site. The panels also served as perch sites. Sheep and goats were permitted access to the remaining half of each site (browsed site) by cutting panel strips 30 cm wide and elevating them to a height of 90 cm above the soil surface (Figure 1). Grazing pressure was maintained at a moderate rate for the entire pasture by adjusting livestock numbers either up or down depending on weather conditions. For most of the forage years, sheep and goats provided the only livestock grazing/browsing in the pasture, and they were equally represented on an animal unit equivalent basis.

Juniper density in the protected and browsed sites averaged 3075 and 618 plants/ha, respectively; these are rather high densities of juniper considering that no juniper plants existed in the sites before the initiation of the study. However, there was approximately 1 linear meter of perch space per 12 m^2 of area, which is a high perch-to-land area ratio. The American robin (*Turdos migratorius*) was the major bird species that appeared to use the perch sites frequently during the period of juniper berry ripening (December through March). During years of juniper fruit production, juniper berries can be the main source of winter fruit for American robins on the Sonora Research Station (Chavez-Ramirez 1992). Because these study sites were popular perch sites, the recruitment of juniper was greater than expected and would not necessarily be representative of juniper recruitment on a larger scale. However, a comparison of the two treatments is interesting because sheep and goat grazing/browsing significantly affected juniper recruitment and tree size. Juniper height averaged 15.6 and 126 cm for the browsed and protected sites,

Figure 1 Effects of goat and sheep grazing/browsing on juniper recruitment under artificial perch sites for 20-year period (1985–2005)

respectively. Redberry juniper represented 100% of the juniper found in the browsed sites compared to a redberry-to-Ashe-juniper ratio of 2.2:1 for the protected sites. These data lend further support to the hypothesis that Ashe juniper seedlings are more vulnerable to browsing than redberry juniper.

Improving Goats for Juniper Management: Super Juniper-Eating Goat Project

A research effort is being made at the Sonora Research Station to select and breed goats based on their ability to consume juniper (Campbell et al. 2007). Preliminary results from the research indicate that percent juniper in goat diets has a heritability of 41%, providing strong evidence for the potential of genetic control over dietary preferences (i.e., in this case, provide an increased capacity for juniper consumption). This finding coupled with the rapid advances in biotechnology and molecular genetics holds the promise for developing goats that will target juniper over other desirable forages, thus improving one of the tools we have to manage vegetation.

Prescribed Fire and Its Effects on Juniper and Herbaceous Vegetation: A Case Study

Burning experiments were initiated in 1986 on the Sonora Research Station to evaluate the effects of warm season and cool season fires along with controls (nonburn treatments). Forty-four different pastures are currently included in this intensive fire research program. Before applying all burning treatments, permanent transect lines were established in each treatment. Vegetation was measured before and after each burn.

The data presented below were collected from a replicated study with two warm season burned pastures, two cool season burned pastures, and two control or nonburned pastures. Juniper density was similar for all treatments before the implementation of the burning treatments (approximately 75 mature plants/ha in 1993). By 2001 the control pastures, the nonburned treatment, had juniper densities that averaged 2500 plants per ha. Most of these plants were small seedlings, but this is a good example of how quickly juniper density can increase in an area without any type of management. The prescribed fire treatment pastures received two burns each by 2001, and the juniper density in the winter and summer burned treatments averaged 100 and 25 plants/ha, respectively.

These data illustrates the importance of a long-term, sustainable management program for juniper. A grassland-dominated range can be maintained by periodic fires. Without fires, or if the severity of fires is reduced because of low fuel, juniper can quickly encroach and start to dominate a range site in a few years.

Warm season fires are more effective in killing juniper than cool season fires. It is the author's opinion that the summer burn pastures in this study would not have to be burned again for 30 years to maintain their grassland dominance. Given their current juniper status, the cool season fire treatment pastures would need to be burned within 15 years to maintain their grassland dominance. Recruitment of new seedlings is occurring at an accelerated rate in the control, nonburn treatments. Within a few years, juniper will start to dominate the control pastures and significantly reduce the herbaceous biomass and carrying capacity for both livestock and wildlife.

Recent interest in warm season fire has increased because the intensity of these fires generally inflicts greater damage to woody plants than do cool season fires (Ansley and Jacoby 1998; Taylor 2001). However, there is concern that warm season fires may harm warm season perennial grasses (Britton 2005). Ansley (2005) published a review of responses of the important plant species found in the southern Great Plains to warm season fires. He concluded that most studies showed warm season fires caused greater short-term damage to herbaceous vegetation than do dormant or cool season fires; however, these negative effects were short lived. This observation was supported by further research wherein Ansley concluded that summer fire in combination with high-intensity, low-frequency defoliation from grazing stimulated C_4 midgrass production over that of winter fire combined with grazing or grazing alone (Ansley et al. 2006).

Effects of warm season fires on herbaceous vegetation on the Sonora Research Station are mostly positive (Figure 2). Warm season fires have significantly increased primary production of warm season grasses compared to cool season burns and control treatments. The summer burned pastures were burned in 1995 and then again in 2000. The 2000 summer burn was characterized by the driest summer on record (over an 87-year period). Burning under these hot, dry conditions was the acid test regarding the effects of warm season burning on herbaceous forage production; however, there was almost twice the grass production in the warm season burn treatments compared to the control and cool season burned pastures following a sufficient period of time for the herbaceous vegetation to recover (see Figure 2).

Management Implications

It is not the author's opinion that all juniper should be removed from a particular landscape. In fact, it is important for land managers to determine their goals and objectives before initiating a juniper management program. Some land managers may want to keep some strategically located dense stands of juniper for aesthetics, wildlife, recreation, or future land management options. Thoroughly planned and selective juniper management programs can optimize the uses of the land while maintaining a healthy ecosystem. For those land managers who want to use goats or prescribed fire or a combination of the two methods to manage juniper, the following are offered as suggestions.

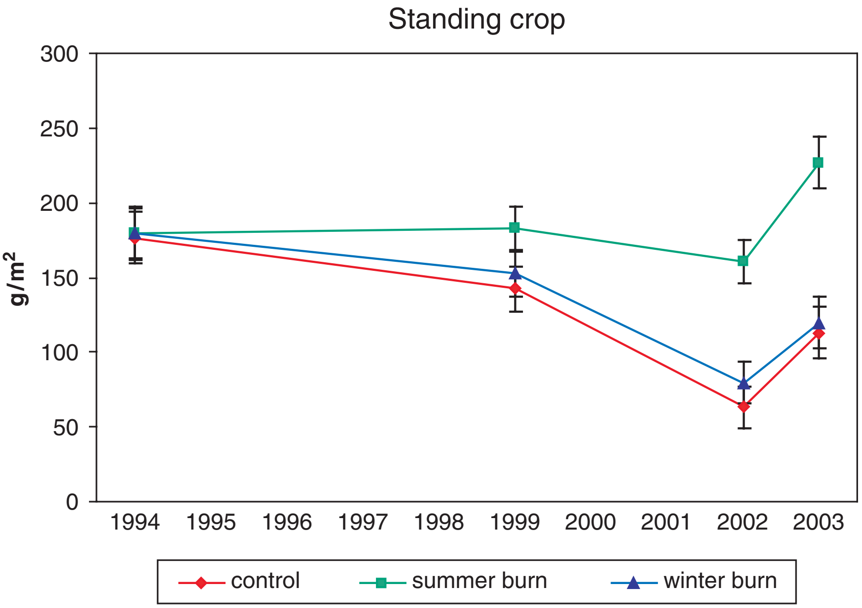

Figure 2 End of growing season standing crop (g/m^2) from control, winter burned, and summer burned pastures (values are means ±SE). Winter burned pastures were burned in 1995 and 1999; summer burned pastures were burned in 1994 and 2000

Goats

As the weakest link in the life cycle of juniper is the early seedling and/or cotyledon growth stage, juniper-invaded sites should be frequently browsed with goats to take advantage of the window of palatability that seedlings experience before they cross over the threshold and become less palatable. Also, include increased grazing pressure (concentration of goats) on target pastures during the winter and browsing with a high ratio of goats to juniper. Initiate a close monitoring program for early detection of juniper seed germination and seedling emergence and monitor use on the preferred forage to ensure that overbrowsing of other plant species does not occur. Using goats to manage juniper is a unique management tool in that they can directly generate income in the short term to help pay for other control methods and to extend the effective treatment life of prescribed fire and/or the more expensive, conventional control methods.

Fire

Young juniper seedlings are also very vulnerable to prescribed fire. Implement prescribed fire before individual juniper plants exceed 1.0 to 1.5 m in height (the shorter the better). Long-term juniper management will require repeated application of management practices (a fire frequency of every 7–10 years may be required for the western part of the Edwards Plateau). The combination of prescribed fire and goats has the potential to be an effective low-cost management method but requires greater levels of expertise than other control methods (i.e., herbicide application or mechanical treatment).

If planned, monitored, and managed correctly, prescribed fire and herbivory with goats can result in increased herbaceous biomass, decreased juniper density, increased species diversity, increased water availability, improved wildlife habitat, and a greater overall quality of rangeland function.

Summary

Before Euro-American settlement, fire and herbivory played a major role in shaping the vegetation, wildlife, and ecology of North America, including the Edwards Plateau region of central Texas. During the 19th century, immigrants from Europe and early pioneers from the United States carved farms and ranches from the Texas landscape. By the beginning of the 21st century, and after 100 years of fire suppression and stocking rates exceeding the carrying capacity of the rangelands, vegetation and wildlife had changed dramatically. Recently, however, interest in using prescribed fire as a restoration tool has increased considerably. Understanding the role of fire and herbivory in vegetation manipulation is critical for managing wildlife habitat and rangeland restoration. The reintroduction of fire into various parts of western North America and central Texas will not be an easy task. The implementation of a sustained prescribed fire/herbivore management regime by ranchers on public or privately owned lands requires cooperation, organization, and education.

References

Ansley, J.R. 2005. Summer fire effects on southern Great Plains vegetation. In: Fire as a tool for managing wildlife habitat in Texas, eds. C.G. Brown and D. Rollins, pp 255–272. San Angelo, TX: Texas Cooperative Extension Service.

Ansley, J.R., and Jacoby, P.W. 1998. Manipulation of fire intensity to achieve mesquite management goals in north Texas. In: Fire in ecosystem management: shifting the paradigm from suppression to prescription. Proceedings of the tall timbers fire ecology conference, eds. L. Pruden and L.A. Brennan. Tallahassee, FL: Tall Timbers Research Station.

Ansley, J.R., and Rasmussen, G.A. 2005. Managing native invasive juniper species using fire. Weed Technol. 19:517–522.

Ansley, J.R., Castellano, M.J., and Pinchak, W.E. 2006. Sideoats grama growth responses to seasonal fires and clipping. Range. Ecol. Manag. 59:258–266.

Archer, S. 1994. Woody plant encroachment into Southwestern grasslands and savannas: rates, patterns, and proximate causes. In: Ecological implications of livestock herbivory in the west, eds. M. Varva, W.A. Laycock, and R.D. Pieper, pp 13–68. Denver, CO: Society for Range Management.

Belsky, A.J. 1996. Viewpoint: western juniper expansion: is it a threat to arid northwestern ecosystems? J. Range. Manag. 49:53–59.

Britton, C. 2005. Observations on fire and wildlife. In: Fire as a tool for managing wildlife habitat in Texas, eds. C.G. Brown and D. Rollins, pp 42–49. San Angelo, TX: Texas Cooperative Extension Service.

Campbell, E.S., Engdahl, B.S., Lupton, C.J., Scott, C.B., Taylor, C.A., Jr., Waldron, D.F., Walker, J.W., and Whitworth, W.R. 2007. The use of fecal NIRS to identify levels of consumption of the toxic shrub juniper in a selective breeding program with goats. Proceedings of the 7th international symposium on poisonous plants, Logan, UT, pp 386–393.

Chavez-Ramirez, F. 1992. The role of birds and mammals in the dispersal ecology of Ashe juniper (*Juniperus ashei*) in the Edwards Plateau, Texas. M.S. thesis. College Station: Texas A&M University.

Dye, K.L., Ueckert, D.N., and Whisenant, S.G. 1995. Redberry juniper-herbaceous understory interactions. J. Range. Manag. 48:100–107.

Frost, C.C. 1998. Presettlement fire frequency regimes of the United States: a first approximation. In: Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall timbers fire ecology conference proceedings, no. 20, eds. T.L. Pruden, and L.A. Brenna, pp 70–81. Tallahasse, FL: Tall Timbers Research Station.

Gershenzon, J., McCaskill, D., Rajaonarivony, J., Mihaliak, C., Karp, F., and Croteau, R. 1992. Isolation of secretory cells from plant glandular trichomes and their use in biosynthetic studies of monoterpenes and other gland products. Anal. Biochem. 200:130–138.

Haley, J.F. 1929. Grassfires of the southern Plains. In: West Texas Historical Association Year Book, pp 24–42. Abilene, TX: The West Texas Historical Association.

Krebs, C.J. 1989. Ecological methodology. New York: Harper Collins.

Owens, M.K., and Schliesing, T.G. 1995. Invasive potential of Ashe juniper following mechanical disturbance. J. Range. Manag. 48:503–507.

Pritz, R.K., Launchbaugh, K.L., and Taylor, C.A., Jr. 1997. Effects of breed and dietary experience on juniper consumption by goats. J. Range. Manag. 50:600–606.

Riddle, R.R., Taylor, C.A., Jr., Kothmann, M.M., and Huston, J.E. 1996. Volatile oil contents of Ashe and redberry juniper and its relationship to preference by Angora and Spanish goats. J. Range. Manag. 49:35–41.

Scifres, C.J. 1980. Brush management: principles and practices for Texas and the Southwest. College Station, TX: Texas A&M University Press.

Smeins, F.E., and Fuhlendorf, S.D. 1997. Biology and ecology of Ashe (blueberry) juniper. In: Proceedings, 1997 juniper symposium, ed. C.A. Taylor, Jr., pp 33–47. Technical report 97-1. San Angelo, TX: Texas A&M University Research and Extension Center.

Smeins, F.E., Fuhlendorf, S.D., and Taylor, C.A., Jr. 1997. Environmental and land use changes: a long-term perspective. In: Proceedings, 1997 juniper symposium, ed. C.A. Taylor, Jr., pp 3–21. Technical report 97-1. San Angelo, TX: Texas A&M University Research and Extension Center.

Taylor, C.A., Jr. 1992. Brush management considerations with goats. In: Proceedings of the international conference of meat goat production, management, and marketing, eds. J.C. Paschal, and C.W. Hanselka, pp 144–155. Laredo, TX: Texas Agricultural Extension Service.

Taylor, C.A., Jr. 2001. Summer fire for the western region of the Edwards Plateau: a case study. Technical report 01-2. Sonora, TX: Texas Agricultural Experiment Station.

Taylor, C.A., Jr., and Smeins, F.E. 1994. A history of land use of the Edwards Plateau and its effect on the native vegetation. In: Juniper symposium, pp 1–8. Technical report 94-2. Sonora, TX: Texas A&M University Research Station.

Taylor, C.A., Jr., and Fuhlendorf, S.D. 2003. Contribution of goats to the sustainability of Edwards Plateau Rangelands. Texas Agricultural Experiment Station Technical Report 03-1. Sonora, TX: Texas Agricultural Experiment Station.

Taylor, C.A., Jr., Launchbaugh, K., Huston, E.J., and Straka, E.J. 1997. Improving the efficacy of goating for biological juniper management. In: Proceedings, 1997 juniper symposium, ed. C.A. Taylor, Jr., pp 5.17–5.22. Technical report 97-1. San Angelo, TX: Texas A&M University Research and Extension Center.

Thurow, T.L., and Hester, J.W. 1997. How an increase or reduction in juniper cover alters rangeland hydrology. In: Proceedings, 1997 juniper symposium, ed. C.A. Taylor, Jr., pp 4.9–4.22. Technical report 97-1. San Angelo, TX: Texas A&M University Research and Extension Center.

Thurow, T.L., Thurow, A.P., Taylor, C.A., Jr., Conner, R.J., and Garriga, M. 1997. Environmental and economic tradeoffs associated with vegetation management on the Edwards Plateau. In: Proceedings, 1997 juniper symposium, ed. C.A. Taylor, Jr., pp 2.3–2.10. Technical report 97-1. San Angelo, TX: Texas A&M University Research and Extension Center.

Ueckert, D.N., Phillips, R.A., Petersen, J.L., Wu, X.B., and Waldron, D.F. 2001. Redberry juniper canopy cover dynamics on western Texas rangelands. J. Range. Manag. 54:603–610.

Wills, F.H. 2005. Structure of historic vegetation on Kerr Wildlife Management Area, Kerr County, Texas. Tex J. Sci. 57:137–152.

Wright, H.A., and Bailey, A.W. 1982. Fire ecology: United States and Southern Canada. New York: Wiley.

Yamaura, T., Tanaka, S., and Tabata, M. 1992. Location of the biosynthesis and accumulation of monoterpenoids in glandular trichomes of thyme. Planta Med. 58:153–158.

14

From the Dust Bowl to the Green Glacier: Human Activity and Environmental Change in Great Plains Grasslands

David M. Engle, Bryan R. Coppedge, and Samuel D. Fuhlendorf

Introduction

Before European settlement, the land between the Rocky Mountains and the Mississippi River of North America formed immense unbroken grasslands devoid of trees except those few forming gallery forests along lower river channels and those located in disjunct topoedaphic sites protected from fire. The Great Plains grasslands are now extensively fragmented by cropland agriculture, human occupation, and woody plant encroachment and altered directly and indirectly by livestock grazing and other anthropogenic disturbances. As a consequence of these processes, today's grasslands bear little resemblance to those of pre-European settlement and are now recognized as one of the most endangered ecosystems in North America (Sampson and Knopf 1994). Awareness of the unique biodiversity of the Great Plains and its importance to our natural heritage has highlighted the need for a regional approach to conservation of remnant grasslands (Joern and Keeler 1995; Mitchell et al. 1999). In part, this need is urgent because many of the species endemic to the region are declining rapidly.

According to the North American Breeding Bird Survey, 70% of the 29 bird species characteristic of North American grasslands have declined between 1966 and 1993, and they are declining at a faster rate than any other guild of terrestrial birds in North America (Knopf 1994; Peterjohn and Sauer 1999). Although many factors have been suggested as contributing causes to the decline (Peterjohn and Sauer 1999), habitat fragmentation and degradation are generally recognized as central issues (Vickery et al. 1999). Cultivation was historically the primary factor fragmenting grasslands, but in most regions cultivated land has stabilized or even decreased over the past 20 years (Laycock 1988). The factor contributing most to the current decline in grassland habitat quality in the Great Plains is the expansion of woody plants, particularly eastern redcedar (*Juniperus virginiana* L.) (Coppedge et al. 2001a). In this chapter, we use population and community properties of the Great Plains avifauna to demonstrate that the spread of woody plants into grasslands, part of a broad process we call the *Green Glacier*, is changing endemic avifauna to an extent equivalent to that of the Pleistocene glaciation.

O.W. Van Auken (ed.), *Western North American Juniperus Communities: A Dynamic Vegetation Type.*

Environmental History and Development of Great Plains Grassland Fauna: The Great Change Events

Understanding the role of climate, drought, grazing animals, and fire on the development and evolution of Great Plains grasslands and associated avifauna is critical to interpreting many of the processes now affecting them. The development of these grasslands is largely attributed to the Miocene uplift of the Rocky Mountains that produced the rain shadow which limits moisture availability and increases the probability of prolonged droughts (Axelrod 1985). Because grasses are generally better adapted to drier conditions than woody plants, the spread of grasslands in the drier environment came at the expense of forests (Daubenmire 1978; Anderson 1990). Fire was a key process in the conversion of central North America from forests to grasslands, and fire remains critical for maintaining the dominance of herbaceous vegetation types (Axelrod 1985; Coupland 1992).

The region is now characterized by an east–west precipitation gradient and a south–north temperature gradient (Epstein et al. 1996). As moisture availability increases from west to east in the Great Plains, grasslands intergrade eventually into the eastern deciduous forests. In the eastern tallgrass prairie region where precipitation is adequate for trees, fire is critical in restricting woody plant intrusion into grasslands (Briggs et al. 2005). But fire plays a significant role even in the drier mixed prairie and shortgrass prairie, and woody plants have also increased in these regions in the absence of fire over most of the past century (Engle et al. 1996; Coppedge et al. 2001b).

Glaciers and Aboriginal Activity

No other recent geological or climatological event has shaped Great Plains fauna more than glaciation (Borchert 1950; Pielou 1992). During the development of grassland dominance at the initiation of the current interglacial period [10,000 to 15,000 years before present (B.P.)], most of the Pleistocene mammalian megafauna became extinct. These extinctions included mammoths, mastodons, camels, giant ground sloths, musk ox, horses, and the precursors to modern species of American bison (*Bos bison* L.). The modern bison form gained dominance in the absence of competition across the Great Plains after the last (Wisconsin) glaciation (McDonald 1981; Stebbins 1981; Mack and Thompson 1982).

Grassland dominance of central North America peaked about 7000 years ago (Wright 1970). Large herds of bison and frequent anthropogenic burning of grassland fuels within the past 5000 years (Pyne 1982; Anderson 1990) together augmented the influence of aridity on the development of Great Plains grasslands. Thus, the relatively young age of the Great Plains grasslands has resulted in an endemic avifauna that is comparatively depauperate (Knopf 1994), making their conservation even more urgent.

Drought, Sodbreaking by Europeans, and the Dust Bowl

Except for perhaps climate, the ecological processes governing Great Plains biota have been altered substantially during the past 150 years. Foremost in these processes is the substitution of native flora for cultivated monocultures. However, settlement and subsequent cultivation patterns varied across the Great Plains depending on soils, climate, and socioeconomic boundaries. Relatively flat topography, nutrient-rich soils, and government policies (e.g., the Homestead Act of 1862) invited and often encouraged cultivation on much of these lands. By the dawn of the 20th century, Euro-American settlement claimed most of the arable lands for cultivation in the Great Plains, and settlement integrated grazing agriculture into most of the remaining land in the region. Cycles of cultivation and cropland abandonment in the 20th century were punctuated periodically by federal conservation and incentive programs driven only in part by the goals of maintaining the productivity, sustainability, and economic viability of the region (Bedenbaugh 1988; Joyce 1989). Given the regional socioeconomic significance of cropland agriculture, drought continues to play havoc with the economic stability of the region (Albertson et al. 1957; Baltensperger 1979; Glantz 1994).

Severe drought plagued European settlers in the Great Plains following settlement, with the droughts of the 1890s, 1930s and 1950s indelibly marking the history of the Great Plains (Flores 1996; Licht 1997). The Dust Bowl, associated with ill-advised cultivation of the western Plains and the drought of the 1930s, is one of the greatest ecological disasters in the history of the United States. Sala et al. (1988) derived an index of variability in primary production, the difference between the maximum and minimum production in above-average and below-average precipitation years divided by the average production. An area centered around southwest Kansas, northwest Oklahoma, and into southeast Colorado and northeast New Mexico has a variability index of 0.9, meaning that fluctuations in forage production are 90% of the average. Much of the Great Plains, including all the states of Kansas and Oklahoma, has an index of 0.5 or more.

The Euro-American culture that settled the New World focused on removing most natural habitats, such as grasslands, forests, and wetlands, which were perceived as impediments to progress (Sopuck 1995). Limited species diversity, apparent monoculture over most of the region, and conversion to cropland agriculture of more than 80% of the landscape is evidence that these strategies have been effective. However, those areas on the Great Plains that escaped cultivation are dominated by vegetation very similar to the potential natural plant community described by Kuchler (1964; O'Neill et al. 1997), and are typically rangelands used for livestock production by private landowners. Because these areas are often extensively managed native plant communities surrounded by intensively managed cropland or pastureland, they are essential to conservation of the native biota of the Great Plains. Economic, social, and political pressures on these rangelands will continue to increase as ecological awareness in the general population grows and economic changes in agriculture also increase.

Eastern Redcedar: The Green Glacier

Juniper (*Juniperus* spp.) expansion is well documented in the Great Plains (Figure 1). Ashe juniper (*J. ashei*) and redberry juniper (*J. pinchotii*) have expanded in the extreme southern portion of the Great Plains (Ansley et al. 1995; Fuhlendorf et al. 1996), whereas eastern redcedar has expanded throughout the Great Plains, except the far north and far west areas (Van Haverbeeke and King 1990; Engle et al. 1996; Schmidt and Wardle 1998; Hoch et al. 2002). Junipers are evergreen species native to the Great Plains, but their historical distribution was limited to rocky outcrops and similar topoedaphic features that limited the spread of fire. Our focus in this chapter is on eastern redcedar, a species that has expanded from the eastern deciduous forests to the west and from isolated refugia along rivers into upland grasslands (Arend 1950).

Size of mature eastern redcedar varies with site, often reaching a height of 15 m on better forest sites (Dirr 1983; Lawson 1990), but trees rarely grow taller than 10 m on upland grassland sites of the Great Plains (Engle and Kulbeth 1992). Encroaching eastern redcedar can rapidly convert grassland to woodland because of crown growth as great as 0.25 m/year (Engle and Kulbeth 1992; Hoch et al. 2002) combined with dense recruitment of individual seedlings enabled by abundant production of a fleshy fruit dispersed by birds (Holthuijzen and Sharik 1985;

Figure 1 Current distribution of eastern redcedar in Great Plains grasslands (lightly stippled area). The *area densely stippled* has largely been converted to woodland, whereas the *medium-density stippled area* is under threat of conversion to woodland within 10 to 20 years

Horncastle et al. 2004). When eastern redcedar and other species of juniper expand into grasslands, they can greatly alter the biotic and abiotic environment of grassland ecosystems. Their increase reduces the productivity of herbaceous vegetation (Engle et al. 1987; Hoch et al. 2002) and the diversity of grassland plant species, especially beneath the crowns of large trees (Gehring and Bragg 1992; Fuhlendorf et al. 1997; Hoch et al. 2002). Conversion of C_4-dominated grasslands to C_3-dominated woodland greatly alters the hydrological and nutrient cycles of these ecosystems (Thurow and Hester 1997; Norris et al. 2001; Hoch et al. 2002). Found in a wide array of climates and soils (Schmidt and Wardle 2002), eastern redcedar establishes readily and competes effectively in virtually every terrestrial ecosystem in the eastern two-thirds of North America.

Upon Euro-American settlement of the Great Plains, fire suppression in most areas allowed juniper and other fire-limited woody plants to expand their distribution from the east to west and from the rough breaks of drainages to uplands (Figure 2). Trees were planted as windbreaks for homes, to reduce erosion, to enhance wildlife habitat, and to provide relief from the vast open grasslands of the Great Plains (Capel 1988; Knopf 1992; Friedman et al. 1997). Much of the landscape was fragmented by the mid-1900s, but intentional plantings dispersed these woody species throughout the Great Plains, thereby bridging barriers imposed by cropland agriculture (Figure 3). Because native species of juniper are drought tolerant, they persist in most Great Plains environments and, unfortunately, are able to reproduce and expand their range. Tree planting, widely considered a wise conservation act that provided wildlife habitat and greened the landscape, was inconsiderate of obligate grassland wildlife. Government

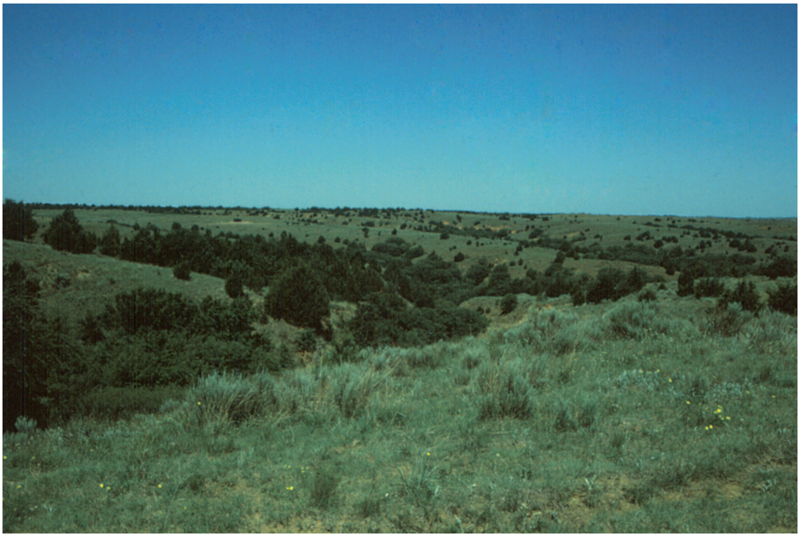

Figure 2 Fire suppression has allowed juniper and other fire-limited woody plants to expand their distribution from east to west and from drainages to uplands, a change ecologically equivalent to glaciation

Figure 3 Intentional tree planting in the Great Plains fragments the remaining patches of grassland and facilitates widespread encroachment. Eastern redcedar is often selected for planting in Great Plains grassland because it is tolerant to a wide range of soil and climate conditions. The species is commonly used for (**a**) living snow fence (eastern redcedar and Russian olive in this case) and (**b**) wildlife habitat improvement. Federal and state programs to control encroachment of eastern redcedar conflict with different programs within the same agency to plant this species as living snow fences within the same counties of Oklahoma. As a wildlife habitat improvement practice, planting eastern redcedar opposes habitat conservation for grassland obligate endemic wildlife

programs to control the expansion of eastern redcedar coexist with other programs in the same agency that plant this species as living snow fences in Oklahoma. A negative feedback of fire suppression resulting from grassland fragmentation leads to reduced herbaceous plant diversity (Leach and Givnish 1996) and an increase in woody plant encroachment, which further fragments grassland (Coppedge et al. 2001b).

Eastern Redcedar Invasion and Grassland Avifauna

Avifauna obligate to the grasslands of the Great Plains is viewed increasingly as important to the U.S. citizenry. Songbirds are considered prime ecological indicators, providing easily observable indices to wildlife habitat structure and ecosystem health (Eyre et al. 1992). Several bird species are locally important to some of the most economically depressed rural economies in the United States. Populations of the greater prairie-chicken, lesser prairie-chicken, and northern bobwhite, the three primary upland game birds of the central and southern Great Plains, are declining across much of their range (Brennan 1991; Church et al. 1993, Silvy and Hagen 2004). With their populations nearing potential listing as endangered, hunting of both species of prairie-chickens has nearly been eliminated (Silvy and Hagen 2004), and hunting remnant populations threatens population viability of all three species in fragmented landscapes (Roseberry and Klemstra 1984:147–148; Woodward et al. 2001; Fuhlendorf et al. 2002; Silvy and Hagen 2004). The increasing rarity of the upland game bird species as well as the entire grassland avifauna has led to increased public and scientific interest in the Great Plains and has fostered interest in development of ecotourism-based enterprises (Henderson 1984; Cordell et al. 1999).

Although causation is debated, obligate grassland birds are the most rapidly declining guild of birds in North America according to the Breeding Bird Survey, an avian survey conducted in late May through June (Bystrak 1981) at more than 3000 sites across North America (Droege 1990). Over the past 30 years these obligate grassland bird species have declined by 70%, and projections indicate the trends will not be reversed. Many factors may be contributing to these declines, but cultivation of grasslands, which in the past contributed to loss of grassland bird breeding habitat, is unlikely to contribute to additional permanent change in land use in the Great Plains (Heimlich and Kula 1991). Recent studies point to the expansion of eastern redcedar as a primary factor responsible for changes in Great Plains avifauna during the past 30 years. Several studies examining the effects of eastern redcedar on the grassland avifauna from regional, landscape, and local spatial scales indicate habitat change resulting from eastern redcedar expansion could extirpate grassland obligate birds from much of the Great Plains.

A recent study documented change in the regional winter bird assemblage associated with differences in regional dominance of eastern redcedar and human population density throughout Oklahoma (Coppedge et al. 2001a). Aside from agricultural activities, Oklahoma landscapes have also experienced significant alteration as a result of low-density urban development, which is highly correlated with the expansion of eastern redcedar (Coppedge et al. 2001a). Junipers produce prolific fruits that are utilized by frugivorous passerines in winter (Holthuijzen and Sharik 1984, 1985; Chavez-Ramirez and Slack 1996). Therefore, the effects of juniper encroachment on long-term winter abundance patterns of common passerines in Oklahoma should be detectable using data from the Audubon Society Christmas Bird Counts (CBC) (Butcher 1990). The abundance of nine species was found to be significantly related to regional juniper levels (Coppedge et al. 2001a). Three known juniper feeders and seed dispersers, the cedar waxwing (*Bombycilla cedrorum*), eastern bluebird (*Sialia sialis*), and yellow-rumped warbler (*Dendroica coronata*), had significant positive abundance trends with regional juniper levels, as did the ruby-crowned kinglet (*Regulus calendula*). Two other know juniper feeders (American robin, *Turdus migratorius*; blue jay, *Cyanocitta cristata*) exhibited unimodal trends, indicating a preference for regions with moderate juniper levels. Four species, the song sparrow (*Melospiza melodia*), white-crowned sparrow (*Zonotrichia leucophrys*), house sparrow (*Passer domesticus*), and American goldfinch (*Carduelis tristis*), were negatively related to regional juniper encroachment levels (Figure 4). With juniper projected to dominate one-half of the grassland remnants in Oklahoma before 2010, the winter abundance of many frugivorous species that are responsible for spreading juniper seeds will likely increase in Oklahoma and other parts of the southern plains. Conversely, continuation of low-density urban sprawl will accompany juniper encroachment and hinder conservation efforts for many grassland habitats and wildlife already in decline.

A landscape-level study utilized Breeding Bird Survey (BBS) data and a geographic information system to compare bird populations to the dynamics of three landscapes in western Oklahoma over a 30-year period (Figure 5; Coppedge et al. 2001b). Dominance of woody vegetation, composed primarily of eastern redcedar, was the best explanatory variable for shifts in the composition of grassland bird communities. Grassland obligate birds declined as woody plants increased, whereas open habitat generalists, woodland species, and successional shrub species increased in abundance. Many of the grassland obligate bird species are those the BBS indicates are declining (Peterjohn and Sauer 1999).

Yet another landscape-level study sheds light on the influence of juniper on grassland obligate avifauna. This study examined habitat elements associated with the lesser prairie-chicken, a grouse species endemic to prairie and shrubland of the Southern Great Plains (Aldrich 1963; Giesen 1998). Population levels and range have declined by more than 90% from historic levels (Crawford 1980; Taylor and Guthery 1980a; Giesen 1994b). As populations declined precipitously in recent decades (Bailey and Williams 2000; Giesen 2000; Horton 2000; Jensen et al. 2000; Sullivan2000), hunting has been discontinued in Oklahoma and New Mexico (Hagen et al. 2004), and the bird has been considered a "warranted, but was precluded" threatened species by the U.S. Fish and Wildlife Service (Giesen 1998). Previous research, focused primarily on habitat requirements at the local level, demonstrated that the lesser prairie-chicken requires a mosaic of prairie and shrubland habitats dispersed across the landscape, albeit the nature of such dispersion remains unknown (Jones 1963; Riley et al. 1992; Riley and Davis 1993; Giesen

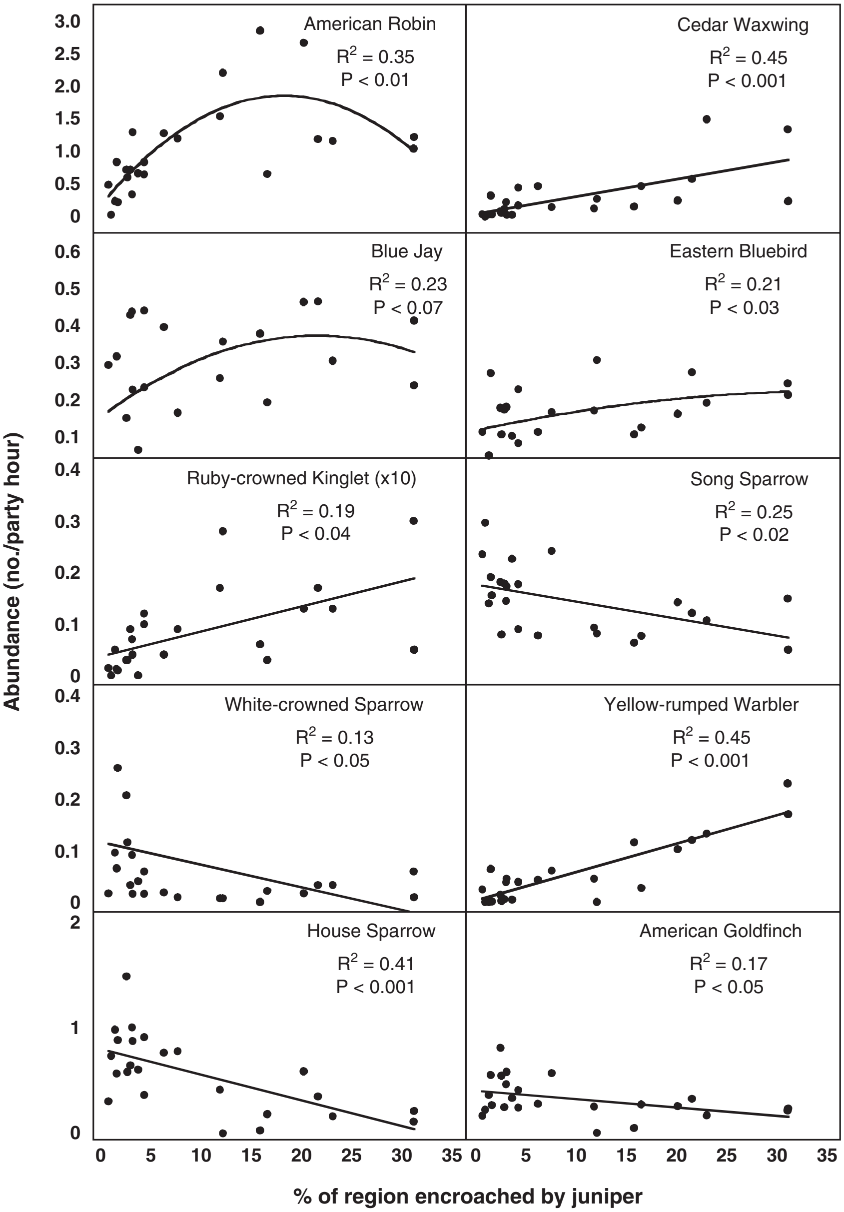

Figure 4 Results of regression models relating mean species abundance of selected birds wintering in Oklahoma to regional encroachment of eastern redcedar for the 1950–1994 time period. (From Coppedge et al. 2001a, with permission from Kluwer Academic Press)

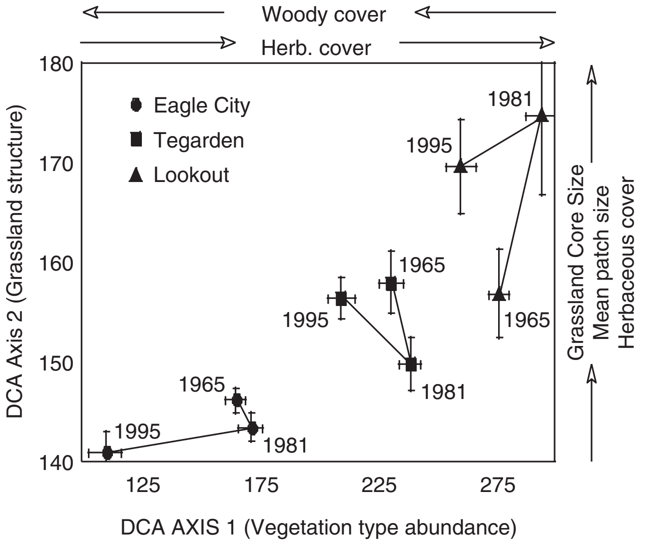

Figure 5 Plot of the results of a detrended correspondence analysis of bird abundance observed on three routes of the North American Breeding Bird Survey. The landscapes surrounding each route varied in proportion of cover of woodlands, primarily composed of eastern redcedar, and fragmented by cropland agriculture. The primary gradient associated with bird community composition was the relative cover of vegetation types, woodland and grassland. (From Coppedge et al. 2001b, copyright Ecological Society of America)

1998). This research also indicated that the lesser prairie-chicken possesses a high degree of site fidelity to habitat surrounding or adjacent to their breeding display grounds (leks), and their home ranges can be several thousand hectares (Taylor and Guthery 1980b; Giesen 1994a; Riley et al. 1994). Several authors have speculated that 1024 to 7238 ha of unfragmented habitat (native grassland and shrubland) might be required to sustain a population, suggesting that populations might be associated with landscape-level structure and patch stability (Davison 1940; Crawford and Bolen 1976; Taylor and Guthery 1980b; Woodward et al. 2001). A study focusing on permanent breeding grounds and the surrounding landscapes found that although cultivation historically fragmented these landscapes, cultivated land had decreased over the past 20 years (Woodward et al. 2001). However, fragmentation continued in recent years because of the increased dominance of trees, primarily eastern redcedar, and decline of some lesser prairie-chicken populations can be attributed to this source of fragmentation (Figure 6).

Coarse-scale habitat features constrain local-level habitat relationships so that the effect of regional juniper expansion is also exhibited at local levels. A study examining the relationship between local habitat structure and bird communities demonstrated that the canopy cover of eastern redcedar explained a greater proportion of the composition of bird communities in southern mixed prairie than did the structure of herbaceous vegetation (Figure 7; Chapman et al. 2004). Structure of

Figure 6 Except for the encroaching eastern redcedar, this shrub-steppe in the western Great Plains provides suitable habitat for lesser prairie-chicken, a grassland obligate species that is declining across its range. Visual cues provided to the birds by the trees might be perceived as unsuitable habitat, perhaps because predators increase with tree encroachment (Bradley and Fagre 1988, Winter et al. 2000)

herbaceous vegetation, manipulated primarily through herbivory and fire, is a key factor in habitat selection by grassland obligate birds in the breeding season (Weins 1974; Cody 1985; Knopf 1996). However, as the canopy cover of eastern redcedar increases, variability in species composition and density decreases, indicating that canopy cover of eastern redcedar will constrain the local influence of herbaceous habitat structure (Figure 8). The practical significance of this is that the application of fire and herbivory, wildlife habitat management practices that ordinarily can be used to enhance habitat in Great Plains grasslands, becomes increasingly influential as eastern redcedar increases in abundance.

Together, these studies indicate encroaching juniper meaningfully influences the avian community at multiple spatial scales. Already declining grassland species decline further as eastern redcedar increases, whereas woodland, shrubland, and some frugivorous species benefit from the presence of this invasive woody species. The expansion of eastern redcedar and other juniper species is at least partially responsible for declining populations of grassland obligate birds. Although an influx of woody vegetation generally increases the resources available to avian communities, it in turn alters avian community composition by attracting avian exotics and habitat generalists and decreasing habitat suitability for endemic and obligate avian grassland species (Blair 1996; Farina 1997; Preiss et al. 1997). The size and diversity of grassland bird communities are already quite low consequent to a limited resource base inherent to North American grasslands because of recurrent

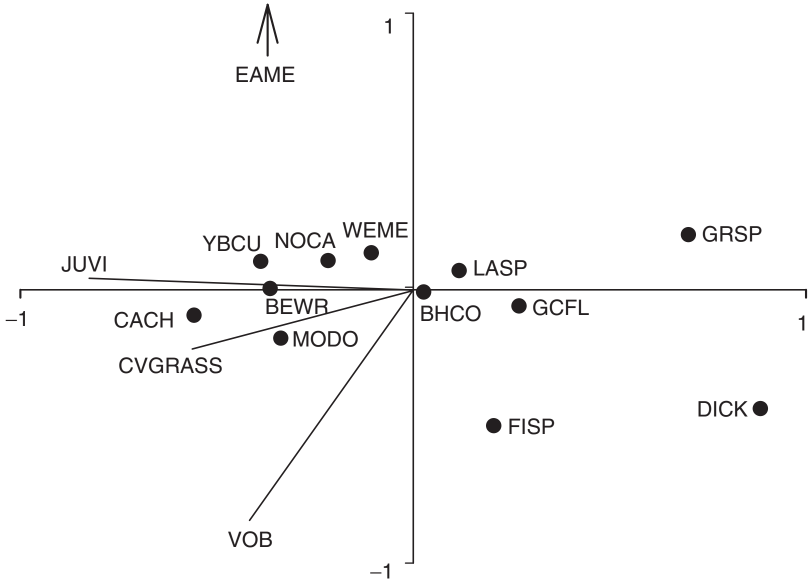

Figure 7 Plot of the results of an ordination (canonical correspondence analysis) relating bird species to habitat variables on sites within the mixed prairie of northwestern Oklahoma. Vectors (*lines with arrows*) show relationships between habitat variables and axes; *length of the vector* indicates the importance of the variable, and *direction* indicates strength of correlation with individual axes. *Axis 1* explains the greatest amount of association between the habitat variables and abundance of bird species, which indicates that eastern redcedar is the primary habitat variable explaining avian species composition. *JUVI*, canopy cover of eastern redcedar; *VOB*, visual obstruction, a measure of vertical structure; *CVGRASS*, coefficient of variability of grass canopy cover, a measure of horizontal structural patchiness; all *four-letter abbreviations* are American Ornithological Union species codes of common bird species of the southern mixed-grass prairie. (From Chapman et al. 2004, copyright Écoscience)

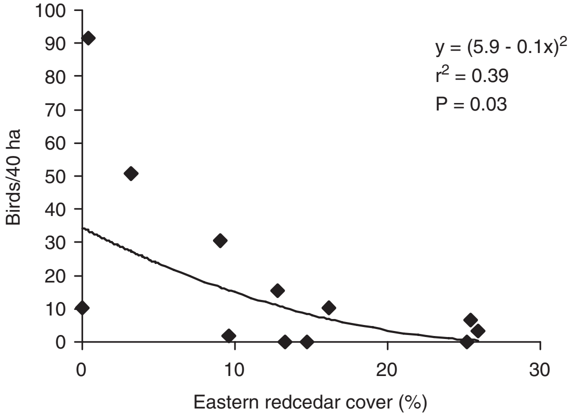

Figure 8 Regression model showing that relative abundance of bird species associated with grassland habitats decreases as canopy cover of eastern redcedar increases. Just as important, variability in bird species composition decreases as canopy cover of eastern redcedar increases, indicating that canopy cover of eastern redcedar constrains the local influence of herbaceous habitat structure created by herbivory and fire. (From Chapman et al. 2004, copyright Écoscience)

drought (Wiens 1974) and fragmentation of grassland habitat (Herkert et al. 2003). In fact, the Great Plains once served as a geographic barrier to woodland avifaunas (Mengel 1970), but westward expansion of species from eastern deciduous forests has been fostered by the development of riparian woodlands along major rivers (Johnson 1994) that provide regional habitat corridors across the Great Plains (Knopf 1986). The mixing of eastern and western avifaunas has resulted in the loss of several subspecific avian forms and the general loss of genetic and community distinctiveness (Rising 1983; Knopf 1986). Using prescribed fire to prevent encroachment of eastern redcedar, and therefore grassland fragmentation and degradation, would contribute significantly to reducing the rates of decline in grassland bird species. Curtailing sponsored, intentional planting of eastern redcedar and other trees by federal and state agencies would also contribute to reducing this decline.

Summary

The Green Glacier or woody plant encroachment into grasslands is creating a 21st-century environmental crisis that might well surpass the ecological impact of the 20th-century Dust Bowl. The Dust Bowl resulted from unwise conversion of large

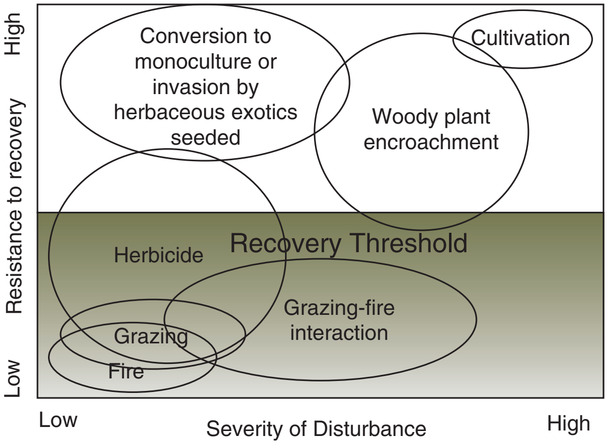

Figure 9 Resistance to recovery of Great Plains grasslands as a function of severity of disturbance. *Circles* indicate the normal bounds of variation in recovery potential for a particular kind of disturbance. The *horizontal midline* indicates the bound above which the grassland will not recover to the state to which it existed before disturbance. Great Plains grasslands evolved with grazing and fire, unlike the anthropogenic disturbances of cultivation and planting of both herbaceous plants and woody plants. Fire exclusion, the result of anthropogenic intervention, also accounts for a current profusion of woody plants in the largely treeless grasslands of the Great Plains

blocks of Great Plains grasslands unsuited to cultivation to cropland agriculture, and it culminated in one of America's most noted environmental disasters. Conversion of native grassland to cropland is no longer the primary threat in the region. A second environmental crisis, the Green Glacier or woody plant encroachment, now accounts for the great majority of land conversion and represents the primary environmental concern for the native grasslands of the Great Plains (Figure 9).The Green Glacier, a present threat perhaps more egregious than the Dust Bowl, has added to the fragmentation accomplished in the original breakout of the prairie sod (Coppedge et al. 2001c). However, in contrast to the original plowing of prairie sod, the Green Glacier is even less selective of sites, and therefore presents conservationists and the general public with perhaps a greater challenge than did the Dust Bowl, which marshaled a national conservation movement for the soil resource.

In this chapter, we used birds as model ecological indicators to quantify the environmental costs of eastern redcedar encroachment into Great Plains grasslands. Other environmental costs will likely be commensurate to the loss incurred by the grassland obligate avifauna. Water yield and water quality will decline with the loss of herbaceous vegetation, human respiratory health will be threatened as eastern redcedar pollen counts increase, and a host of other ecosystem-related goods and services will be negatively affected. Lacking the Black Sunday that caught the nation's attention of the Dust Bowl, we wonder what lever must be tripped before the nation's conservation consciousness is raised on the more insidious Green Glacier.

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References

Albertson, F.W., Tomanek, G.W., and Riegel, A. 1957. Ecology of drought cycles and grazing intensity on grasslands of central Great Plains. Ecol. Monogr. 27:27–44.

Aldich, J.W. 1963. Geographic orientation of American *Tetraonidae*. J. Wildl. Manag. 27:529–545.

Anderson, R.C. 1990. The historic role of fire in the North American grassland. In: Fire in the North American tallgrass prairies, eds. S.L. Collins and L.L. Wallace, pp 8–18. Norman, OK: University of Oklahoma Press.

Ansley, J.A., Pinchak, W.E., and Ueckert, D.N. 1995. Changes in redberry juniper distribution in northwest Texas (1948–1982). Rangelands 17:49–53.

Arend, J.L. 1950. Influence of fire and soil on distribution of eastern redcedar in the Ozarks. J. For. 48:129–130.

Axelrod, D.I. 1985. Rise of the grassland biome, central North America. Bot. Rev. 51:163–202.

Bailey, J.A., and Williams, S.O., III. 2000. Status of the lesser prairie-chicken in New Mexico. Prairie Nat. 32:157–168.

Baltensperger, B.H. 1979. Agricultural adjustments to Great Plains drought, the Republican Valley, 1870–1900. In: The Great Plains, environment and culture, eds. B.W. Blouet and F.C. Luebke, pp 43–59. Lincoln, NE: University of Nebraska Press.

Bedenbaugh, E.J. 1988. History of cropland set aside programs in the Great Plains. In: Impacts of the conservation reserve program in the Great Plains, ed. J.E. Mitchell, pp 14–17. General technical report RM-158. Fort Collins, CO: United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Blair, R.B. 1996. Land use and avian species diversity along an urban gradient. Ecol. Appl. 6:506–519.

Borchert, J.R. 1950. The climate of the central North American grassland. Ann. Assoc. Am. Geogr. XL:1–39.

Bradley, L.C., and Fagre, D.B. 1988. Coyote and bobcat response to integrated ranch management practices in south Texas. J. Range. Manag. 41:322–327.

Brennan, L.A. 1991. How can we reverse the northern bobwhite population decline? Wildl. Soc. Bull. 19:544–555.

Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S., and McCarron, J.K. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. BioScience 55:243–254.

Butcher G.S. 1990. Audubon Christmas bird counts. In: Survey designs and statistical methods for the estimation of avian population trends, eds. J.R Sauer and S. Droege, pp 5–13. Biological report 90. Washington, DC: United States Department of the Interior.

Bystrak, D. 1981. The North American Breeding Bird Survey. In: Estimating numbers of terrestrial birds, eds. C.J. Ralph and J.M. Scott. Studies Avian Biol. 6:34–41.

Capel, S.W. 1988. Design of windbreaks for wildlife in the Great Plains of North America. Agric. Ecosyst. Environ. 22/23:337–347.

Chapman, R.N., D.M. Engle, R.E. Masters, and Leslie, D.M., Jr. 2004. Tree invasion constrains the influence of herbaceous structure in grassland bird habitats. Écoscience 11:55–63.

Chavez-Ramirez, F., and Slack, R.D. 1996. Winter phenology and frugivory of American robins and cedar waxwings on the Edwards Plateau of central Texas. Tex. J. Sci. 48:129–136.

Church, K.E., Sauer, J.R., and Droege, S. 1993. Population trends of quails in North America. Proc. Natl. Quail Symp. 3:44–54.

Cody, M.L. 1985. Habitat selection in grassland and open-country birds. In: Habitat selection in birds. ed. M.L. Cody, pp 191–226. Orlando: Academic Press.

Coppedge, B.R., Engle, D.M., Fuhlendorf, S.D., Masters, R.E., and Gregory, M.S. 2001a. Urban sprawl and juniper encroachment effects on abundance of wintering passerines in Oklahoma. In: Avian ecology and conservation in an urbanizing world. eds. J.M. Marzluff, R. Bowman, and R. Donnelly, pp 225–242. Norwell, MA: Kluwer.

Coppedge, B.R., Engle, D.M., Masters, R.E., and Gregory, M.S. 2001b. Avian response to landscape change in fragmented Southern Great Plains grasslands. Ecol. Appl. 11:47–59.

Coppedge, B.R., Engle, D.M., Fuhlendorf, S.D., Masters, R.E., and Gregory, M.S. 2001c. Landscape cover type and pattern dynamics in fragmented southern Great Plains grasslands, USA. Landsc. Ecol. 16:677–690.

Cordell, H.K., McDonald, B.L., Teasley, R.J., Bergstrom, J.C., Martin, J., Bason, J., and Leeworthy, V.R. 1999. Outdoor recreation participation trends. In: Outdoor recreation in American life: a national assessment of demand and supply trends compared, ed. H.K. Cordell. Champaign: Sagamore.

Coupland, R.T. 1992. Overview of the grasslands of North America. In: Ecosystems of the world: natural grasslands, vol 8A, ed. R.T. Coupland, pp 147–150. Amsterdam: Elsevier.

Crawford, J.A. 1980. Status, problems, and research needs of the lesser prairie-chicken. In: Proceedings, prairie grouse dymposium, eds. P.A. Vohs and F.L. Knopf, pp 1–7. Stillwater, OK: Oklahoma State University.

Crawford, J.A., and Bolen, E.G. 1976. Effects of land use on lesser prairie-chickens in Texas. J. Wildl. Manag. 40:96–104.

Daubenmire, R.F. 1978. Plant geography. New York: Academic Press.

Davison, V.E. 1940. An eight year census of lesser prairie-chickens. J. Wildl. Manag. 4:55–62.

Dirr, M.A. 1983. Manual of woody landscape plants. Champaign: Stipes.

Droege, S. 1990. The North American breeding bird survey. In Survey designs and statistical methods for the estimation of avian population trends, eds. J.R. Sauer and S. Droege, pp 1–4.

Biological report 90(1). Washington, DC: United States Department of the Interior, Fish and Wildlife Service.

Engle, D.M., and Kulbeth, J.D. 1992. Growth dynamics of eastern redcedar at three locations in Oklahoma. J. Range. Manag. 45:301–305.

Engle, D.M., Stritzke, J.F., and Claypool, P.L. 1987. Herbage standing crop around eastern redcedar trees. J. Range. Manag. 40:237–239.

Engle, D.M., Bidwell, T.G., and Moseley, M.E. 1996. Invasion of Oklahoma rangelands and forests by eastern redcedar and ashe juniper. Circular E-947. Stillwater, OK: Cooperative Extension Service, Oklahoma State University.

Epstein, H.E., Lauenroth, W.K., Burke, I.C., and Collins, D.P. 1996. Ecological response of dominant grasses along two climatic gradients in the Great Plains of the United States. J. Veg. Sci. 7:777–788.

Eyre, M.D., Rushton, S.P., Young, A.G., and Hill, D. 1992. Land cover and breeding birds. In: Land use change: the causes and consequences, ed. M.C. Whitby, pp 131–136. London: ITE Symposium 27.

Farina, A. 1997. Landscape structure and breeding bird distribution in a sub-Mediterranean agroecosystem. Landsc. Ecol. 12:365–378.

Flores, D.L. 1996. A long love affair with an uncommon country: environmental history of the Great Plains. In: Prairie conservation: preserving North America's most endangered ecosystem, eds. F.B. Samson and F.L. Knopf, pp 3–17. Washington, DC: Island Press.

Friedman, J.M., Scott, M.L., and Auble, B.T. 1997. Water management and cottonwood forest dynamics along prairie streams. In: Ecology and conservation of Great Plains vertebrates, vol 125, eds. F.L. Knopf and F.B. Samson, pp 49–71. New York: Springer-Verlag.

Fuhlendorf, S.D., Smeins, F.E., and Grant, W.E. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecol. Model. 90:245–255.

Fuhlendorf, S.D., Smeins, F.E., and Taylor, C.A. 1997. Browsing and tree size influences on Ashe juniper understory. J. Range. Manag. 50:507–512.

Fuhlendorf, S.D., Woodward, A.J.W., Leslie, D.M., Jr., and Shackford, J.S. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. Landsc. Ecol. 17:617–628.

Giesen, K.M. 1994a. Movements and nesting habitat of lesser prairie-chicken hens in Colorado. Southwest. Nat. 39:96–98.

Giesen, K.M. 1994b. Breeding range and population status of lesser prairie-chickens in Colorado. Prairie Nat. 26:175–182.

Giesen, K.M. 1998. Lesser prairie-chicken (*Tympanuchus pallidicinctus*). In: The birds of North America, eds. A. Poole and F. Gill. Account no. 364. Philadelphia: Academy of Natural Sciences; Washington, DC: American Ornithologists' Union.

Giesen, K.M. 2000. Population status and management of lesser prairie-chicken in Colorado. Prairie Nat. 32:137–148.

Gehring, J.L., and T.B. Bragg. 1992. Changes in prairie vegetation under eastern redcedar (*Juniperus virginiana*) in an eastern Nebraska bluestem prairie. Am. Midl. Nat. 128:209–217.

Glantz, M.H. 1994. Drought, desertification and food production. In: Drought follows the plow, ed. M.H. Glantz, pp 9–30. New York: Cambridge University Press.

Hagan, C.A., Jamison, B.E., Giesen, K.M., and Riley, T.Z. 2004. Guidelines for managing lesser prairie-chicken populations and their habitats. Wildl. Soc. Bull. 32:69–82.

Heimlich, R.E., and Kula, O.E. 1991. Economics of livestock and crop production on post-CRP lands. In: The conservation reserve: yesterday, today and tomorrow, eds. L.A. Joyce, J.E. Mitchell, and M.D. Skold, pp 11–23. General technical report RM-203. Fort Collins, CO: United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Henderson, F.R. 1984. Guidelines for increasing wildlife on farms and ranches: with ideas for supplemental income sources for rural families. Great Plains Agricultural Council, Wildlife

Resources Committee. Manhattan, KS: Cooperative Extension Service, Kansas State University.

Herkert , J.R., Reinking, D.L., Wiedenfeld, D.A., Winter, M., Zimmerman, J.L., Jensen, W.E., Finck, E.J., Koford, R.R., Wolfe, D.H., Sherrod, S.K., Jenkins, M.A., Faaborg, J., and Robinson, S.K. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. Conserv. Biol. 17:587–594.

Hoch, G.A., Briggs, J.M., and Johnson, L.C. 2002. Assessing the rate, mechanism and consequences of conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 6:578–586.

Holthuijzen, A.M.A., and Sharik, T.L. 1984. Seed longevity and mechanisms of regeneration of eastern redcedar (*Juniperus virginiana* L.). Bull. Torrey Bot. Club 111:153–158.

Holthuijzen, A.M.A., and Sharik, T.L. 1985. The avian seed dispersal system of eastern redcedar (*Juniperus virginiana* L.). Can. J. Bot. 63:1508–1515.

Horncastle, V.J., Hellgren, E.C., Mayer, P.M., Engle, D.M., and Leslie, D.M., Jr. 2004. Differential consumption of eastern redcedar (*Juniperus virginiana*) by avian and mammalian guilds: implications for tree invasion. Am. Midl. Nat. 152:255–267.

Horton, R.E. 2000. Distribution and abundance of lesser prairie-chicken in Oklahoma. Prairie Nat. 32:189–195.

Jensen, W.E., Robinson, D.A., Jr., and Applegate, R.D. 2000. Distribution and population trend of lesser prairie-chicken in southwestern Kansas. Prairie Nat. 32:169–175.

Joern, A., and Keeler, K. 1995. The changing prairie: North American grasslands. New York: Oxford University Press.

Johnson, W.C. 1994. Woodland expansion in the Platte River, Nebraska: pattern and causes. Ecol. Monogr. 64:45–84.

Jones, R.E. 1963. Identification and analysis of lesser and greater prairie-chicken habitat. J. Wildl. Manag. 27:757–778.

Joyce, L.A. 1989. An analysis of the range forage situation in the United States: 1989–2040. General technical report RM-180. Fort Collins, CO: United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Knopf, F.L. 1986. Changing landscapes and the cosmopolitanism of eastern Colorado avifauna. Wildl. Soc. Bull. 14:132–142.

Knopf, F.L. 1992. Faunal mixing, faunal integrity, and the biopolitical template for diversity conservation. Trans. N. Am. Wildl. Nat. Res. Conf. 57:330–342.

Knopf, F.L. 1994. Avian assemblages on altered grasslands. Studies Avian Biol. 15:247–257.

Knopf, F.L. 1996. Prairie legacies—birds. In: Prairie conservation. preserving North America's most endangered ecosystem, eds. F.B. Samson and F.L. Knopf, pp 135–148. Washington, DC: Island Press.

Kuchler, A.W. 1964. Potential natural vegetation of the conterminous United States. Special publication no. 36. Washington, DC: American Geographical Society.

Lawson, E.R. 1990. *Juniperus virginiana* L. eastern redcedar. In: Silvics of North America, vol 1. Conifers, eds. R.M. Burns and B.H. Honkala, pp 131–140, Agriculture handbook 654. Washington, DC: United States Department of Agriculture, Forest Service.

Laycock, W.A. 1988. History of grassland plowing and grass planting on the Great Plains. In: Impacts of the conservation reserve program in the Great Plains, ed. J.E. Mitchell, pp 3–8. General technical report RM-158. Fort Collins, CO: United States Department of Agriculture, Forest Service.

Leach, M.K., and Givnish, T.J. 1996. Ecological determinants of species loss in remnant prairies. Science 273:1555–1558.

Licht, D.S. 1997. Ecology and economics of the Great Plains. Lincoln, NE: University of Nebraska Press.

Mack, R.N., and Thompson, J.N. 1982. Evolution in steppe with few large, hooved mammals. Am. Nat. 119:757–773.

McDonald, J.N. 1981. North American bison: their classification and evolution. Berkeley: University of California Press.

Mengel, R.M. 1970. The North American central plains as an isolating agent in bird speciation. In: Pleistocene and recent environments of the central Great Plains, eds. W. Dort and J.K. Jones, Jr., pp 279–340. Lawrence, KS: University of Kansas Press.

Mitchell, J.E., Louda, S.M., and Gillam, B. 1999. Background and synopsis: symposium on the Great Plains grasslands at the millennium. Great Plains Res. 9:211–222.

Norris, M.D., Blair, J.M., Johnson, L.C., and McKane, R.B. 2001. Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. Can. J. For. Res. 31:1940–1946.

O'Neill, R.V., Hunsaker, C.T., Jones, K.B., Riitters, K.H., Wickham, J.D., Schwartz, P.M., Goodman, I.A., Jackson, B.L., and Baillargeon, W.S. 1997. Monitoring environmental quality at the landscape scale. Bioscience 47:513–519.

Peterjohn, B.G., and Sauer, J.R. 1999. Population status of North American grassland birds. Studies Avian Biol. 19:27–44.

Pielou, E.C. 1992. After the Ice Age: the return of life to glaciated North America. Chicago: University of Chicago Press.

Preiss, E., Martin, J.L., and Debussche, M. 1997. Rural depopulation and recent landscape changes in a Mediterranean region: consequences to the breeding avifauna. Landsc. Ecol. 12:51–61.

Pyne, S.J. 1982. Fire in America: a cultural history of wildland and rural fire. Princeton, NJ: Princeton University Press.

Riley, T.Z., and Davis, C.A. 1993. Vegetative characteristics of lesser prairie-chicken brood foraging sites. Prairie Nat. 25:243–248.

Riley, T.Z., Davis, C.A., Ortiz, M., and Wisdom, M.J. 1992. Vegetative characteristics of successful and unsuccessful nests of lesser prairie chickens. J. Wildl. Manag. 56:383–387.

Riley, T.Z., Davis, C.A., Candelaria, M.A., and Suminski, H.R. 1994. Lesser prairie-chicken movements and home ranges in New Mexico. Prairie Nat. 26:183–186.

Rising, J.D. 1983. The Great Plains hybrid zones. Curr. Ornithol. 1:131–157.

Roseberry, J.L., and Klimstra, W.D. 1984. Population ecology of the bobwhite. Carbondale, IL: Southern Illinois University Press.

Sala, O.E., Parton, W.J., Joyce, L.A., and Lauenroth, W.K. 1988. Primary production of the central grassland region of the United States: spatial pattern and major controls. Ecology 69:40–45.

Sampson, F., and Knopf, F. 1994. Prairie conservation in North America. Bioscience 44:418–421.

Schmidt, T.L., and Wardle, T.D. 1998. The forest resources of Nebraska. Research paper NC-332. St. Paul, MN: United States Department of Agriculture, Forest Service, North Central Research Station.

Schmidt, T.L., and Wardle, T.D. 2002. Impact of pruning eastern redcedar (*Juniperus virginiana*). West. J. Appl. For. 17:189–193.

Silvy, N.J., and Hagen, C.A. 2004. Introduction: management of imperiled prairie grouse species and their habitat. Wildl. Soc. Bull. 32:2–5.

Sopuck, R.D. 1995. Sustaining the Great Plains ecosystem: integrating people economics and the landscape. In: Conservation of Great Plains ecosystems: current science, future options, eds. S.R. Johnson and A. Bouzaher, pp 83–95. Amsterdam: Kluwer.

Stebbins, G.L. 1981. Coevolution of grasses and herbivores. Ann. Mo. Bot. Gard. 68:75–86.

Sullivan, R.M., Hughes, J.P., and Lionberger, J.E. 2000. Review of the historical and present status of the lesser prairie-chicken (*Tympanuchus pallidicinctus*) in Texas. Prairie Nat. 32:178–188.

Taylor, M.S., and Guthery, F.S. 1980a. Status, ecology, and management of the lesser prairie-chicken. General technical report RM-77. Fort Collins, CO: United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Taylor, M.S., and Guthery, F.S. 1980b. Fall-winter movements, ranges, and habitat use of lesser prairie-chickens. J. Wildl. Manag. 44:521–524.

Thurow, T.L., and Hester, J.W. 1997. How an increase or reduction in juniper cover alters rangeland hydrology. In: 1997 juniper symposium, ed. C.A. Taylor, pp 4.9–4.22. Technical report 97-1. Sonora, TX: Texas Agricultural Experiment Station.

Van Haverbeeke, D.F., and King, R. 1990. Genetic variation in Great Plains *Juniperus*. Research paper RM-292. Fort Collins, CO: United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Vickery, P.D., Tubaro, P.L., Da Silva, J.M.C., Peterjohn, B.G., Herkert, J.R., and Cavalcanti, R,B. 1999. Conservation of grassland birds in the western hemisphere. Studies Avian Biol. 19:2–26.

Wiens, J.A. 1974. Habitat heterogeneity and community structure in North American grassland birds. Am. Midl. Nat. 91:195–213.

Winter, M., Johnson, D.H., and Faaborg, J. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor 102:256–266.

Woodward, A.J., Fuhlendorf, S.D., Leslie, D.M., Jr., and Shackford, J. 2001. Influence of landscape composition and change on lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations. Am. Midl. Nat. 145:261–274.

Wright, H.E., Jr. 1970. Vegetational history of the Central Plains. In: Pleistocene and recent environments of the Central Great Plains, eds. W. Dort and J.K. Jones, Jr., pp 157–172. Lawrence, KS: University of Kansas Press.

15

Reversing the Woodland Steady State: Vegetation Responses During Restoration of *Juniperus*-Dominated Grasslands with Chaining and Fire

R. James Ansley and Harold T. Wiedemann

Introduction

Junipers (*Juniperus* spp.) are native woody shrubs that have expanded beyond their normal historical ranges in the western and southwestern United States since the late 1800s (Johnson 1962; Burkhardt and Tisdale 1976; Gehring and Bragg 1992; Ansley et al. 1995; Miller and Tausch 2001; Ueckert et al. 2001). The most likely reason for this is the change in the disturbance regimes associated with these communities and the lengthening of the time between disturbances that removed juniper. Increases in juniper can be attributed to fire suppression, climate change, and overgrazing by livestock. Overgrazing had the dual effect of weakening the competitive ability of grasses against emerging juniper seedlings and reducing the amount of herbaceous fine fuel that normally supported fires (Archer et al. 1995; Van Auken 2000).

Junipers have encroached upon 8.8 million ha of rangeland in Texas and 1.4 million ha in Oklahoma and negatively influenced land use (SCS 1983, 1988; Snook 1985). Increases in density and distribution of these species has increased remarkably in the last 50 to 60 years. For example, from 1948 to 1982, redberry juniper (*Juniperus pinchotii* Sudw.) distribution in northwest Texas increased from 2.5 to 4 million ha, or 61% (Ansley et al. 1995). Distribution of eastern redcedar (*Juniperus virginiana* L.) and Ashe juniper (*Juniperus ashei* Buchholz) in Oklahoma has increased from 1.4 to 2.4 million ha, or 71%, during the short period of 1985 to 1994 (McNeill 2000).

The Woodland Steady State

Junipers threaten grassland ecosystems through a steady encroachment and ultimate domination (Bragg and Hulbert 1976; Tausch et al. 1981; Ansley and Rasmussen 2005). This change is largely a function of a consistent pattern of seed dispersal and a favorable competitive environment for emerging juniper seedlings. Juniper seedling survival is often increased when the herbaceous layer is overgrazed by livestock.

O.W. Van Auken (ed.), *Western North American Juniperus Communities:*
A Dynamic Vegetation Type.

Once a certain threshold of woody encroachment into grasslands is reached, normal graminoid-driven succession patterns give way to a shrub-driven succession, as illustrated by Archer (1990). Succession patterns among herbaceous species become modified by the shrub effect. Moreover, the presence of a woody overstory may modify wildlife migration patterns, such that the potential for changes in wildlife-mediated seed dispersal patterns increases, and this may add to shrub-driven succession through the introduction of new plant species into the ecosystem.

Woody plant dominance in grasslands is often considered a "woodland steady state" because the system will not likely shift back to grassland without anthropogenic manipulation of the woody vegetation (i.e., fire, mechanical, chemical), especially if the dominant woody species can sprout from the subterranean meristem following destruction of aboveground tissue. Examples are redberry juniper and honey mesquite (*Prosopis glandulosa*). Juniper species in general provide one of the more robust examples of how woody species maintain a steady state, and the probability of juniper woodlands naturally crossing the threshold and reverting back to an intermediate shrub-steppe or to grassland is very low in the absence of a major disturbance or costly anthropogenic inputs (Miller et al. 2000).

Juniper Effects on Herbaceous Production

Several studies have quantified the competitive effects of individual juniper trees on herbaceous growth and have documented a progressive increase in herbaceous production with increasing lateral distance from an individual juniper tree (Engle et al. 1987; Dye et al. 1995). Shading caused by evergreen foliage and the dense canopy structure of junipers prevents herbaceous vegetation from growing beneath the canopy. The lateral root system can cause extreme soil drought conditions at the canopy dripline and just beyond. It appears from these studies, however, that the lateral roots of individual junipers do not exert much of an effect on herbaceous production beyond 2 m from the dripline in redberry juniper (Dye et al. 1995), or 1 m beyond the dripline in eastern redcedar (Engle et al. 1987). These studies suggest the lateral root system of junipers is more restricted to the immediate environment of the juniper canopy, in contrast to honey mesquite, which has an extensive lateral root system.

Most community-level studies indicate that the functional relationship between percent juniper canopy cover (or density) and herbaceous production (or cover) follows either a negative linear or a negative exponential function (Jameson 1967; Clary 1971, 1987; McPherson and Wright 1990; Miller et al. 2000). These relationships are fairly consistent across a variety of juniper species and ecosystems, although the amplitude of this relationship changes with precipitation patterns and site (McPherson and Wright 1990). A common response in all these studies is that herbaceous production declines significantly with as little as 10% to 20% of juniper canopy cover, which appears to be somewhat inconsistent with the individual tree studies described above. If the competitive influence of single juniper trees was restricted to 1 to 2 m beyond the dripline, then one would not expect to see such a sharp decline in herbaceous production at relatively low juniper cover values. Clearly, there are synergistic effects among juniper trees that occur at the community level that are not well understood; these are no doubt a function of the size of the individual juniper trees.

Many other studies, although not focused on quantifying a functional relationship between juniper cover and herbaceous production, have demonstrated an increase in herbaceous production following juniper removal. Increases in herbaceous plant production are often substantial the first few years after treatment, even doubling or tripling that of pretreatment levels (Arnold 1964; Clary 1971; Steuter and Wright 1983). However, little is known about what factors are involved and how they interact to affect herbaceous recovery. Certainly, condition of the herbaceous community before treatment, soil health (amount of A and B horizon remaining; soil organic matter content, etc.), and posttreatment precipitation patterns are important. Because juniper domination tends to increase the amount of bare ground in addition to reducing growth of existing herbaceous patches, posttreatment recovery is also dependent on the rate of recruitment of herbaceous plants into bare soil areas (Miller et al. 2000). If the herbaceous community is dominated by bunchgrasses, then recruitment must come from seed. In the Intermountain region of Nevada and Utah, because of lower rainfall and generally more shallow soils, unaided rates of recovery are often too slow and seeding of herbaceous species is required.

Junipers and Herbaceous Composition

Posttreatment vegetation composition and succession trajectories following juniper control can be highly variable (Tausch et al. 1993). Postfire succession models presented by Barney and Frischknecht (1974) and Everett and Ward (1984) portray a progression from annuals to perennial grasses to grass/shrub mix to juniper dominance over time. In these models, juniper encroachment gradually gains over time. In the case of a resprouting species such as redberry juniper, a postfire increase to the point of dominance would be expected to occur much earlier (perhaps within 20 years) than that expected with juniper species, which depend on seedling recruitment. Annual forbs in this model would increase rapidly in the immediate postfire years (Koniak 1985) and may increase later as annual grasses and/or forbs when juniper is dominant. As juniper begins to dominate, the diversity of herbaceous species will likely decline.

The succession models portrayed by Barney and Frischknecht (1974), West and Van Pelt (1987), and others may still apply toward much of the southern prairie of Oklahoma and Texas where perennial grasses remain dominant. However, in many areas of the Intermountain region, the increase in annual grasses such as cheatgrass (*Bromus tectorum*) has largely altered this basic succession model by replacing the intermediate seral stages (i.e., perennial grass, shrub-steppe/grass mix) with an annual grass-dominated phase that has potential for high fire frequency. If true, Miller and Tausch (2001) suggest these communities may have difficulty returning to perennial grass or juniper woodland stages. In these regions, annual grasses may become a more important concern than reducing juniper stands with fire. Cool season (C_3) annual grasses have increased in many areas of the southern Great Plains, and it is worth considering that these may also have the potential to alter succession patterns in juniper woodlands (Ansley et al. 2004).

Restoration of Juniper-Dominated Grasslands

Numerous efforts have been made to return juniper-dominated areas to grasslands. Much of the motivation for earlier restoration efforts was to increase grass production for livestock grazing (Clary 1971; Steuter and Wright 1983). Although this remains an important consideration, there are other reasons for juniper control in addition to or in lieu of increasing livestock production. Juniper domination reduces habitat for wildlife species, particularly grassland birds that depend on open spaces (Belsky 1996). Moreover, juniper domination can cause increases in bare ground and severe soil erosion and can mine soil nutrients from interstitial spaces (Schlesinger et al. 1990; Davenport et al. 1998). The presence of a closed canopy stand of juniper also creates the potential for a catastrophic summer season crown fire that may threaten property. Thus, in many areas of the southern Great Plains there may be adequate justification for anthropogenically shifting the woodland steady state back to grasslands. It is acknowledged that certain woodland obligate species such as the golden-cheeked warbler (*Dendroica chrysoparia*) and black-capped vireo (*Vireo atricapillus*) are trigger points for the argument against juniper reduction. Perhaps the basis for decisions should focus more on the conservation of the soils resource than other factors (Davenport et al. 1998). The potential for long-term soil erosion is high in closed-canopy juniper areas that have had a crown fire disturbance because of the high amount of bare soil and slow herbaceous recovery rates.

Fire Disturbance Regimes

The consensus of opinion remains that many areas in the Great Plains and Intermountain region were once grasslands that have become dominated by junipers (Steuter and Britton 1983; Burkhardt and Tisdale 1976; Miller and Tausch 2001). Pre-settlement fire return interval was less than 10 years for much of the Great Plains and 12 to 25 years in the Intermountain region (Frost 1998;

Miller and Tausch 2001). Grassland communities in the Great Plains had more frequent fires than the Intermountain region because of an even distribution of readily combustible fuel (grass) and a greater frequency of ignition potential from lightning strikes or native Indian activities than that found in the Intermountain region. The lengthening of the fire return intervals associated with settlement by Europeans in the late 1800s likely stimulated juniper encroachment.

A fire return interval less than 10 years may have been key toward preventing encroachment by resprouting juniper species such as redberry juniper. Fire-induced mortality of redberry juniper was 90% when trees were less than 0.16 m tall but 37% in plants 0.16 to 0.34 m tall (Steuter and Britton 1983). With a growth rate of 0.04 m/year, redberry juniper plants that were less than 0.16 m tall were assumed to be 4 years old or younger. Thus, 4- to 8-year-old plants were twice more resistant to fire than younger plants, presumably because the basal bud zone began to be covered with soil and was protected from fire. Smith et al. (1975) found that redberry juniper survived ground-level clipping of all stems when plants were about 8 years of age. Resistance to aboveground disturbances is a function of the rate at which the basal caudex became covered with soil (McPherson and Wright 1989). The species sprouts from this meristem if aboveground tissue is killed. Thus, if pre-settlement fire frequency was less than 10 years in the southern Great Plains, it is likely that most seedling and juvenile redberry juniper plants were killed by wildfires before they became fire resistant.

Other juniper species in the Great Plains such as eastern redcedar and Ashe juniper can be killed by fire because they will not resprout following destruction of aboveground tissue (Wink and Wright 1973). However, size plays a role, and complete aboveground mortality achieved by fire declines considerably when trees are more than 2 m tall (Dalrymple 1969; Martin and Crosby 1955; Owensby et al. 1973). Moreover, these species have a net effect of lengthening the fire return interval because of their competitive effects on herbaceous production.

Prescribed Fire in Combination with Other Treatments

Prescribed burning has been used to accelerate the fire return interval in juniper-dominated grassland ecosystems and restore herbaceous dominance (Wright and Bailey 1982; Steuter and Britton 1983; Rasmussen and Wright 1989). Most prescribed fires in the southern Great Plains have been conducted during winter months. As a single treatment, winter fires are most effective when juniper encroachment is in early stages when juniper size and densities are low and the ecosystem is still primarily herbaceous. However, because of the influence of juniper on herbaceous production, it is difficult to send a fire through stands of mature junipers because of the lack of herbaceous fuel between juniper canopies. Because of this, moderate to dense stands of junipers are often mechanically treated to reduce juniper competition and increase the herbaceous growth that fuels a subsequent fire (Wink and Wright 1973; Rasmussen et al. 1986; Ansley and Rasmussen 2005). Another alternative is to burn under conditions when fire intensity is high enough to generate a crown fire, thus bypassing the need for herbaceous fuel links between juniper plants (Bryant et al. 1983). Research into the potential of summer season fires is currently underway at several locations. For the time being, however, this chapter focuses on the mechanical + fire treatment option.

A common mechanical treatment is chaining, in which trees are felled by an anchor chain pulled between crawler tractors (Fisher et al. 1973). Typically, chaining costs about \$30 to \$45 ha^{-1} (\$12–\$18 ac^{-1})(Johnson et al. 1999), but in dense stands of large junipers on rocky sites, chaining can be much more expensive because of greater resistance to pulling. Wiedemann and Cross (1996) determined that an elevated chaining technique could reduce pulling requirements of individual trees by 84% in redberry junipers and 67% in Ashe juniper while maintaining tree felling efficacy similar to that of ground-level chaining. The elevated chain, suspended 0.6 m above ground through the use of a rotating ball attached to the chain midway between the two tractors, will partly uproot juniper trees exposing the bud zone and potentially increase plant mortality by using fire to destroy the exposed bud zone. In theory, a ground level chain scrapes across the soil surface and has a greater chance of damaging herbaceous plants and soil crusts and increasing bare ground and the potential for soil erosion than does an elevated chain. In addition, the elevated chain is less likely to spread unwanted species such as prickly pear cactus (*Opuntia* spp.) than is a ground level chain. Thus, from a herbaceous restoration standpoint, an elevated chain may achieve the desired result on juniper yet have a less drastic effect on the herbaceous community and accelerate the restoration process over that of a ground level chain.

Many studies have observed vegetative responses of juniper to fire alone or chaining alone (Clary 1971; Tausch and Tueller 1977; Steuter and Britton 1983; Rippel et al. 1983; Barnitz et al. 1990), but few have quantified effects of combined mechanical + fire treatments on dense juniper stands over a long enough period to measure responses after each treatment. Recently, Johnson et al. (1999) determined in an economic modeling study that chaining followed by burning in 7-year intervals was an economical method of redberry juniper control in north Texas. Increased livestock production (cattle) in response to increased herbaceous production was used as the basis to calculate net present values of the investment in brush control treatments over a 30-year period. However, these projections were not based on quantified herbaceous responses to chaining + fire. Relatively few studies in the southern Great Plains have actually quantified ecosystem responses to mechanical treatment of juniper followed by a maintenance fire, and none of these monitored responses on the same site for more than 2 years (Wink and Wright 1973; Steuter and Wright 1983; Rasmussen and Wright 1989). Thus, there is a need for quantification of long-term effects of such combined treatments for juniper control.

A New Study: Combined Effects of Chaining and Fire

Scientists at the Texas Agricultural Experiment Station in Vernon, Texas, have recently completed a study to determine the potential of chaining followed by prescribed fire on restoration of a badly degraded site in north Texas dominated by redberry juniper (see Ansley et al. 2006). Specifically, the study quantified the effect of two types of chaining (ground-level and elevated), each followed by fire 4 years later, on juniper canopy reduction and mortality, herbaceous production by functional group (C_3 vs. C_4), herbaceous composition, bare ground, and litter cover. Another objective of the study, not documented here (see Wiedemann et al. 2006), was to quantify effects of these treatments on populations of the horse fly (*Tabanus abactor* Philip, also known as the “cedar fly”), a pest to livestock in juniper-dominated rangeland. The remainder of this chapter reports results from this study.

Study Area and Treatments

The study occurred on two sites in the Rolling Plains ecological region of northwest Texas (Johnson: 33°59’ N, 99°50’ W; Halsell: 33°50’ N, 99°48’ W). Soils at both sites were complexes of the Cottonwood (silt loam; thermic Lithic Ustorthents), Talpa (loam; thermic Lithic Calciustolls), and Knoco (clay loam; thermic shallow Aridic Ustorthents) soil series (NRCS office, Vernon, TX). Mean annual precipitation is 616mm, most occurring between April and October (NOAA 2003). Herbaceous vegetation at both ranch locations is dominated by C_4 (warm season) perennial grasses, including sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), little bluestem (Schizachyrium scoparium), tobosagrass (*Hilaria mutica* (Buckl.] Benth), buffalograss (*Buchloe dactyloides* (Nutt.] Engelm.), silver bluestem (*Bothroichloa laguroides* (DC.) Herter. spp. *torreyana* (Steud.), and red threeawn (*Aristida purpurea*). Also present is the C_3 (cool season) perennial Texas wintergrass (*Nassella leucotricha* Trin. and Rupr.). There are numerous forb species, but none occurs in great quantities.

The study had three treatments with four replicate plots per treatment. Plot size ranged from 12 to 17ha. Treatments were (1) untreated control, (2) ground level chaining followed by fire 4 years later (GLC + F), and (3) elevated chaining followed by fire 4 years later (EC + F). A dense stand of redberry juniper (>30% cover) occurred in each plot before treatments.

Chaining was conducted in March 1997 when adequate soil moisture was present. Two crawler tractors, pulled 54-m of 52-mm-diameter anchor chain (12.4kg/link or 58.4kg/m) for ground-level chaining. For the elevated chaining treatment, a spherical ball, 1.2m in diameter, was fabricated from 13-mm steel plate and attached midway in the chain. The chain was thus suspended between the ball and the two crawlers such that the average striking height of the chain was 0.6m above ground (for more details, see Wiedemann and Cross 1996).

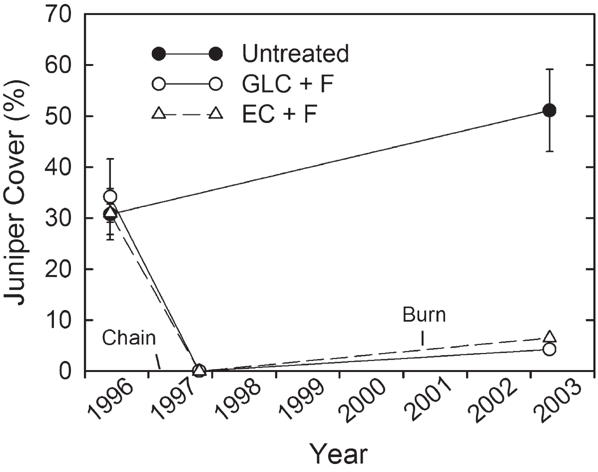

Figure 1 Redberry juniper canopy cover in response to the three treatments: *untreated*, *GLC + F*, standard chain + fire; *EC + F*, elevated chain + fire). *Vertical bars* are ±1 standard error (SE) (from Ansley et al. 2006)

Fires were applied as head fires in February and early March 2001, 4 years after the chaining treatments, following guidelines by White and Hanselka (1991). Plots were burned as individual units with a total of eight plots burned (four at each site). Fire intensity was moderate because droughts in 1998, 2000, and 2001 had the cumulative effect of lowering fuel moisture content and limiting fine fuel accumulation.

Timing of the fire treatment at 4 years after chaining mimicked a typical situation for such a combined treatment management scenario (Rasmussen and Wright 1989). It is usually too hazardous to burn downed juniper within the first 2 years of felling by chaining because of highly volatile fuels and the potential for fire brands to travel great distances.

Juniper Responses

Both chaining treatments reduced juniper canopy cover to less than 1% and juniper tree height from 2.8 m to less than 1.0 m. By 2003, 2 years after the fire treatments were imposed, juniper regrowth had increased canopy cover in the GLC + F and EC + F treatments to 4% and 6%, respectively, which were both significantly different from the control (see Figure 1). Juniper canopy cover increased in the untreated control from 30% to 51% (1996 to 2003).

Juniper mortality in 1997 at 8 months postchaining averaged 20% for both methods of chaining. However, by 2003, 6 years postchaining and 2 years after the fire treatment, mortalities were 8% and 4% in SC + F and EC + F treatments, respectively. We hypothesized that the fire treatment 4 years after chaining would increase juniper mortality over that of chaining alone by killing exposed meristem on trees that had been partly uprooted. Thus, the reduction in juniper mortality from 1997 to 2003 was unexpected. Some uprooted stumps that were counted as dead in 1997 may have sprouted between 1997 and 2003, thus lowering the mortality percentage. In addition, herbaceous fuel remained patchy at the time of burning, and an even flame front was not achieved. Areas that were initially dense, closed-canopy patches of juniper likely did not have sufficient growth of herbaceous fuel between 1997 and 2001 for fire to have an effect on the chained junipers.

The low juniper mortality rates contributed to the observation of no net change in juniper densities during the course of the study. Although the chaining + fire treatments did not reduce juniper density, they did reduce tree height and canopy cover such that the competitive effect of juniper was greatly reduced.

Precipitation

Annual precipitation was above the long-term average in 4 years (1997, 1999, 2000, and 2002) (Figure 2). Drought conditions prevailed in 1996, 1998, 2001, and 2003. Droughts in 1998 and 2001 were especially severe with very little precipitation occurring during the growing season. Precipitation patterns were similar between the Halsell and Johnson sites.

Herbaceous Standing Crop

End-of-growing-season grass standing crop ranged from 20 to 120 g m^{-2} throughout the study (see Figure 2). Pretreatment standing crop, collected in April 1996, was near 70 g m^{-2} in all treatments. In the year following chaining treatments, standing crop decreased to a greater degree relative to pretreatment levels in the standard chain treatment than in the other treatments, probably because of the scraping effects of standard chaining on the soil surface. The 1998 drought reduced grass standing crop in all three treatments, but the decline was most severe in the control.

Grass standing crop did not increase in treated plots over the control until 1999, four growing seasons after chaining. At this point, standing crop in both chaining treatments was similar and about twice that of the control. These differences between treatments continued into the next year, although standing crop in the ground level chain treatment was slightly greater than in the elevated treatment. Both remained significantly greater than the control.

After fire treatments were imposed in early 2001, grass standing crop declined in both chain + fire treatments. Standing crop also declined in the control treatment, probably because of the drought in this year. Thus, standing crop reductions in the chain + fire treatments may have been caused by the combined effects of fire followed by drought. However, because the rate of decline was similar in all three

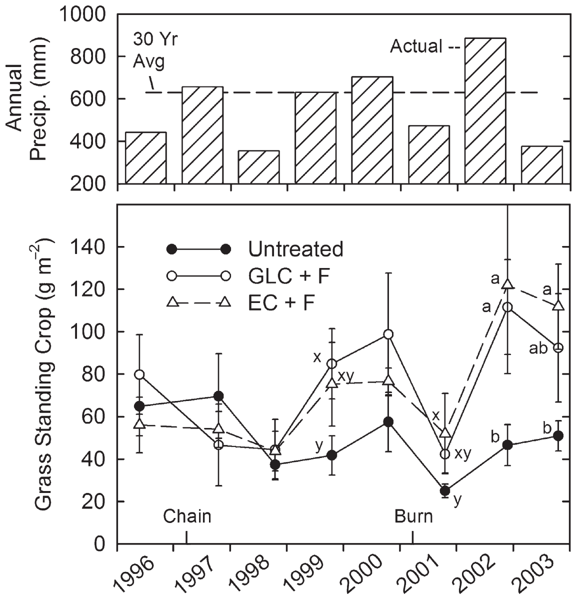

Figure 2 Annual precipitation and 30-year mean annual precipitation at the site (*top*) and end-of-growing-season grass standing crop (live + dead) in response to the three treatments (*bottom*). Treatment codes: *GLC + F*, standard chain + fire; *EC + F*, elevated chain + fire. *Letters within a sample date* that are different indicate a significant difference at $P > 0.05$; any sample dates without letters indicates no significant differences among treatments (from Ansley et al. 2006)

treatments, we may assume that drought was more responsible than fire in explaining the reduction in grass standing crop in the treated plots.

Grass standing crop in treated plots increased to two to three times that in the untreated control the second and third year after fire. A peak standing crop of 110–120 g m^{-2} occurred in 2002, an above-normal precipitation year. There was no difference in standing crop between standard and elevated chaining treatments after 2000. In the control, grass standing crop declined gradually over the course of the study but declined most notably in the drought years of 1998 and 2001.

End-of-season standing crop of all perennial grass functional groups (C_3 perennial grasses, C_4 midgrasses, C_4 shortgrasses) indicated a general trend toward decreasing in the control and either increasing or remaining unchanged in the treated plots, but there were no statistically significant differences (data not shown). Significant differences in standing crop between treatments were only found when these functional groups were treated collectively.

A positive linear relationship occurred between annual precipitation and end-of-growing-season grass standing crop during posttreatment years of 1998–2002 (Figure 3). The slope of the relationship was much steeper in treated plots that had less than 5% *Juniperus* cover than in the untreated control, which had 40% to 50% *Juniperus* cover during this time period.

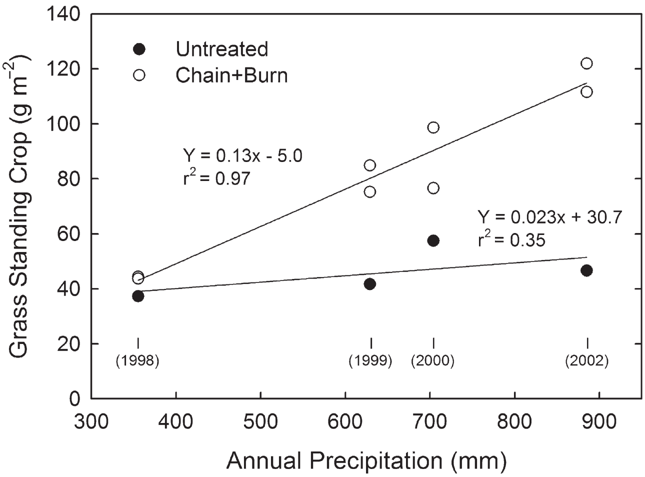

Figure 3 Regression between annual precipitation and end-of-growing season grass standing crop in treated (*open circles*) and untreated (*closed circles*) rangeland from 1998–2002. Each *point* represents the mean of a treatment. Data from the SC + F and EC + F treatments were grouped into the "chain + fire" treatment. Juniper cover was 40%–50% in the control plots and >5% in the treated plots (from Ansley et al. 2006)

End-of-growing-season forb standing crop was low in all treatments throughout the study, ranging from 0.4 to 14 g m^{-2} (data not shown). Forb standing crop was similar among all three treatments except in 1999, 2002, and 2003 when it was greater in the treated plots than the control. The fire treatment in 2001 appeared to increase forb standing crop.

Few studies in the region have quantified long-term herbaceous production following the combined treatments of chaining and burning of juniper woodlands. Wink and Wright (1973), in a study in which juniper was dozed in 1965 and burned in 1970, found that grass production was 131 g m^{-2} in untreated controls and 185 g m^{-2} in dozed + burned plots the first growing season post fire. Grass data were collected only in that year. Steuter and Wright (1983), in a study where juniper was chained in 1974 or 1975 and burned in 1979, found first-year postfire grass production was 61 g m^{-2} in untreated plots and 75 g m^{-2} in chained + fire plots. Again, only first-year postburn data were collected. In our study, increases in grass biomass did not occur until the second growing season post fire and these were more than twice that in the control. We know of no studies that have quantified grass responses under a combined treatment scenario for as many years as the current study.

Herbaceous Cover Responses

Total grass cover was lower in treated plots relative to the control immediately after chaining, but this difference disappeared by 1998 (Figure 4). Total grass cover did

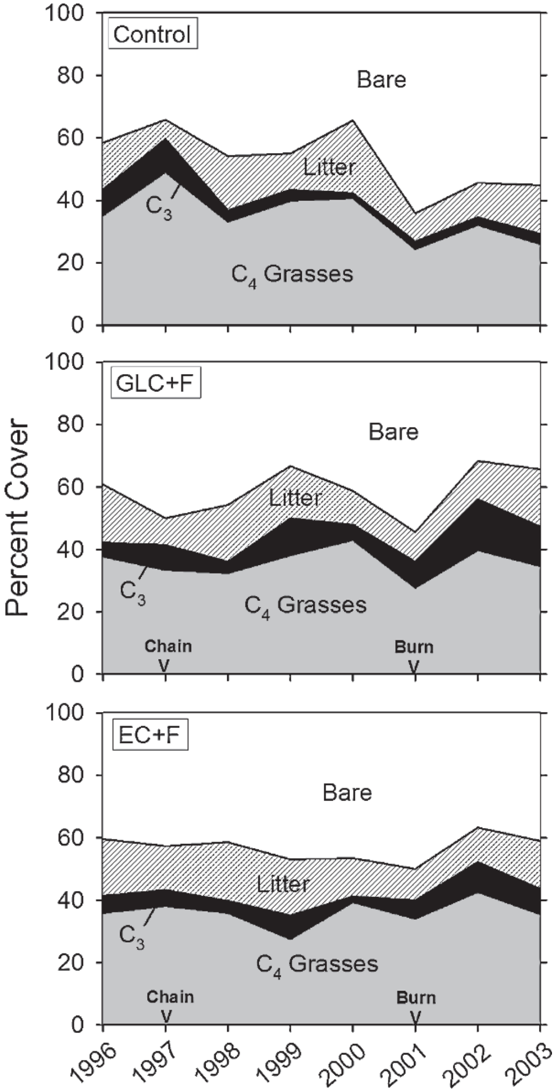

Figure 4 Total grass foliar (C_3 and C_4) cover and percent bare ground in response to chaining and fire treatments. Treatment codes: *GLC* + *F*, standard chain + fire; *EC* + *F*, elevated chain + fire

not increase in treated plots over the control until after the fire treatment. This response differs from that found with grass standing crop, which was greater in chained treatments than the control for 2 years before burning. These results suggest that increases in grass standing crop from chaining alone (in 1999 and 2000) were caused by increased growth of existing grass patches. The fire treatment may have stimulated recruitment of grass species into bare soil areas and, as such, postfire increases in grass standing crop in 2002 and 2003 were probably a combination of increased growth in existing grass patches plus increased recruitment into bare soil areas. Above-normal precipitation in 2002 also may have contributed to the accelerated growth and/or recruitment into bare soil areas.

Bare ground was near 40% in all treatments at study initiation and did not change much between treatments over the course of the study until the severe drought in 2001 (see Figure 4). At this time, bare ground in the control plots increased from 35% to 65% and remained above 55% in 2002–2003. In the treated plots, bare ground remained fairly constant from 1996 to 2001, with a slight but not significant increase from fall 2000 to fall 2001 in response to the spring 2001 fire. In the second and third growing seasons following fire (2002 and 2003), bare ground in both the GLC + F and EC + F treatments decreased from about 50% to between 30% and 40%. Thus, although 4 years of drought during an 8-year period ultimately increased bare ground in juniper woodlands, percent bare ground remained unchanged or slightly decreased in the chaining + fire treatments. We expected bare ground area to significantly decrease in the treated plots over 8 years, but in a community largely dominated by C_4 bunchgrasses, any reduction in bare ground would need to come from recruitment of new plants via seed. The droughts may have prevented this from happening.

Forb cover remained less than 4% in all treatments (data not shown). Forb cover showed a trend of being greater in treated plots than the control, especially after the fire treatments, but these differences were not significant.

Herbaceous Composition

Changes in cover of all herbaceous functional groups during the period of the study are shown in Figure 4. The immediate impression from this figure is that treatments did not alter composition at the functional group level much beyond that which was found in the untreated control. However, some subtle differences were apparent. C_4 grasses slightly declined in the control while they remained unchanged or slightly increased in the treated plots. The C_3 grasses and forbs, shown collectively in Figure 4, increased slightly in the treated plots and slightly decreased in the control. As mentioned before, bare ground increased in the control, while it remained unchanged or was slightly decreased in treated plots. Litter cover was similar in all treatments, remaining about 10% to 20% of the total cover. These responses, when viewed collectively, suggest that the treated sites were moving toward a greater herbaceous domination. Total herbaceous cover increased to nearly 50% in treated plots compared to 30% in the control by study's end.

There were no clear differences in species composition responses between the GLC + F and EC + F treatments during the study, with the possible exception that, for reasons unknown, responses were less variable from year to year in the EC + F treatments than in the GLC + F treatment. This observation may relate to the greater degree of soil disturbance that was assumed (not quantified) to occur as a result of ground-level chaining in the GLC + F treatment, but the mechanism as to how this caused greater variability in composition from year to year is unknown.

Postfire succession models developed in the Intermountain region by Barney and Frischknecht (1974), Everett and Ward (1984), and West and van Pelt (1987) portray a progression from annuals to perennial grasses to grass/shrub mix to juniper dominance over time. In these models, annual forbs increase rapidly in the immediate postfire years (Koniak 1985). Juniper encroachment gradually gains over time and, as juniper begins to dominate, herbaceous species diversity and perennial grass production decline. In the case of a resprouting species such as redberry juniper, a postfire increase to the point of dominance would be expected to occur much earlier (perhaps within 20 years) than that expected with juniper species that depend on seedling recruitment.

Results from the current study do not lend support to these models, however, as we did not find a strong shift toward forbs in the first few years post fire. Although there was a slight increase in C_3 grasses and forbs in the burned plots in 2002 and 2003, 2 and 3 years after the fire, species composition remained dominated by C_4 grasses and bare ground. It should be noted that, because we monitored postfire responses for only 3 years, we have no basis to compare our study with the projected intermediate succession stages in the Barney and Frischknecht (1974) model.

Ecological and Management Implications

Combined treatments of mechanical chaining followed by repeated fires will likely accelerate the restoration process of juniper-dominated rangelands (Ansley and Rasmussen 2005). In Ashe juniper communities, a single mechanical treatment allowed juniper to significantly recover within 15 years, whereas the same treatment followed by fire 5 years later minimized juniper recovery. Prescribed fire altered the successional pattern to a more diverse shrub and herbaceous community (Rasmussen and Wright 1989).

Figure 5 illustrates hypothetical long-term ecological responses to three management scenarios applied to a mature juniper stand: using mechanical treatments alone, prescribed fire alone, or an initial mechanical treatment followed by repeated fire treatments. If a mechanical treatment such as chaining was used alone, it probably would not be applied more frequently than every 40 years due to prohibitive costs. Such a treatment scenario probably would not keep pace with the overall deleterious effects of increasing juniper encroachment. Both peak perennial grass production as well as juniper production would likely gradually decline over time due to soil loss during the periods of juniper domination (Figure 5). Fire, because of lower cost, could be applied more frequently than mechanical treatments, shown in Fig. 5 at every 20 years, but would not be as effective initially as a mechanical on reducing mature juniper cover and density. After several burns, fire may gradually reduce the peak to

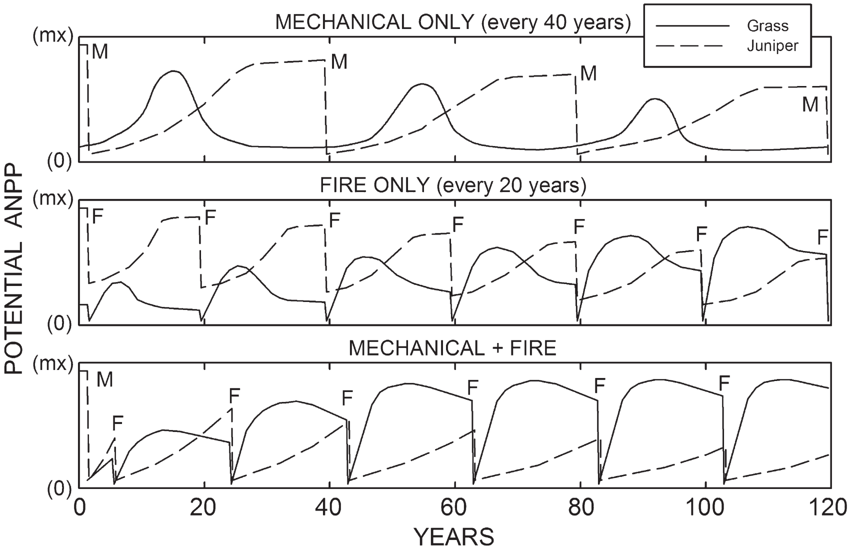

Figure 5 Potential ANPP (annual net primary productivity) of grass (*solid line*) and juniper (*dashed line)* over 120 years in each of the three treatments: mechanical (*M*) only, fire (*F*) only, and mechanical + fire (*mx*, maximum) (from Ansley and Rasmussen 2005)

which juniper production could recover. Moreover, assuming a constant precipitation pattern, repeated fires would likely gradually increase both peak production and duration high production of grasses, but it might take a century and 6 or 7 fires to ultimately shift the balance to grass dominance. In contrast, if an initial high-cost mechanical treatment were followed with fire 4–5 years after mechanical and then at 20 year intervals, juniper dominance might be avoided indefinitely and perennial grass production would more rapidly increase to a sustained maximuim. These scenarios are all based on the assumption that high cost seeding is not part of the treatment plan.

Data from Ansley et al. (2006) suggest that complete restoration of juniper-dominated regions, even under a combined treatment scenario, may not occur rapidly on badly degraded sites; hence we show in the bottom panel of Figure 5 a slow herbaceous recovery in the first 20 years. Condition of the resource before treatment and weather conditions following treatment are key variables in determining rates of restoration (Everett and Ward 1984; Tausch and Tueller 1977).

Although grass biomass and cover increases in the treated plots were not as great as hypothesized, one revealing element of this study was the observation of the progressive impacts of juniper domination on the herbaceous community. During the droughts of 1998 and 2001, herbaceous production declined sharply. Coupled with this, the herbaceous community was not able to make significant gains during wet years, as responses in the control in 1997, 1999, and especially 2002, revealed. A long-term pattern of herbaceous species losing ground in drought years and failing to recover in wet years suggests a trend toward degradation. These responses imply that a “do-nothing” custodial management of juniper-dominated rangelands in the southern prairie may not be an acceptable option.

Summary

Juniper (*Juniperus* spp.) encroachment in grasslands usually progresses toward a woodland “steady state” of mature trees that requires a significant disturbance to shift succession in another direction. Fire alone is often inadequate and must be preceded by a mechanical treatment such as chaining to reduce juniper competition and increase herbaceous growth that fuels a subsequent fire. The objective of this study was to quantify the potential of chaining followed by fire on restoration of a badly degraded site in north Texas dominated by redberry juniper (*J. pinchotii*). Chaining was conducted in 1997 and fires were applied in March 2001. Treated areas (chaining + fire) were compared to untreated controls (four plots per treatment). Livestock grazing was excluded. Juniper cover was reduced to less than 5%, but mortality was less than 15% as most plants basal sprouted. Herbaceous production did not increase in treated plots over the control until 3 years after chaining. Production declined in all treatments the first growing season following fire but increased in treated plots to three times the control the second and third year after fire. Total grass cover in treated plots did not increase over the control until the second year after fire treatment. Results suggest herbaceous production increases from chaining alone were caused by increased growth of existing vegetation patches. The fire treatment appeared to stimulate herbaceous recruitment into bare soil areas.

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References

Ansley, R.J., Pinchak, W.E., and Ueckert, D.N. 1995. Changes in redberry juniper distribution in northwest Texas. Rangelands 17:49–53.

Ansley, R.J., Pinchak, W.E., Teague, W.R., Kramp, B.A., and Jones, D.L. 2004. Long-term grass yields following chemical control of honey mesquite. J. Range. Manag. 57:49–57.

Ansley, R.J., and Rasmussen, G.A. 2005. Managing native invasive juniper species using fire. Weed Technology 19:517–522.

Ansley, R.J., Wiedemann, H.T., Castellano, M.J., and Slosser, J.E. 2006. Herbaceous restoration of juniper dominated grasslands with chaining and fire. Rangeland Ecol. Manag. 59:171–178.

Archer, S. 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. J. Biogeogr. 17:453–462.

Archer, S., Schemil, D.S., and Holland, E.A. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2? Clim. Change 29:91–99.

Arnold, J.F. 1964. Zonation of understory vegetation around a juniper tree. J. Range. Manag. 17:41–42.

Barnitz, J.A., Jr., Armentrout, S.M., Howard, V.W., Jr., Pieper, R.D., and Southward, G.M. 1990. Vegetational changes following two-way cabling of pinyon-juniper in south-central New Mexico. N. M. Agric. Exp. Stat. Bull. 749:1–36.

Barney, M.A., and Frischknecht, N.C. 1974. Vegetation changes following fire in the pinyon-juniper type of west-cental Utah. J. Range. Manag. 27:91–96.

Belsky, A.J. 1996. Viewpoint: western juniper expansion: is it a threat to arid northwestern ecosystems? J. Range. Manag. 49:53–59.

Bragg, T.B., and Hulbert, L.C. 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range. Manag. 29:19–24.

Bryant, F.C., Launchbaugh, G.K., and Koerth, B.H. 1983. Controlling mature ashe juniper in Texas with crown fires. J. Range. Manag. 36:165–168.

Burkhardt, J.W., and Tisdale, E.W. 1976. Causes of juniper invasion in southwestern Idaho. Ecology 57:472–484.

Clary, W.P. 1971. Effects of Utah juniper removal on herbage yields from Springerville soils. J. Range. Manag. 24:373–378.

Clary, W.P. 1987. Herbage production and livestock grazing on pinyon-juniper woodlands. In: Proceedings of the pinyon-juniper conference, ed. R.L. Everett, pp 440–447. General technical report INT-215. Ogden, UT: United States Forest Service.

Dalrymple, R.L. 1969. Cedar control in southern Oklahoma. Proc. Soc. Weed Sci. Soc. 22:272–273.

Davenport, D.W., Breshears, D.D., Wilcox, B.P., and Allen, C.D. 1998. Viewpoint: sustainability of pinon-juniper ecosystems—a unifying perspective of soil erosion thresholds. J. Range. Manag. 51:231–240.

Dye, K.L., Ueckert, D.N., and Whisenant, S.G. 1995. Redberry juniper-herbaceous understory interactions. J. Range. Manag. 48:100–107.

Engle, D.M., Stritzke, J.F., and Claypool, P.L. 1987. Herbage standing crop around eastern redcedar trees. J. Range. Manag. 40:237–239.

Everett, R.L., and Ward, K. 1984. Early plant succession on pinyon-juniper controlled burns. Northwest Sci. 58:57–68.

Fisher, C.E., Wiedemann, H.T., Meadors, C.H., and Brock, J.H. 1973. Mechanical control of mesquite. Tex. Agric. Exp. Sta. Res. Mon. 1:46–52.

Frost, C.C. 1998. Presettlement fire frequency regimes of the United States: a first approximation. Tall Timb. Fire Ecol. Conf. 20:70–81.

Gehring, J.L., and Bragg, T.B. 1992. Changes in prairie vegetation under eastern red cedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie. Am. Midl. Nat. 128:209–217.

Jameson, D.A. 1967. The relationship of tree overstory and herbaceous understory vegetation. J. Range. Manag. 20:247–249.

Johnson, P., Gerbolini, A., Ethridge, D., Britton, C., and Ueckert, D. 1999. Economics of redberry juniper control in the Texas Rolling Plains. J. Range. Manag. 52:569–574.

Johnson, T.N. 1962. One-seed juniper invasion of northern Arizona grasslands. Ecol. Monogr. 32:187–207.

Koniak, S. 1985. Succession in pinyon-juniper woodlands following wildfire in the Great Basin. Great Basin Nat. 45:556–566.

Martin, S.C., and Crosby, J.S. 1955. Burning on a glade range in Missouri. Technical paper 147. Forest Service Central States Forest Experiment Station: United States Department of Agriculture.

McNeill, A. 2000. Burn baby burn. The Cattleman Magazine, February, pp 56–64.

McPherson, G.R., and Wright, H.A. 1989. Direct effects of competition on individual juniper plants: a field study. J. Appl. Ecol. 26:979–988.

McPherson, G.R., and Wright, H.A. 1990. Effects of cattle grazing and *Juniperus pinchotii* canopy cover on herb cover and production in western Texas. Am. Midl. Nat. 123:144–151.

Miller, R.F., and Tausch, R.J. 2001. The role of fire in juniper and pinyon woodlands: a descriptive analysis. In: Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species, eds. K.E.M. Galley and T.P. Wilson, pp 15–30. Miscellaneous publication 11. Tallahassee, FL: Tall Timbers Research Station.

Miller, R.F., Svejcar, T.J., and Rose, J.A. 2000. Impacts of western juniper on plant community composition and structure. J. Range. Manag. 53:574–585.

NOAA. 1996–2003. Climatological data: north Texas stations. Rocket Center, WV: National Oceanic and Atmospheric Administration.

Owensby, C.E., Blan, K.R., Eaton, B.J., and Russ, O.G. 1973. Evaluation of eastern redcedar infestations in the northern Kansas Flint Hills. J. Range. Manag. 26:256–260.

Rasmussen, G.A., and Wright, H.A. 1989. Succession of secondary shrubs on Ashe juniper communities after dozing and prescribed burning. J. Range. Manag. 42:295–298.

Rasmussen, G.A., McPherson, G.R., and Wright, H.A. 1986. Prescribed burning juniper communities in Texas. Range and wildlife management note 10. Lubbock, TX: Texas Technical University.

Rippel, P., Pieper, R.D., and Lymbery, G.A. 1983. Vegetational evaluation of pinyon-juniper cabling in south-central New Mexico. J. Range. Manag. 36:13–15.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., and Whitford, W.G. 1990. Biological feedbacks in global desertification. Science 247:1043–1048.

Smith, M.A., Wright, H.A., and Schuster, J.L. 1975. Reproductive characteristics of redberry juniper. J. Range. Manag. 28:126–128.

Snook, E.C. 1985. Distribution of eastern redcedar on Oklahoma rangelands. In: Proceedings of eastern redcedar in Oklahoma conference, eds. R.F. Wittner and D.M. Engle, pp 45–52. Publication E-849. Stillwater, OK: Cooperative Extension Service, Oklahoma State University.

Soil Conservation Service (SCS). 1983. Oklahoma resource inventory. Stillwater, OK: United States Department of Agriculture.

Soil Conservation Service (SCS). 1988. Texas brush inventory. Temple, TX: United States Department of Agriculture.

Steuter, A.A., and Britton, C.M. 1983. Fire induced mortality of redberry juniper (*Juniperus pinchotii* Sudw.). J. Range. Manag. 36:343–345.

Steuter, A.A., and Wright, H.A. 1983. Spring burning effects on redberry juniper-mixed grass habitats. J. Range. Manag. 36:161–164.

Tausch, R.J., and Tueller, P.T. 1977. Plant succession following chaining of pinyon-juniper woodlands in eastern Nevada. J. Range. Manag. 30:44–49.

Tausch, R.J., West, N.E., and Nabi, A.A. 1981. Tree age and dominance patterns in Great Basin pinyon-juniper woodlands. J. Range. Manag. 34:259–264.

Tausch, R.J., Wigand, P.E., and Burkhardt, J.W. 1993. Viewpoint: plant community thresholds, multiple steady states, and multiple successional pathways: legacy of the Quaternary. J. Range. Manag. 46:439–447.

Ueckert, D.N., Phillips, R.A., Petersen, J.L., Wu, X.B., and Waldron, D.F. 2001. Redberry juniper canopy cover dynamics on western Texas rangelands. J. Range. Manag. 54:603–610.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–215.

West, N.E., and van Pelt, N.S. 1987. Successional patterns in pinyon-juniper woodlands. In: Proceedings of the pinyon-juniper conference, ed. R.L. Everett, pp 43–52. General technical report INT-215. Ogden, UT: United States Forest Service.

White, L.D., and Hanselka, C.W. 1991. Prescribed range burning in Texas. Bulletin B-1310. College Station, TX: Texas Agricultural Extension Service.

Wiedemann, H.T., and Cross, B.T. 1996. Draft requirements to fell junipers. J. Range. Manag. 49:174–178.

Wiedemann, H.T., Slosser, J.E., and Ansley, R.J. 2006. *Tabanus abactor* Philip responses to chaining and burning redberry juniper stands. Southwest. Entomol. 30:203–214.

Wink, R.L., and Wright, H.A. 1973. Effects of fire on an Ashe juniper community. J. Range. Manag. 26:326–329.

Wright, H.A., and Bailey, A.W. 1982. Fire ecology: United States and Southern Canada. New York: Wiley.

Section 4

The Future

16

Conclusions: Present Understanding and Future Research in *Juniperus* Communities

O.W. Van Auken

> Prediction is very difficult, especially about the future. … Niels Bohr (Danish physicist, 1885–1962)

With the foregoing quote in mind, I will proceed. It seems clear after examining what has been presented here and in many other places in the published literature that understanding *Juniperus* savanna and woodland biomes is a difficult task. Managing these is even more difficult. Because many of these *Juniperus* savannas and woodlands were probably grasslands at some time in the past, we should add grasslands to the mix of what is required to understand *Juniperus* communities. Thus, the task is complicated, but it is even more difficult when we add time as a factor that further complicates the equation.

It seems clear that grasslands and *Juniperus* savanna and woodland communities will not remain the same as they are unless they are burned at certain intervals. Fire intensity and frequency are factors of paramount importance to understanding the functioning of these communities. The intensity and fire interval depend on a number of factors including grazing intensity, precipitation, temperature, soil depth, and probably others. If grasslands are not burned, woody species such as the various *Juniperus* species and other species will encroach into the grasslands and the grassland communities will become savannas. If savannas are not burned, encroachment of woody species will continue and the savanna communities will become woodlands.

What happens if the woodlands are not burned? This is unclear. In more mesic areas, succession continues and the woodland will be replaced in time with other species that may be more tolerant to shaded understory conditions or possibly other undefined conditions. This woodland successional sequence has been shown to occur in eastern North America, and a similar sequence probably occurs in northwestern North America as well. However, in the grasslands, savannas, and woodlands of the Great Plains of central North America and in arid and semiarid biomes in western North America, the picture or outcome is not as clear. Will other drought-tolerant and or shade-tolerant species replace the various *Juniperus* species in these habitats? This question is unanswered at this time. What are the potential replacement species? They are also unidentified at this time.

O.W. Van Auken (ed.), *Western North American Juniperus Communities:
A Dynamic Vegetation Type.*

Could the succession be cyclic? If the woodlands are burned, would these communities revert to open grasslands or savannas? This question too is unanswered. What is the timeline of these changes? Also largely undefined at present, this is dependent on local conditions that modify the rate of change.

Would the removal of grazing animals prevent the encroachment of various *Juniperus* species and other species into the arid and semiarid communities of western and southwestern North America? The answer seems to be no: removal of the herbivores would not prevent woody plant encroachment. Heavy and continuous cattle grazing would speed up the encroachment process and lower levels of grazing would slow the process down. The presence and competition of the various species of C_3 and C_4 grasses with the woody species would not prevent encroachment. The grasses would slow down the woody plant encroachment process but not prevent it from occurring. The dead grass biomass is important as fuel for fires that move through these areas. Without the dead grass mass, there would be no fuel for the fires. If there is enough fuel, and the fires are at a high enough temperature and frequency, the fires would prevent *Juniperus* and other woody plant encroachment into these communities. Seasonality of the fires is also important, and effects of summer fires on woody plant encroachment need to be examined more carefully.

This is not the end of the story: it is much more complicated. The atmosphere of the Earth is changing because of natural and anthropogenic factors. Atmospheric carbon dioxide levels are increasing at rates modified by human activities. The elevated levels of CO_2 in the atmosphere have exacerbated the greenhouse effect, causing a measurable increase in the mean annual temperature of the Earth. These higher levels of CO_2 in the atmosphere will stimulate plant photosynthetic activity and may increase annual net primary production, providing another required nutrient or factor is not limiting to the plants. Increased temperatures will also probably increase photosynthetic rates and should promote the spread of more-temperate or tropical species with a concomitant contraction of the ranges of more cold-tolerant species.

What does this mean for the distribution of the *Juniperus* savannas and woodlands of western and southwestern North America and to other plant communities and species throughout the world? Effects are hard to see over the short term because of the age or potential age of the woody plants and communities involved. In addition, there are no controls, and humans were not here the last time changes such as these occurred. Elevated temperatures at the surface of the Earth suggest that temperate species will migrate farther north and to higher elevations in the mountains. More cold-adapted or cold-tolerant species that are already present in the more northern regions and higher elevations will be displaced. They in turn will move further north and up until they cannot move further and, unfortunately, they will probably be extirpated.

The previous suggestions are relatively long-term changes. What about short-term changes? Some of the expected changes in water and nitrogen and other nutrient cycling have been investigated and are reported here. However, longer-term effects are speculative at this time. Additional studies are needed to clarify the longer-term effects of modifications in water use and storage. These changes will no doubt cause modifications in the overall water cycle as well; the same is true for carbon and nitrogen storage, use, and metabolism. As the use and cycling of these resources change, the plant and animal species in the *Juniperus* savanna and woodland communities will also change. These physical and chemical changes will also cause changes in the vertebrate, invertebrate, plant, bacteria, and fungi populations and diversity, changes that will be beneficial to some and detrimental to others.

Evaluation of gas-exchange rates for the various *Juniperus* species present in these communities should be expanded. Other woody species present in these communities should also be examined, especially understory species and incidental or low-density species. Carbon uptake of these species should be examined at various soil moisture levels, light levels, and elevated CO_2, nitrogen, and temperature levels. Potential *Juniperus* replacement species from dry, southern environments should be examined and evaluated as well.

The importance of soil organisms and soil processes should not be ignored. Changes in soil microbial communities will undoubtedly occur as atmospheric conditions including CO_2 and temperature levels change. Additional atmospheric inputs will change as well, including nitrogen type and amount and probably other airborne chemicals. All these factors taken together may modify the soil biotic communities and alter soil biotic and abiotic reactions. How these potential changes will alter surface plant and animal communities is unknown.

Global and regional long-term climate changes are expected, but there is still considerable uncertainty associated with predictions. Increases in extreme events may be important in the future, but the frequency and intensity of the events are uncertain. Changes in water movement and flow seem a certainty, but directions and amounts of these changes, and the effects of altered climate, are further unknowns. The same is true for the other abiotic components present in this system. Certainly as the abiotic components change, the biotic components will follow and change as well.

The future of these *Juniperus* communities is difficult to predict. It seems certain that they will change and that they will be different in the world of the future. The communities are dynamic and important biologically, ecologically, and economically. The knowledge gained from past work and what has been presented in this volume is very important and is the foundation for future work and future understanding of these communities. Predicting the future of these communities is an exciting and important adventure: I think we are on the right tract.

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