Holocene Changes in Semiarid Pinyon-Juniper Woodlands

Response to climate, fire, and human activities in the US Great Basin

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With the prospect of global warming, it is interesting to look back at past climate change and its effects on vegetation. Although the greatest change in climate probably occurred during deglaciation, 12,500 to 11,000 years ago, significant climate changes have occurred more recently in the intermountain region of the western United States, the vast area in the West lying between the Sierra Nevadas and Cascades and the Rocky Mountains (Antevs 1938, Davis 1982, Mehringer and Wigand 1990). Climate changes during this period caused major shifts in plant distribution and composition throughout the region. However, rates of vegetation change during the past 120 years, primarily due to anthropogenic factors, have been unprecedented in the intermountain region (Miller et al. 1994).

One of the most pronounced vegetational changes in recent time occurred in the juniper and pinyon-juniper woodlands, a major vegetation type characterizing the intermountain region (Figure 1). These woodlands currently occupy 17 million ha in the intermountain region and 24 million ha in the western United States (West 1984). Juniper species common in the intermountain region are western juniper (*Juniperus occidentalis*), Utah juniper (*Juniperus osteosperma*), single-seeded juniper (*Juniperus monosperma*), alligator juniper (*Juniperus deppeana*), redberry juniper (*Juniperus eythrocarpa*), and rocky mountain juniper (*Juniperus scopulorum*) (Figure 2). Except for western juniper, these species are commonly associated with pinyon pine.

Controversy has developed over past and present juniper restoration projects

Since settlement, juniper woodlands have significantly increased both in density and distribution throughout the West and are still expanding into adjacent shrub steppe communities, grasslands, aspen groves, and riparian communities. However, evidence strongly suggests that juniper woodlands in the West increased and decreased during prehistoric times. In this article, we look at the prehistoric and historic expansions of juniper, with an emphasis on western juniper, and the environmental conditions in which these expansions occurred. We also briefly describe possible impacts of currently expanding woodlands on the landscape.

Prehistoric expansion of juniper

During the Holocene, the last 12,000 years, climate has fluctuated with periods of cooler/wetter, cooler/drier, warmer/drier, and warmer/wetter weather patterns than those of the present (Antevs 1938, Davis 1982). There is also evidence that season of maximal precipitation has varied across the intermountain sagebrush region (Davis 1982, Wigand and Nowak 1992). Within the intermountain west, fluctuations in lake levels and salinity, glacial advances and retreats, regionally correlated tree-ring widths, and changing animal assemblages provide proxy data for these climatic changes (Grayson 1993).

In addition, changes in plant community composition inferred from pollen data and plant macrofossils recovered from ancient packrat middens; dry caves; sediments from lake, fen, and marsh; and Native American archaeological sites have been used as evidence indicating climatic variation. Changes in the relative abundance of plant species have been used to document climatic variations over the span of hundreds and thousands of years. Pollen productivity has been used to document changes on scales of less than five years (Mehringer and Wigand 1990).

The paleobotanical record provided by fossil pollen and plant

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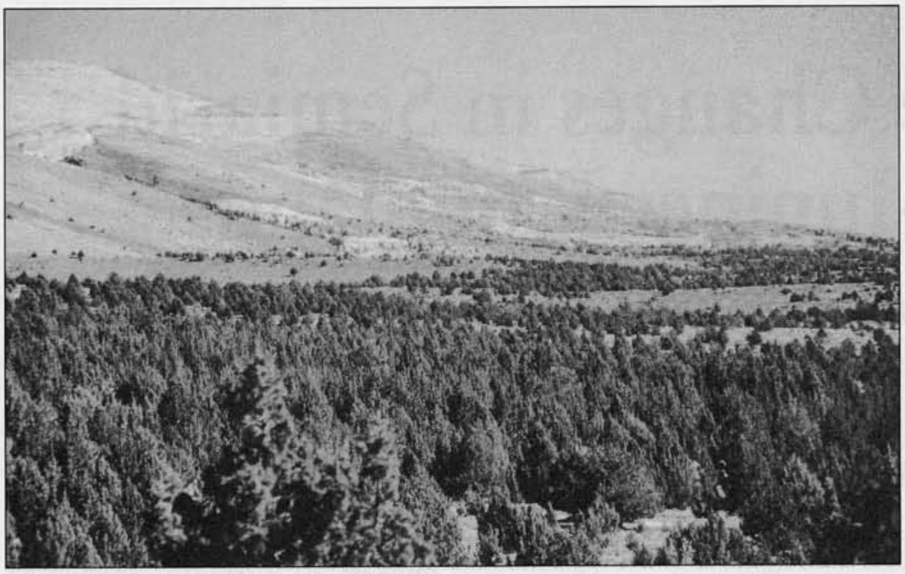

Figure 1. Western juniper woodland on Steens Mountain, southeastern Oregon. Succession towards a juniper woodland from a shrub steppe plant community began in the mid-1880s.

macrofossils from lake sediments and ancient packrat middens provides the basis for reconstruction of past juniper distributions. Pollen data provide the framework for reconstructing the regional abundance of juniper on the landscape. The direction and rates of change in pollen abundance and packrat midden data provide the evidence needed to corroborate species identification and the limits to which this expansion occurred.

Prostrate juniper (*Juniperus horizontalis*) and common juniper (*Juniperus communis*) were growing in southeastern Oregon during portions of the late Pleistocene (Wells 1983). Packrat middens suggest the more drought-tolerant juniper species, which comprise the semiarid woodlands of today in the intermountain west, were distributed 500 to 640 km farther south, and 1000 to 1500 meters lower in elevation, during peak glaciation than their current range (Thompson 1990, Wells 1983, Wigand and Nowak 1992). Utah juniper or occasionally pinyon-juniper woodlands (having single-needle pine, *Pinus monophylla*) occupied the Mojave Desert of southern California and southern Nevada, the southern Sierra Nevada Mountains, the south central valley of California (Thompson 1990), and arid regions of the Sonoran Desert in Arizona. In most of western Utah and in Nevada as far north as the present location of Reno, juniper woodlands were also dominated by Utah juniper, but locally they may have included admixtures of Rocky Mountain and California juniper (*Juniperus californica*) (Wigand and Nowak 1992).

Other packrat midden data indicate western juniper (probably the southern variety, var. *australis*) was growing in Kings Canyon, California, during maximal glaciation (Thompson 1990). Western juniper (probably the northern variety, var. *occidentalis*) also appears in the fossil midden record on the east shore of Lake Lahontan in Nevada approximately 12,000 years ago (the more mesic side receiving the benefit of lake effect) (Thompson et al. 1986). At the same time Utah juniper characterized the woodlands of the western shores, which are drier due to the rain shadow (Wigand and Nowak 1992).

The earliest evidence of western juniper reported within its historic range of northeastern California and eastern Oregon occurs between 4000 and 7000 years ago. This range is indicated from charcoal sediments immediately beneath Mazama ash in Fort Rock Cave, Oregon, 6700 years ago (Bedwell 1973), seeds and twiglets from ancient woodrat middens at Lava Beds, California, 5400 years ago, and Diamond Craters, Oregon, 4000 years ago (Mehringer and Wigand 1987). Evidence from pollen records indicates that western juniper (based upon inference from the packrat midden record) has been in the area at least since the middle Holocene; it may have arrived during the early Holocene (Mehringer and Wigand 1987). Since its arrival in the northwestern Great Basin, western juniper numbers and distribution have fluctuated greatly.

Prior to western juniper's first clearly evidenced appearance in the paleoenvironmental record of the northwestern portion of the Great Basin, climate was much drier and warmer than at present. This period, traditionally termed the Hypsithermal or Altithermal (meaning warmer and/or drier) interval has been assigned various time spans between 8000 and 4500 years ago (Antevs 1938, Thompson 1990, Wigand 1987). During this interval, lakes and marshes were desiccated and pollen of drought-tolerant salt desert species increased substantially (Mehringer and Wigand 1990, Wigand 1987). The dramatic decline in Native American activity throughout the Great Basin at this time corroborates the severity of this extreme period of drought (Aikens 1993).

Approximately 5400 years ago, this period of extreme drought came to an end, but conditions remained warm. Plant pollen and macrofossil data indicate gradually increasing winter and summer precipitation punctuated by dramatic but brief increases in moisture (Antevs 1938, Davis 1982, Wigand 1987). From 4000 to 2000 years ago, conditions were significantly wetter than present (Davis 1982, Wigand 1987). Temperatures cooled and winter precipitation increased dramatically with respect to summer precipitation. Juniper pollen values began to rise approximately 4500 years ago, increased dramatically in the Diamond Pond area of the northwestern Great Basin 4000 years ago, and remained high, with intermittent drops, until approximately 1900 years ago (Figure 3; Mehringer and Wigand 1990, Wigand 1987). The downslope expansion of the lower juniper tree line by as much as 150 meters is confirmed by western juniper macrofossils from packrat middens at Diamond Craters (Mehringer and Wigand 1990) and Lava Beds National Monument (Mehringer and Wigand 1987).

Increasingly wetter conditions in the northern Great Basin between 4000 and 1900 years ago (the Neoglacial period) enabled juniper to expand down slope into more xeric communities (Wigand 1987). Rising grass:sagebrush ratios and higher regional water tables indicate more mesic climatic conditions during this period. The more mesic conditions brought on by a combination of increased rainfall and lowered summer temperatures would have promoted vigorous juniper growth (Fritts and Xiangdig 1986). Three very pronounced periods of abundant grass between 4000 and 2000 years ago suggest dramatic local grass expansion following local fires. Periodic increased abundance of grass pollen values in proportion to those of big sagebrush pollen at Diamond Pond and Steens Mountain (Figures 3 and 4; Mehringer and Wigand 1990, Wigand 1987) indicate a more grass-dominated sagebrush steppe than today.

Juniper pollen values during the Neoglacial period above 2200 meters at Fish Lake on Steens Mountain remained lower than those presently found in Fish Lake (Mehringer and Wigand 1987). This observation suggests that during prehistoric juniper woodland maximum, the upper tree line lay below that of today. Severe winter conditions at the higher elevations probably restricted the upslope expansion of juniper (Mehringer 1987). However, juniper did seem to expand slightly upslope at the end of the middle Holocene when conditions were much warmer but increasingly wetter (Mehringer 1985, Mehringer and Wigand 1987).

During Neoglacial expansion, these lower elevation juniper woodlands on Steens Mountain (1200 meters elevation) were less dense than twentieth-century western juniper woodlands (1500–1800 meters in elevation). Juniper pollen at Diamond Pond during periods of prehistoric woodland maximum are less abundant than levels found currently in juniper woodlands at intermediate elevations (Wigand 1987). Abundant grass pollen during prehistoric expansion also indicates a vigorous herbaceous understory.

Although climatic conditions at the lower elevations were good for juniper growth and establishment, periodic fires fueled by abundant herbaceous understory vegetation probably helped maintain the low-density open tree stands. Recent stable isotopic data from the northern Great Basin indicate that juniper were often water stressed as a result of drought or frequent freezing during the growing season of the Neoglacial and other late Holocene periods of expansion (Wigand et. al in press).

Since the end of the Neoglacial period 1900 years ago, climate became generally warmer and drier across the Great Basin (Davis 1982, Wigand 1987, Wigand and Nowak 1992, Wigand and Rose 1990). The plant macrofossil record from Diamond Pond indicates the decline in regional water tables (Wigand 1987). Dramatically declining juni-

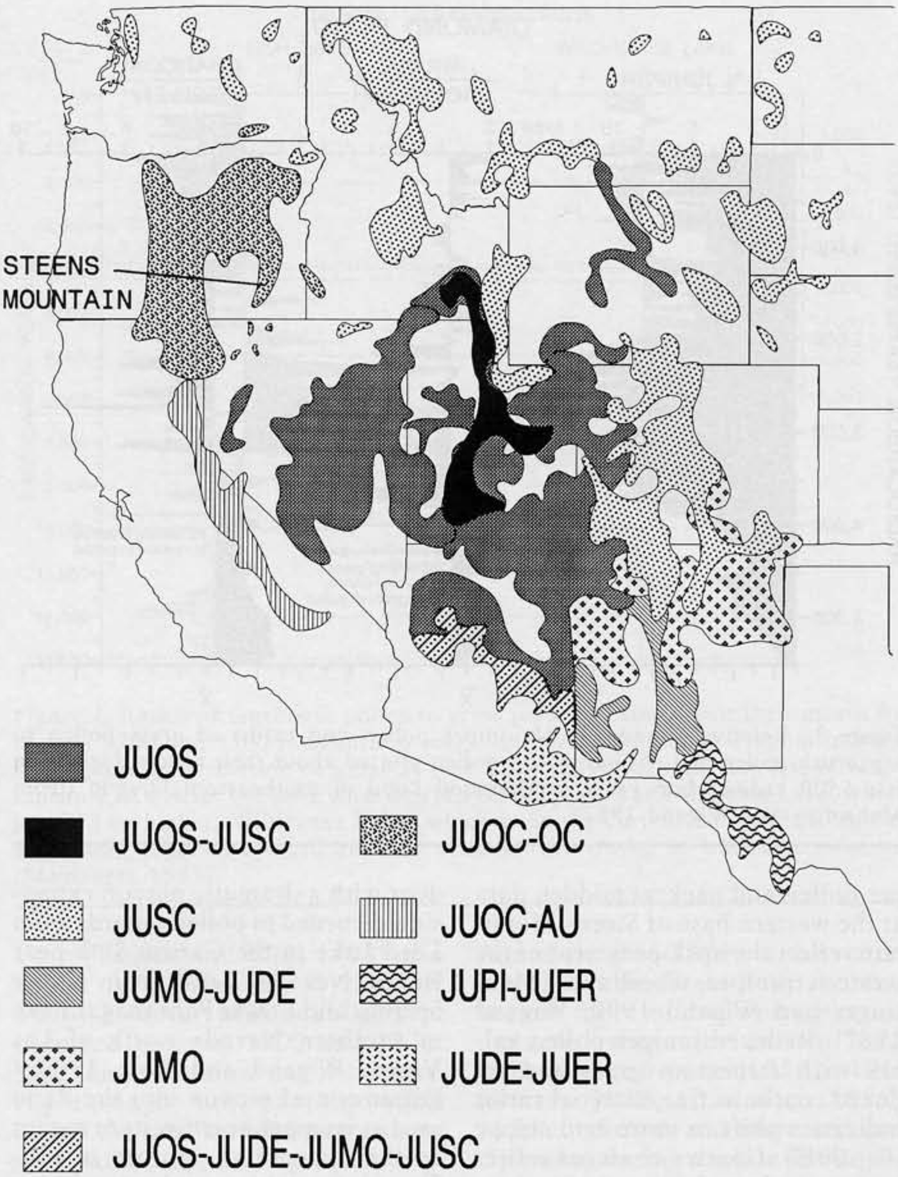

Figure 2. Generalized distributions of common juniper species in the western United States; JUOS = Utah juniper, JUSC = Rocky Mountain juniper, JUMO = one-seeded juniper, JUDE = alligator juniper, JUOC-OC = western juniper var. *occidentalis*, JUOC-AU = western juniper var. *australis*, JUPI = Pinchot's juniper, JUER = redberry juniper (partially derived from Critchfield and Little 1966).

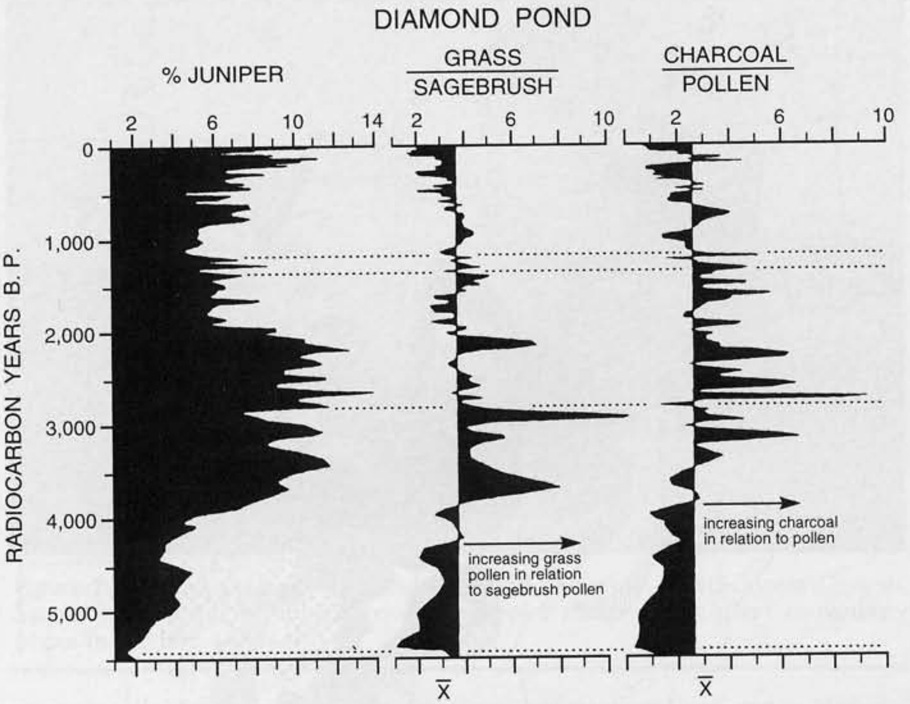

Figure 3. Relative abundance of juniper pollen and ratios of grass pollen to sagebrush pollen and of charcoal to pollen plotted about their means during the last 5500 radiocarbon years at Diamond Pond in southeastern Oregon (from Mehringer and Wigand 1987).

per pollen and packrat midden data at the western base of Steens Mountain reflect the upslope retreat of the western juniper woodland (Mehringer and Wigand 1990, Wigand 1987). Reduced juniper pollen values with respect to grass and reduced coarse to fine charcoal ratios indicate a shift to more arid steppe (Figure 5). Coarser charcoal reflect juniper fuels and finer charcoal indicate shrub and forb fuels. At higher elevations on Steens Mountain increased sagebrush pollen relative to grass pollen reflects a more xeric, less grass-dominated sagebrush steppe (Figure 4; Mehringer 1987). Expansion of salt deserts at the expense of shrinking marshes, evidenced by greater chenopod pollen values at Diamond Pond, indicates a period of increasing aridity, particularly between 1900 and 1000 years ago (Wigand 1987).

Approximately 1000 years ago, major increases in juniper pollen at Diamond Pond and western juniper macrofossils in the packrat middens on Diamond Craters and Hart Mountain, coincide with increased large versus small charcoal values (Figure 5). This expansion is coincident with a dramatic pinyon expansion recorded in pollen records from Lead Lake in the Carson Sink near Reno, Nevada,[1] and from Cofer Springs and Lower Pahranagat Lake in southern Nevada north of Las Vegas (Wigand and Rose 1990).[2] Expansion of pinyon into the Reno area at its most northwestern extent at the expense of juniper is confirmed from the packrat midden records of the Virginia range (Wigand and Nowak 1992).

Tree-ring records suggest severe drought and fire occurred at all three localities between 700 and 500 years ago. This period coincides with dramatically reduced pollen values of juniper in the north (Wigand 1987) and of juniper and pinyon in the south (Wigand and Rose 1990),[3] indicating a dramatic retreat of Great Basin woodlands. A sudden gap in the packrat midden evidence for this period also suggests a decline in the forests (Wigand and Nowak 1992).

Beginning 400 to 500 years ago, a pattern of stronger winter precipitation developed, initiating a gradual re-expansion of juniper woodland in the northern Great Basin (Mehringer and Wigand 1990). Farther south in the Lead Lake, Lower Pahranagat Lake, and Cofer Springs, records of increasing amounts of pinyon pine pollen with respect to juniper indicate that it was pinyon that benefited from more mesic climate conditions (Wigand and Nowak 1992, Wigand and Rose 1990).[4] The greatest Holocene juniper pollen values in the Fish Lake record suggest that western juniper woodland may have been expanding at higher elevations during this period (Mehringer and Wigand 1987). It is clear that re-expansion of Great Basin woodlands was just getting underway when Europeans first entered the area.

Historic expansion of juniper

Abundance of juniper pollen has gradually increased since A.D. 1500, fluctuating in the early 1800s and sharply increasing in the mid-1900s (Mehringer 1987). Since the culmination of the Little Ice Age in the mid-1800s, temperature has been rising (Ghil and Vautgard 1991). Rising temperatures have been accompanied by an increase in sagebrush pollen relative to grass pollen and a decrease in the water table at Diamond Pond near Steens Mountain in eastern Oregon (Wigand 1987).

Relict juniper woodlands, tree-age class ratios, fire scars, and historical documents generally indicate pinyon-juniper and juniper woodlands, before the Euro-American settlement, were open, sparse, and savannah-like or confined to rocky ridges and rocky low sagebrush flats where fine fuels were too low in abundance to carry a fire (Miller and Rose in press, West 1984). However, during the last 150 years, juniper species have increased both in distribution and density throughout their range (Tausch et al. 1981, West 1984).

Juniper species began to increase throughout much of the intermountain region during the late 1800s (Cottam and Stewart 1940, Miller

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[1] P. E. Wigand, 1993, unpublished data.

[2] See footnote 1.

[3] See footnote 1.

[4] See footnote 1.

and Rose in press, West 1984). Expansion has occurred into open meadows, grasslands, sagebrush steppe communities, and aspen groves (Eddleman 1987, Miller and Rose in press, West 1984), and junipers have been invading riparian communities.[5] In southwestern Utah between 1864 and 1940, woodlands expanded downslope covering fivefold as much land area as the original pinyon-juniper stands, and tree densities increased 6- to 20-times (Cottam and Stewart 1940). In Nevada, a basin-wide survey of pinyon-juniper woodlands showed that tree populations have increased in density and almost 2.5-fold in distribution during the past 150 years (Tausch et al. 1981).

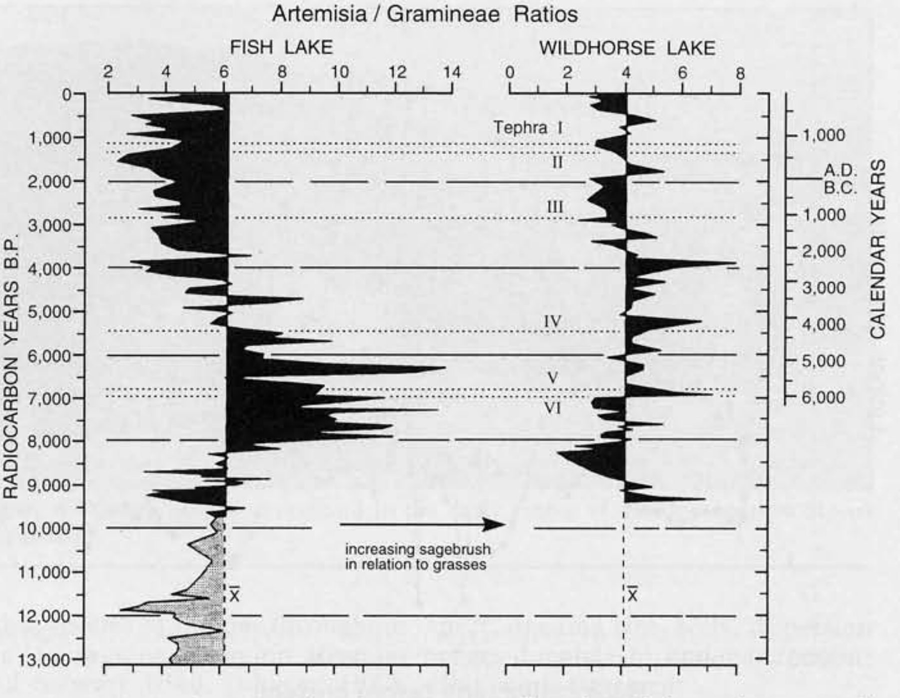

Figure 4. Ratios of sagebrush pollen to grass pollen plotted about their means for the last 9700 and 9300 radiocarbon years for Steens Mountain, Oregon. Increasing sagebrush in relation to grass at Fish Lake (2250 m) indicates less effective moisture. A similar but somewhat delayed trend appears at Wildhorse Lake, which lies 315 m higher. Wildhorse Lake, which is at the current elevational limit of sagebrush, suggests upward advance of sagebrush owing to warmer conditions (Mehringer 1985).

Western juniper has followed a similar pattern of expansion as its southern neighbors, currently occupying more than 1 million ha in eastern Oregon, southwestern Idaho, and northeastern California (Figure 2). In 1901, D. Griffiths, a representative from the USDA, was sent to tour and evaluate the condition of the western rangelands. He observed only scattered stands of juniper in southeastern Oregon (Griffiths 1902). Western juniper began increasing in both density and distribution in the late 1800s (Eddleman 1987, Miller and Rose in press), Young and Evans 1981). Current densities of trees less than 100 years old on these rocky low sagebrush flats and recently occupied mountain big sagebrush communities average 338 trees/ha (Figure 6; Miller and Rose in press). Although western juniper is a long-lived species (the oldest tree reported is nearly 3000 years old), the majority of present-day woodlands are less than 100 years old.

In southeastern Oregon, western juniper expansion began in the 1880s, the rate increasing as trees reached maximal reproductive maturity, 60 to 70 years of age (Figure 7; Miller and Rose in press). Well-developed western juniper woodlands in central Oregon[6] and Utah juniper woodlands in south central Utah (Tausch and West 1988) also began establishment in the late 1800s; however, peak establishment occurred between 1900 and 1930. Seed dissemination occurs primarily through movement by water across the land surface, particularly on frozen soils, and by birds, coyotes, and rabbits (Gabrielson and Jewett 1970, Johnsen 1962). The Townsend solitare (*Myadestes townsendii*) (Poddar and Lederer 1982), American robin (*Turdus migratorius*), Steller's jay (*Cyanocitta stelleri*), and scrub jay (*Aphelocoma coerulescens*) are primary avian vectors of juniper seed dispersal in the Great Basin (Gabrielson and Jewett 1970).

The factors most frequently implicated in the recent expansion of juniper species throughout the West are climate, fire, and grazing. Climate was likely the cause of juniper expansion and retraction during prehistoric times, but could climate change be fully responsible for the expansion of western juniper woodlands during the last 100 years? Following the end of the Little Ice Age in the mid-1800s in the northern half of the Great Basin, winters became more mild and precipitation increased above the current long-term average between 1850 to 1916 (Antevs 1938, Graumlich 1985). Mild conditions and increased precipitation during the late 1800s and early 1900s, which promote vigorous juniper growth (Fritts and Xiangdig 1986), probably contributed to the expansion of juniper. However, these conditions would also have increased the potential for fire due to the increased production of light fuels: grasses and forbs.

Reduced fire frequency has been one of the primary factors attributed to the expansion of juniper throughout the West (Burkhardt and Tisdale 1976, Johnsen 1962, Young and Evans 1981). Before settlement, fire frequencies in mountain big sagebrush (*Artemisia tridentata spp. vaseyana*) communities varied from 15 to 25 years (Agee 1993). Western juniper less than 40 to 50 years old are easily killed by fire (Burkhardt and Tisdale 1976). Fire probably maintained both shrubs and trees at

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[5] R. F. Miller, 1993, unpublished observation.

[6] EOARC Eastern Oregon Agricultural Research Center data file, 1993.

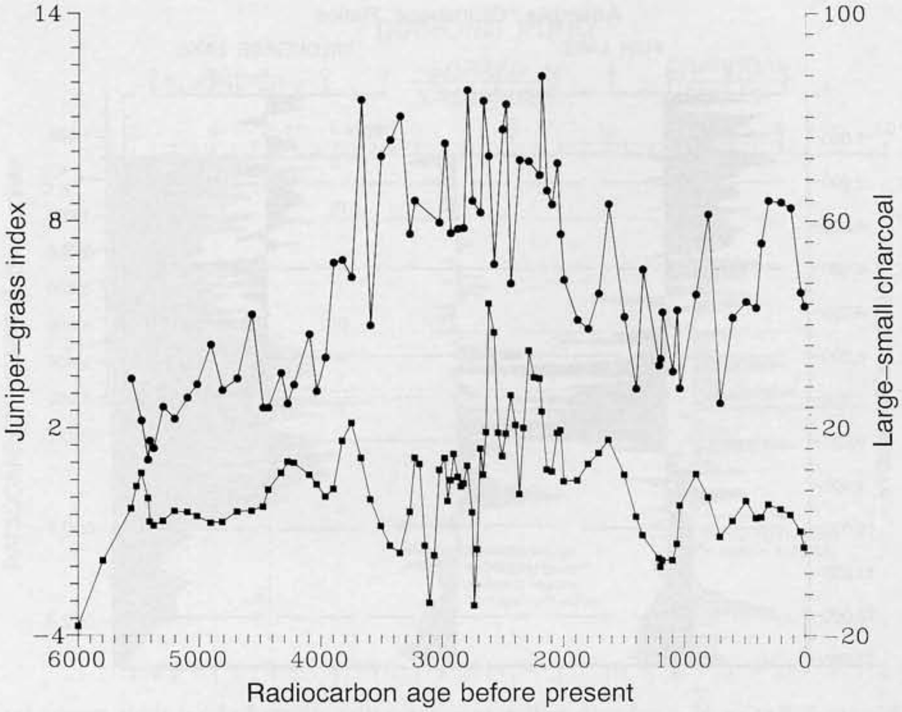

Figure 5. Comparison of juniper-grass index (dots) with large charcoal–small charcoal index (squares) from Diamond Pond, Oregon. The juniper-grass index was generated by standardizing both juniper and grass pollen values for the period of record and then subtracting the grass index from the charcoal index. High values indicate increased juniper abundance relative to grass. The large charcoal--small charcoal index was generated by standardizing charcoal values above 50 microns and below 50 microns for the period of record and then subtracting the charcoal values below 50 microns from those above 50 microns. High values indicate both periods of major fire activity and the shift to juniper as the dominant fuel type, whereas low values indicate periods when more regional fires were typical and the main fuel was shrubs, forbs, and grasses.

low densities and often restricted trees to rocky sites.

Before the late 1700s, Native American–caused fires augmented lightning fires in the more mesic sagebrush communities (Agee 1993). Fire was used to improve forage for game, maintain or increase the yield of certain wild edible plants, and increase seed production. By the close of the eighteenth century, native populations throughout the intermountain region were reduced 80% by European diseases such as smallpox, measles, venereal disease, and possibly typhus (Cressman 1981). Despite this decline in population, fur trapper Peter Skene Ogden noted in the 1820s abundant evidence of Native American fires in the Harney and Malheur Lakes region.

Settlement of the region by European Americans in the late 1800s and early 1900s led to a reduction of fine fuels through grazing high densities of domestic livestock (Burkhardt and Tisdale 1976). Possibly the greatest influence livestock had on the expansion of juniper throughout the West was the reduction of fine fuels resulting in a decrease in the occurrence of fire. In 1901, on his trip from Nevada to eastern Oregon, Griffiths (1902) stated: "No open-range lowland was seen on the whole trip which had much feed upon it excepting that consisting of the tough and persistent salt grass. On the whole trip of three days we found no good feed, except in very steep ravines." Removal of fine fuels was probably of particular importance during the wet and mild climate conditions of the late 1800s and early 1900s initiating the development of western juniper woodlands. The effects of fire suppression did not become a major factor in reducing fires until after World War II.

Livestock grazing has also been implicated in causing the increase in juniper in ways other than altering fire regimes. Livestock may have encouraged juniper expansion through seed dissemination, reducing competition from preferred forage species, and increasing safe sites for juniper seedling establishment through shrub increases. The reduction in competition from herbaceous forage species through grazing has been implicated in opening up many communities to juniper invasion (Cottam and Stewart 1940).

Cottam and Stewart (1940) concluded that the combination of grass competition and fire in the meadows kept Utah juniper from invading these communities. Cool-season grasses can be effective in competing for soil resources during the critical time of conifer seedling establishment. However, once juniper is established, density of understory species appears to have little affect on juniper growth regardless of the presence or absence of grazing. Competition may not be a factor inhibiting western juniper seedling establishment (Burkhardt and Tisdale 1976, Eddleman 1987, Miller and Rose in press).

A more recent argument attributes the expansion of pinyon-juniper woodlands in the southwest to increased atmospheric carbon-dioxide concentrations (Johnson et al. 1990). Bazzaz et al. (1985) reported cool-season C_3 plants respond more favorably to increased carbon-dioxide levels than do warm-season C_4 plants. In the southwest, increased atmospheric carbon-dioxide may increase growth of cool-season C_3 junipers at the expense of associated warm season C_4 grasses in the understory. In the northern portions of the juniper (e.g., western juniper) zone understory species are also cool-season C_3 forbs and grasses. However, water-use efficiency has been shown to be enhanced more in woody than herbaceous cool-season plants (Polley et al. 1993).

Effects of historic juniper expansion

During the past 35 years thousands of acres of juniper woodlands have been burned, chained, cut, plowed, and poisoned in attempts to restore various ecosystem values. As with many of today's resource issues relating to land use and management, considerable controversy over past and current juniper restoration projects has developed. Various interest groups have different views of the role of juniper on the landscape. Recently this has led to a large increase in contested proposed juniper-restoration projects developed by both federal agencies and private landowners.

The controversy will likely continue to grow in the future due to a large increase in the commercial market value of juniper wood products. Historically, only small amounts of juniper have been harvested for fence posts and firewood. However, due to the increased value of wood products, tens of thousands of acres of juniper may be harvested annually in the near future. Timely questions to address are: how do these newly developed juniper woodlands affect various ecosystem processes, such as nutrient cycling, hydrologic cycles, erosion, atmospheric carbon-dioxide enrichment, and energy flows; and what impact do these woodlands have on biodiversity and wildlife habitat.

Plant community structure and composition play a significant role in nutrient, water, and energy cycles, and they influence the amount and type of use by wildlife species. There is often an inverse relationship between overstory cover of juniper and/or pinyon with understory plant cover. Closed juniper stands may virtually exclude all herbaceous vegetation (Tausch and Tueller 1990). However, the relationship between overstory and understory plants varies across sites and across the intermountain region.

Increases in western juniper density appear to have the greatest impact on plant community composition and structure on sites with shallow soils (40 to 60 cm) or south-facing slopes. On these drier sites, canopy cover of fully developed juniper woodlands frequently ranges from 20 to 30% with less than 5% cover of shrubs, grasses, and forbs, and nearly 70% bare ground. The large decline of understory plant species as juniper increases on rocky shallow soils has been reported for other species of juniper throughout the intermountain region (Cottam and Stewart 1940, Johnsen 1962, Tress and Klopatek 1987). On deep soil sites, understory vegetation appears to better withstand juniper invasion. This difference may be due to a lower density of juniper roots directly competing with the more shallow-rooted herbaceous plants in the upper soil layer on deeper soils. Plant species richness and seed reserves also decline as juniper dominance increases on a site (Koniak and Everett 1982).[7]

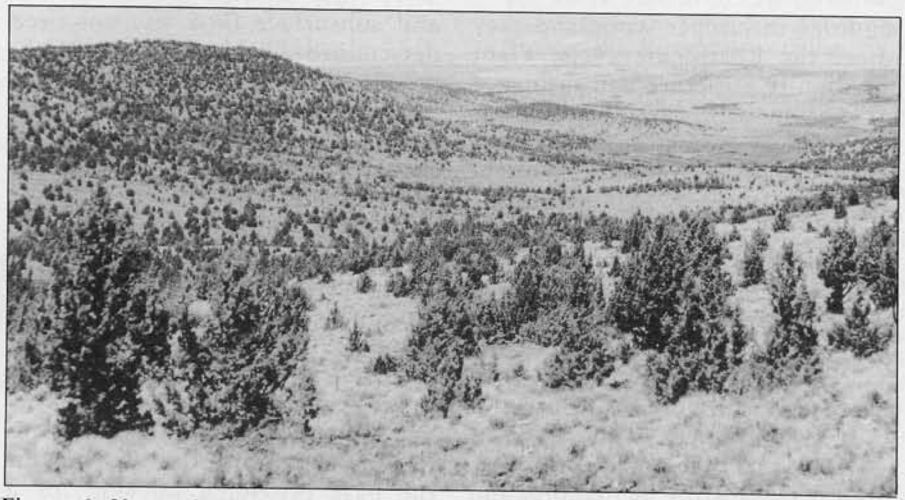

Figure 6. Young juniper woodland in the early stages of development on Steens Mountain.

The response of plant community composition and structure following juniper removal is also highly variable. During the second growing season following tree removal in a western juniper woodland occupying a south-east exposure in southeastern Oregon, the annual primary productivity of native perennial forbs and grasses increased more than eightfold, and total number of species increased 1.7 times.[8] However, removal of juniper may also enhance an increase in undesirable species such as cheat grass (*Bromus tectorum*) or medusahead (*Taeniatherum asperum*). The potential for these exotic weeds to form closed communities usually depends upon the composition of the understory prior to removal. Plant response following juniper removal is a function of initial floristics, seed pools, aspect, opening size, soils, dispersion of residues (slash), and management following treatment.

As communities shift from shrub steppe to juniper woodlands, spatial distribution of nutrients, nitrification, and nutrient import:export ratios may change. Dense juniper stands influence nutrient distribution on a site by extracting nutrients from the interspace between the trees and recycling them beneath the tree canopy (Klopatek 1987). Both carbon and total nitrogen levels were nearly fourfold greater beneath the juniper canopy than in the space between trees (Klopatek et al. 1988). Nitrification was also reduced beneath the tree canopy (Klopatek 1987). Increased bare ground may also promote nutrient loss through increased overland flow of water and erosion.

The shift of plant community structure from shrub steppe com-

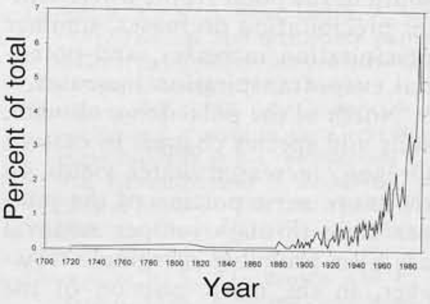

Figure 7. Years when western juniper trees established on Steens Mountain, estimated from tree-ring counts (sample size = 1400 trees) (from Miller and Rose in press).

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[7] See footnote 6.

[8] See footnote 6.

munities to juniper woodland may affect the hydrologic cycle. Plant community structure can influence infiltration rates, overland and subsurface flow of water, evapotranspiration, and precipitation interception. Hydrologic processes are probably most altered where juniper woodlands have significantly reduced the understory cover or where plant cover has changed from widely dispersed to clumped. Carrara and Carroll (1979) estimated that soil erosion in pinyon-juniper woodlands has increased fourfold during the past century.

On-site moisture availability and seasonal depletion patterns in the upper 60 cm of soil are also affected.[9] This is reflected by an increase in herbaceous and shrub production and an increase in the length of the growing season. Juniper woodlands influence soil-moisture depletion patterns and on-site moisture availability through transpiration (Angell and Miller 1994). A significant amount of precipitation can also be intercepted by the tree canopy and lost through evaporation. Evans (1988) estimated a juniper woodland with 40% cover intercepted 15 to 20% of the precipitation.

A contested issue is the influence of juniper woodlands on subsurface flow of water. Subsurface water flow provides an important source of water to springs, streams, and rivers, helping to maintain summer water flows and cooler water temperatures. Results from the southwestern pinyon-juniper zone generally showed only marginal increases in water yields following tree removal (Clary et al. 1974, Schmidt 1987). However, this work was done south of the polar front, where winter precipitation decreases, summer precipitation increases, and potential evapotranspiration increases.

North of the polar-front climate, soils and species change. In eastern Oregon, increased water yields on the more xeric portion of the juniper zone through juniper removal are also probably marginal. However, in the mesic portion of the juniper zone, which generally receives good snow accumulation, the relationship of juniper woodlands and subsurface flow has not been determined. Results from the southwest or drier juniper woodlands cannot be applied to the more mesic northern woodlands, which receive the majority of their precipitation during the winter.

Shifts from sagebrush steppe and aspen communities to juniper woodlands also impact populations of wildlife species. Although juniper trees provide forage for several wildlife species, cover is probably one of the more important functions of the woodlands. Old juniper trees frequently contain hollow cavities at the base providing housing for a number of wildlife species. Juniper woodlands modify severe weather conditions during the winter season for large ungulates (Leckenby 1986). Mule deer frequently shift use from the more preferred shrubland communities to the woodlands during winter stress periods. Juniper woodlands also provide nesting, migratory corridors, winter food, and cover for numerous bird species (Poddar and Lederer 1982). However, plant community structure and composition greatly affect animal use of these woodlands. Unfortunately good inventory data of species use of juniper woodlands is limited.

Although juniper can benefit wildlife species, the restoration of shrub steppe communities from juniper woodlands also benefits wildlife. Deer readily use forage in plant communities where juniper has been removed. Small mammal populations also increased in plant communities following juniper removal where tree limbs were scattered and left on the ground (Severson 1986). However, response of individual species varies among uncut areas, those cut with slash left on the ground, and those cut with slash removed. There is little argument that juniper benefits wildlife habitat. Disagreement rises, however, in how much juniper is optimal, size of treated areas, the effects of thinning versus total removal, and what sites should or should not be treated.

Conclusions

Several factors appear to be different for periods of juniper expansion in the prehistoric and historic record, including climate, fire frequency, plant community composition and structure, and atmospheric carbon-dioxide levels. During prehistoric expansion, increased annual and growing-season moisture coincided with the downslope movement of juniper into drier shrub steppe communities (Wigand 1987). Pollen and charcoal records also suggest an increase in grasses in proportion to sagebrush and an increase in fire events in the region.

In contrast, the historic expansion of western juniper occurred during a period of increasing aridity, decreasing fire-return intervals, a decrease in the proportion of grasses to sagebrush, and the presence of newly introduced noxious species. Historic expansion occurred primarily within the more mesic sagebrush steppe communities rather than downslope into the drier Wyoming big sagebrush (*Artemisia tridentata spp. wyomingensis*) communities as it did in the prehistoric past. Western juniper also appears to have expanded slightly at higher elevations (e.g., above 2200 m on Steens Mountain), suggesting milder winter conditions at these elevations than during prehistoric expansion. The increase in atmospheric carbon-dioxide levels may have also contributed to recent juniper expansion in the West.

The development of these present-day woodlands under a different combination of environmental variables has led to woodland communities with a different plant composition and structure than those of the past. Current conditions have allowed present-day juniper woodlands to become considerably more dense than in the recent past. The abundance of western juniper pollen appears to be greater in the twentieth century than during the past 5000 years (Mehringer and Wigand 1990).

Current climate conditions are also less favorable than those in the past for the development of a competitive herbaceous understory. Greater tree densities under drier conditions have a different impact on watershed properties, nutrient cycling, fauna, biodiversity, and ecosystem processes than the juniper/

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[9] See footnote 6.

grass communities of the past. Management of juniper woodlands through prescribed fire or thinning is probably important to maintaining or restoring various resource values. However, selection of sites to be treated, the pattern of treated and untreated juniper stands on the landscape, and proper management following treatment will probably determine the success or failure of juniper woodland management. Monitoring ecosystem responses following treatment will also determine ability to make proper land management decisions in the future.

Acknowledgment

This paper is approved as Oregon State Agricultural Experiment Station Technical Paper Number 10,461.

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