Comparative Rates of Western Juniper Afforestation in South-Central Oregon and the Role of Anthropogenic Disturbance*

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We examine changes in canopy cover for adult western juniper from the 1960s to 1994 in central Oregon using repeat aerial photography. We compare changes at four sites with a land-use history of minimal anthropogenic disturbance to changes on adjacent sites that have a disturbance history more typical of central Oregon rangelands. Canopy cover increased at all sites, but afforestation on sites with domestic livestock grazing was greater. The potential driving forces common to all sites include a long fire-free interval, early twentieth-century favorable climatic conditions, biological inertia, and atmospheric CO_2 enrichment.
Key Words: afforestation, canopy-cover increases, repeat aerial photography, western juniper.

Introduction

Western juniper (*Juniperus occidentalis* var. *occidentalis* Hook.), a dominant tree species in the semiarid Pacific Northwest, has undergone a rapid range expansion in the last 150 years. Western juniper forests (>10% crown cover) and savanna (<10% crown cover) now cover more than two million hectares in eastern Oregon (Gedney et al. 1999), with additional hectares (although considerably fewer) extending into Washington, Idaho, California, and Nevada. One inventory of woodlands in eastern Oregon reports that the area covered by western juniper forests quintupled between the mid-1930s and late 1980s (Gedney et al. 1999). Rates of establishment are generally found to have increased dramatically on disturbed sites during the twentieth century (Burkhardt and Tisdale 1976; Young and Evans 1981; Eddleman 1987; Miller and Rose 1995). However, even in the absence of significant human interaction, some locations exist at which establishment rates show geometric increases over the last several decades (Soulé and Knapp 2000). While the forcing mechanisms for this recent afforestation are debatable, primacy has been attributed to factors such as fire suppression, domestic livestock grazing, favorable climatic conditions, and biological inertia (Burkhardt and Tisdale 1976; Miller and Rose 1995, 1999; Knapp and Soulé 1998; Soulé and Knapp 2000).

The expansion of western juniper into areas in which it previously did not exist is an issue with both scientific and practical concerns. By expanding into what were once communities dominated by big sagebrush (*Artemisia tridentata* Nutt.), western juniper is changing the species composition of the region and potentially reducing range productivity (Eddleman 1987; Bedell et al. 1993; Miller and Wigand 1994) and soil-moisture balances (Bedell et al. 1993; Gedney et al. 1999). Management of western juniper woodlands has become a policy issue for the Bureau of Land Management (BLM) and other federal agencies charged with maintenance of public lands in the semiarid

*This study was funded by the National Science Foundation Grant #SBR-9809245, and by an Appalachian State University Research Council Grant. We thank Harry Blount, Stacy Carnine, Joel Davis, Betsy Herrmann, Kimberly Eldridge, Allison Miller, Paul Mitchell, Andrew Paul, and Mark Pelfrey for field and/or laboratory assistance. We also thank Chris Larson for image analysis, Jeffery McMichael of the Georgia State University Cartography Laboratory for production of Figures 1 and 5, and Truman Hartshorne and three anonymous reviewers for their constructive comments.

The Professional Geographer, 55(1) 2003, pages 43–55
Initial submission, May 2001; revised submission, January 2002; final acceptance, March 2002.
Published by Blackwell Publishing, 350 Main Street, Malden, MA 02148, and 9600 Garsington Road, Oxford OX4 2DQ, UK.

Pacific Northwest. Belsky (1996, 55) argues that western juniper "should not be referred to as an invasive weed that is threatening natural communities, but as a native species that becomes a community dominant under certain environmental conditions" and that many of the negative impacts associated with its expansion (e.g., extensive water use, reduced biodiversity) are unfounded. However, attempts to control the expansion of juniper through mechanical removal, controlled burning, and chemical treatment are occurring (BLM 1993), and multimillion-dollar treatment programs have been proposed within the BLM (Liverman 1993).

One of the unresolved issues in the study of western juniper afforestation is the role of disturbance. A commonly held view is that domestic livestock grazing has accelerated the rates of expansion by reducing the amount of fine fuels needed to sustain and carry fire and stimulating the growth of shrubs that serve as nurse plants for juvenile western junipers (Young and Evans 1981; Eddleman 1987; Miller and Rose 1995). With longer fire-free intervals, the biological inertia effect of an increasing seed rain can result in a rapid expansion of the species. One means of testing the validity of this viewpoint is to compare rates of afforestation on sites that have been actively disturbed by human activities with adjacent physically comparable sites that are substantially less disturbed. As demonstrated by Soulé and Knapp (1999), recent rates of western juniper afforestation can be monitored through the use of repeat aerial photography. They examined changes in cover and density of western juniper on a single research natural area (RNA) in central Oregon and found that expansion in the last half of the twentieth century occurred at a rate comparable to that observed on nearby disturbed sites (Soulé and Knapp 1999).

In this study, we document recent (1960s to mid-1990s) changes in canopy cover of adult western junipers on four minimally disturbed sites in central Oregon and compare these changes to those observed on matched disturbed sites with similar physical characteristics (e.g., soil type, aspect, climate). The primary objective is to determine the relative importance active disturbance (primarily domestic livestock grazing) plays in short-term afforestation of western juniper. A secondary goal is to expand on the results presented in previous analyses of afforestation rates of western juniper (Soulé and Knapp 1999, 2000) by examining rates of afforestation across a substantially broader range of environmental conditions (i.e., topoedaphic and climatic variability that exists among the four macrosites). A third goal is to examine the suite of potential driving forces responsible for western juniper afforestation and present arguments for or against these mechanisms.

Study Sites

The four study sites are located in central Oregon (Figure 1). Each includes an established or proposed RNA (as designated by the BLM or the United States Department of Agriculture Forest Service) and a matched study site that is considerably more disturbed (Table 1). These RNAs were established, in part, because they have a history of minimal human impacts (e.g., livestock grazing, logging) and thus represent areas that are well suited for ecosystem studies (BLM 1995). Our search for minimally disturbed sites was guided by the absence and presence of exotic plants, particularly cheatgrass (*Bromus tectorum* L.). While we designate the sites as disturbed (e.g.,

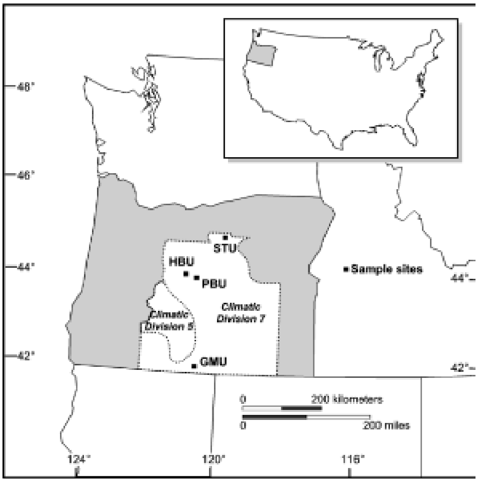

Figure 1 *Study-site locations (study-site pairs are adjacent, e.g., STU/STD) and the boundaries of the High Plateau (division 5) and South Central (division 7) Oregon climatic divisions.*

Table 1 *Basic Characteristics of the Eight Study Sites*

Site	Status	Elevation (in Meters)	Slope (in Degrees)	Aspect	Fire Information	Other Information
STU	Proposed RNA	800	16–40	Southwest	None since 1968; no evidence of widespread fires.	No evidence of recent grazing. Sheep grazed in region from 1870s to 1940. High frequency of summer thunderstroms.
STD	Downslope	730	5–20	Southwest	None since 1968; no evidence of widespread fires.	Grazing is active (hoof prints, manure, cattle trails).
PBU	RNA	1,220	5–25	South	None since 1968; no evidence of widespread fires.	Topography limits grazing; high frequency of summer thunderstorms.
PBD	Downslope	1,145	5–20	South	No evidence of fire within study area; prescribed burns on adjacent land.	Recent grazing allotments up to 200 cattle (manure on site).
GMU	RNA	1,555	1–2	N.A.–flat	No evidence of fire within study area; prescribed burns on adjacent land.	RNA created in 1942, fenced. High water table (meadows). Pre-1942 grazing was light to moderate.
GMD	Outside RNA fence	1,555	1–4	N.A.–flat	No evidence of fire within study area; prescribed burns on adjacent land.	Very minimal disturbance (limited manure on site).
HBU	Proposed RNA	1,185	30–44	Southwest	No evidence of fires spreading through the site (too rocky).	Topography limits grazing.
HDB	Downslope	1,065	2–20	Southwest	Large prescribed burn in 1982; study area selected to avoid the burned area.	Active grazing (manure, hoof prints, cow trails), old 4-wheel-drive road crosses transect.

Note: RNA, research natural area; N.A., not applicable.

Powell Butte Disturbed—PBD) or undisturbed (e.g., Powell Butte Undisturbed—PBU), perhaps a better descriptor is either *typical* or *atypical* for central Oregon rangelands, as most areas either have been or are now actively grazed by livestock and may have experienced other human pressures, such as wood-cutting and active fire suppression. The minimally disturbed sites have largely escaped extensive and widespread grazing by cattle (BLM 1995), because the excessively steep and rocky upper slopes were not conducive to foraging. The role of sheep grazing on these sites is less well documented, but the absence of exotic plants on the higher slopes of the RNAs suggests that their influence was small.

The sites we selected represent western juniper growth under a diverse range of physical characteristics (e.g., slope, elevation, soil characteristics, climate) (Table 1). At three of these sites, Powell Butte Research Natural Area (PBU/PBD), Sutton Mountain (STU/STD), and Haystack Butte (HBU/HBD), the primary factor limiting disturbance is topography, so the matched disturbed site is downslope. Goodlow Mountain Research Natural Area (GMU) is a fenced exclosure, so all domestic livestock grazing has been eliminated since 1942. The matched disturbed site for Goodlow is outside the fenced boundary.

Methods

Canopy-Cover Determination

Aerial photography is commonly used to examine changes in arid and semiarid vegetation cover over time (e.g., Knapp, Warren, and Hutchinson 1990; Soulé and Knapp 1999; Ansley, Wu, and Kramp 2001; Ueckert et al. 2001). We assessed changes in canopy cover of adult western juniper using large-scale (1:20,000 or 1:40,000) black-and-white aerial photographs of the study sites. All sites had usable imagery beginning in 1960, 1961, 1962, or 1968 and ending in 1994. Because a varying number of usable photographs were available for each site between the 1960s and 1994, we present only results from these two time periods. We scanned the photos at either 1015 dpi (1:20,000) or 2030 dpi (1:40,000) to obtain a spatial resolution of equivalent size for the various photographic scales. We converted the scanned photos into JPEG format and imported them into ERDAS IMAGINE as unsigned 8-bit gray scales. On each photograph, we determined the location of the field transects used for dendrochronological sampling using ArcInfo. These transects were approximately 700 m in length. We noted the latitude and longitude of the endpoints in the field using a hand-held global positioning system. We reprojected the transects from LAT/LONG to Universal Transverse Mercator coordinates (zone 10, NAD27).

For the rectification process, we used either digital line graphs from the U.S. Geological Survey or TIGER (topologically integrated geocoding and referencing) files to establish ground-control points. We rectified one image in each series using a polynomial order one, with four to nine ground-control points. We then registered the remaining images to the rectified image. We performed an unsupervised classification of the images using ERDAS IMAGINE. This created three or four classes. We then recoded the classified images into juniper/nonjuniper. This was possible because juniper woodlands are largely monospecific in our sampled areas. We created buffer files approximately 70,000 m^2 in size (usually rectangular and roughly centered on our field transects) using ArcView, and then imported these files into ArcInfo. We converted the ArcInfo buffer files to raster format and masked the classified images to hide everything outside our 70,000-m^2 sample areas. We then used the attribute table in ERDAS IMAGINE to count the number of pixels that were either juniper or nonjuniper. Because each pixel covered 0.25 m^2, we multiplied the number of juniper pixels by 0.25 to obtain the total area covered by juniper. Dividing this value by the actual total area covered in the buffer files (i.e., it was always close to, but never exactly 70,000 m^2) returned the percent cover of adult western juniper at each site from each image. Western junipers often remain small, understory species until approximately twenty-five to thirty-five years of age, and are not detectable on the aerial photographs. Thus, our study documents cover changes of young adult to adult western juniper trees. Furthermore, we minimized potential problems caused by shadowing effects by using only vertical imagery taken during late spring or summer months at or near midday (Aerial Photography Field Office 2001; James L. Fischer, Aerial Photography Field Office, United States Department of Agriculture, personal communication, e-mail, 15 November 2001).

Dendrochronology

Analyzing the effects of climate on tree growth required a dendrochronological analysis that used measured tree-ring widths of western juniper trees for comparison with regional climate records. We randomly sampled between 105 and 200 trees per site. We first established twenty 0.05-ha plots systematically along a transect through the study site, then sampled the 10 trees closest to the plot center, regardless of age. We extracted two or more core samples from each tree using a Haglof increment borer at approximately 30-cm height. Cores were taken from the sides of each tree along the contour of the slope to avoid sampling the reaction wood occasionally found in trees growing on slopes. All core samples were placed in narrow-gauge storage containers and allowed to air-dry. Once dry, all cores were glued to wooden core mounts, then sanded using progressively finer sandpaper until the cellular features of the wood were identifiable under standard magnification (usually after using a 320-grit sanding belt). The tree rings on all cores were then cross-dated by using both the list method (Phipps 1985; Yamaguchi 1991) and skeleton plots (Stokes and Smiley 1968; Swetnam, Thompson, and Sutherland 1985) to ensure each and every ring was assigned its precise calendrical year of formation.

For trees too narrow to be cored, we measured their height and determined their age using regression models that predicted age as a function of height. To develop these models, we collected separate whole-tree samples of forty-five juvenile western junipers less than 30 cm in height at each site and determined their age, again using standard dendrochronological techniques. We also used these regression models to correct tree ages for all

Table 2 *Percent Canopy Cover of Western Juniper in the Early 1960s and 1994, Mean Age of Trees, Radial Growth Indices, and Mean Z-scores for October–June Precipitation for Multiple Time Periods*

Site	196x Cover (%)	1994 Cover (%)	Mean Tree Age		Mean Radial Growth Index		
			Years	SD	196x–1994	196x–1977	1978–1994
STU	9	9.6	89	82.6	1.12 (−0.20)	0.82 (−0.23)	1.29**[a] (−0.05)
STD	5	9.7	63	67.5	1.20 (−0.20)	0.82 (−0.23)	1.43** (−0.05)
PBU	9.6	12.3	70	79.6	1.09 (−0.16)	0.92 (−0.26)	1.27* (−0.05)
PBD	3.4	10.8	55	68.7	1.05 (−0.16)	0.99 (−0.26)	1.12 (−0.05)
HBU	8.7	9.6	211	186.9	1.10 (−0.14)	1.02 (−0.23)	1.19 (−0.05)
HBD	4.7	16.3	30	33.9	1.01 (−0.14)	0.82 (−0.23)	1.20** (−0.05)
GMU	5	9.2	65	82	1.01 (−0.63)	0.97 (−0.40)	1.06 (−0.87)
GMD	2.2	6.3	62	57.8	1.05 (−0.63)	1 (−0.40)	1.09 (−0.87)
All undisturbed	8.1	10.2	109	68.9	1.08	0.96	1.20**
All disturbed	3.8	10.8	53	15.4	1.07	0.94	1.21**

Note: Numbers shown parenthetically are mean Z-scores based on October-June precipitation.
[a] For all figures in this column, significance between index values based on one-tailed difference of means t-test with unequal variance based on 196x–1977 versus 1978–1994 periods.
** $p < 0.05$. ** $p < 0.01$.*

cross-dated samples (i.e., the number of years it took the tree to reach 30 cm in height).

We developed standard index (tree-ring) chronologies for each site using a subsample (generally 30 to 40) of the total cores (210 to >400 per site) collected at each site. In general, the core samples included in chronology development offered the clearest ring structure and greatest temporal sample depth. We then used these chronologies to determine the mean radial growth rate of trees across a site for each calendar year (i.e., how much growth occurred, on average, across a given site each year). We developed all chronologies using the ARSTAN program (Cook and Holmes 1997) and used conservative ring-width standardization techniques (e.g., negative exponential curves) to ensure that low-frequency trends in climate, if any, would be preserved.

Climate

To determine the potential impact of climate on changes in canopy cover over time, we first identified the monthly or seasonal climate variable that most strongly affects radial growth of western juniper trees at these eight sites using correlation techniques. We examined data from Oregon's High Plateau (division 5—matched with GMU/GMD) and South Central (division 7—matched with all other sites) climatic divisions (Figure 1) from 1896 to 1994 for long-term trends (1896 to 1994) and short-term trends (1960 to 1994) using least squares regression. We then tested for significant differences between the 1960–1994 period and the 1896–1959 period using a two-tailed Wilcoxon signed-ranks test (Burt and Barber 1996).

Results

Canopy-Cover Changes

Canopy cover increased at all sites between the 1960s (PBU/PBD 1960, HBU/HBD 1961, GMU/GMD 1962, STU/STD 1968) and 1994 (Table 2; Figure 2). Cover increases were generally greater on disturbed sites. Disturbed sites on slopes (HBD, PBD, STD) had greater cover increases compared to GMD, which is flat (Figure 3). However, the relative cover increase at GMD (2.9×, or a near tripling of cover) was greater than at STD (1.9×), and GMU had the largest relative cover increase (1.8×) among the four undisturbed sites. Mean age of trees was inversely related to both absolute (Spearman r_s: −0.91, $p < 0.0001$) and relative cover changes (Spearman r_s: −0.98, $p < 0.0001$) (Table 2; Figure 4). Thus, comparatively younger woodlands had greater relative cover increases.

Radial Growth and Climate

We found that total precipitation from October of the previous year to June of the current year explained the greatest amount of variance in tree growth (see Knapp, Soulé, and Grissino-Mayer 2001a, 2001b). Analyses of October–June rainfall for the South Central Climatic Division revealed no significant long-term (slope = −0.002, $p < 0.56$) or short-term trends

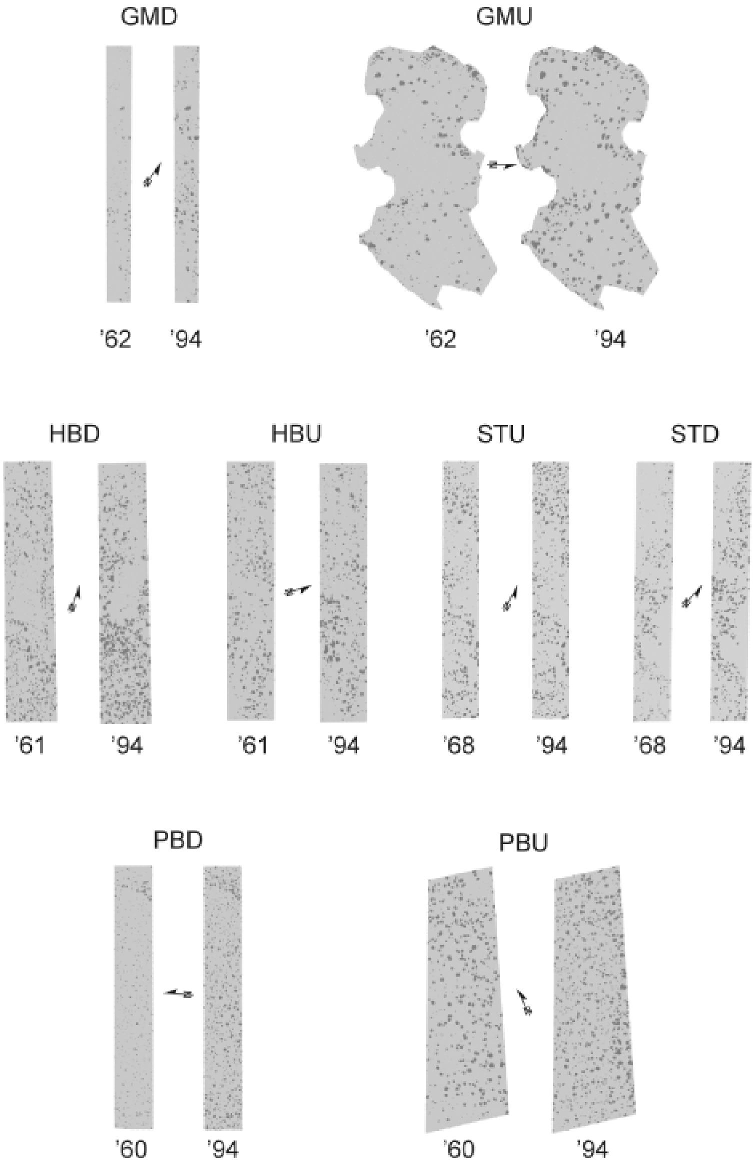

Figure 2 *Enhanced aerial photograph pairs at Goodlow Mountain Research Natural Area (GMU/GMD, 1962 and 1994), Haystack Butte (HBU/HBD, 1961 and 1994), Sutton Mountain Research Natural Area (STU/STD, 1968 and 1994), and Powell Butte Research Natural Area (PBU/PBD, 1960 and 1994). The light gray pattern represents area not covered by canopy of western juniper, and the dark gray represents area classified as being covered by western juniper canopy. Photographs are not to scale, but each study area (e.g., GMD) encompasses approximately 70,000 m²$^{}$. Western juniper and ponderosa pine (*Pinus ponderosa *Laws.) both occur within the GMU study site. To ensure that only western juniper trees were counted on the aerial photographs, we had to use an irregularly shaped boundary for the area sampled at GMU.*

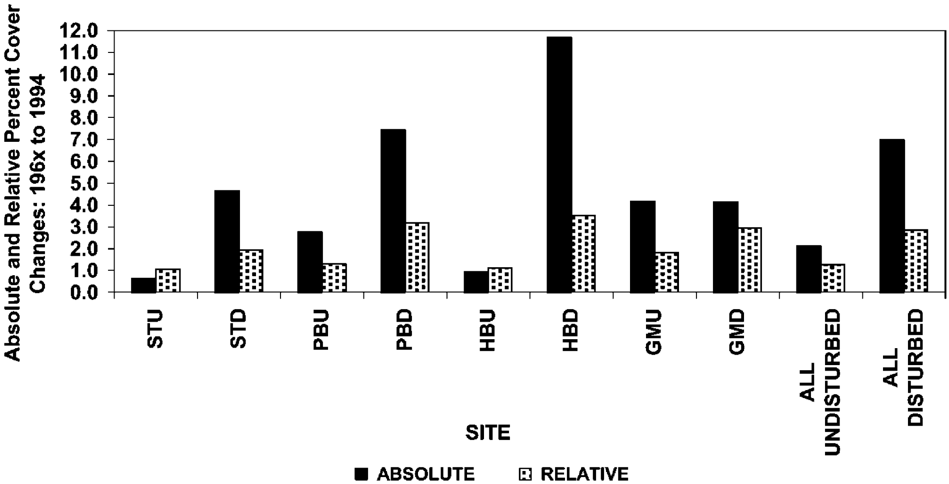

Figure 3 *Absolute (1994 minus 196x) and relative (1994/196x times 100) percent cover changes in western juniper canopy cover at the eight study sites and for the combined undisturbed and distrubed sites.*

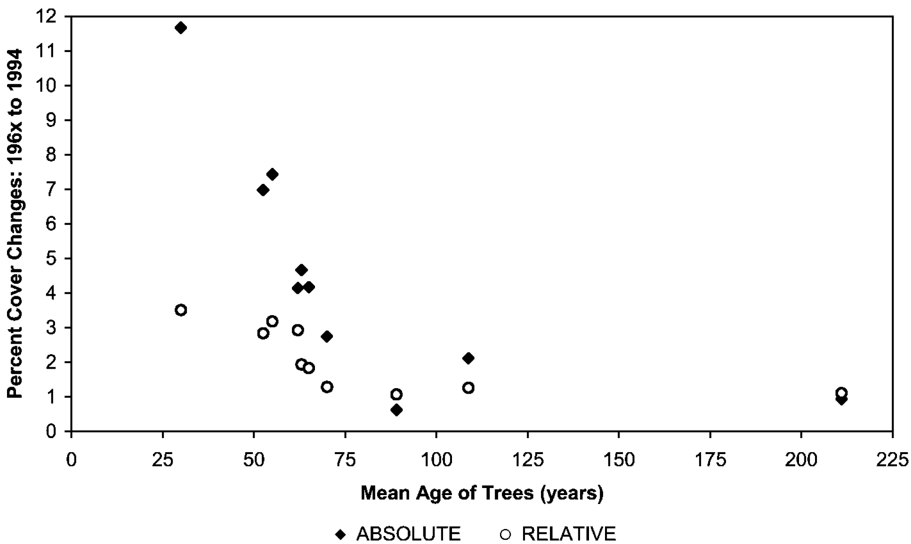

Figure 4 *Scatterplot showing the relationship between mean age of trees and absolute/relative percent cover changes from 196x to 1994 at the eight study sites and for the combined undisturbed and disturbed sites.*

(slope $= -0.009$, $p < 0.62$), and no significant differences ($p < 0.37$) between the 1960–1994 and 1896–1959 periods (Figure 5). Significant, negative long-term (slope $= -0.017$, $p < 0.001$) and short-term (slope $= -0.033$, $p < 0.029$) trends in October–June precipitation and a significant reduction in precipitation during the 1960–1994 period relative to 1896–1959 ($p < 0.0001$) were found at the High Plateau Climatic Division (Figure 5). Further, when the study interval was split into an early period (196x–1977) and a late period (1978–1994), no significant differences ($p > 0.05$) existed in October–June precipitation (Table 2; Figure 5).

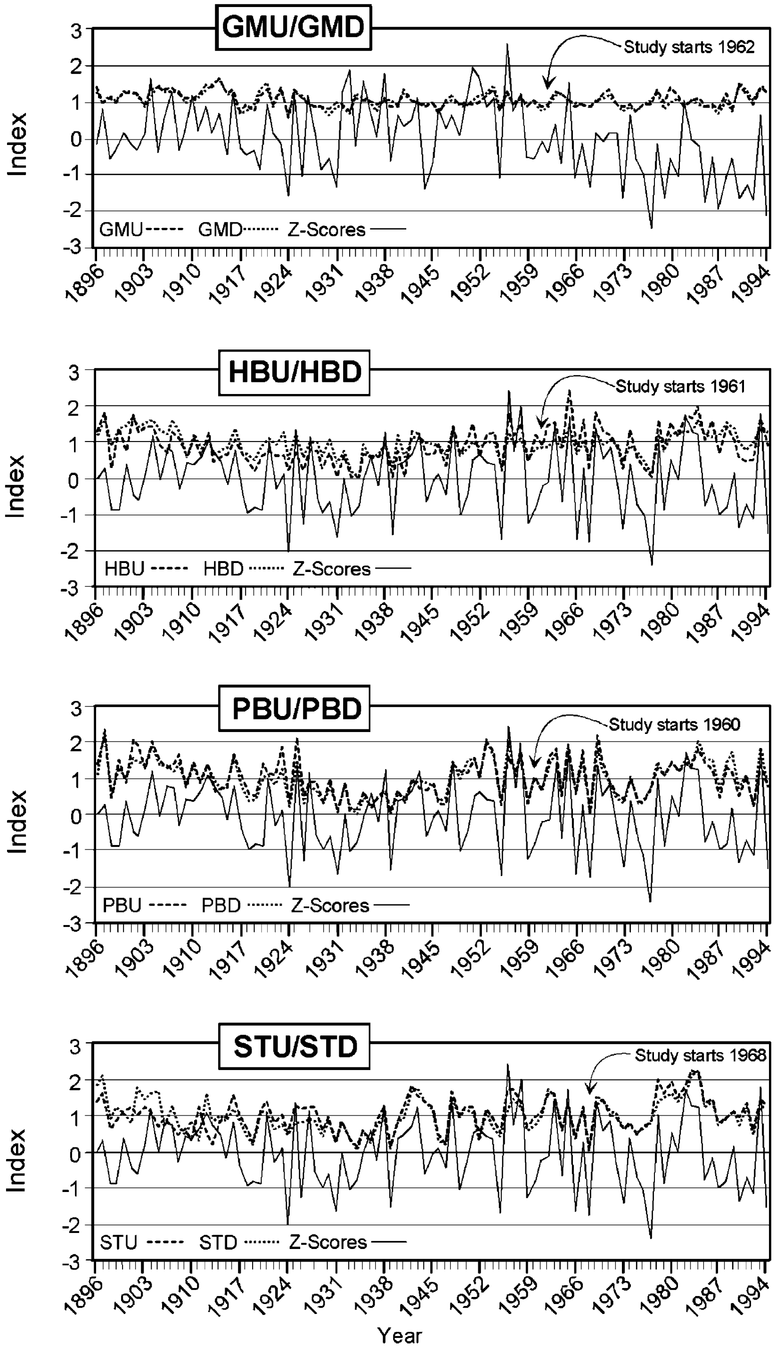

Figure 5 *Radial growth index values for disturbed and undisturbed study sites (dashed lines, mean = 1) and standardized October–June precipitation (solid line, mean = 0). Oregon Climatic Division 7 data were used for all sites except GMU and GMD, where Oregon Climatic Division 5 data were used. Period of record is 1896–1994.*

In summary, total October–June precipitation—the key determinant of radial growth for western juniper in eastern Oregon—either remained unchanged (South Central Climatic Division) or decreased (High Plateau Climatic Division) over the period of study.

Mean radial growth during the 196x to 1994 period was above average (mean = 1) at all sites, ranging from an increase of 18% at STD to 1% at both HBD and GMU (Table 2; Figure 5). Differences between undisturbed and disturbed sites were minor. These increases in radial growth, however, largely occurred from 1978 to 1994 (Table 2). This period followed the severe 1977 drought, but included the 1985–1994 drought at HBU/HBD, PBU/PBD, and STU/STD and a severe ongoing drought at GMU/GMD. At GMU/GMD, only two years between 1978 and 1994 had above-average October–June precipitation (Figure 5).

Discussion

Our results reveal an average doubling of cover for mature western juniper over a twenty-seven- to thirty-five-year period across eight sites and agree with findings from previous studies that western juniper afforestation is occurring within its range (e.g., Miller and Rose 1995; Knapp and Soulé 1998; Gedney et al. 1999; Soulé and Knapp 1999). The finding that the three largest absolute cover increases and the two largest relative cover increases occurred on sites that are downslope from what are considered to be the historical habitat of western juniper (i.e., steep, rocky slopes near ridgetops) suggests that downslope invasion of the species is an important component of recent afforestation. As the dispersal of western juniper berries is at least partially gravity-driven (Burkhardt and Tisdale 1969, 1976; Bedell et al. 1993), downslope expansion of the species would be expected in the absence of other limiting factors. Cover increased at all sites, but was greater on the disturbed sites, suggesting that some of the driving forces behind afforestation are ubiquitous to all sites, and that some forces are more dominant than others.

Potential Driving Forces

Climate and Biological Inertia The synergistic effects of favorable climatic conditions in the late 1800s through early 1900s and widespread domestic livestock grazing have been suggested as probable causes for western juniper expansion during the last century (Miller and Rose 1995, 1999; Gedney et al. 1999). This theory suggests that expansion began during the late 1800s with the establishment of trees in environments where previously they had been unable to establish and survive (e.g., downslope locations) due to aridity and short fire-return intervals (Burkhardt and Tisdale 1976; Young and Evans 1981; Agee 1993; Miller and Rose 1999). Western junipers require between twenty-five and seventy-five years to reach reproductive maturity (Eddleman 1984; Bedell et al. 1993; Miller and Rose 1995). We suspect that as these trees matured, the effects of biological inertia (i.e., increasing seed rain) emerged and the species continued to prosper. Our analyses of October–June precipitation do suggest that the early 1900s were climatically favorable for western juniper establishment, as was the period generally extending from the early 1940s to late 1950s (Figure 5). Trees establishing during the early 1900s would be reaching maturity within the 1960–1994 time period, and some trees establishing in the 1940s–1950s may have reached maturity, resulting in increased cover as they became large enough to be visible on the large-scale photographs. In addition, some of the cover increases are likely associated with a radial increase in stem growth from the central trunk as trees mature (Knapp and Soulé 1998). Both long- and short-term trends in October–June precipitation point toward increasing aridity, and increased cover is most pronounced at the lower elevation and more xeric sites, conditions not favorable for stimulating growth and establishment (hence increasing cover). We conclude that regional-scale changes in long-term climate are unlikely to be responsible for afforestation, but short-term (decadal) periods of wetter conditions are a potentially significant influence behind the observed increases in canopy cover.

Fire Fire records reveal that one site, HBD, has been affected by fire since the late 1960s (Table 1). The lack of other physical indicators, such as burned stumps and surface charcoal, suggests that our study sites have experienced substantially longer periods without a major fire event. Juniper seedlings have a high survival rate (Burkhardt and Tisdale 1976). Thus, in the absence of wildfire, which is often lethal to junipers less than fifty years old (Burkhardt and Tisdale 1976; Agee 1993), most juvenile western junipers would have reached maturity, adding to the increases in cover. In various parts of its range, a decreasing frequency of fire has been identified as one of the most likely causes for the increasing rates of expansion for western juniper (e.g., Burkhardt and Tisdale 1976; Miller and Rose 1995, 1999). While the prescribed burn of some of the lower slope at HBD may have reduced cover on portions of the area sampled on the aerial photography, we were careful to place the transect for dendroecological sampling outside the burned area. Conversely, the prescribed burn may have contributed to increased establishment of younger trees at HBD by stimulating growth through a release of nutrients (Burkhardt and Tisdale 1976). However, because this prescribed fire occurred in the early 1980s, it is doubtful that the younger and much smaller junipers that possibly established following nutrient release from this burn would be noticeable on aerial photographs.

Livestock Grazing Domestic livestock grazing has occurred on all the disturbed sites and continues to be an active component of their use (Table 1). Grazing may favor expansion (and, subsequently, increases in cover) by: (1) removing grasses that would compete with junipers for resources; (2) reducing fine fuels needed to carry fire; (3) promoting shrub understory dominance that then serve as nurse-plant sites for juvenile western juniper; and (4) accelerating seed dispersal (Burkhardt and Tisdale 1976; Bedell et al. 1993). These mechanisms should have contributed directly to the increases in cover observed on our disturbed sites. Further, the undisturbed sites have likely been impacted indirectly by grazing, because fires that may have historically started on adjacent lands and then spread into the undisturbed sites have been reduced.

Resource Competition: Emerging versus Established Woodlands Overall, trees on the disturbed sites are substantially younger than those on the undisturbed sites (Table 2). With a mean age of forty-nine years, the downslope, disturbed sites (STD, PBD, HBD) likely represent emerging juniper woodlands, with a majority of trees reaching reproductive maturity within the time frame of our analyses (1960–1994). In addition, percent cover on the undisturbed sites in the 1960s was generally double that of the matched disturbed sites (Table 2). We hypothesize that rates of afforestation have been more rapid on the disturbed sites in part because there was more room for expansion and thus less competition for resources (such as water and nutrients). For example, if wildfires were the historic limiting factor that hindered establishment and growth in downslope environments, the absence of fires would allow western junipers to establish across the site. Conversely, there were fewer areas for establishment and growth in upslope sites, as western junipers already dominated many of the preferred sites (the fire-proof, rocky outcrops commonly found on the steep upper slopes). Older stands of junipers common to the upslope sites may represent more steady-state conditions. Many of the trees we sampled on the upslope site showed signs of stress (i.e., strip-bark morphology, limited seed production) that are not conducive to establishment and expansion.

Carbon Dioxide Enrichment Atmospheric CO_2 enrichment may be an additional factor favoring the increase of western juniper cover. Recent studies on western junipers suggest that this species became much less sensitive to dry conditions in the later part of the twentieth century because the ameliorating effects of elevated CO_2 increase water-use efficiency (Knapp, Soulé, and Grissino-Mayer 2001b). As a consequence, canopy-cover reductions in response to drought are likely to be reduced. Additionally, radial growth of western juniper has exceeded that predicted from climate alone (i.e., significant positive trends in residuals from climate/growth models) (Knapp, Soulé, and Grissino-Mayer 2001a). Thus, growth (and coverage) continue, despite less-than-favorable moisture conditions found on the lower slope of the disturbed study areas and/or progressively drier climatic conditions.

Our results show that the greatest increase in radial growth occurred in the second half of our study period (Figure 5; Table 2). If radial growth acts as proxy for cover, then the largest increases in cover also occurred during a period of rapidly increasing atmospheric CO_2. These results are consistent with the findings of Tausch and West (1995), who showed that biomass accumulation (as measured via leaf-area indices) over the life history of pinyon-juniper woodlands is ten times that of shrub-steppe communities on comparable sites. Because of increasing atmospheric CO_2, junipers may have the ability to assimilate more carbon dioxide for photosynthesis than other competitive species, giving them a long-term growth advantage (Richard F. Miller, personal communication, phone, 15 November 2000).

Conclusions

Western juniper canopy cover increased from the 1960s to 1994 across all eight sites in central Oregon with variable disturbance histories and considerable topoedaphic and climatic variability. These results indicate that afforestation is occurring more rapidly on disturbed sites, and that younger stands of western juniper are experiencing greater rates of cover increase. Further, these cover increases are not unique to this genus: our results are consistent with those of Ueckert and colleagues (2001) who identified similar increases in redberry juniper (*Juniperus pinchotti* Sudw.) cover between disturbed and undisturbed woodland sites in the southwestern U.S. during an almost identical study period. We suspect that the driving forces behind afforestation are likely synergistic, and because of similar findings in other western North America woodlands (e.g., Tausch and Nowak 1999 [single leaf pinyon pine—*Pinus monphylla* Torr. & Fre.; Utah juniper—*Juniperus osteosperma* (Torr.) Lit.], Ansley, Wu, and Kramp 2001 [honey mesquite—*Prosopis glandulosa* var. *glandulosa* Torr.]), at least partially driven by some macroscale level mechanism.

All sites appear to be evolving within an extended period without major stand-replacing fire events. Because fire is one of the main causes of mortality for juvenile western juniper, lack of fire enhances chances for maturation of western juniper on our sites. Domestic livestock grazing has potentially been a factor in afforestation, both directly (e.g., by stimulating growth of shrubby nurse-plants) and indirectly (e.g., by making major stand-replacing wildfires less frequent). Extended periods of favorable climate in the early 1900s and again in the 1940s–1950s could be a contributing factor for growth increases observed from 1960 to 1994 when we relate the timing of establishment to maturation (typically twenty-five to seventy-five years). However, long-term trends in precipitation are not conducive for *sustaining* growth and cover increase. Finally, the impacts of increasing levels of atmospheric CO_2 on western juniper afforestation should be considered a possible driving force because of an atmospheric CO_2 enrichment effect on growth of this species. Substantially higher mean radial growth indices occurred during the last seventeen years of the study in the absence of favorable climatic conditions. Thus, some exogenous (i.e., nonclimatic) factor beneficial to western juniper growth rates has likely been operative over a large suite of environmental conditions. ■

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