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Structure and development of expanding western juniper woodlands as influenced by two topographic variables

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Abstract

Juniper and pinon woodlands have been expanding throughout the Intermountain West, USA since the late 1800s. Although causal factors attributed to woodland expansion have been documented, data are lacking that describe the influence of topographic features on rates of development and structural attributes of expanding woodlands. Our primary objective was to determine the relationship between stand-level developmental and structural attributes of four expanding western juniper (*Juniperus occidentalis*) woodlands with two topographic features commonly important to forest vegetation patterns, site exposure (an index of insolation exposure based on slope and aspect) and elevation. To accomplish this we measured tree density and age across four western juniper woodlands in Oregon and Idaho. Site exposure and elevation were consistently correlated with spatial and temporal components of woodland development and structure. Holding slope constant, a shift from a north to south aspect resulted in a 4.9 trees/ha/year decrease in tree establishment at a similar elevation. A 200 m rise in elevation was associated with a 1.8 trees/ha/year increase in tree establishment with similar exposure. A 100 m rise in elevation was associated with a 5-year decrease in the time required for a stand to reach dominance and a 22% increase in dominant tree density among stands with similar site exposure. Although significant, site exposure and elevation only explained a portion of the process of woodland dynamics. However, our data suggest exposure and elevation are contributing variables influencing woodland expansion across landscapes, resulting in spatial and temporal heterogeneity in stand structure and development. Models of woodland expansion incorporating landscape topographic features may be practical for identifying windows of opportunity for less costly restoration.
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1. Introduction

The increase in abundance of woody species has been reported in many semiarid and arid ecosystems throughout the world (Walker and Gillison, 1982; Schofield and Bucher, 1986; Archer et al., 1988). In the Intermountain West, USA, juniper and pinon woodlands have been actively expanding since the late 1800s (Tausch et al., 1981; Miller and Tausch, 2001; Wall et al., 2001). Prior to this time period, juniper and pinon woodlands were primarily confined to fuel-limited or fire-insulated sites (Dealy et al., 1978; Martin, 1978; Miller and Rose, 1995, 1999). Encroachment of juniper and pinon from fire-protected areas on the landscape to more productive, deeper

soils sites supporting shrub steppe, riparian, and aspen communities has largely been attributed to broad-scale reductions in the frequency of fire in the Intermountain West (Burkhardt and Tisdale, 1976; Miller and Rose, 1999; Miller and Tausch, 2001). Miller and Wigand (1994) speculated that the rate and extent of expansion of pinon and juniper woodlands in the past 150 years is unprecedented compared to any other time during the Holocene. Presently, these semiarid woodlands occupy around 19 million hectares (Miller and Tausch, 2001). Studies have described the chronology of post-settlement establishment (after 1850) of juniper and pinon woodlands (Burkhardt and Tisdale, 1976; Tausch et al., 1981; Tausch and West, 1988; Knapp and Soulé, 1996; Miller and Rose, 1999; Miller et al., 2000, 2005) and the spatial variation of woodlands across the Great Basin (West et al., 1978). In addition, impacts of woodland encroachment on plant community composition and structure, hydrologic processes, nutrient cycling, and

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wildlife habitat have also been evaluated (Klopatek, 1987; Reinkensmeyer, 2000; Bates et al., 2002; Miller et al., 2000, 2005). Other studies have looked at the relationships linking soils and plant associations with woodland structure and the interaction between increasing juniper dominance and understory species (Koniak and Everett, 1982; Tausch and West, 1995; West, 1999; Miller et al., 2000). However, little work has been conducted from a landscape perspective to determine how topographic elements influence stand-level rates of development and structural attributes. To effectively manage or restore woodland encroached ecosystems it is important that we can describe spatial and temporal patterns of woodland development and structure and understand the underlying causes.

Western juniper (*Juniperus occidentalis*) (Cronquist et al., 1972) woodland expansion probably has had the greatest impact on the mountain big sagebrush (*Artemisia tridentata* var. *vaseyana*) alliance based on area invaded (Miller et al., 2000, 2005). The process of woodland encroachment in these communities can be described with three phases directly linked to increasing tree dominance over site ecological processes (Miller et al., 2005). In phase I, trees are present but shrubs and herbs are the dominant vegetation that influence ecological processes on the site; phase II, trees are co-dominant with shrubs and herbs and all three vegetation layers influence ecological processes on the site; and phase III, trees are the dominant vegetation and the primary plant layer influencing ecological processes on the site. Miller et al. (2000) reported there were repeatable stand characteristics in the mountain big sagebrush alliance that can be used to define the phase of stand development. An important transition in this model occurs between phases II and III with the onset of dominant tree stress (i.e. reductions in leader growth and reproductive effort) resulting from intraspecific competition. It is the point where trees begin to influence the interspace causing changes in community structure that alter ecological processes, fire regimes, wildlife habitat suitability, and restoration options. Miller et al. (2000) speculated that by the mid to late phases of this transition, the reversal to shrub steppe by fire becomes unlikely because juniper dominance causes a significant enough loss of understory shrub and herbaceous species to preclude surface fires. Once an ecological threshold has been crossed, restoration usually becomes difficult and expensive, and outcomes become less predictable (Archer, 1989; Miller et al., 2000).

Resource availability has long been recognized as an important factor influencing composition, structure and development of plant communities (Whittaker, 1975; Tilman, 1982; Ohmann and Spies, 1998; Iverson et al., 1997; McNab, 1989, 1993). Gradients of resource availability on the landscape are often associated with topographically induced gradients of climate, the most apparent of which are related to changes in elevation and site insolation exposure (slope and aspect). A long tradition in gradient analysis by vegetation scientists has pointed to temperature (proxied as elevation) and moisture (proxied as various "exposure" indices) as primary constraints on vegetation pattern (Whittaker, 1975; Stephenson, 1990). Our primary study objective was to determine the relationship

between stand-level rates of development and structural attributes of expanding western juniper woodlands with two topographic features commonly important to forest vegetation patterns, site exposure (slope and aspect) and elevation (e.g. Taylor, 1990; Parker, 1989, 1991, 1992, 1995). Describing stand-level variation in the development of expanding woodlands over topographically diverse environments is important for forecasting windows of opportunity for management actions in restoration planning.

Specific questions we addressed in this study were:

1. Does the rate of tree establishment increase with elevation and decrease with site exposure?
2. Do total and dominant tree densities increase with elevation and decrease with site exposure?
3. Does the length of time from stand establishment to the onset of dominant tree stress resulting from intraspecific competition decrease with elevation and increase with site exposure?

2. Study area and methods

2.1. Study region

Two study areas were located in the semiarid region of the Intermountain West on Steens Mountain, Harney County, southeastern Oregon (42°N 118°W), and two on South Mountain and Juniper Mountain, which form a part of the Owyhee Mountains, Owyhee County, southwestern Idaho (42°N 116°W). Climate, soils, and vegetation across the study areas are characteristic of those found in the High Desert, Klamath, Humboldt and the Snake River ecological provinces (Anderson et al., 1998; Bailey, 1994). Steens Mountain is approximately 80 km long and oriented in a northeast direction (Baldwin, 1981). Elevation of Steens Mountain ranges from 1268 to 2949 m, with a steep east-facing escarpment and a gentle west-facing slope. Geomorphology of Steens Mountain is characterized by nearly level basins and valleys that are bordered by long, gently sloping alluvial fans. Pliocene volcanic and shallow intrusive igneous rocks occur, along with andesite, breccias, and basalt flows. The geomorphology of the Owyhee Mountains is characterized as an uplifted region with doming and fault blocking common. The Owyhee Mountains are predominantly comprised of granite overlain by rhyolites and welded tuffs with silicic volcanic flows, ash deposits, and wind-blown loess. Topographic features of this area include mountains dissected by deep canyons, rocky tablelands, and rolling plains ranging in elevation between 1200 and 2375 m. Soils across the four woodlands vary from shallow rock outcrops to moderately deep gravelly, sandy, or silt loams. Predominant soil taxa are Aridisols, Entisols, Alfisols, Inceptisols, and Mollisols that occur in combination with mesic and frigid soil temperature regimes and xeric and aridic soil moisture regimes.

Climate across the two mountain ranges is characteristic of the northern Great Basin in that it is cool and semiarid. Mean annual precipitation within the juniper belt ranges between 300 mm at lower elevations increasing to >400 mm at higher

elevations (Oregon Climate Services, 2004). The majority of the annual precipitation is received as snow in November, December, and January and as rain March through June. Average temperatures vary from −6.6 °C in January to 34.5 °C in July. The growing season ranges from 90 to 120 days.

Western juniper woodlands form a discontinuous belt between 1450 and 2100 m in elevation on Steens Mountain and a near continuous belt on South and Juniper Mountains between 1300 and 2100 m. Above 2100 m, extremes in temperatures and severe winter conditions limit western juniper establishment (Miller and Rose, 1995). Limited western juniper distribution in the basins or below the toe-slopes of the mountains is likely an artifact of late spring frosts (Billings, 1954) coupled with limiting moisture. The Resources Conservation Service has described the areas' potential natural vegetation as sagebrush-grassland. Current vegetation is predominantly of two types, sagebrush-grasslands and western juniper woodlands (Burkhardt and Tisdale, 1976; Miller et al., 2000). Predominant potential vegetation occupying the uplands are: (1) mountain big sagebrush associated with bluebunch wheatgrass (*Agropyron*

spicatum), Idaho fescue (*Festuca idahoensis*), or Thurber needlegrass (*Stipa thurberiana*) on relatively deep, well-drained soils and (2) low sagebrush (*Artemisia arbuscula* var. *arbuscula*) associated with bluebunch wheatgrass, Idaho fescue, or Sandberg bluegrass (*Poa secunda*) over restrictive layers of claypan or bedrock (Burkhardt and Tisdale, 1976).

2.2. Methods

We established four transects extending a total of 68 km in 2001 across four different western juniper woodlands (Fig. 1). Each of the four transects were located along an elevational gradient extending from the lower to upper boundaries of each woodland. We used both field reconnaissance and aerial photos to position transects in areas where there was minimal evidence of woodland disturbance since the early 1900s and to ensure sampling represented a wide array of environmental variables typical of sites occupied by western juniper.

To determine how site exposure and stand elevation affect woodland development and structure, circular plots were
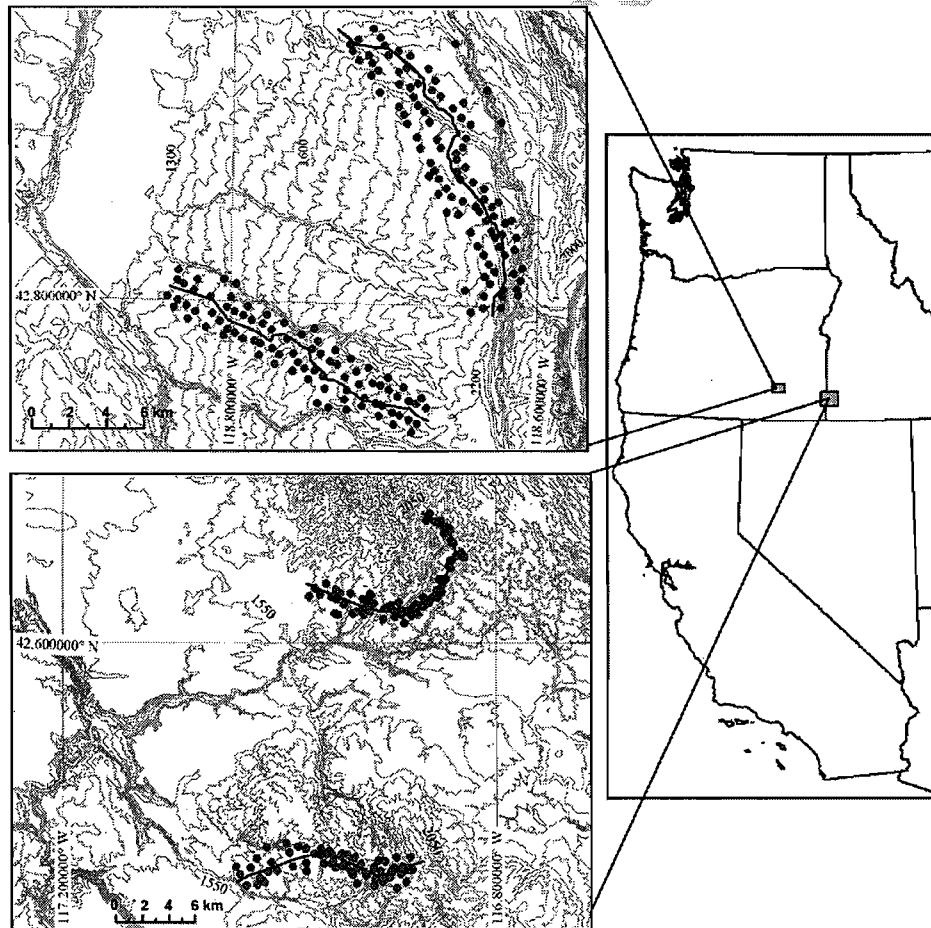

Fig. 1. Map of the study locations in Oregon (top left) and Idaho (bottom left). Three plots circular plots were placed approximately every 500 m along three parallel transects spaced 500 m apart; plot locations were adjusted to fit within a uniform stand at least 0.5 ha in size with uniform characteristics (e.g. aspect, topography, soil, and vegetation). Middle transect lines were located along roads to optimize sampling efficiency and extended from the low to upper elevation boundaries of each woodland.

placed approximately every 500 m along three parallel transects spaced roughly 500 m apart (Fig. 1). For this study we only report plots falling within the mountain big sagebrush alliance ($n = 186$). We adjusted plot locations to fit within a uniform stand at least 0.5 ha in size and representing a single ecological site with uniform characteristics (e.g. aspect, topography, soil, and vegetation). A variable plot radius was employed, scaled to tree density. The plot radius was selected at each location based on a cursory estimation of stand density: 15, 20, and 30 m radiuses were employed on plots with greater than 600 trees/ha, between 200 and 600 trees/ha, and with less than 200 trees/ha, respectively.

We identified and recorded dominant understory plant species and wood remnants to determine the potential plant alliance and association. UTM coordinates, percent slope, aspect, elevation, and topographic position were recorded for each plot. Due to its circular nature, aspect is a poor variable for quantitative analysis. Although 1° and 360° represent about the same aspect, the numbers are very different. To alleviate difficulties in using aspect as a variable in our analyses, we used the following equation (Balice et al., 2000) that rescales aspect to a north/south axis and weights aspect exposure by steepness of slope to generate a unitless index of a site's insolate exposure:

site exposure

$$= \text{percent slope} \times \text{cosine}(\pi(\text{aspect} - 180)/180) \quad (1)$$

where cosine is in radians and degrees east of north.

For each plot we also identified the phase of woodland development (i.e. I, II, III or early, mid, and late successional) following the guidelines developed by Miller et al. (2000, 2005). Tree canopy cover during phase I is typically less than 10%, comprised primarily of juveniles (<1 m) and saplings (1–3 m), whereas phase II stands can be comprised of interspersed older dominant trees among young trees and commonly approach cover values of 10–49%, depending on the ecological site. Characteristics employed for differentiation between phases II and III follow: (1) terminal and lateral leader growth exhibited by understory trees located in tree interspace are suppressed by intraspecific competition as stands approach phase III (threshold ∼ terminal 10 cm, lateral 6 cm) (Miller et al., 2000), and (2) during phase II a portion the shrub layer remains intact but with obvious mortality, whereas during phase III live shrubs are nearly to completely absent and dead shrub skeletons are common to abundant.

Tree density was counted and recorded in size classes. Classes were based on tree height and age consisting of the following: (1) juvenile <1 m, (2) sapling 1–3 m, (3) sub-dominant 3 m to 75% of the potential maximum height yielded by a particular site, (4) dominant >75% of the potential maximum height, and (5) pre-settlement >150 years. Potential height was assumed to be the height of the tallest mature tree present in the primary canopy of the stand. Pre-settlement trees (>150 years) were identified in the field using morphological characteristics described by Waichler et al. (2001) and Miller et al. (2005).

To estimate the period of initial western juniper post-settlement encroachment, the three tallest post-settlement trees were aged. An increment core was collected at 30 cm above ground level. Cores were brought back to the laboratory at the Eastern Oregon Agricultural Research Center, mounted, sanded until the cell structure was visible with a binocular microscope, and rings counted. Most cores (98%) intersected or were within 10 rings of the pith. For samples that did not include the pith, we used transparent overlays of concentric circles to estimate the number of rings to pith (Villaba and Veblen, 1997). Thirty juvenile trees (15–45 cm) growing in the tree interspace of open (phase I) woodlands were sampled and aged to correct for core sample height.

To estimate the number of years for the development of woodlands to approach the onset of dominant tree stress (i.e. transition from phase II to phase III) we collected an additional 12 tree cores per plot from sub-canopy and dominant trees in a subsample of 13 phase III plots to attain relative growth rates. We also collected 12 cores from 7 phase I stands for comparison. Individual years were identified and ring widths (i.e. distance between successive growth rings) were measured on each core sample to the nearest 0.001 mm using an Acu-Rite Slide Table, Velmex Quick-Check 100 Meter, and Measure J2X v. 3.1 release 25 software. We did not include ring widths for the first 25 years (juvenile stage) for each core. During the early stages of growth western juniper trees are putting a greater proportion of growth into root development (Kramer, 1990) resulting in slower above ground growth (Tausch and West, 1995; Miller and Tausch, 2001). Samples were compiled for each plot and a mean ring width was calculated for each year. Tree rings were cross-dated to ensure years were properly matched across core samples within plots. The mean ring width for each year was divided by the overall mean ring width across years for each plot, and resulting relative growth rates were plotted graphically to estimate years transpired from the beginning of stand development to phase III woodlands. For phase III stands, relative growth curves were evaluated to determine when a constriction in ring widths occurred. A persistent constriction in ring widths remaining below the long term average was assumed to be indicative of the onset of dominant tree stress resulting from intraspecific competition, thereby signifying the approximate time the woodland transitioned to phase III. This procedure yielded estimates of time in years transpired since initial post-settlement tree establishment, estimated by aging the three tallest trees, until phase III.

2.3. Data analyses

To address the question of the relationship of the response variables (Table 1) with site exposure and elevation among phase III juniper stands the following regression model was fit to the data:

$$Y_i = \beta_0 + \beta_1 \times X_{1i} + \beta_2 \times X_{2i} + \varepsilon_i \quad (2)$$

where Y_i is any of the response variables, βs are the linear regression coefficients, $\varepsilon_i \sim N(0, \sigma_\varepsilon^2)$ and ε_i and $\varepsilon_{i'}$ are

Table 1
Description of the response variables

Model	n	Description of response variable	Mean	Min	Max
Rate of post-settlement juniper establishment	77[a]	Number of post-settlement trees established per hectare per year	5.7 ± 3.7	1.2	15.9
Time required to reach phase II	13[b]	Time transpired since initial tree establishment until phase III	90.2 + 17.1	75	135
Total tree density[c]	77[a]	Total density of trees	737.9 + 451.4	155.0	2037.0
Dominant tree density[c]	77[a]	Density of dominant trees (i.e. those trees comprising the primary canopy of a stand)	154.3 ± 88.0	24.0	399.0

[a] Analysis limited to late phase juniper stands associated with mountain big sagebrush.

[b] Analysis limited to late phase juniper stands associated with mountain big sagebrush that were sampled on Juniper Mountain, Idaho in 2002 in which relative growth curves were developed.

[c] Initial analyses suggested the need for log transformation of the response variable to equalize variance over the range of explanatory variables.

independent. X_{1i} is the site exposure index for the ith stand, X_{2i} the elevation in meters for the ith stand, β_1 the estimate of the regression of Y on site exposure, β_2 the estimate of the regression of Y on elevation and ε_i is the random effect of each stand that adds variability to the value of Y.

This model assumes a linear relationship between the response and the explanatory variables. In addition, the model assumes that variance in the response variables among stands with similar values of the explanatory variables is the same as the variance in the response variables among stands with different values of the explanatory variables. The need for log transformation of the response variables in order to meet model assumptions was evaluated prior to interpretation of models.

3. Results

3.1. Influence of site exposure and elevation on rates of tree establishment

Based on the year of stand initiation and tree density at the time of measurement, the rate of tree establishment (# trees established/ha/year): (1) decreased with increasing site exposure (i.e. increasing southerly exposure) and (2) increased with increasing stand elevation (Fig. 2). The regression model describing this relationship was (standard errors in parentheses below parameter estimates):

rate of juniper establishment

$$= \underset{(4.73)}{-10.41} - [\underset{(0.028)}{0.25}\,(\text{exposure}) + \underset{(0.0026)}{0.009}\,(\text{elevation})] \quad (3)$$

with residual error = 2.4. The adjusted r^2 was 0.6.

A 20-unit increase in site exposure (e.g. contrast of stands developing on similar hill slopes and elevation but facing south instead of north) was associated with a 4.9 trees/ha/year decrease in the mean rate of woodland establishment among stands developing at similar elevation (95% CI: 3.8–6.0 trees/ha/year). A 200 m rise in elevation was associated with a 1.8 trees/ha/year increase in the rate of woodland establishment among stands with similar exposure (95% CI: 0.8–2.9 trees/ha/year).

3.2. Influence of site exposure and elevation on rates of stand development

Relative growth rates in phase III stands all showed a distinct decline in ring width during stand development. Relative growth rates among phase III stands that initiated expansion between 1850 and 1870 began a decline 70–120 years later depending on insolation exposure and elevation. Although similar climatic signatures are apparent, tree ring widths in phase I stands, occupied by a low density of trees, did not show a similar decline in relative growth rate that was observed in phase III stands (Fig. 3).

The number of years required to reach phase III (the number of years from stand initiation to a persistent decline in relative growth rate) increased with increasing southerly exposure and decreased with increasing elevation (Fig. 4). The regression
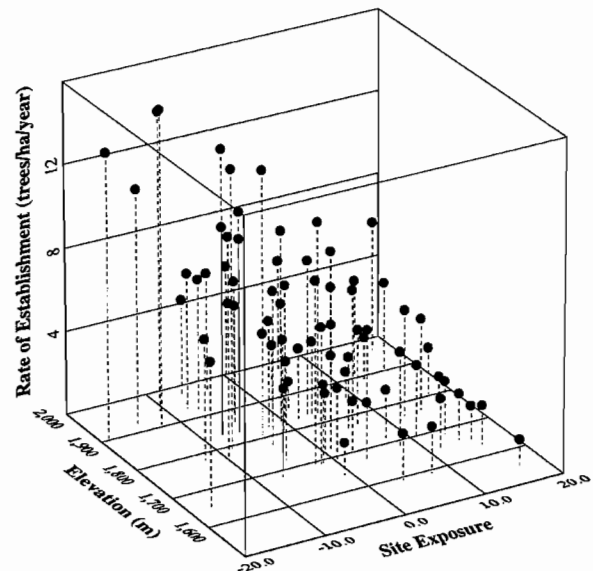

Fig. 2. Relationship of rate of establishment with elevation (m) and site exposure in stands associated with mountain big sagebrush. Site exposure becomes increasingly warmer to the right.
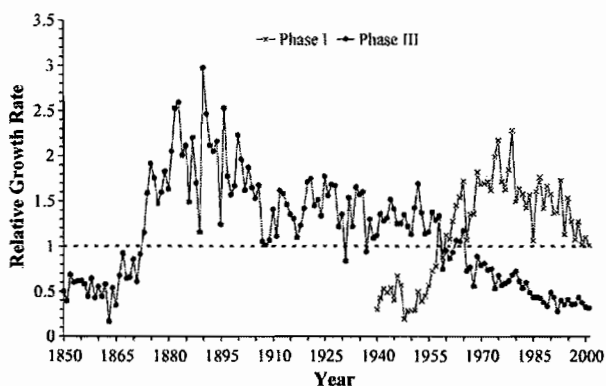
Fig. 3. Display showing relative growth rates (ratio of annual ring width over mean ring width) over time of a phase I juniper stand that established in 1940 and a phase III stand that established in 1850 on Juniper Mountain, Idaho. Notice the dashed line represents a 1:1 ratio with the overall mean tree ring width and during the time period 1950–1960 ring widths declined to well below the long term average suggesting increased competition among trees in phase III. Also notice this trend was not observed in phase I stands.

model describing this relationship was (standard errors in parentheses):

years until phase III

$$= \underset{(45.58)}{193.66} + [\underset{(0.117)}{0.48} (\text{exposure})] - [\underset{(0.025)}{0.052}(\text{elevation})] \tag{4}$$

residual error = 4.29, adjusted r^2 was 0.73.

A five-unit increase in site exposure (e.g. contrast of stands on similar hill slopes and elevation but facing south instead of east) was associated with a 2.4 year increase in the time required to reach phase III among stands that have developed at

similar elevations (95% CI: 1.13–3.67 year). A 100 m rise in elevation was associated with a 5-year decrease in the time required for a stand to reach phase III on sites with similar exposure (95% CI: 0.37–10.81 years).

3.3. Influence of site exposure and elevation on tree density

Total density of western juniper in phase III stands ranged between 155 and 2037 trees/ha. Total live juniper density increased with increasing elevation and decreased with increasing site exposure (i.e. increasing southerly exposure) in stands associated with mountain big sagebrush (Fig. 5). To meet the models assumptions the response variable (total tree density) was log transformed. The final regression model was:

log(total tree density)

$$= \underset{(0.705)}{2.59} - [\underset{(0.004)}{0.036}(\text{exposure})] + [\underset{(0.0004)}{0.0022}(\text{elevation})] \tag{5}$$

residual error = 0.356 and adjusted r^2 was 0.65.

A five-unit increase in site exposure (e.g. contrast of stands on similar hill slopes and elevation but facing south instead of east) was associated with an 18% decrease in total tree density (95% CI: 14–22%). A 100 m rise in elevation was associated with a 22% increase in total tree density among stands with similar site exposure (95% CI: 14–30%). Density of dominant trees in phase III plots varied from 24 to 399 trees/ha. Dominant tree density (number of trees/ha comprising the upper 75% of the canopy) increased with increasing elevation and decreased with increasing site exposure (i.e. increasing southerly exposure) in stands associated with mountain big sagebrush (Fig. 6). The final regression model describing this relationship was as follows with standard errors in parentheses below the
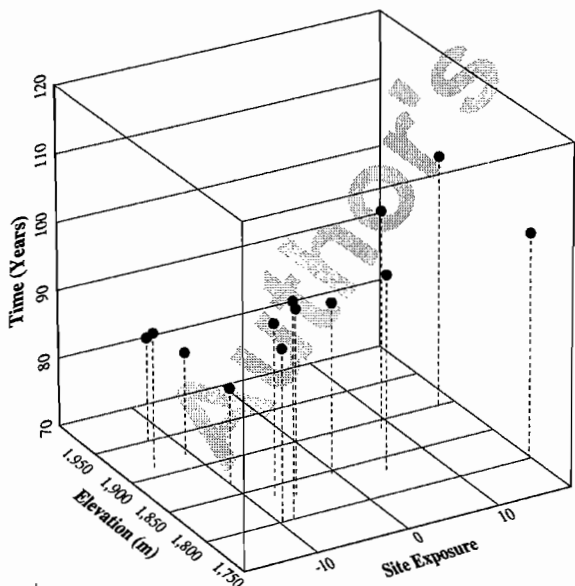

Fig. 4. Relationship of time required to reach phase III with elevation (m) and site exposure in stands associated with mountain big sagebrush. Site exposure becomes increasingly warmer to the right.
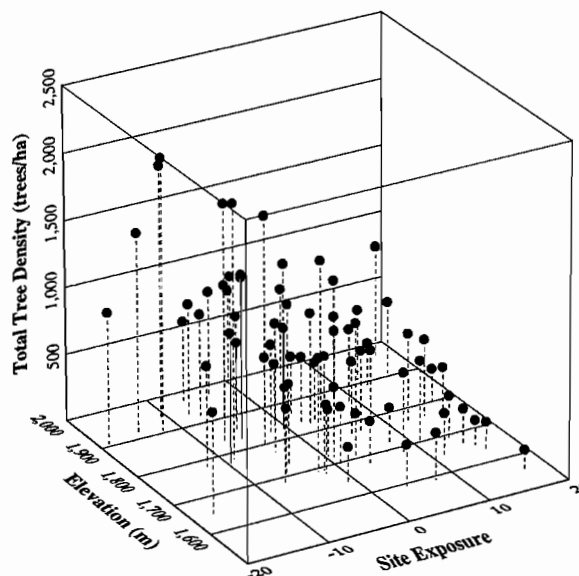

Fig. 5. Relationship of total live juniper density with elevation (m) and site exposure in stands associated with mountain big sagebrush. Site exposure becomes increasingly warmer to the right.
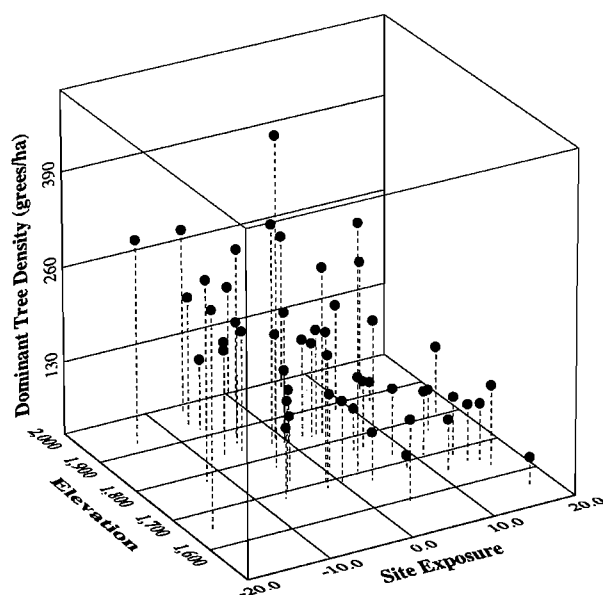
Fig. 6. Relationship of dominant juniper density with elevation (m) and site exposure in stands associated with mountain big sagebrush. Site exposure becomes increasingly warmer to the right.

estimates (response variable log transformed to meet model assumptions):

log(dominant tree density)

$$= \underset{(0.836)}{2.62} - \underset{(0.005)}{[0.026(\text{exposure})]} + \underset{(0.0001)}{[0.001\,(\text{elevation})]} \quad (6)$$

residual error = 0.36 and adjusted r^2 was 0.49.

A five-unit increase in site exposure (e.g. contrast of stands on similar hill slopes and elevation but facing south instead of east) was associated with a 15.4% decrease in the density of dominant overstory trees (95% CI: 9.6–21%). A 100 m rise in elevation was associated with a 22% increase in dominant tree density among stands with similar site exposure (95% CI: 8–11%).

4. Discussion

Many authors have speculated that fire played a significant role influencing landscape vegetation pattern and plant composition in shrub steppe, riparian, and aspen communities in Intermountain West prior to the late 1800s (Tausch et al., 1981; Miller and Tausch, 2001; Wall et al., 2001). However, during the process of woodland encroachment in these communities, an ecological threshold is crossed in which disturbance, in the form of fire, ceases to operate as an important driving factor of landscape vegetation patterns and plant composition (Miller et al., 2000, 2005). Instead, environmental factors pertaining to the site become important determinants of structure and developmental rates of expanding woodlands. Our findings indicate that two topographic features commonly important to forest vegetation patterns, site exposure and elevation, explained much of the variation in the structure and development of western

juniper stands occurring on different landscape positions. We assumed site exposure and elevation created a gradient of site available moisture over the landscape, resulting in varying rates of tree establishment and growth. Similar to the results presented in this study, several authors have also inferred that topographic position creates variable patterns of resource availability influencing the composition and productivity of forests (e.g. Iverson et al., 1997; McNab, 1989, 1993; Taylor, 1990; Parker, 1991, 1992, 1995).

The decline we observed in relative growth rates by phase III suggested the intensity of intraspecific competition had approached a sufficient level to cause dominant tree stress. Although similar climatic signatures are apparent, tree ring widths in phase I stands, occupied by a low density of trees, did not show a similar decline in relative growth rates that was observed in phase III stands. We speculated that during the period of decline in relative tree growth rates, transitional shrub-steppe woodlands were crossing a threshold from phase II to III. This transition occurred over a 10-year period that likely coincided with a rapid loss of shrubs and possibly a decline in herbaceous vegetation in response to a reduced availability of resources. Several studies have reported declines in shrub and herbaceous layers throughout the Intermountain West as juniper and pinon increase in dominance (Cottam and Stewart, 1940; Adams, 1975; Tausch and West, 1995; Miller et al., 2000). Tausch and West (1995) and Miller et al. (2000) estimated that as trees approached 50% of maximum potential stocking for a site, big sagebrush cover and biomass declined to approximately 20–25% of maximum potential.

Based on western juniper age chronology, Johnson (2005) reported stands on northerly exposures and in the upper elevation of the woodland belt were capable of attaining minimum stocking densities (approximate density of seedlings, once mature and comprising the dominant primary canopy, that uses site resources to the exclusion of the understory) of around 250 trees/ha over a 20-year period. On drier sites, 40+ years were required to achieve minimum stocking densities of fewer than 100 trees/ha. In this study we observed similar trends in time required to reach critical stages in stand development. We found that although dry sites supported fewer total trees in phase III than mesic sites (<350 trees/ha as opposed to >800 trees/ha, respectively), phase III occurred within >120 years on warm dry sites compared to only 80 years on mesic sites. These results are similar to those reported by Miller et al. (2000) who concluded phase III western juniper stand densities varied from 222 to 481 trees/ha in mountain big sagebrush/Thurber needlegrass (warm dry) associations to 247–716 trees/ha in mountain big sagebrush/Idaho fescue (cool wet) associations. Based on tree age chronology they also concluded that the time required for woodland closure was highly variable depending on site potential and estimated the minimum time for stands to approach phase III on mesic sites was 60–70 years. Several others have reported that the minimum time required reaching phase III is 60–90 years (Barney and Frischknecht, 1976; Tausch and West, 1995; Miller and Rose, 1999; Miller et al., 1999). The rate of juniper above ground shoot and leaf development may also influence the timing when stands

approach the threshold of tree dominance on a site. Tree canopy development in western and Utah junipers (*Juniperus osteosperma*) is usually relatively slow during the first 45–50 years compared to the second 50 years of growth (Tausch and West, 1995; Miller and Tausch, 2001). This would suggest that the rate of woodland development would begin to increase as tree stands approach 50 years of age. These estimates were found to be reasonable in this study on more productive sites (i.e. northerly exposed sites at higher elevations), however, it was generally found that less productive sites (i.e. southerly exposed sites at lower elevations), although supporting fewer total trees, require a longer time period to reach phase III.

Our findings indicated that the rate of western juniper establishment and tree density increased with elevation and northerly exposure. The conceptual model shown in Fig. 7 represents three hypothesized phases of stand development for western juniper encroachment in mountain big sagebrush steppe communities. The three dashed lines in the model represent mean rates of tree establishment (trees/ha/year) for stands developing under varying levels of insolate exposure and at different elevations. The estimates in the conceptual model represent mean rates of tree establishment for specific levels of site exposure and elevation, thus one needs to realize that a continuum exists between them. In addition, rates of tree establishment during phase I is a major factor determining the rate of woodland development. Initial stocking density is a function of successful establishment, which is influenced by the spatial distribution of seed dissemination, resource availability, climate, and safe sites. Johnson (2005) found a significant relationship between the presence of nearby pre-settlement trees (>150 years) and the initiation of post-settlement (<150 years) stands of western juniper. Pre-settlement juniper was primarily confined to fuel-limited or fire-insulated sites (Dealy et al., 1978; Martin, 1978; Miller and Rose, 1995, 1999). Thus, with a greater probability of the historic seed trees occurring on more fuel-limited south exposures, the dispersal distance was likely greater and encroachment may have been slower on more

mesic aspects. Therefore, our estimates of enhanced juniper encroachment on less severe sites may be conservative in nature. Seed dispersal mechanisms and safe sites were assumed to be in place and not limiting tree establishment in our conceptual model, so transitions between phases occur as a function of density of established trees, canopy cover, and time.

The model presented in Fig. 7 provides an estimate of the time required for stands to achieve critical stages in their development based on elevation and site exposure. Since we know that juniper is most easily controlled early in development prior to displacement of understory shrub and herbaceous species (Martin, 1978; Bunting, 1984; Miller et al., 2000), this model points out windows of opportunity for less costly management. It also estimates the time required during woodland development for transition across an important management threshold. Once trees begin competing with one another and understory shrub and herbaceous components decline during the transition from phase II to III, management is relegated to mechanical means of treatment prior to prescribed fire.

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References

Adams, A.W., 1975. A brief history of juniper and shrub populations in southern Oregon. Oregon State Wildl. Comm. Res. Div. Wildl. Res. Rep. No. 6, Corvallis, OR.

Anderson, E.W., Borman, M.M., Krueger, W.C., 1998. Ecological Provinces of Oregon: A Treatise on the Basic Ecological Geography of the State. Ore. Agric. Exp. Sta., Oregon State University, Corvallis, OR.

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

Archer, S., Scifres, C., Bassham, C.R., 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecol. Monogr. 58, 111–127.

Bailey, R.G., 1994. Descriptions of the Ecoregions of the United States. U.S. For. Ser., Misc. Pub. 1391.

Baldwin, E.M., 1981. Geology of Oregon. Kendal/Hunt Publishing Co., Dubuqe, IA.

Balice, R.G., Miller, J.D., Oswald, B.P., Edminister, C., Yool, S.R., 2000. Forest surveys and wildfire assessment in the Los Alamos region, 1998–1999. Los Alamos Nat. Lab., LA-13714-MS.

Barney, M.A., Frischknecht, N.C., 1976. Vegetation changes following fire in the pinyon-juniper type of west-central Utah. J. Range Manage. 27, 91–96.

Bates, J.D., Svejcar, T.J., Miller, R.F., 2002. Effects of juniper cutting on nitrogen mineralization. J. Arid Environ. 51, 221–234.

Billings, W.D., 1954. Temperature Inversion in the Pinyon-Juniper Zone of a Nevada Mountain Range, vol. 12. Bulter Univ. Bot. Studies.

Bunting, S.C., 1984. Prescribed burning of live standing western juniper and post-burning succession. In: Bedell, T.E. (compiler), Proceedings of the Western Juniper Short Course. Ore. State Univ. Ext. Ser, Corvallis, OR, pp. 69–73.

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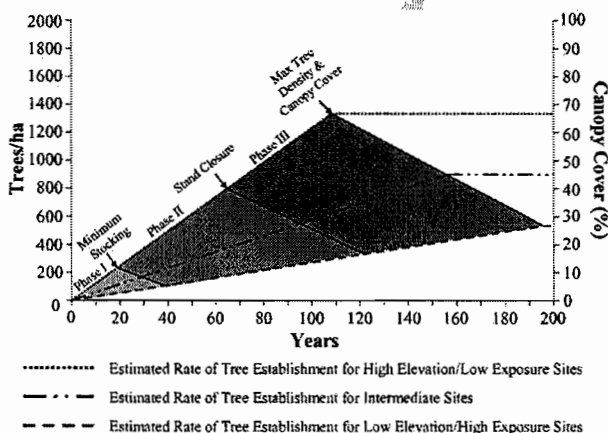

Fig. 7. Display showing the hypothesized time periods from initial tree establishment (early phase I) to minimum stocking adequate for phase III, and estimated maximum potential for tree density and cover for stands developing on varying insolation exposures and elevations.

Cronquist, A., Holmgren, A.H., Holmgren, N.H., Reveal, J.L., 1972. Inter-mountain Flora: Vascular Plants of the Intermountain West, USA. Hafner Publishing Co., Inc., NY.

Cottam, W.P., Stewart, G., 1940. Plant succession as a result of grazing and of meadow desiccation by erosion since settlement in 1862. J. For. 38, 613–626.

Dealy, J.E., Geist, M.J., Driscoll, R.S., 1978. Communities of western juniper in the Intermountain northwest. In: Martin, R.E., Dealy, J.E., Caraher, D.L. (Eds.), Proceedings of the Western Juniper Ecology and Management Workshop. U.S. For. Ser. Gen. Tech. Rep. PNW-74. pp. 11–29.

Iverson, L.R., Dale, M.E., Scott, C.T., Prasad, A., 1997. A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (USA). Landsc. Ecol. 12, 331–348.

Johnson, D.D., 2005. The influence of environmental attributes on temporal and structural dynamics of western juniper woodland development and asso-ciated fuel loading characteristics. MS Thesis, Oregon State University, Corvallis, OR, 112 pp.

Klopatek, J.M., 1987. Nitrogen mineralization and nitrification in mineral soils of pinyon juniper ecosystems. Soil Sci. Soc. Am. J. 51, 453–457.

Knapp, P.A., Soulé, P.T., 1996. Vegetation change and the role of atmospheric CO_2 enrichment on a relict site in central Oregon: 1960–1994. Ann. Assoc. Am. Geogr. 86, 387–411.

Koniak, S., Everett, R.L., 1982. Seed reserves in soils of successional stages of pinyon woodlands. Am. Midl. Nat. 108, 295–303.

Kramer, S., 1990. Development and morphology of juvenile western juniper (*Juniperus occidentalis* Hook.). MS Thesis, Oregon State University, Corvallis, OR.

Martin, R.E., 1978. Fire manipulation and effects in western juniper (*Juni-perus occidentalis* Hook.). In: Martin, R.E., Dealy, J.E., Caraher, D.L. (Eds.), Proceedings of the Western Juniper Ecology and Management Workshop. U.S. For. Ser. Gen. Tech. Rep. PNW-74. pp. 121–136.

McNab, H.W., 1989. Terrain shape index: quantifying effect of minor landforms on tree height. For. Sci. 35, 91–104.

McNab, H.W., 1993. A topographic index to quantify the effects of mesocsale landform on site productivity. Can. J. For. Res. 23, 1100–1107.

Miller, R.F., Bates, J.D., Svejcar, T.J., Pierson, F.B., Eddleman, L.E., 2005. Biology, Ecology, and Management of Western Juniper (*Juniperus occi-dentalis*). Ore. State Univ. Agric. Exp. Sta. Tech. Bull. No. 152, 77 pp.

Miller, R.F., Rose, J.A., 1999. Fire history and western juniper encroachment in sagebrush steppe. J. Range Manage. 52, 550–559.

Miller, R.F., Rose, J.A., 1995. Historic expansion of western juniper (*Juniperus occidentalis*) in southeastern Oregon. Gt. Basin Nat. 55, 37–45.

Miller, R.F., Svejcar, T.J., Rose, J.A., 2000. Impacts of western juniper on plant community composition and structure. J. Range Manage. 53, 574–585.

Miller, R.F., Tausch, R.J., 2001. The role of fire in pinyon and juniper woodlands: a descriptive analysis. In: Galley, K.E.M., Wilson, T.P. (Eds.), Proceedings of the Invasive Species: The Role of Fire in the Control and Spread of Invasive Species. Misc. Publ. No. 11, Tall Timbers Res. Sta., Tallahassee, FL, pp. 15–30.

Miller, R.F, Tausch, R.J., Waichler, W., 1999. Old-growth juniper and pinyon woodlands. In: Monsen, S.B., Stevens, R., Tausch, R.J., Miller, R.F. (compilers), Proceedings of the Ecology and Management of Pinyon-juniper Communities within the Interior West. U.S. For. Ser. Proc. RMRS-P-9, pp. 375–384.

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

Ohmann, J.L., Spies, T.A., 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forest. Ecology 81, 3237–3243.

Oregon Climate Services, 2004. Spatial climate analysis service, Oregon State University. http://www.ocs.oregonstate.edu/prism/.

Parker, A.J., 1989. Forest/environment relationships in Yosemite National Park, California, USA. Vegetation 82, 41–54.

Parker, A.J., 1991. Forest/environment relationships in Lassen Volcanic National Park, California, USA. J. Biogeogr. 18, 543–552.

Parker, A.J., 1992. Spatial variation in diameter structures in forest of Lassen Volcanic National Park, California. Prof. Geogr. 44, 147–160.

Parker, A.J., 1995. Comparative gradient structure and forest cover types in Lassen Volcanic and Yosemite National Parks, California. Bull. Torrey Bot. Club 122, 58–68.

Reinkensmeyer, D.P., 2000. Habitat associations of bird communities in shrub-steppe western juniper woodlands. MS Thesis, Oregon State University, Corvallis, OR, 85 pp.

Schofield, C.J., Bucher, E.H., 1986. Industrial contributions to desertification in South America. Trends Ecol. Evol. 1, 78–80.

Stephenson, N.L., 1990. Climatic controls on vegetation distribution: the role of the water balance. Am. Nat. 135, 649–670.

Tausch, R.J., West, N.E., 1988. Differential establishment of pinyon and juniper following fire. Am. Midl. Nat. 119, 174–184.

Tausch, R.J., West, N.E., 1995. Plant species composition patterns with differences in tree dominance on a southwestern Utah piñon-juniper site. In: Shaw, D.W., Aldon, E.F., LoSapio, C. (tech. coordinators), Proceedings of the Desired Future Conditions for Piñon-Juniper Ecosystems. U.S. For. Ser. Gen. Tech. Rep. RM-258, pp. 16–23.

Tausch, R.J., West, N.E., Nabi, A.A., 1981. Tree age and dominance patterns in Great Basin pinyon-juniper woodlands. J. Range Manage. 34, 259–264.

Taylor, A.H., 1990. Habitat segregation and regeneration patterns of red fir and mountain hemlock in ecotonal forest, Lassen Volcanic National Park, California. Phys. Geogr. 11, 36–48.

Tilman, D., 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, NJ.

Villaba, R., Veblen, T.T., 1997. Regional patterns of tree age structures in northern Patagonia: climate and disturbance effects. J. Ecol. 85, 113–124.

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

Walker, J., Gillison, A.N., 1982. Australian savannas. In: Huntely, B.J., Walker, B.H. (Eds.), Ecology of Tropical Savannas. Springer-Verlag, NY, pp. 5–24.

Wall, T.G., Miller, R.F., Svejcar, T.J., 2001. Western juniper encroachment into aspen communities in the northwest Great Basin. J. Range Manage. 54, 691–698.

West, N.E., 1999. Juniper-pinyon savannas and woodlands of western North America. In: Anderson, R.C., Fralish, J.S., Baskin, J.M. (Eds.), Savannas, Barrens, and Rock Outcrop Plant Communities of North America. Cam-bridge University Press, London, England, pp. 288–308.

West, N.E., Tausch, R.J., Rea, K.H., Tueller, P.T., 1978. Phytogeographical variation within juniper-pinyon woodlands of the Great Basin. Gt. Basin Nat. Mem. 2, 119–136.

Whittaker, R.H., 1975. Communities and Ecosystems, 2nd ed. Macmillan, NY.