Intermountain Presettlement Juniper: Distribution, Abundance, and Influence on Postsettlement Expansion

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Abstract

Successful implementation of watershed restoration projects involving control of piñon and juniper requires understanding the spatial extent and role presettlement trees (> 140 yr) play in the ecology of Intermountain West landscapes. This study evaluated the extent, abundance, and spatial pattern of presettlement western juniper (*Juniperus occidentalis* Hook.) in four woodlands located in southeast Oregon and southwest Idaho. The potential for modeling presence/absence of presettlement juniper using site characteristics was tested with logistic regression and the influence presettlement trees had on postsettlement woodland (trees < 140 yr) expansion was evaluated with a Welch's *t*-test. Pre- and postsettlement tree densities, tree ages, site characteristics, and understory vegetation were measured along four 14–27 km transects. Presettlement juniper occurred in 16%–67% of stands in the four woodlands and accounted for 1%–10% of the population of trees > 1 m tall. Presettlement trees were generally widely scattered and more common in lower elevation stands with greater surface rock cover and higher insolate exposure. Presettlement trees sparsely occupied productive sites on deeper soils in southwest Idaho, suggesting the area had sustained a different disturbance regime than southeast Oregon. Southwest Idaho might have experienced a high frequency of lower severity fire that afforded survival to widely distributed legacy trees. This supposition is in contrast to most reports of a disturbance regime including either stand replacement or frequent fire of sufficient intensity to preclude survival of trees to maturity. Stands sustaining presettlement trees initiated woodland expansion 24 yr earlier than stands lacking presettlement trees. Presettlement trees may serve as a seed source potentially reducing the longevity of juniper control treatments. For areas with greater abundances and spatial distribution of presettlement trees such as southwest Idaho, management maintaining low intensity fire or cutting treatments at frequencies of less than 50 yr should sustain relatively open stands.

Resumen

La implementación exitosa de proyectos de restauración de cuencas hidrológicas que involucran el control de "Piñon" y "Juniper" requiere de entender la cantidad espacial y el papel que los árboles (> 140 años) existentes desde antes de la colonización (precolonización) juegan en la ecología de los paisajes de los valles del oeste. Este estudio evaluó la cantidad, abundancia y patrón espacial del "Western juniper" (*Juniperus occidentalis* Hook.) de la precolonización en cuatro bosques localizados en el sudeste de Oregon y sudoeste de Idaho. El potencial para modelar la presencia/ausencia del "Juniper" de la precolonización usando características del sitio se probó con regresión logística; la influencia que los árboles de la precolonización tuvieron en la expansión de del bosque en la postcolonización (árboles < 140 años) fue evaluada con la prueba de t de Welch. Las densidades de árboles pre- y postcolonización, las edades de los árboles, las características del sitio y la vegetación del estrato herbáceo fueron medidas a lo largo de 14 transectos de 27 km. El "Juniper" precolonización ocurrió en 16%–67% de las poblaciones de los cuatro bosques y aportó de 1%–10% de la población de árboles mayores a 1 m de altura. Los árboles precolonización, generalmente estuvieron muy dispersos y fueron más comunes en las poblaciones de baja elevación con una mayor cobertura de rocas en la superficie y mayor exposición a la insolación. Los árboles precolonización ocuparon escasamente los sitios productivos de suelos profundos del sudoeste de Idaho, sugiriendo que el área había sostenido un régimen de disturbio diferente al sudeste de Oregon. El sudoeste de Idaho pudo haber experimentado una mayor frecuencia de fuegos de baja severidad que permitió la supervivencia de un legado de árboles ampliamente distribuido. Esta suposición esta en contraste a la mayoría de los reportes de un régimen de disturbio que incluye tanto el reemplazo de poblaciones o de fuegos frecuentes de intensidad suficiente para imposibilitar la supervivencia de los árboles en la madurez. Las poblaciones con árboles de precolonización iniciaron la expansión del bosque 24 años antes que las poblaciones carentes de ellos. Los árboles precolonización pueden servir como fuente de semilla, reduciendo potencialmente la longevidad de los tratamientos de control de "Juniper." Para áreas con altas abundancias y mayor distribución espacial de árboles precolonización, tales como las del sudoeste de Idaho, el manejo para mantener fuegos de baja intensidad o tratamientos de corte a frecuencias menores de 50 años deben mantener poblaciones relativamente abiertas.

Key Words: low sagebrush, mountain big sagebrush, old-growth, succession, western juniper

INTRODUCTION

Over the past several decades there has been an increasing emphasis on control of expanding piñon (*Pinus* spp.) and juniper (*Juniperus* spp.) woodlands throughout the Intermountain West for the purpose of restoring shrub–steppe plant

All scientific names used throughout the text are from USDA, NRCS. 2007. The PLANTS Database (http://plants.usda.gov, 3 August 2007). National Plant Data Center, Baton Rouge, LA 70874-4490, USA.

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communities, watersheds, wildlife habitat, and forage for livestock. The potential for accumulation of heavy fuels and associated impacts to the fire regime in mature postsettlement piñon and juniper woodlands has recently generated an even greater impetus for controlling expanding woodlands. The widespread removal of piñon and juniper, however, has increased awareness and concern over the proper identification and maintenance of presettlement woodlands ($>$ 140 yr of age). The current estimate of area occupied by piñon and juniper woodlands in the Intermountain West is 18.9 million ha (Miller and Tausch 2001). Although not based on quantitative data, woodlands present prior to Eurasian settlement of this region (approximately 1860) are estimated to have occupied less than 10% of the current distribution (Miller et al. 1999; Azuma et al. 2005). Past literature reporting on piñon and juniper, however, often has not distinguished between pre- and postsettlement woodlands. Thus, the abundance and spatial distribution of presettlement woodlands is poorly documented and probably varies across mountain ranges and ecological provinces and might account for well over 10% in some areas occupied by piñon or juniper (Miller et al. 2005).

With individual longevities commonly exceeding 500 yr, piñon–juniper woodlands comprise some of the oldest plant communities in the Intermountain West (Swetnam and Brown 1992; Waichler et al. 2001). Presettlement western juniper (*Juniperus occidentalis* Hook.) woodlands exhibit considerable diversity in structure and composition, varying from open shrub–tree savannas to nearly closed-canopy woodlands (Miller et al. 2005). These woodlands differ from expanding postsettlement woodlands in a variety of characteristics including tree size and morphology, accumulation of large dead wood, species composition, wildlife habitat structure, and ecosystem function (Waichler et al. 2001). Presettlement woodlands often provide unique values such as plant and animal habitat, biodiversity and genetic pools, and long-term climate records (Spices et al. 1988; Kaufmann et al. 1992). For example, Reinkensmeyer et al. (2007) reported significantly greater numbers of cavity-nesting birds and overall avian diversity in presettlement western juniper woodlands compared to postsettlement woodlands in eastern Oregon.

Successful implementation of watershed restoration projects involving control of piñon and juniper requires understanding the spatial extent and role presettlement trees ($>$ 140 yr) play in the ecology of Intermountain West landscapes. To address these issues, we developed three study objectives: 1) determine the distribution and composition of presettlement western juniper, both spatially and as a proportion of the total population sampled, of four woodlands located in southeast Oregon and southwest Idaho; 2) evaluate the potential for predicting presence/absence of presettlement juniper using site and vegetation characteristics; and 3) determine the influence presettlement trees had on initiation of postsettlement woodland expansion.

STUDY AREA

Four study areas were located in the semiarid region of the Intermountain West. Two woodlands were measured on Steens Mountain, in southeast Oregon, and two were measured on South and Juniper Mountains of the Owyhee Mountains in southwest Idaho (Fig. 1). Climate, soils, and vegetation across these areas are commonly found in portions of the High Desert, Klamath, Humboldt, and the Snake River ecological provinces. The Owyhee Mountains are located in Owyhee County, Idaho between the towns of Grand View, Idaho, and Jordan Valley, Oregon (lat 42°N, long 116°W), in the Humboldt Ecological Province. The geomorphology of this area is characterized as an uplifted region with doming and fault blocking common. Elevations range between 1 200 and 2 650 m. Steens Mountain is an isolated volcanic fault block that lies in the extreme northwest Basin and Range Province (Fenneman 1931) in Harney County, Oregon, south-southeast of Burns (lat 42°N, long 118°W) in the High Desert Ecological Province. The mountain is approximately 80 km long and oriented in a northeast direction (Baldwin 1981). Elevation of Steens Mountain ranges from 1 268 to 2 949 m.

Climate across the study areas is cool and semiarid. Mean annual precipitation within the juniper woodland belts ranges from 300 mm at lower elevations to $>$ 400 mm at higher elevations (National Oceanic and Atmospheric Administration 1982). The majority of 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. Soils vary from shallow rock outcrops to moderately deep gravelly, sandy, or silt loams.

Western juniper woodlands form a discontinuous belt between 1 450 and 2 100 m in elevation on Steens Mountain and a near continuous belt on South and Juniper Mountains between 1 300 and 2 100 m. Above 2 100 m, extremes in temperatures limit western juniper establishment (Miller and Rose 1995). Limited distribution below 1 500 m is probably the result of late spring frosts (Billings 1954), coupled with limiting moisture. The Natural Resources Conservation Service has described the areas as having sagebrush–grassland potential natural vegetation. Current vegetation is predominantly of two types, sagebrush–grasslands and western juniper woodlands (Burkhardt and Tisdale 1976; Johnson and Miller 2006). Predominant sagebrush–steppe vegetation occupying the uplands are 1) mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana* [Rydb.] Beetle) associated with either bluebunch wheatgrass (*Psuedorogenaria spicata* [Pursh] A. Love) or Idaho fescue (*Festuca idahoensis* Elmer) on relatively deep, well-drained soils and 2) low sagebrush (*Artemisia arbuscula* subsp. *arbuscula* Nutt.) associated with bluebunch wheatgrass, Idaho fescue, or Sandberg bluegrass (*Poa secunda* J. Presl.) over restrictive layers of claypan or bedrock (Burkhardt and Tisdale 1976).

METHODS

Field Sampling

Transects lines, varying in length from 14 to 27 km, were established in four woodlands located on north and south Steens Mountain and on South Mountain and Juniper Mountain in the Owyhee Mountains (Fig. 1). Transects were placed along an elevational gradient extending from the lower to upper boundaries of each woodland. Field reconnaissance and aerial photos were used to locate transects in areas with minimal evidence of woodland disturbance since the early

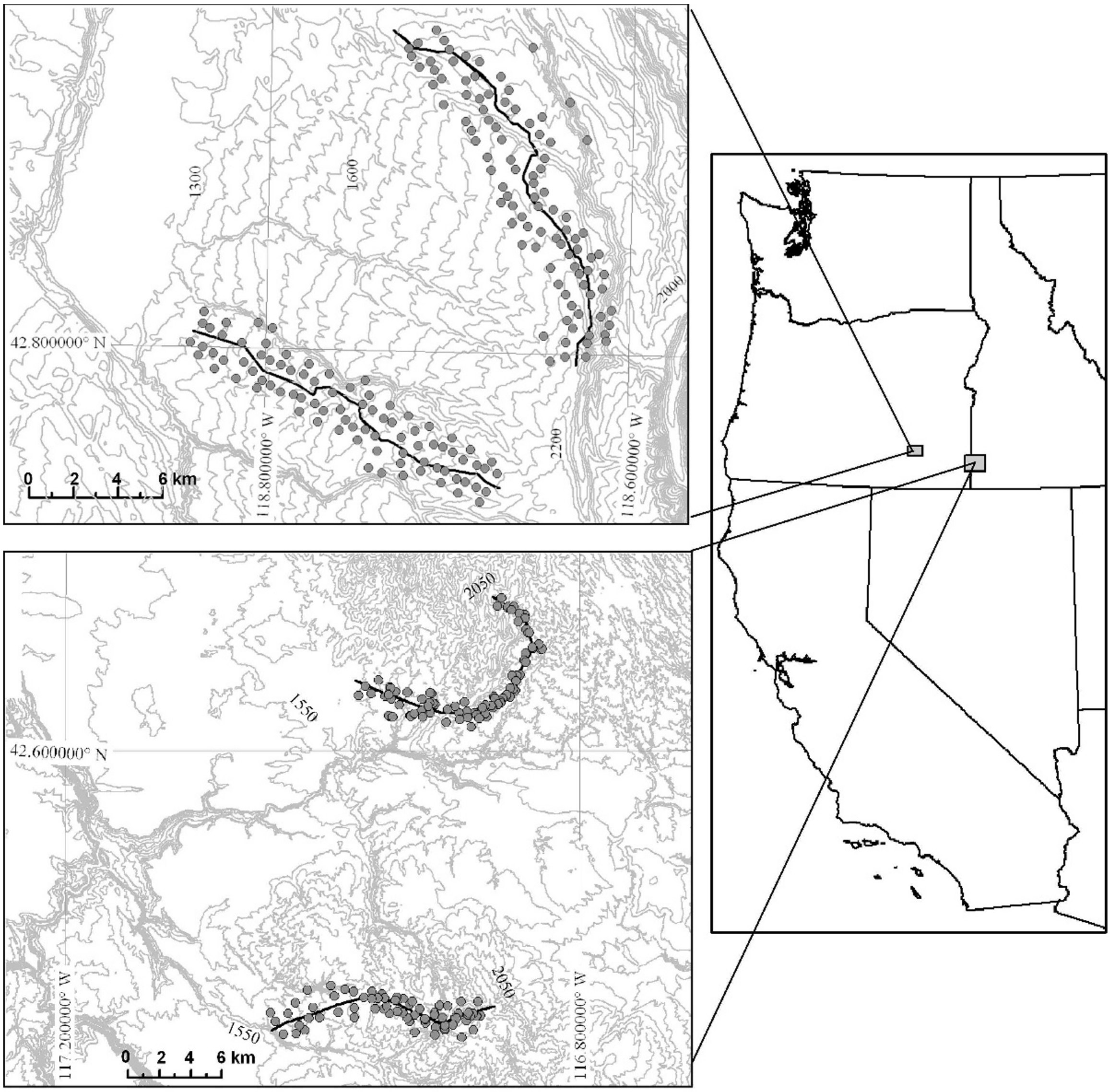

Figure 1. Map of the study locations on North and South Steens Mountain in southeast Oregon (top left) and South Mountain and Juniper Mountain in southwest Idaho (bottom left). Three circular plots were placed approximately every 500 m along three parallel transects spaced 500 m apart; plot locations 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).

1900s. Transects were denoted by their respective locations as follows: North Steens, South Steens, South Mountain, and Juniper Mountain.

Circular plots were placed approximately every 500 m along three parallel transects spaced roughly 500 m apart ($n = 342$; Fig. 1). 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 radii were employed on plots with greater than 600 trees $\cdot$ ha^{-1}, between 200 and 600 trees $\cdot$ ha^{-1}, and less than 200 trees $\cdot$ ha^{-1}, respectively. Because presettlement trees generally occurred in low densities, they were recorded in 30-m-radius plots.

We identified and recorded dominant understory plant species based on cover to determine the potential plant alliance and association (Grossman et al. 1998). Tree density was counted and recorded in three classes based on tree height and morphological characteristics: 1) juvenile, < 1 m; 2) postsettlement, > 1 m; and 3) presettlement, including remnants of large trees. In this study we defined presettlement trees as those establishing prior to Eurasian settlement in the region around 140 yr before present, an age when trees begin to morphologically differentiate from younger trees (Waichler et al. 2001; Miller et al. 2005). Presettlement trees were identified in the field using morphological differences between pre- and postsettlement-age-class trees as described by Waichler et al. (2001) and Miller et al. (2005). To determine the decadal frequency of postsettlement expansion, the three tallest postsettlement trees were aged using an increment core collected 30 cm above ground level. Cores were mounted, sanded until the cell structure was visible with a binocular microscope, and rings were 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

Table 1. Description of the response and candidate explanatory variables for the forward stepwise variable selection procedure.

Variable	Units	Description
Y	binomial response	Response variable equaling 1 if a presettlement tree was present in the stand and 0 if absent.
Elevation	meters	Height (m) above sea level of the stand.
Exposure	index	Unitless index of a site's insolation exposure.[1]
Rock	percent	Ocular estimate of the amount of soil surface covered by rock in each stand determined by averaging 30 regularly placed, 1-m^2 plots.
Topography	class	Categorical variable with three classes describing the topographic position on which the stand occurred: ridgetop, terrace, or sideslope.
Concavity	class	Categorical variable with three classes describing the curvature along the contour of sloping terrain: flat, convex, or concave.
Shrub	class	Categorical variable with four classes[2] describing the dominant shrub with which stands were associated.

[1]To alleviate difficulties in using aspect as a continuous 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 insolation exposure, calculated as: exposure = percent slope × cosine(π × [aspect − 180]/180).

[2]Classes consisted of mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana* [Rydb.] Beetle), low sagebrush (*Artemisia arbuscula* Nutt.), mountain snowberry (*Symphoricarpos oreophilus* A. Gray), and curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.).

number of rings to pith (Villaba and Veblen 1997). For each woodland, 30 juvenile trees (15 to 45 cm tall) were aged from interspace areas to correct for core sample height. In the early 1980s, the Laboratory of Tree Ring Research at the University of Arizona conducted an extensive sample of conifer species in the Pacific Northwest, including western juniper, to determine their tree-ring series dependability (Holmes et al. 1986). They reported that western juniper was one of several species that yield dependable tree-ring series for aging, cross-dating, and developing chronologies.

Analyses

Descriptive Analyses. Stands ($n = 340$) were stratified by study area, presence/absence of trees, presence/absence of presettlement trees, and associated shrub species to determine the potential plant alliance. We separated these strata into three classes: 1) postsettlement, trees > 140 yr of age absent; 2) mixed age, at least one tree to 75% of the trees were > 140 yr of age; and 3) presettlement, > 75% of the trees were > 140 yr. General comparisons of the abundance and distribution of pre- and postsettlement trees were made between study areas and plant alliances. Pre- and postsettlement tree densities were determined to describe general changes in the abundance of juniper across the study area since settlement.

Influence of Site Characteristics on Presence/Absence of Presettlement Juniper. The analysis employed binary logistic regression (SAS v.8.0; SAS Institute Inc., Cary, NC), which is used when the dependent variable is dichotomous and the independent variables are either categorical or continuous. Logistic regression overcomes many of the restrictive assumptions of ordinary least squares regression. It does not require the assumption of a linear relationship between the independent and dependent variables, and it is not necessary for the dependent variable to be normally distributed. There is no assumption of homogeneity of variance or normally distributed error terms, and the independent variables do not need to be unbounded. Logistic regression applies a maximum likelihood estimation after transforming the dependent into a logit variable, or the natural log of the odds of the dependent occurring or not. Logistic regression estimates the probability of a certain event occurring in the dependent variable; it calculates changes in the log odds of the dependent variable, not the changes in the dependent variable itself. It is the likelihood, or probability, that the observed values of the dependent variable can be predicted from the observed values of the independent variables. Hosmer and Lemeshow (1989) and Menard (2002) present a more extensive discussion of logistic regression. The analysis used a forward approach in model selection. In the first step, presence/absence of presettlement juniper was regressed against each of the independent variables individually. The most important variable (i.e., with the highest improvement χ^2 test) was then included in the model if significant, and the procedure repeated. A significance level of 0.05 for an improvement χ^2 test was specified for explanatory variable retention in the model. The improvement χ^2 tests the null hypothesis that the addition of a variable does not change the model; a small *P* value indicates improvement of the model with the addition of that variable. Candidate explanatory variables are described in Table 1. Classes of explanatory variables that were represented by < 5 stands were omitted from the analysis. The equation expressing the relationship between site/vegetation characteristics and the response variable was $\text{logit}(Y) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots \beta_k X_k$. Separate analyses were conducted for southeast Oregon ($n = 184$) and southwest Idaho ($n = 156$).

Covariate means (i.e., percent rock covering the soil surface, elevation, and exposure) were compared between presettlement and non-presettlement stands for each study area using Welch's *t* tests ($\alpha = 0.05$). The analysis is robust to violations against the assumption of equal variances among groups, but still assumes data are normally distributed in both groups. An examination of histograms indicated data in each group were normally distributed. The power of the Welch's *t* test is similar to that of the Student's *t* test even when the population variances are equal (Moser et al. 1989).

Relationship of Presence/Absence of Presettlement Trees with Postsettlement Woodland Age. A Welch's *t* test ($\alpha = 0.05$) was used to determine if there was a difference in mean postsettlement woodland age between stands with and without the presence of presettlement trees. Presettlement tree ages were excluded from the analysis. An examination of histograms suggested data in each group were normally distributed. Because we were interested in estimating the effect presettlement western juniper had on the initiation of postsettlement woodland expansion in the Intermountain region, data from southeast Oregon and southwest Idaho were combined for analysis ($n = 340$).

Table 2. The percentage of presettlement (primary canopy comprised predominantly of trees > 140 yr), mixed (≥ 1 tree present > 140 yr), and postsettlement (all trees < 140 yr) age class stands for each woodland ($n = 340$). Note that a higher proportion of Juniper and South Mountains supported presettlement trees than North and South Steens Mountain. The percentages of the total trees sampled ($n = 12\,672$) for each woodland that exhibited presettlement age class morphologic characteristics are displayed. A range of presettlement tree densities in mixed and presettlement age class stands for each woodland are presented. Totals are also displayed in bold for southwest Idaho and southeast Oregon.

	Stand age class					Tree age class			Presettlement tree density	
Woodland[1]	Presettlement (%)	Mixed (%)	Postsettlement (%)	Trees absent (%)	*n*	Presettlement (%)	Postsettlement (%)	*n*	Mixed aged range (trees · ha^{-1})	Presettlement range (trees · ha^{-1})
JM	11.6	36.2	50.7	1.5	69	4.6	95.4	4 261	1–31	34–175
SM	6.9	45.9	35.6	11.5	87	10.4	89.6	2 406	1–40	49–80
SW Idaho	**9**	**42**	**42**	**7**	**156**	**6.7**	**93.3**	6 667	**1–40**	**34-175**
STN	0.0	10.4	88.7	0.9	106	1.0	99.0	3 444	1–10	n/a
STS	1.3	25.6	69.2	3.9	78	1.6	98.4	2 561	1–21	25[2]
SE Oregon	**0.5**	**17**	**80**	**2**	**184**	**1.3**	**98.7**	6 005	**1–21**	**25[2]**

[1]JM = Juniper Mountain, SM = South Mountain, STN = North Steens Mountain, STS = South Steens Mountain.
[2]One presettlement stand was sampled in southeast Oregon.

RESULTS

Postsettlement Distribution and Composition

Western juniper occurred in 96% of the sampled stands ($n = 340$). Approximately 95% of these trees established after 1860. Although only accounting for 5% of the population, presettlement trees were recorded in 33% of the sampled stands. Four percent of these stands had primary canopies comprised of ≥ 75% presettlement trees (i.e., presettlement stands), and the balance had a minimum of one presettlement tree present within the stand. Woodlands comprised exclusively of postsettlement trees accounted for 63% of the stands.

Both the abundance and spatial distribution of presettlement trees were greater in southwest Idaho than in southeast Oregon (Table 2). On Juniper and South Mountains ($n = 156$), 42% of stands established after 1860, 42% had at least one presettlement tree or remnants of large trees (i.e., mixed woodlands), 9% had a canopy predominantly comprised of presettlement trees, and 7% lacked trees. On Steens Mountain ($n = 184$), 80% of stands established after 1860 and were classed as postsettlement woodlands, 17% had at least one presettlement tree present or remnants of large trees, 0.5% were predominantly occupied by presettlement trees, and 2% lacked trees. Presettlement tree density of mixed age stands varied from 1 to 40 trees · ha^{-1} and 1 to 21 trees · ha^{-1} in southwest Idaho and southeast Oregon, respectively. Presettlement tree density of presettlement stands varied from 34 to 175 trees · ha^{-1} in southwest Idaho. The only presettlement stand sampled in southeast Oregon had 25 presettlement trees · ha^{-1}. Approximately 80% of the mixed and presettlement age class stands had presettlement tree densities ranging between 1 and 26 trees · ha^{-1}.

The composition of stands also varied among alliances. Mountain big sagebrush (*Artemisia tridentata* Nutt. subsp. *vaseyana* [Rydb.] Beetle) occurred most frequently across the four woodlands accounting for 186 sampled stands (55%), followed by low sagebrush (*Artemisia arbuscula* Nutt.; 24%), curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.; 12%), mountain big sagebrush/mountain snowberry (*Symphoricarpos oreophilus* A. Gray; 6%), mountain big sagebrush/antelope bitterbrush (*Purshia tridentata* Pursh; 2%), and basin big sagebrush (*Artemisia tridentata* subsp. *tridentata* Beetle and Johnson; 1%). With the exception of South Mountain, the majority (≥ 67%) of mountain big sagebrush communities were comprised exclusively of postsettlement trees with no evidence of presettlement wood present within the plot (Table 3). Approximately 25% of plots in mountain big sagebrush contained at least one presettlement tree across the four woodlands. However, a higher proportion of mixed age and presettlement stands

Table 3. Number and percent of different stand age classes occurring in different plant alliances averaged across the four woodlands in southeast Oregon and southwest Idaho.

	Southwest Idaho																Southeast Oregon															
	Juniper Mountain								South Mountain								North Steens Mountain								South Steens Mountain							
	artrv[1]		arar[2]		cele[3]		syor[4]		artrv		arar		cele		syor		artrv		arar		cele		syor		artrv		arar		cele		syor	
Age Class	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
< 140 yr	61	20	18	2	50	12	0	0	40	19	30	8	40	2	33	1	94	65	79	19	0	0	100	8	71	25	50	10	80	8	88	7
> 140 yr	6	2	36	4	8	2	0	0	0	0	15	4	20	1	0	0	0	0	0	0	0	0	0	0	0	0	5	1	0	0	12	1
Mixed	33	11	37	4	42	10	0	0	56	27	33	9	40	2	33	1	4	4	21	10	100	1	0	0	20	4	45	10	20	2	0	0
No trees	0	0	9	1	0	0	0	0	4	2	22	6	0	0	33	1	2	1	0	0	0	0	0	0	9	3	0	0	0	0	0	0
Totals		33		11		24		0		48		27		5		3		70		29		1		8		32		21		10		8

[1]Mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana* [Rydb.] Beetle).
[2]Low sagebrush (*Artemisia arbuscula* Nutt.).
[3]Curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.).
[4]Mountain snowberry (*Symphoricarpos oreophilus* A. Gray).

Table 4. Mean (± SE) elevation, exposure, and percent of rock covering soil surface for stands with (i.e., presettlement) and without (i.e., postsettlement) presettlement trees for the southwest Idaho and southeast Oregon woodlands. Ninety-five percent confidence intervals for the difference between covariate means between presettlement and postsettlement stands are also provided.[1]

Variable	Southwest Idaho			Southeast Oregon		
	Presettlement	Postsettlement	95% CI	Presettlement	Postsettlement	95% CI
Elevation	1 769.39 ± 15.73*	1 855.67 ± 24.91	−147.37 to −5.18	1 755.28 ± 22.95	1 819.32 ± 15.58	−133.54 to 5.45
Exposure	1.71 ± 1.61	−0.42 ± 1.56	−2.32 to 6.58	2.36 ± 1.54**	−3.83 ± 1.11	−2.36 to 3.83
Rock	10.99 ± 1.06*	5.06 ± 0.66	3.54 to 8.32	22.85 ± 3.05**	8.17 ± 0.74	−22.84 to −8.17

[1]* indicates presettlement and non-presettlement significantly different ($P < 0.01$); **, presettlement and non-presettlement significantly different ($P < 0.02$).

occurred in the two Idaho woodlands. Stands with at least one presettlement tree within the mountain big sagebrush alliance accounted for 8% and 49% of the plots sampled in southeast Oregon and southwest Idaho, respectively. In the majority (~75%) of mixed-age stands, presettlement trees accounted for only a small proportion (< 25%) of the overstory tree canopy.

Low sagebrush had the greatest proportion (~48%) of stands sustaining presettlement trees of all the alliances sampled (Table 3). Presettlement juniper was also found in 42% of the mountain mahogany and 10% of mountain snowberry stands (Table 3). In the limited number of antelope bitterbrush and basin big sagebrush stands, western juniper was present in 95%, 100%, and 100% of sampled stands, respectively, with presettlement trees accounting for less than 2% of the population (data not shown).

Relationship of Site Characteristics with Presettlement Western Juniper Distribution

In southwest Idaho, presettlement and non-presettlement stands differed in elevation and percent rock covering the soil surface ($P \leq 0.01$), but did not differ in insolate exposure ($P > 0.05$; Table 4). Percent of rock covering the soil surface was the most important variable (i.e., with the highest improvement χ^2 statistic) in differentiating stands that supported presettlement trees from stands that did not ($P < 0.05$; Table 5). With only percent rock cover in our logistic regression model, the equation correctly classified 40.3% of presettlement stands and 88.9% of non-presettlement stands (Table 6). The only other explanatory variable included in the model was site concavity ($P < 0.05$), which increased the percentage of correctly classified presettlement and non-presettlement stands to 43.3% and 90.1%, respectively:

$$P = 1/[1 + \exp(-1.23 - 0.84 \times \mathrm{CONCAVE} + 0.60 \times \mathrm{CONVEX} + 0.11 \times \mathrm{ROCK})] \quad [1]$$

where P = probability of a presettlement stand, CONCAVE = categorical variable coded 1 if the stand occurred on a concave site, CONVEX = categorical variable coded 1 if the stand occurred on a convex site (a stand occurring on a flat site was denoted in the model when both CONCAVE and CONVEX were coded 0), and ROCK = percent of the soil surface covered by rock.

In southwest Idaho, presettlement juniper occurred more frequently on convex sites with a higher percent rock cover. Other candidate explanatory variables were excluded from the model at the 0.05 significance level.

In southeast Oregon, presettlement and non-presettlement stands differed in insolate exposure and percent of rock covering the soil surface ($P \leq 0.02$), but did not differ in elevation ($P > 0.05$; Table 4). Percent of rock covering the soil surface was again the most important variable (i.e., with the highest improvement χ^2 statistic) in differentiating stands that supported presettlement trees from stands that did not ($P < 0.05$; Table 5). With just the percent of rock covering the soil surface in the model, the equation correctly classified 34.4% of presettlement stands and 93.9% of non-presettlement stands (Table 6). The addition of topographic position ($P < 0.05$) increased the percentage of stands correctly classified to an average of 75.8% for the two stand types. The addition of the associated shrub species ($P < 0.05$) enhanced the percentage of correctly classified stands to 80.9%. Insolate exposure was the last variable to enter the model ($P < 0.05$). The final model correctly classified 72.9% and 96.9% of the presettlement and non-presettlement stands, respectively:

$$P = 1/[1 + \exp(-8.18 + 0.096 \times \mathrm{EXPOS} - 0.313 \times \mathrm{TERR} + 1.8464 \times \mathrm{RIDGE} + 0.162 \times \mathrm{ROCK} + 6.17 \times \mathrm{ARAR} + 3.99 \times \mathrm{ARTRV} - 6.30 \times \mathrm{CELE})] \quad [2]$$

where P = probability of a presettlement stand, EXPOS

Table 5. Results of logistic regression analysis of variables characterizing stands with and without presettlement trees in southwest Idaho and southeast Oregon.

Model	Step number	Variable[1] entered	Log likelihood	Model[2] χ^2	Improvement[3] χ^2
Southwest	1	ROCK	−90.3	20.9*	20.9*
Idaho	2	CONCAVITY	−87.1	27.0*	6.1*
Southeast	1	ROCK	−48.2	63.2*	63.2*
Oregon	2	TOPO POSITION	−42.7	74.7*	11.5*
	3	SHRUB SPP.	−38.1	83.6*	8.9*
	4	EXPOSURE	−34.7	89.8*	6.2*

[1]ROCK indicates percent of rock covering the soil surface (%); CONCAVITY, classification of the curvature along the contour of sloping terrain as either flat, concave, or convex; TOPO POSITION, classification of the topographic position as either side slope, ridgetop, or terrace; SHRUB SPP., classification of the associated shrub species as either mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana* [Rydb.] Beetle), low sagebrush (*Artemisia arbuscula* Nutt.), mountain snowberry (*Symphoricarpos oreophilus* A. Gray), or curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.); and EXPOSURE, unitless index of a site's insolation exposure.

[2]The model χ^2 tests the null hypothesis that there is no difference between the constant and the model presented; a small *P* value indicates a significant change in the model. * indicates significant at $P < 0.05$.

[3]The improvement χ^2 tests the null hypothesis that the addition of a variable does not change the model; a small *P* value indicates improvement of the model with the addition of that variable. * indicates significant at $P < 0.05$.

Table 6. Classification rates at each step of forward stepwise logistic regression analysis of variables characterizing stands with and without presettlement trees in southwest Idaho and southeast Oregon.

Model	Step	Variable[1]	Observed stand type	Number predicted		Classification rate
				non-presettlement	presettlement	
Southwest Idaho	1	ROCK	non-presettlement	72	9	88.9
			presettlement	40	27	40.3
			AVERAGE			64.6
	2	CONCAVITY	non-presettlement	73	8	90.1
			presettlement	38	29	43.3
			AVERAGE			66.7
Southeast Oregon	1	ROCK	non-presettlement	123	8	93.9
			presettlement	21	11	34.4
			AVERAGE			64.2
	2	TOPO POSITION	non-presettlement	129	2	98.5
			presettlement	15	17	53.1
			AVERAGE			75.8
	3	SHRUB SPP.	non-presettlement	126	5	96.2
			presettlement	11	21	65.6
			AVERAGE			80.9
	4	EXPOSURE	non-presettlement	127	4	96.9
			presettlement	9	23	72.9
			AVERAGE			84.9

[1]ROCK indicates percent of rock covering the soil surface (%); CONCAVITY, classification of the curvature along the contour of sloping terrain as either flat, concave, or convex; TOPO POSITION, classification of the topographic position as either side slope, ridgetop, or terrace; SHRUB SPP., classification of the associated shrub species as either mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana* [Rydb.] Beetle), low sagebrush (*Artemisia arbuscula* Nutt.), mountain snowberry (*Symphoricarpos oreophilus* A. Gray), or curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.); and EXPOSURE, unitless index of a site's insolation exposure.

= index of a stand's insolate exposure, ROCK = estimate of the percent of the soil surface covered by rock, TERR = categorical variable coded 1 if the stand occurred on a terrace, RIDGE = categorical variable coded 1 if the stand occurred on a ridgetop (a stand that occurred on a sideslope position was denoted in the model when both TERR and RIDGE were coded 0), ARAR = categorical variable coded 1 if the stand was associated with low sagebrush, ARTRV = categorical variable coded 1 if the stand was associated with mountain big sagebrush, and CELE = categorical variable coded 1 if the stand was associated with curlleaf mountain mahogany (a stand associated with mountain snowberry was denoted in the model when ARAR, ARTRV, and CELE were coded 0).

In southeast Oregon, presettlement juniper occurred more frequently on ridgetop and sideslope topographic positions with a higher insolate exposure and greater cover of rock on the soil surface. Presettlement juniper were also most frequently associated with low sagebrush ($n = 21$, 64% of presettlement stands).

Relationship of Presence/Absence of Presettlement Trees with Postsettlement Woodland Age

Stands with at least one presettlement tree began postsettlement establishment 24 yr earlier ($P < 0.001$, 95% CI: 16 to 32 yr) than stands where presettlement trees were absent. The greater abundance and spatial distribution of presettlement trees in the Idaho stands was associated with an earlier initiation of postsettlement woodland expansion compared to Steens Mountain (Fig. 2). Tree establishment in 18% of the sampled stands in southwest Idaho occurred prior to 1860, compared to < 1% of sampled stands in southeast Oregon. A total of approximately 21% of initial tree establishment occurred before 1900 in southeastern Oregon. Conversely, greater than 50% of initial establishment corresponding to the southwestern Idaho sites occurred prior to the turn of the century.

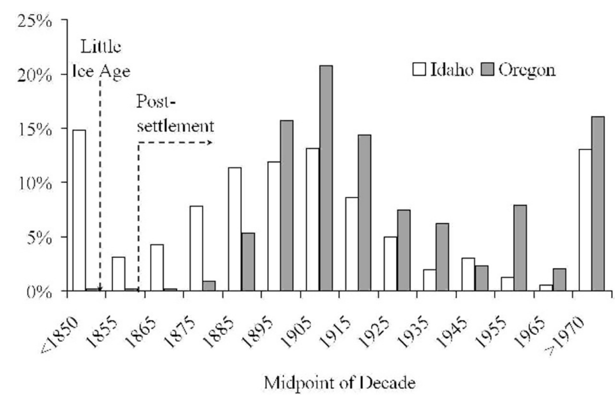

Figure 2. Combined decadal frequency of initial establishment of postsettlement trees for stands in southwest Idaho ($n = 158$) and southeast Oregon ($n = 184$). These data represent the initiation dates of postsettlement tree establishment (approximately 1860), for the sampled stands. Each column denotes the proportion of sampled stands that established during the corresponding time period. The last two bars on the right represent early stages of woodland development (i.e., only young trees present) and stands lacking trees. The first two bars on the left represent trees establishing before 1850, a decade reported to be the end of the Little Ice Age. Note the periods of earlier tree establishment for the Idaho study area.

DISCUSSION

Postsettlement Distribution and Composition

Western juniper older than 140 yr accounted for a small proportion (< 10%) of the overall population in southwest Idaho and southeast Oregon. Other studies have reported that presettlement trees accounted for less than 10% of the population across portions of the Great Basin (Miller et al. 1999; Miller and Tausch 2001). Abundances of presettlement trees were greater in the two southwest Idaho woodlands compared to those measured in southeast Oregon. Greater abundances of presettlement trees have been similarly reported for other areas. For instance, in the Mazama Ecological Province in central Oregon, composition of presettlement western juniper trees on a population basis was over 50% of the trees greater than 1 m tall (Waichler et al. 2001). In addition, over half the stands of piñon and juniper measured on the Uncompahgre Plateau, in western Colorado were considered presettlement (Eisenhart 2004) and the majority of piñon and juniper woodlands measured in Mesa Verde, Colorado, also predated 1860 (Floyd et al. 2000).

The extent that presettlement juniper occurred on the landscape varied among woodlands in southwest Idaho and southeast Oregon. At least one presettlement tree was recorded in 58% of stands measured in southwest Idaho compared to only 23% in the southeast Oregon woodlands. Both the spatial distribution and density of presettlement trees suggest stand structure prior to 1860 was open with tree densities generally ranging from 1 to $26 \cdot ha^{-1}$. We also observed that stands characterized by higher densities of presettlement trees were usually small (i.e., < 0.5 ha). The relatively open and scattered nature of trees in these woodlands prior to 1860 allowed for a greater abundance and diversity of understory species to dominate or codominate (Miller et al. 2000). With the exception of South Mountain, the lack of presettlement trees or large wood in the majority of measured stands indicates a large portion of these landscapes were treeless and probably dominated by grassland and shrub–steppe vegetation prior to 1860. Since 1860, substantial increases of western juniper in both density and spatial distribution occurred across all four woodlands. Gedney et al. (1999) compared two US Forest Service surveys conducted in 1938 and 1988 across eastern Oregon and similarly reported a 600% increase in tree density and area occupied by western juniper. Cottam and Stewart (1940) also reported a 600% increase in tree density and area occupied by Utah juniper in southwest Utah between 1864 and 1940.

On Steens Mountain, a larger proportion of the low sagebrush alliance supported presettlement trees than the mountain big sagebrush alliance. The prevalence of presettlement western juniper in low sagebrush areas as well as other areas lacking sufficient fine fuels to carry fire, such as rocky ridges, rock outcrops, and pumice soils, has been well described (Burkhardt and Tisdale 1976; Vasek and Thorne 1977; Holmes et al. 1986; Miller and Rose 1995; Waichler et al. 2001). Fire return intervals in low sagebrush sites are usually considerably longer (150+ yr) than in more productive mountain sagebrush communities, increasing the potential for tree establishment and survival to maturity (Miller and Rose 1999). Interestingly, this was not the case on Juniper and South Mountains. In fact, the proportion of stands occupied by presettlement trees was greater in the mountain big sagebrush alliance than areas supporting low sagebrush on South Mountain, but was similar between the two plant alliances on Juniper Mountain.

Relationship of Site Characteristics with Presettlement Western Juniper Distribution

Western juniper is capable of successfully establishing under a wide range of environmental conditions (Miller et al. 2005). However, in contrast to the broad distribution of postsettlement trees, the spatial location of presettlement trees is usually restricted to fire-insulated habitats on the landscape (Burkhardt and Tisdale 1976; Vasek and Thorne 1977; Holmes et al. 1986; Miller and Rose 1995; Waichler et al. 2001). We found significant differences in site characteristics between stands containing presettlement trees and postsettlement stands. In southwest Idaho, presettlement trees tended to occur on lower elevation sites with a higher percent of rock covering the soil surface. In southeastern Oregon, presettlement trees tended to occur on sites with greater insolate exposure and higher percent rock covering the soil surface. These landscape attributes are typically associated with lower levels and/or discontinuity of fine fuels that reduce the potential for fire spread. The relationship between elevation and the occurrence of presettlement trees (i.e., presettlement trees were more abundant at the lower compared to the higher elevations) might be closely linked with the colder conditions that persisted during the Little Ice Age. Western juniper appears to be limited by colder temperatures above 2 100 m in elevation (Miller and Rose 1995). Shorter frost-free periods might have limited establishment of western juniper prior to 1850 at the upper elevation boundaries of current woodlands.

Our ability to model the presence/absence of presettlement juniper using site characteristics as predictors met varying success. We observed greater success predicting the presence/absence of presettlement juniper when data from southeast Oregon were modeled. These results corroborated our observation that, in southeast Oregon, presettlement trees were more restricted in spatial distribution compared to the broader dispersal of presettlement trees in southwest Idaho. Although the stepwise procedure similarly included the percent of rock covering the soil surface and the microtopographic curvature (indicative of soil deposition and moisture accumulation) in the southwest Idaho regression model, the overall fit and classification success of the model was poor (69% overall hit rate) relative to the model fitted to the southeast Oregon data (92% overall hit rate). These results suggest trees in southwest Idaho were not always restricted to fire-safe sites prior to the mid-1800s as described in the literature. In contrast, the environmental and vegetation variables included in the model for southeast Oregon are indicative of those reported in the literature limiting presettlement juniper habitat to fire-safe sites on shallow rocky soils lacking understory fine fuels (Burkhardt and Tisdale 1976; Vasek and Thorne 1977; Holmes et al. 1986; Miller and Rose 1995; Waichler et al. 2001).

The broader spatial distribution of presettlement trees in southwest Idaho woodlands, particularly in the mountain big sagebrush alliance, could suggest a different disturbance regime than is typically reported for most piñon and juniper woodlands in the Intermountain West (Miller and Tausch 2001; Baker and Shinneman 2004). Burkhardt and Tisdale (1976) estimated presettlement mean fire return intervals to have been 11 yr in the two southwest Idaho woodlands, which might have disallowed the accumulation of heavier fuels associated with woody species. In the stands we measured, occasional charred trunks or stumps indicated a fire event that killed from one to several trees. In addition, we also observed that fire scars on presettlement trees were relatively common. The spatial arrangement of presettlement trees growing on mountain big sagebrush sites usually occurred in scattered clumps of three to six trees. Similar clumping has been reported for ponderosa pine in the southwest as a result of frequent surface fires (Cooper 1960; White 1985). Thus, we speculate presettlement fire intensities might have been low enough to afford survival to a scattering of legacy trees on deeper soil sites while still maintaining a relatively low density of juniper over the landscape. This supposition is in contrast to most reports in the literature of a disturbance regime characterized by either stand replacement fire events (Miller and Tausch 2001; Baker and Shinneman 2004; Miller et al. 2005) or frequent fire (Miller and Rose 1999; Miller and Tausch 2001) of sufficient intensity to preclude the survival of trees to maturity in big sagebrush grassland communities.

Relationship of Presence/Absence of Presettlement Trees with Postsettlement Woodland Age

Our tree age data from north and south Steens Mountain parallel most reported age chronologies for western juniper in the mountain big sagebrush alliance that suggest woodland expansion initiated after 1870 (Adams 1975; Eddleman 1987; Miller and Rose 1995; Gruell 1999). However, our age data from South Mountain and Juniper Mountain indicate woodland expansion began around 1850 in southwest Idaho. This time period occurred prior to the introduction of large numbers of livestock in 1869 (Oliphant 1968). The start of woodland expansion does, however, coincide with the end of the Little Ice Age around 1850, which resulted in milder temperatures throughout the second half of the 19th century (Antevs 1948; Easterling 1990; Ghil and Vautgard 1991). In addition, from about 1850 to 1916 precipitation was greater across this region than the current long-term average (Antevs 1938; LaMarche 1974; Graumlich 1987), which can promote vigorous growth in juniper (Fritts and Xiangdig 1986; Holmes et al. 1986).

An earlier expansion of the woodlands in southwest Idaho might have resulted from a combination of factors, including favorable climatic conditions for tree establishment and growth following the Little Ice Age and enhanced seed dissemination from a relatively broad distribution of presettlement trees over the landscape. Seed dispersal of western juniper occurs by gravity, overland flow, and animal transport (Chambers et al. 1999). In a southwest Idaho study, western juniper seed dispersed an average of only 1.29 m down slope during a 6-mo winter period (Burkhardt and Tisdale 1976). Although birds are a primary mechanism for seed dissemination of western juniper (Lederer 1977; Poddar and Lederer 1982), they have limited gut-retention times and fly short distances to perch and process the fruit, thus limiting the distance of most seed dispersal (Schupp et al. 1997; Chambers et al. 1999). After feeding on Ashe juniper fruits, American robins flew an average distance of 44 m to a postforaging perch (Chavez-Ramirez and Slack 1994). Because long-distance dispersal of western juniper seed is limited, we speculate the presence of scattered but widely distributed presettlement trees in southwest Idaho provided an on-site seed source for earlier initiation of woodland expansion. Conversely, without the benefit of an on-site seed source, stands comprised strictly of postsettlement trees exhibited a lagged establishment period of 16 to 32 yr relative to stands with presettlement trees present.

MANAGEMENT IMPLICATIONS

The ability to model reference presettlement conditions can be applied to management of western juniper woodlands in two ways. First, reference conditions are a standard against which to evaluate current conditions and future alternatives. Second, reference conditions can serve as a goal for ecological restoration treatments. Our attempts to model the landscape location of presettlement western juniper as a proxy for reference conditions using site vegetation and environmental parameters as predictors met varying success. In contrast to previous reports in the literature, presettlement juniper was not spatially constrained to fire-safe areas on the landscape in southwest Idaho, thus it was not surprising that our efforts to model its location were unsuccessful. Conversely, the spatial distribution of presettlement trees and woodlands in southeast Oregon more closely paralleled narrower presettlement habitat descriptions found in the literature, and our success in modeling the landscape location of presettlement juniper increased correspondingly. Although the spatial distribution and abundance of presettlement juniper were greater in Idaho, comparisons to reference conditions suggest contemporary woodlands are well above the range of presettlement variability in tree density, and both live and dead fuel structures have developed that can support high-intensity wildfire.

Presettlement trees can serve as a seed source potentially shortening the long-term effectiveness of woodland control treatments. Where presettlement trees occur on a small portion of the landscape, repercussions to treatment effectiveness and longevity of leaving presettlement trees generally will be inconsequential. For areas with greater abundances and spatial distribution of presettlement trees such as southwest Idaho, management that maintains low-intensity fire or cutting treatments at frequencies of less than 50 yr should sustain relatively open conifer stands (Miller and Tausch 2001). If left untreated, however, fire regimes in mixed age stands have the potential to change from low-intensity surface fires to high-intensity stand replacement fires, displacing old growth that has persisted on-site after centuries of disturbance (Tausch 1999).

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