

Understory Vegetation and Ponderosa Pine Abundance in Eastern Oregon

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Abstract

Management prescriptions for contemporary ponderosa pine (*Pinus ponderosa* Dougl.) forests often incorporate the restoration to a structure that more closely resembles pre-European contact forests. Successful restoration programs should incorporate the herbaceous understory component; however, published research specifically addressing changes in understory species composition is minimal. Ponderosa pine influence on the undercanopy environment may be an important factor in understory vegetation distribution. In this study, we addressed the relationships among ponderosa pine abundance, undercanopy environment, and understory species composition and made inferences with respect to restoration potential. Data representing vegetation, soil, and environmental attributes were measured in 28 plots in an eastern Oregon ponderosa pine forest. Relationships among the parameters measured were evaluated using cluster analysis, indicator species analysis, and ordination. Ponderosa pine occupancy was inversely related to understory perennial bunchgrass abundance and species diversity and appeared to regulate the undercanopy habitat through alterations in light intensity, nitrogen availability, and soil temperature. Light availability was the most important ponderosa pine-influenced undercanopy environmental parameter associated with understory vegetation distribution. These data suggested that degradation in the undercanopy environment associated with higher levels of ponderosa pine abundance may be temporary and that restoration practices that reduce pine occupancy should promote undercanopy conditions favorable to perennial bunchgrass growth. However, understory vegetation recovery in stands with excessive pine ingrowth may be constrained by desired understory species loss or invasion by more competitive understory vegetation.

Resumen

Las recomendaciones de manejo para los bosques contemporáneos de pino ponderosa (*Pinus ponderosa* Dougl.) incorporan a menudo la restauración de la estructura que se asemeje más a los bosques que había antes del contacto por los Europeos. Los programas exitosos de restauración deberían incorporar el componente herbáceo debajo de los árboles. Sin embargo, la investigación publicada que se enfoque específicamente en los cambios en la composición de las especies debajo de los árboles es mínima. La influencia del pino ponderosa en el ambiente debajo de la cubierta puede ser un factor importante en la distribución de la vegetación debajo de la cubierta de los árboles. En este estudio vimos las relaciones entre la abundancia del pino ponderosa, el medioambiente debajo de la cubierta de los árboles, y la composición de las especies debajo de la cubierta. Asimismo, se hicieron inferencias con respecto al potencial de restauración. Los datos representan vegetación, suelo, y los atributos del medio ambiente que se midieron en 28 parcelas en el bosque de pino ponderosa, en el oeste de Oregon. Las relaciones entre los parámetros medidos fueron evaluadas usando análisis cluster, análisis de las especies del indicador, así como la ordenación. La presencia del pino ponderosa fue inversamente relacionada con la abundancia de las gramíneas perenes amacolladas y con la diversidad de las especies y parece que regula el hábitat debajo de la cubierta de los árboles a través de las alteraciones de la intensidad de la luz, disponibilidad de nitrógeno, y la temperatura del suelo. La disponibilidad de la luz fue el factor más importante en el pino ponderosa que influencia los parámetros del medio ambiente debajo de la cubierta asociados con la distribución de la vegetación debajo de la cubierta de los árboles. Estos datos sugieren que la degradación en el medio ambiente debajo de la cubierta de los árboles asociada con niveles más altos de la abundancia del pino ponderosa quizá sea temporal y que la práctica de restauración que reduce la presencia del pino debe promover las condiciones favorables debajo de la cubierta para el crecimiento de gramíneas perenes amacolladas. Sin embargo, la recuperación de la vegetación en grupos con un excesivo crecimiento del pino se puede forzar por la pérdida o la invasión de vegetación más competitiva.

Key Words: ecological restoration, *Festuca idahoensis*, Oregon, *Pinus ponderosa*, threshold, understory–overstory interactions

INTRODUCTION

Throughout their range, contemporary ponderosa pine (*Pinus ponderosa* Dougl.; nomenclature follows Hitchcock and Cronquist 1973) forests are generally thought to exist outside their historic range of variability (Covington and Moore 1994; Johnson 1994; Tiedemann et al. 2000; Allen et al. 2002; Wienk et al. 2004). Activities associated with European settlement in the late 1800s, including road and trail development, intensive livestock grazing, and active fire suppression, triggered a

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substantial increase in the fire return interval and, combined with favorable conditions for ponderosa pine seed germination and seedling establishment, generated unprecedented changes in the fire regime and vegetation structure in ponderosa pine forests (Covington and Moore 1994; Johnson 1994).

Management of ponderosa pine forests toward a structure that more closely resembles presettlement conditions is often prescribed and is desirable from many perspectives. Most restoration programs focus on the manipulation of overstory structure without consideration of understory species; however, dynamics in understory species composition should also be considered in ponderosa pine restoration activities (Moore et al. 2006). The herbaceous understory in ponderosa pine forests is important for maintaining soil stability, site hydrology, and nutrient dynamics; it provides important wildlife habitat and livestock forage and is a major component of the fire regime, natural variability, and aesthetic value of these ecosystems. In established ponderosa pine forests, overstory pine trees are favored in competitive interactions with the understory herbaceous and shrub components. By eliminating the majority of pine regeneration, fire, in a low-intensity, high-frequency regime, confers a competitive advantage to understory forbs and grasses. Over time and in the absence of fire, increased pine stem density, canopy cover, and/or root density effects an increasing level of stress on understory species by reducing available light, water, or nutrient resources (Krueger 1981; Riegel et al. 1991, 1992, 1995) and may eventually lead to localized extirpation of understory species (Moore et al. 1999; Stephenson 1999).

Although overstory–understory interactions are well documented with respect to ponderosa pine and herbaceous understory biomass (Ffolliott and Clary 1982; Riegel et al. 1991, 1992), the effects of increased ponderosa pine abundance on under canopy resource availability and the subsequent influence on understory species composition are generally not well understood. Moreover, the bulk of published research on ponderosa pine ecology has occurred in southwestern pine types that differ from Pacific Northwest forests in both climatic regime and understory species physiology: southwestern forests have both cool- and warm-season plants, while understories in Pacific Northwest forests are comprised of only cool-season plants. Thus, research is needed in Pacific Northwest Ponderosa pine forests to assist in developing appropriate restoration and management strategies. This study was designed to characterize relationships among ponderosa pine abundance, undercanopy resource availability (i.e., nitrogen, light, moisture, and temperature), and understory vegetation and to make inferences with respect to restoration potential of similar ponderosa pine stands.

METHODS

Study Area

The study area was located in eastern Oregon (lat 44°12'52"N, long 118°59'16"W) in a Ponderosa pine/Idaho fescue plant association (Johnson and Clausnitzer 1992) within the John Day ecological province (Anderson et al. 1998). The area ranges from 1 500 m to 1 560 m in elevation and is situated in an area of gently sloping (~8% slope gradient) north-facing hillsides. The average daily high and low summer and winter temperatures, recorded between 1971 and 2000 at Seneca,

Oregon (~8 km south of the study area), were 24°C and 1.5°C and 4°C and –9°C, respectively (Western Regional Climate Center [WRCC] 2010). Approximately 32 cm of precipitation is received annually, most occurring in the winter months and primarily in the form of snow (WRCC 2010).

Soils of the study area were composed of a variable-thickness ash mantle overlaying serpentinite gravel and cobble. Soils were classified as either fine-loamy, mixed, superactive, frigid Vitrandic Haploxerolls or clayey-skeletal, smectitic, Lithic Ultic Argixerolls. Thickness of the ash-influenced mantle is a distinguishing feature of these soil types, Vitrandic Haploxerolls having an ash-influenced layer that is 20–30 cm thicker. Although soils derived from air-fall volcanic ash deposited over serpentinite bedrock residuum have been shown to moderate serpentine influences on soil properties (Bulmer et al. 1992), the potential influence of ultramafic mineralogy should be considered before broadly applying the results of this study.

The study area was located in a climax ponderosa pine forest consisting of large-diameter ponderosa pine trees scattered across a landscape dominated primarily by patches of smaller trees. Over 90% of the trees in the study area were less than 100 yr old, while approximately 3% survived for more than 250 yr (Carr 2007). The area was historically grazed by sheep and cattle; however, since the 1960s, it has been grazed primarily by cattle in the summer from July to October. No evidence of recent fire or logging activity was apparent in the study plots.

Data Collection

Twenty-eight 15 × 15-m plots were established in the summer of 2005 along a gradient of ponderosa pine abundance ranging from 133 stems · ha⁻¹ to 4 800 stems · ha⁻¹. Plots were limited to areas with similar site characteristics, including slope, aspect, elevation, and soils, and had no obvious evidence of recent logging or fire activity.

In each plot, trees > 1.4 m in height were tallied and their diameters at 1.4 m height recorded. Individual tree basal area was calculated from the diameter and tallied across all trees in the plot to generate a plot-level basal area value. Canopy closure was evaluated from three randomly located upward-looking hemispherical photographs using HemiView version 2.1 (Delta T Devices Ltd, Burwell, Cambridge, UK). Canopy closure was calculated as 100 minus the percent visible sky.

In each plot, the density of each understory species (plants · m⁻²) was subsampled in 0.5-m² (1 × 0.5-m) quadrats. Vegetation sampling occurred through the first 3 wk of July 2006. Quadrats were systematically positioned from a random starting point along randomly located transects in each plot. The number of subsamples in each plot differed in accordance with plant community heterogeneity and was determined through pilot sampling and sample size calculation (Elzinga et al. 1998). A minimum of 30 quadrats were sampled in plots with relatively uniform understory vegetation, while up to 80 quadrats were sampled in plots with more heterogeneous understories.

Undercanopy light conditions were modeled in each plot from the three hemispherical photographs using HemiView version 2.1 (Delta T Devices). The total yearly below-canopy radiation (MJ · m⁻² · yr⁻¹) was calculated as the sum of the

undercanopy direct and diffuse radiation values. The Hemi-View solar model incorporated latitude, longitude, and altitude to generate an expected radiation value (assumes no sky obstructions) and, using the geometry of sky visibility and sky obstruction determined through hemispherical image classification, estimated the below-canopy radiation as the proportion of the expected radiation that could reach the undercanopy environment (Rich et al. 1999). Plot values were averages of the three subsamples and provided a relative comparison among plots.

Gravimetric soil moisture integrated over the top 15 cm of the soil was determined for each plot by averaging four randomly located soil samples removed by auger to a depth of 15 cm. A 15-cm depth was selected, as it represented the general rooting depth of understory species in the study area. Soil moisture was sampled biweekly throughout the growing season, during which approximately 5.3 cm of precipitation were received (data from Seneca, Oregon; WRCC 2010).

Plant-available nitrogen was evaluated using PST-1 mixed bed ion exchange resin capsules (UNIBEST Inc, Bozeman, MT). Four capsules were placed at 15-cm depth in the soil at each of four randomly selected locations in each plot. One capsule from each sampling location was removed at four different times throughout the growing season (11 June, 12 July, 12 August, and 9 September). Samples at each removal date were composited within the plot to provide a plot-level value of nitrogen availability. Capsules were stored in labeled plastic bags and refrigerated until desorption. Capsules were desorbed with 2 M KCl, and the resultant solution was analyzed using an Astoria Pacific autoanalyzer at the Central Analytical Lab at Oregon State University. As the soil volume sampled by each resin capsule was unknown, the nitrogen values do not represent absolute nitrogen amounts; however, they do provide a relative index of nitrogen bioavailability (Kolberg et al. 1997).

Soil temperature was measured at 5-cm depth in three randomly selected locations in each plot using Stowaway® XTI thermistors (Onset Computer Corp, Bourne, MA) programmed to log temperature every 2 h. To characterize soil temperature in each plot, the daily maximum and minimum temperature for five randomly selected days (5 July, 16 July, 26 July, 21 August, and 26 August) were averaged among each thermister in each plot, providing a plot-level value for the average daily maximum and minimum soil temperature.

Data Analyses

The data set analyzed consisted of a matrix of 28 plots (rows) and 63 species (columns). Individual species density values were log transformed to account for an approximately four-orders-of-magnitude difference between the smallest and largest values in the data set. To moderate the influence of dominant species, density values were relativized by species maxima, while species occurring in fewer than four plots were excluded from the analyses to reduce the bulk of and noise in the data set (McCune and Grace 2002). Outlier analyses of these data did not indicate any unusual plots.

Hierarchical agglomerative cluster analysis with Sørensen distance and flexible beta linkage ($\beta = -0.25$) was used to group plots based on understory species density. The resultant

dendrogram was pruned at a location where natural, stable groupings were evident and where the information remaining in the data allowed for a straightforward and practical ecological interpretation. Indicator species analysis (ISA; Dufrene and Legendre 1997), using 1 000 randomizations in Monte Carlo tests of indicator significance, was used to describe individual species value for representing the environmental conditions associated with each of the groups formed through cluster analysis. Nonmetric multidimensional scaling ordination (NMS; Kruskal 1964; Mather 1976) of plots in species space was used to display differences in understory species composition among the groups identified through cluster analysis. NMS analyses were based on Sørensen distance measure and utilized 40 runs with real data from a randomized starting configuration, a maximum of 400 iterations, and an instability criterion of 0.00001. Fifty runs with randomized data were used in a Monte Carlo test to evaluate if the reduction in stress achieved was lower than expected by chance. Joint-plot overlays of understory species functional groups and diversity indices were used to illustrate understory species variability among the groups identified through cluster analysis. Cluster analysis, ISA, and NMS were performed using PC-ORD version 4.39 (McCune and Mefford 1999).

To capture the relationships among understory species distribution, ponderosa pine abundance, and undercanopy environment, joint plots of soil moisture, soil temperature, soil nitrogen availability, undercanopy light conditions, and ponderosa pine occupancy were overlaid on the NMS ordination of understory species density. Synthetic variables representing soil moisture, soil nitrogen, and pine site occupancy were created using the strongest principle components generated by principal components analysis (PCA) of each parameter. The PCA were performed using correlation matrices in PC-ORD version 4.39 (McCune and Mefford 1999). The PCA of ponderosa pine site occupancy incorporated values for pine stem density, canopy closure, and basal area and pine occupancy was defined as the relative magnitude of ponderosa pine influence on a site. The PCAs of soil moisture and soil nitrogen availability incorporated values for each parameter measured at different times throughout the growing season.

RESULTS

The hierarchical cluster analysis dendrogram was pruned at four groups (Fig. 1) identified as groups A, B, C, and D (38.6% information remaining, Wishart's objective function; Wishart 1969). ISA identified perennial bunchgrasses, including *Festuca idahoensis* Elmer (IV = 32.6, $P = 0.001$), *Poa scabrella* (Thurb.) Benth. (IV = 40.5, $P = 0.005$), and *Agropyron spicatum* (Pursh) Scrib. & Smith (IV = 50.7, $P = 0.012$) as indicators of group A. Group B was indicated by the presence of perennial bunchgrasses *Koeleria cristata* Pers. (IV = 36.2, $P = 0.002$) and *Sitanion hystrix* (Nutt.) Smith (IV = 42.0, $P = 0.003$) and by the presence of a variety of forb species; seven forb species expressed significant indicator values for this group. The presence of *Poa nervosa* (Hook.) Vasey var. *wheeleri* (Vasey) Hitchc. (IV = 43.0, $P = 0.036$) appeared to characterize group C, while group D was identified by the presence of *Berberis repens* Lindl. (IV = 97.0, $P = 0.001$), *Silene menziesii* Hook. var. *menziesii* (IV = 75.0,

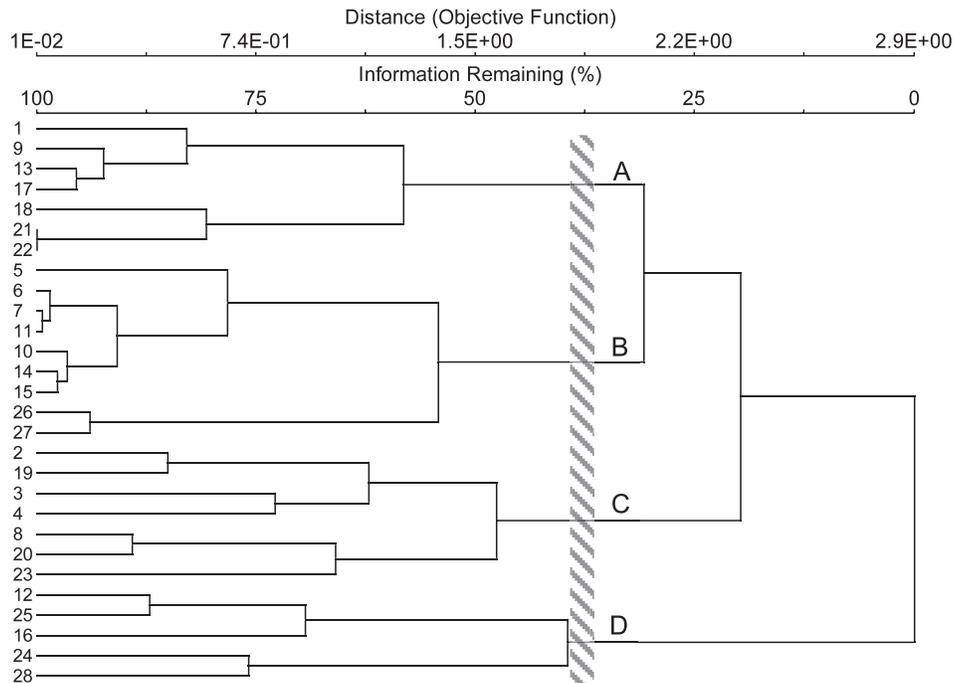


Figure 1. Hierarchical cluster analysis of understory species density. Numbers along the left edge of the dendrogram identify plots, the hashed column identifies the pruning location, and letters identify plots groups as described in the text.

$P = 0.001$), and *Calamagrostis rubescens* Buckl. (IV = 59.1, $P = 0.002$). A two-dimensional solution to NMS ordination of plots in species density space was the best fit for these data (final stress = 13.053, final instability = 0.00001). The accumulated proportion of variance represented by the two axes in this ordination was 90.2%.

Plant functional group overlays corresponded well with the ISA on cluster-generated groupings (Fig. 2A). The presence or absence of perennial bunchgrasses was associated exclusively with the gradient represented by axis 1, while the occurrence of forbs and other grasses (predominantly the rhizomatous species *C. rubescens*) were also associated with axis 2. Groups A and B existed at higher values (to the right) along the axis 1 gradient, while groups C and D existed at lower values, corroborating the significance of perennial bunchgrasses to the understory species composition of groups A and B identified through ISA. Group B plots associated with high forb diversity in the ISA occupied the upper portions of the axis 2 gradient, which was also related to the presence of the forb functional group. Although uniform in the absence of perennial bunchgrasses, some plots in group D were higher in other-grass abundance, associated primarily with very high densities of *C. rubescens*. The average densities of plants were estimated in each functional group (Table 1).

The strongest correlations between perennial bunchgrass species and axis 1 were *F. idahoensis* ($r = 0.907$), *P. scabrella* ($r = 0.83$), and *K. cristata* ($r = 0.78$), indicating that plots in groups A and B had high densities of these species while plots in groups C and D were lacking. As suggested by the diagonal trend of the forb functional group joint plot, numerous forbs shared strong correlations with both axes; however, *Phlox hoodii* Rich., *Achillea millifolium* L., and *Lomatium triternatum* (Pursh) Coult & Rose expressed a substantially stronger alliance with

axis 1 ($r = 0.838$, $r = 0.776$, and $r = 0.849$, respectively). Both *B. repens* ($r = -0.756$) and *S. mensiezii* ($r = -0.756$) expressed strong negative correlations with axis 1, confirming the ISA that identified these two species as indicators of group D. *C. rubescens* expressed a strong correlation with axis 2 ($r = 0.661$) and a weaker negative correlation with axis 1 ($r = -0.397$), supporting the significance of *C. rubescens* in the other-grasses functional group. The density of *Lupinus argenteus* Pursh showed the strongest correlation with axis 2 ($r = 0.732$).

Overlaying indices of species diversity (Fig. 2B) suggested that plots in groups A and B, trending to the right along axis 1, were higher in species diversity relative to groups C and D. Although Simpson's (D) and Shannon's (H) diversity values integrate different aspects of community structure, both incorporate species richness and evenness, and higher values suggest greater diversity (McCune and Grace 2002). Group B plots, in the upper right of the ordination space, had higher species richness than the remaining plots, a reflection of the high forb abundance evident in this group. Similar results were obtained when the ordination was rotated to maximize the correlation between Shannon's and Simpson's diversity values and axis 1.

Average ponderosa pine densities were estimated for each group (Table 1). The synthetic variable of pine occupancy incorporated only the first principal component (85% of variance explained) of the PCA on basal area, density, and canopy closure and, because of the negative association between the component and tree occupancy variables, represented a lack of pine occupancy. Basal area, density, and canopy closure did not emerge as dominant indicators of tree occupancy; rather, the first principal component was strongly correlated with and integrated all three tree occupancy measures (Table 2). To aid in display and interpretation, the

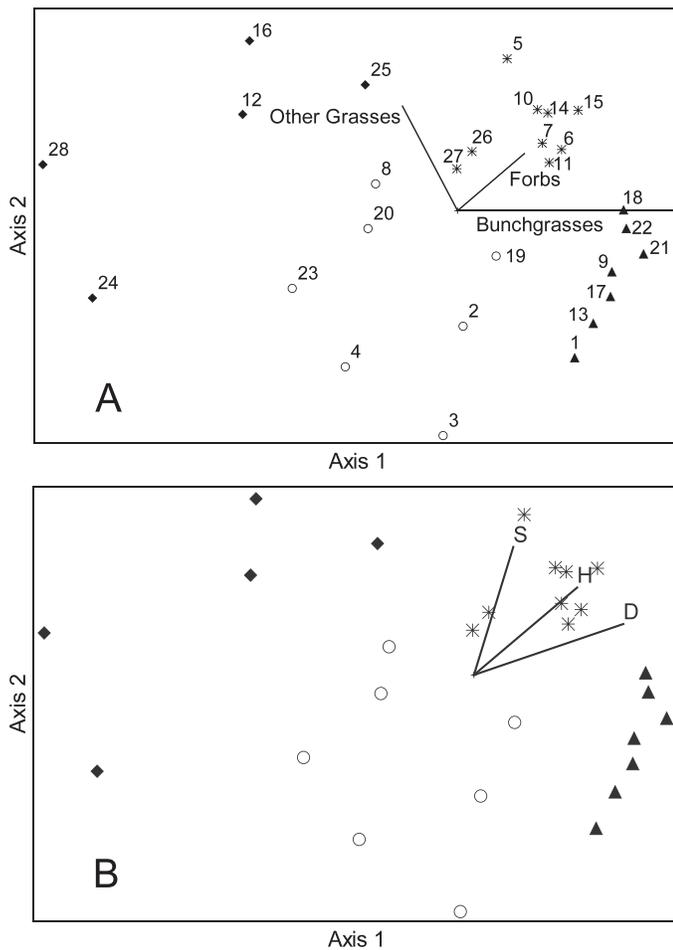


Figure 2. Nonmetric multidimensional scaling ordination of understory species density showing plots in species space. Symbols represent plot groups identified through cluster analysis: group A (\blacktriangle), group B ($*$), group C (\circ), and group D (\blacklozenge). Joint plots represent relationships with ordination axes where the strength and direction of the relationship are represented by line length and angle. **A**, Displays relationships among plot groups and understory plant functional groups. **B**, Identifies patterns in diversity indices (D = Simpson's, H = Shannon's, S = species richness). Plot numbers are identified in **A**.

PCA coordinates of the first component were multiplied by (-1) , creating a variable that represented pine occupancy rather than pine vacancy. Ponderosa pine occupancy was strongly correlated to axis 1 of the NMS ordination of understory species density (Table 3), indicating that plots in groups A and B existed in stands of low pine occupancy while

Table 1. Group mean (SE) densities for plant functional groups, *Festuca idahoensis*, *Calamagrostis rubescens*, and ponderosa pine. Units are in plants $\cdot m^{-2}$ except for ponderosa pine, which is stems $\cdot ha^{-1}$.

	Group A	Group B	Group C	Group D
Perennial bunchgrass	25.70 (2.05)	21.96 (0.98)	7.63 (2.08)	2.01 (1.27)
Other grasses	0.18 (0.12)	16.11 (6.27)	9.54 (5.16)	85.32 (28.68)
Forbs	27.77 (6.89)	32.58 (3.59)	5.69 (1.22)	14.67 (3.55)
<i>F. idahoensis</i>	16.32 (1.73)	12.95 (1.00)	5.50 (1.60)	1.53 (1.10)
<i>C. rubescens</i>	0	18.33 (6.11)	0	71.56 (24.08)
<i>Pinus ponderosa</i>	268 (44.6)	1215 (195.8)	2041 (306.0)	3036 (719.7)

Table 2. Correlations between variables and principal components from principal components analyses of soil moisture, nitrogen availability, and pine occupancy.

	Principal component	
	1	2
Soil moisture		
1 June soil moisture	-0.5163	0.7238
20 June soil moisture	-0.2683	-0.0666
4 July soil moisture	-0.5806	0.6411
22 July soil moisture	-0.9564	-0.1213
3 August soil moisture	-0.9378	-0.2973
1 August soil moisture	-0.9132	-0.3648
Nitrogen availability		
11 June nitrogen	0.8009	-0.0232
12 July nitrogen	0.8825	-0.0951
12 August nitrogen	0.7365	-0.2520
9 September nitrogen	0.3060	0.9418
Pine occupancy		
Basal area	-0.8927	— ¹
Density	-0.9360	— ¹
Canopy closure	-0.9393	— ¹

¹Components were not interpreted.

plots in Group D generally existed in high pine occupancy stands (Fig. 3D).

The first two components from the PCA of soil moisture combined to explain 75% of the variability in soil moisture (Table 4) across plots (55% and 20% of variance explained for principal components 1 and 2, respectively). The first component clearly represented the absence of late-season moisture, showing very high negative correlations with 22 July, 3 August, and 15 August soil moisture measurements (Table 2). Principal component 2 was highly correlated with 1 June and 4 July soil moisture and represented early-season soil moisture. To aid in display and interpretation, the PCA coordinates of the first component were multiplied by (-1) , creating a variable that represented higher late-season soil moisture rather than lower late-season soil moisture. Early-summer soil moisture displayed a strong relationship with the gradient represented by axis 2 of the NMS ordination (Table 3), indicating that the plots in group B and most of the group D plots experienced higher early-season soil moisture (Fig. 3A).

The first component of the PCA of mineral nitrogen availability (Table 4) accounted for 51% of the variation in the data and

Table 3. Pearson correlations between ordination axes and understory growing conditions for the nonmetric multidimensional scaling ordination of understory species density as presented in Figure 3.

	Axis 1	Axis 2
Early-summer H ₂ O	-0.068	0.792
Maximum soil temperature	0.727	0.178
Minimum soil temperature	0.656	-0.201
Light availability	0.703	0.026
Pooled N	0.309	-0.037
Pine occupancy	-0.864	0.068

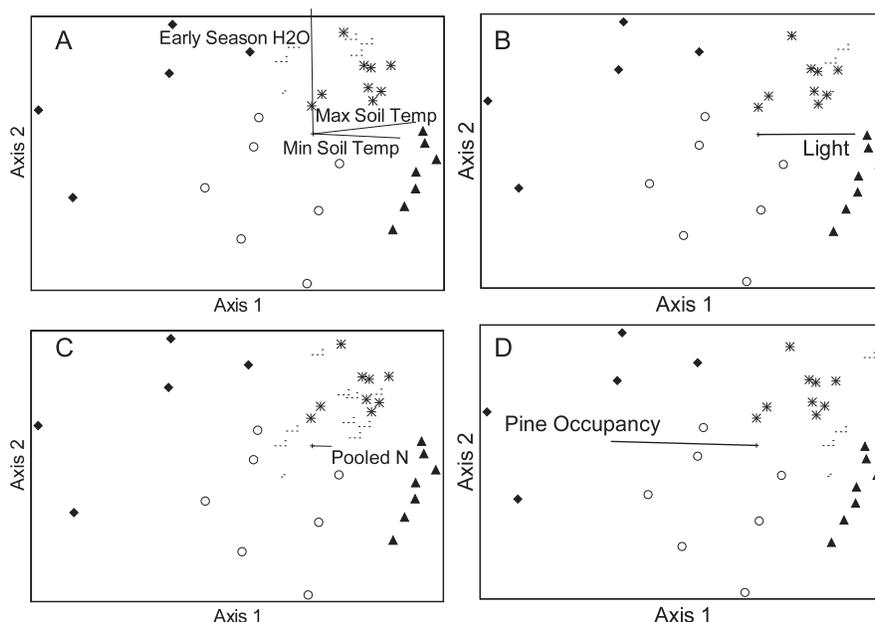


Figure 3. Nonmetric multidimensional scaling ordination of understory species density showing plots in species space. Symbols represent plot groups identified through cluster analysis: group A (▲), group B (*), group C (○), and group D (◆). Joint plots represent relationships with ordination axes. Relationship strength and direction are represented by line length and angle. **A**, Relationships among plot groups and soil moisture and temperature. **B**, Relationships among plot groups and undercanopy light availability. **C**, Relationships among plot groups and nitrogen availability. **D**, Relationships among plot groups and ponderosa pine occupancy.

represented an index of mineral nitrogen availability pooled across sampling dates (i.e., pooled nitrogen availability; Table 2). Plots with higher scores on component 1 generally had more nitrogen available than plots with low scores. The second component accounted for an additional 24% of the variance and represented September nitrogen availability (Table 2). Of the nitrogen availability variables generated through PCA, pooled nitrogen availability showed the strongest association with the distribution of plots in the NMS space, and, although a weak

correlation with axis 1 (Table 3), this relationship indicated that plots in groups A and B were generally higher in nitrogen availability than plots in groups C and D (Fig. 3C).

Both daily maximum and daily minimum soil temperatures were correlated with the gradient represented by axis 1 (Table 3), suggesting that plots to the right along this axis experienced higher soil temperatures (Fig. 3A). Undercanopy radiation was also strongly aligned with axis 1 (Table 3), evidence of substantially higher light intensities in plots

Table 4. Mineral nitrogen availability, soil moisture, below-canopy radiation, and maximum and minimum soil temperatures for the four understory density groups identified through cluster analyses. Values are group means (SE) for each sampling period.

	Group A	Group B	Group C	Group D
Mineral nitrogen (ppm)				
11 June	0.19 (0.03)	0.18 (0.04)	0.22 (0.05)	0.13 (0.03)
12 July	0.34 (0.06)	0.38 (0.05)	0.31 (0.05)	0.27 (0.06)
12 August	0.52 (0.10)	0.31 (0.08)	0.23 (0.04)	0.25 (0.05)
9 September	0.21 (0.03)	0.28 (0.04)	0.13 (0.02)	0.21 (0.03)
Soil moisture (%)				
1 June	32.89 (0.78)	37.37 (1.10)	34.66 (1.36)	39.33 (1.00)
20 June	30.75 (1.05)	30.70 (0.84)	28.53 (0.94)	31.37 (0.74)
4 July	24.18 (1.11)	26.72 (0.57)	22.29 (1.69)	27.34 (1.48)
22 July	12.14 (0.87)	13.18 (0.75)	11.61 (1.00)	14.51 (1.88)
3 August	9.81 (0.71)	10.52 (0.57)	9.38 (1.07)	10.51 (1.67)
15 August	9.89 (0.79)	10.22 (0.57)	9.47 (1.16)	10.27 (1.59)
Radiation ($\text{MJ} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)				
	4 430 (357)	4 079 (362)	2 339 (296)	2 416 (477)
Soil temperature ($^{\circ}\text{C}$)				
Maximum	22.44 (0.77)	23.11 (0.82)	18.18 (0.87)	16.90 (0.85)
Minimum	14.76 (0.20)	14.37 (0.18)	13.86 (0.28)	13.40 (0.20)

associated with groups A and B (Fig. 3B). Soil temperatures and light availability for each plot group are presented in Table 4.

DISCUSSION

The results from this study demonstrated an association among understory herbaceous species composition, the undercanopy environment, and ponderosa pine site occupancy. It can be inferred that increasing ponderosa pine basal area, stem density, or canopy closure may diminish or even eliminate the perennial bunchgrass dominated understory community. Several studies have reported an increase in understory graminoid biomass associated with reductions in ponderosa pine abundance (e.g., Moir 1966; Barrett 1982; Riegel et al. 1992; Uresk and Severson 1998; Griffis et al. 2001); however, only a few studies have evaluated understory species compositional changes. In the US Southwest, Naumburg and DeWald (1999) reported an increase in graminoid presence associated with pine thinning, while Laughlin et al. (2006) found that the understory grass community of ponderosa pine stands where all postsettlement trees were removed trended toward the species composition of relict grassy patches. In the Pacific Northwest, Riegel et al. (1995) also found that understory species composition was altered when ponderosa pine influences were reduced through either root trenching or thinning or their combination. Ponderosa pine can influence the understory environment and growing conditions for understory species by altering soil moisture (Barrett 1970; Helvey 1975), light availability (Naumburg and DeWald 1999), or nutrient cycling and availability (Kaye and Hart 1998a). Our results indicated that light and nitrogen availability and soil temperature were inversely related to ponderosa pine site occupancy, while the dominant soil moisture gradient appeared unrelated to the gradient observed in pine occupancy.

F. idahoensis accounted for over 60% of the understory perennial bunchgrass density in plots associated with lower levels of pine occupancy, and a substantial reduction in *F. idahoensis* was evident when comparing these plots and those with high pine abundance, suggesting that habitat quality for this species was diminished under high pine occupancy conditions. Although *F. idahoensis* is a ubiquitous western rangeland grass (Zouhar 2000), it appears to favor more open forests or woodland environments when it exists as an understory component in these ecosystems (US Department of Agriculture [USDA] 1937; Stubbendieck et al. 2003). The increase in *C. rubescens* abundance in some high pine occupancy plots suggested the potential for an additional shift in understory species not only away from perennial bunchgrasses but also toward a highly competitive rhizomatous grass species. *C. rubescens* accounted for over 83% of the other-grasses functional group density in group D plots.

Undercanopy light availability increased as tree occupancy decreased, reaching a maximum in those plots least influenced by ponderosa pine. Perennial bunchgrass abundant plots (groups A and B) experienced very similar light conditions and were present under the highest light availability encountered in the study, while those plots classified as low or no perennial bunchgrass abundance (groups C and D) existed at

lower light intensities and higher pine occupancies. Light availability has been identified as an important parameter with respect to understory species composition in ponderosa pine ecosystems. Riegel et al. (1995) and Naumburg and DeWald (1999) suggested that variable light availability associated with differing pine abundance was significant with respect to understory species presence. In our study, there were markedly fewer *F. idahoensis* plants in low light intensity plots. *F. idahoensis* has been shown to have a negative response in growth and vigor to increasing levels of shade (Moir 1966; Carr 2007), and these reduced light conditions may have limited the persistence of *F. idahoensis* populations, whose habitat preference is for higher light environments (USDA 1937; Stubbendieck et al. 2001). In contrast, *C. rubescens* is tolerant of lower light conditions (Stubbendieck et al. 2001), and although, in drier sites, its abundance can decline with increases in canopy openness (McLean 1970; Pfister et al. 1977), its competitive nature may also preclude the reestablishment of desired perennial bunchgrasses (Page and Bork 2005).

Soil temperatures in low ponderosa pine occupancy and high perennial bunchgrass plots were higher than plots with low or no perennial bunchgrasses and high ponderosa pine influence. Soil temperature can influence plant growth and is a major driver of plant distribution (Lambers et al. 1998). However, it is unclear what role soil temperature played in the observed differences in understory plant species composition along the pine occupancy gradient. The optimum temperature for root growth of plants in temperate regions is between 10°C and 30°C (Bowen 1991; Lambers et al. 1998), within the range of temperatures encountered in this study. Furthermore, Nasri and Doescher (1995), who evaluated the growth response of *F. idahoensis* to experimentally controlled temperature variation, found very few differences among fescue plants grown at 5°C, 10°C, or 15°C. As the coolest temperatures on our sites were around 13°C, it is unlikely that the temperatures associated with higher pine occupancy played a major role in the apparent decline in perennial bunchgrass abundance.

Pooled nitrogen availability displayed a relatively weak, inverse association with the gradient in tree abundance, and a reduction in mineral nitrogen availability was observed between groups with low tree occupancy and those with higher tree occupancy (Table 4). Reduced rates of nutrient cycling have been observed under higher ponderosa pine abundance (Covington and Sackett 1984) and may be attributed to the relative recalcitrance of ponderosa pine needle litter when compared to herbaceous derived material (Klemmedson et al. 1985; Kaye and Hart 1998b). Rates of decomposition are also influenced by soil temperature (Wolf and Wagner 2005), and warmer soil temperatures evident in plots with higher abundances of fine-leaved grass litter likely contributed to increased rates of decomposition and nitrogen mineralization in these plots.

The drop in *F. idahoensis* abundance evident between high and low perennial bunchgrass abundance plot groups corresponded with a reduction in nitrogen availability, and although this relationship was intriguing, the influence of nitrogen availability on the distribution of perennial bunchgrasses is uncertain. Others who have investigated understory response to increased nitrogen availability associated with restoration

treatments in ponderosa pine forests found no influence on understory plant growth (Riegel et al. 1991, 1992) or understory plant nitrogen uptake (Kaye et al. 2005) and suggested that nitrogen availability was not a driver of posttreatment plant growth and that herbaceous understory species were not nitrogen limited (Riegel et al. 1991, 1992; Kaye et al. 2005). Moreover, increased nitrogen availability had no significant effect on root biomass, shoot biomass, or foliar cover of *F. idahoensis* plants that were harvested from our study area and grown in a greenhouse experiment (Carr 2007). Although nitrogen availability may not be a major driver of perennial bunchgrass loss in our study, others have suggested its importance in vegetation dynamics (e.g., Tillman 1985, 1987), and a more robust evaluation of nitrogen transformations may provide a more complete understanding of the relationships among nitrogen cycling, ponderosa pine abundance, and understory species dynamics. This may be particularly important when considering ecosystem response to restoration treatments and the potential, under conditions of higher nutrient availability (Kaye and Hart 1998a; Kaye et al. 2005), for invasion of exotic annual grasses whose presence may continue to alter the undercanopy growing conditions to the detriment of native perennials through adjustments in the fire return interval (Vasquez et al. 2008; McGlone et al. 2009). Moreover, evidence suggests that *C. rubescens*, adapted to low nitrogen environments, positively responds in growth and vigor to increases in nitrogen availability (Freyman and van Ryswyk 1969; Wikeem et al. 1993), and this could impede perennial bunchgrass recovery following restoration treatments.

Although ponderosa pine forest structural changes have been shown to generate differences in soil moisture status (Barrett 1970; Helvey 1975), soil moisture at 15-cm depth did not appear correlated with the gradient of tree occupancy identified in the present study. The strongest relationship between soil moisture and understory plant species composition was observed for early-season soil moisture, and this relationship was nearly orthogonal to the gradient exhibited in tree occupancy. Elevated early-season soil moisture was associated with high diversity and abundance of forb species and with the presence of other grass species, led primarily by the abundance of *C. rubescens*. The relationship between *C. rubescens* abundance and soil moisture suggested that the potential for a shift in understory species toward *C. rubescens* dominance may exist only in more mesic sites, as the drier plots did not have elevated *C. rubescens* densities.

The lack of a consistent trend in soil moisture along the gradient of tree occupancy is not surprising, as several authors have observed only a short-term fluctuation in soil moisture status associated with stand manipulations. Increased understory plant growth under conditions of low tree occupancy can provide adequate leaf area and transpirational demand to rival the moisture depletion in the upper soil horizons observed in more dense pine types (Barrett and Youngberg 1965; Helvey 1975; Baker 1986). Although competition for soil moisture between overstory trees and understory vegetation can influence understory vegetation dynamics (Riegel et al. 1991, 1992, 1995), in our study, a stand-level effect of reduced soil moisture associated with increased ponderosa pine occupancy was not evident, as soil moisture availability across the gradient in ponderosa pine abundance we sampled was apparently

adequate to satisfy the requirements of the understory vegetation found in more open ponderosa pine stands.

MANAGEMENT IMPLICATIONS

Our study suggests that pre-European settlement understory structure and species composition in contemporary ponderosa pine forests may be at risk because of the increase in pine density, basal area, and canopy closure associated with lengthened fire return intervals. The loss of perennial bunchgrasses represents a significant reduction in available high-quality forage for livestock and wildlife, a decline in biological diversity, and an alteration of the fuel structure and fire regime responsible for maintaining the classic open canopy forest. Others have also recognized the potential for a substantial loss in understory species (Moore et al. 2006), and this may represent an ecological threshold from which natural recovery of desired understory species is constrained by a lack of available plant propagules, substantially altered undercanopy environmental conditions or invasion by more competitive understory species. Thresholds occur where conditions are sufficient to modify ecosystem structure and function beyond the limits of ecological resilience (Briske et al. 2008). In our case, a threshold may be triggered by the lengthened fire return interval, which results in an increasingly modified undercanopy growing environment and subsequent reduction and potential loss of the perennial bunchgrass-dominated community. The loss of perennial bunchgrasses and increase in canopy closure may combine to effect a transition away from stabilizing feedback mechanisms associated with fire-maintained open ponderosa pine stands (i.e., fire-promoted open stand structures favor abundant herbaceous understories, which in turn provide the fine fuels required for frequent low-intensity stand-maintaining surface fire). The degree of reduction in ecosystem resilience and the probability of crossing this threshold are dependent on the availability of disseminules of desired understory vegetation subsequent to the reduction of ponderosa pine influence on the undercanopy environment, the permanence of the undercanopy environmental change, and the presence and abundance of other more competitive understory vegetation. From the perspective of understory perennial bunchgrass habitat suitability, our study suggested that undercanopy environmental degradation may be reversible, and in the case of light availability—the primary pine-influenced undercanopy environmental parameter associated with the loss of perennial bunchgrass understory—reducing pine occupancy will create more suitable habitat for desired understory vegetation. However, perennial herbaceous species tend to exhibit poor seed-banking abilities (Rees 1994), and in the absence of sufficient residual perennial bunchgrass plants, recovery will require off-site sources. Moreover, a shift to a highly competitive understory species (Page and Bork 2005) or the invasion of exotic annual grasses (McGlone et al. 2009) may further limit perennial bunchgrass reestablishment.

Further experimental research is needed to corroborate the observations from our study and to elucidate potential understory species responses to specific restoration treatments in Pacific Northwest ponderosa pine forests. Moreover,

establishing field indicators of ponderosa pine occupancy would be beneficial for identifying the characteristics of those stands at risk to losing understory vegetation and where restoration efforts may be the most fruitful.

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