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Overstory and Shrub Influences on Seedling Recruitment Patterns in an Old-growth Ponderosa Pine Stand

Abstract

Seedling recruitment dynamics in old-growth ponderosa pine forests are poorly understood, but in very dry environments these processes are believed to be especially influenced by facilitation and competition from adjacent vegetation. Seedling recruitment in an old-growth ponderosa pine stand in central Oregon was studied to determine its relationship with overstory trees and nearby shrubs, and to identify the spatial patterns resulting from these relationships. From tests of significance using Poisson regression it was found that the influence of adjacent vegetation was greatest among smaller size classes of regeneration. The strongest relationship (negative) between overstory basal area and germinant and seedling density was observed when calculated at a very local scale (5-m radius). Seedling and germinant densities were also adversely affected by adjacent saplings. However, they were positively associated with shrubs, indicating that the facilitative influence of shrub presence exceeds its competitive effect for these regeneration stages. Unlike germinants and seedlings, saplings were most strongly related to shrubs, and this relationship was negative. Spatial analysis revealed significant aggregation of germinants, seedlings, and saplings, with the intensity of aggregation decreasing from smaller to larger size classes. These results suggest that regeneration is most sensitive to adjacent vegetation during early stages, that the facilitative influence of shrubs diminishes relative to their competitive effect once regeneration reaches the sapling stage, and that the early aggregated condition of regeneration gradually transforms toward a more regular pattern as stand development progresses.

Introduction

Seedlings of ponderosa pine (*Pinus ponderosa*) often face a harsh physical environment and can experience competition for scarce resources. In ponderosa pine forests, it is likely that tree recruitment is influenced by the spatial patterns of existing vegetation. In extreme environments, seedlings are especially influenced by competitive and facilitative forces imposed by adjacent vegetation (Callaway and Walker 1997). Shrubs and overstory trees may inhibit a seedling's survival and growth by competing for limited resources; conversely, they may ameliorate the seedling's physical environment. These influences may be borne simultaneously by an individual seedling (Holmgren et al. 1997), with their net effect determining the seedling's probability of survival and rate of growth. Because competitive

forces are repulsive and facilitative forces are attractive, the cumulative effect of competition and facilitation at the stand level should be reflected in the spatial patterns of regeneration density.

In this study we analyzed the spatial patterns of recruitment in an undisturbed old-growth ponderosa pine stand in central Oregon. The first objective of the study was to determine the relationship of neighboring trees and shrubs to regeneration. We hypothesized that the density of regeneration would be associated with the density of nearby overstory trees, shrubs, and regeneration in larger size classes. Information from this analysis would indicate whether the net relationships between tree regeneration and the components of stand structure were competitive or facilitative. The second objective of the study was to characterize the spatial distribution of regeneration and to identify possible differences in those patterns across different sizes of regeneration. We hypothesized that if overstory trees and shrubs influenced seedling recruitment and survival, then these influences would be evidenced by aggregated

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spatial patterns of recruitment, rather than by regular or random patterns, as a result of net facilitative attraction or net competitive repulsion.

Methods

Study Area

The study area is located 22 km northwest of Sisters, Oregon, in the Metolius Research Natural Area (RNA) on the east slope of the Cascade Range. The Metolius RNA covers parts of sections 25, 26, 35, and 36 of T12S/R9E, Willamette meridian (roughly 44.5° N latitude, 121.6° W longitude). Elevation is approximately 920 meters. The area's continental climate is typical of central Oregon, with cold winters (-0.5° C mean January temperature; weather data from Sisters, Oregon) and warm summers (17.4° C mean July temperature). Mean annual precipitation at Sisters is 408 mm, occurring mostly as snow. Only 36 mm of rain falls during the summer months (June through August), resulting in an annual period of drought.

The study was conducted at a forested site on flat terrain not dissected by streams. The soils are derived of basaltic pumice parent material erupted from volcanoes of the High Cascades, and are deep, coarse-textured, and poorly developed (Hall 1972). The open-canopy, old-growth stand consists of ponderosa pine with trace amounts of grand fir (*Abies grandis*). Overstory trees were moderately clumped rather than randomly or regularly dispersed. The understory vegetation is composed primarily of the deciduous antelope bitterbrush (*Purshia tridentata*), with some western needlegrass (*Stipa occidentalis*).

Data Collection and Analysis

A 4.5-hectare inventory unit was established at the study area in 1981, with trees greater than or equal to 10-cm diameter at breast height (140 cm; dbh) inventoried and mapped. In 1986, dbh was recorded for all live trees in the unit. During the same year, a grid of 28 2-m radius, circular regeneration plots was established at the unit. Plot centers were located at 25-m intervals along the grid. Measurements at these plots included tallies of three size classes of regeneration: 0.1-10.0 cm height, 10.1-140.0 cm height, and 0.1-10.0 cm dbh. In this study, these classes are referred to as germinants, seedlings, and saplings, respec-

tively. Diagrams of bitterbrush cover were sketched in the field, and were later used to visually estimate shrub cover as absent, trace (1 percent), or in increments of 5 percent. Data from one of the regeneration plots was lost, so the number of plots used in the analysis was 27.

Data from the shrub samples and overstory tree census were used for stand-level calculations of percent shrub cover, trees per hectare, basal area per hectare, quadratic mean dbh (diameter at breast height of tree of mean basal area), and the dbh frequency distribution. They were also used to calculate basal area per hectare in circular areas centered on the regeneration plots. Regeneration plot data were used to calculate density (stems per hectare) of germinants, seedlings, and saplings.

A preliminary assessment of spatial autocorrelation was performed for each of the three regeneration classes to assess whether the assumptions of linear regression were violated. Tests were based on calculations of Moran's I statistic, a coefficient that measures the dependence among variable values between spatial points (Upton and Fingleton 1985). Moran's I was calculated at six regular distance classes, with the number of pairs in each class ranging between 28 and 92. The Bonferroni approximation procedure (Rawlings et al. 1998) was used to determine overall significance ($P=0.05$).

Simple and multiple Poisson regressions were conducted to quantify the explanatory value of stand structure variables that were hypothesized to influence regeneration density ($n=27$). There were three response variables: number of stems per plot for each of the three regeneration size classes. Because these data were counts expected to follow the Poisson distribution, the Poisson regression model was the appropriate statistical model for the tests (Neter et al. 1996). The primary explanatory variable tested was overstory tree basal area per hectare, which was calculated for each regeneration plot. This measure was used as a plot-specific estimate of overstory density, and was assumed independent of the sizes of constituent trees. Two variants of overstory basal area were used in order to test whether the effects of overstory trees on regeneration were manifested at different spatial scales for the different sizes of regeneration. The two overstory density variants were calculated by summing the basal area of trees within radii of 5 and 15 meters from the

center of each regeneration plot, then using the appropriate expansion factor to express basal area on a per-hectare basis. Because the sapling class included relatively large stems with potentially substantial competitive impact, the number of saplings per plot was also tested as an explanatory factor for germinant and seedling densities. The effect of shrubs, using percent shrub cover measured within each regeneration plot, was tested for significance alone and with adjustments for overstory density. All tests of significance were conducted at the $P=0.05$ level.

Quadrat-based spatial analysis tools were used to characterize the spatial distribution of regeneration density. Variance/mean ratio, Index of Dispersion (a statistical test to determine the significance of the variance/mean ratio), and standardized Morisita's Index were calculated for each regeneration size class to determine whether they occurred in clumped, random, or regular patterns (Greig-Smith 1983, Krebs 1989).

Results & Discussion

Stand Structure

Stand density in 1986 was 349 trees per hectare, with 24.1 m²/ha of basal area. Nearly all of the overstory was ponderosa pine (> 99% of basal area). Average bitterbrush cover was 27.4% (standard deviation = 18.1%). Quadratic mean dbh was 29.6 cm, but the largest tree was 121.3 cm dbh. The frequency distribution of dbh (Figure 1) illustrates the broad range of tree sizes in the stand.

More than 75% of stems were in the smallest (10.0-19.9 cm) diameter class, presumably indicating a substantial increase in tree density in recent decades.

The total density of regeneration in all classes in 1986 was 9,402 stems per hectare. Variation among plots was high, but the mean number of stems decreased markedly with increasing size class of regeneration. There were 66% fewer seedlings than germinants, and 36% fewer saplings than seedlings. The drop in numbers between saplings (0.1-9.9 cm) and the smallest overstory diameter class (10.0-19.9 cm) was 79%.

Influence of Stand Structure on Regeneration

TABLE 1. Results of the Moran's I tests for spatial autocorrelation of regeneration density by regeneration classes. Moran's I statistic was almost uniformly non-significant ($\alpha=0.05$) at each distance class. The overall correlogram was non-significant for each regeneration class.

Distance Class (m)	Moran's I (P-value)		
	Germinants	Seedlings	Saplings
0-36	-0.199 (0.132)	0.041 (0.277)	0.088 (0.207)
36-71	-0.108 (0.237)	0.000 (0.336)	-0.226 (0.035)
71-107	-0.009 (0.354)	0.035 (0.159)	0.001 (0.320)
107-142	0.049 (0.165)	-0.095 (0.252)	0.059 (0.157)
142-177	0.020 (0.295)	-0.205 (0.053)	-0.95 (0.315)
177-213	-0.130 (0.272)	0.008 (0.375)	-0.038 (0.498)
Overall Significance	(0.792)	(0.317)	(0.212)

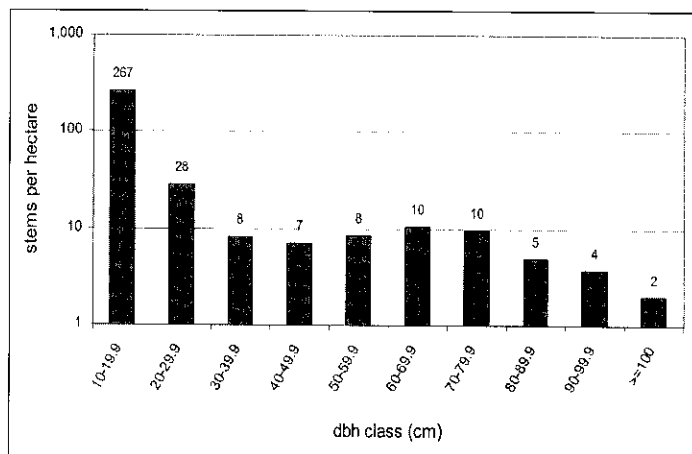


Figure 1. Frequency distribution of overstory trees by diameter class (note logarithmic scale of y-axis).

For each of the three regeneration classes, the Moran's I tests indicated no spatial autocorrelation. Table 1 shows the distance classes tested and the significance of Moran's I for each class. Using Bonferroni approximation, spatial autocorrelation was not significant for germinants ($P=0.792$), seedlings ($P=0.317$), and saplings ($P=0.212$). Given the lack of spatial autocorrelation, it was

possible to carry out the regression tests without violating the underlying assumption of independent observations.

For the smaller regeneration classes, the influence of the overstory was most apparent when basal area per hectare was calculated for the trees closest to the regeneration plot (Table 2). Calculations

TABLE 2. Response variables (Y), explanatory variables (X), and regression coefficients (β_x) of single-factor and two-factor regression models ($n=27$; significant factors at $\alpha=0.05$ in bold).

Y	X	β_x	P-value	
Germinants	<i>One-factor models</i>			
		5-m Overstory Basal Area	-0.0089	0.0007
		15-m Overstory Basal Area	0.0007	0.9559
		Number of Saplings	-0.1120	0.0029
		Percent Shrub Cover	0.0094	0.0141
	<i>Two-factor models</i>			
		5-m Overstory Basal Area	-0.0091	0.0003
		Number of Saplings	-0.1174	0.0014
		5-m Overstory Basal Area	-0.0119	<0.0001
		Percent Shrub Cover	0.0154	0.0005
Seedlings	<i>One-factor models</i>			
		5-m Overstory Basal Area	-0.0143	0.0043
		15-m Overstory Basal Area	-0.180	0.4094
		Number of Saplings	-0.1568	0.0269
		Percent Shrub Cover	0.0112	0.0888
	<i>Two-factor models</i>			
		5-m Overstory Basal Area	-0.0140	0.0031
		Number of Saplings	-0.1582	0.0205
		5-m Overstory Basal Area	-0.0194	0.0006
		Percent Shrub Cover	0.0221	0.0070
Saplings	<i>One-factor models</i>			
		5-m Overstory Basal Area	-0.0062	0.2467
		15-m Overstory Basal Area	0.0565	0.0341
		Percent Shrub Cover	-0.0354	0.0003
	<i>Two-factor model</i>			
		15-m Overstory Basal Area	0.0348	0.1847
		Percent Shrub Cover	-0.0340	0.0008

lated with the 5-m radius, overstory basal area per hectare was the most significant factor (negative) on density of germinants ($P=0.0007$) and seedlings ($P=0.0043$). Germinants and seedlings were also negatively related to sapling density ($P=0.0029$ and $P=0.0269$, respectively). The effect of sapling density was also significant when overstory basal area per hectare within a 5-m radius was included in the model. Scatterplots and tests of overstory basal area per hectare calculated with the 15-m radius did not reveal any relationships with germinants or seedlings. These results indicate that although the presence of overstory trees does adversely affect density of small regeneration, that influence is exerted only by those trees in close proximity. Saplings were not significantly related to overstory basal area per hectare within a 5-m radius, but there appears to be an upper limit on regeneration density in scatterplots of saplings and the other two regeneration classes versus overstory basal area per hectare (Figure 2). Despite scale differences on the Y-axis, the response patterns are consistent across the three regeneration classes.

Germinant density was positively associated with percent bitterbrush cover ($P=0.0141$), a relationship that was also significant when 5-m overstory basal area per hectare was included in the model. Since stems in the germinant class are probably too small to exert any influence on shrubs, this trend appears to represent a facilitative effect of shrubs on germination and small seedling survival. For seedling density, bitterbrush cover was not a significant factor when tested alone, but did have a significantly positive effect when 5-m overstory basal area was included in the model.

Saplings displayed a different pattern than the germinants and seedlings. In contrast to germinants, sapling density was most significantly related to bitterbrush cover ($P=0.0003$), not overstory density. The regression coefficient for bitterbrush cover was negative, indicating a net competitive relationship between saplings and bitterbrush. The relationship of saplings to overstory basal area within a 5-m radius was not significant ($P=0.2467$). In contrast, the effect of 15-m overstory basal area was significantly positive ($P=0.0341$). We cannot explain why the sapling-overstory relationship was positive, whereas the reverse was found for germinants and seedlings, or why it was significant whereas the 5-m basal area per hectare

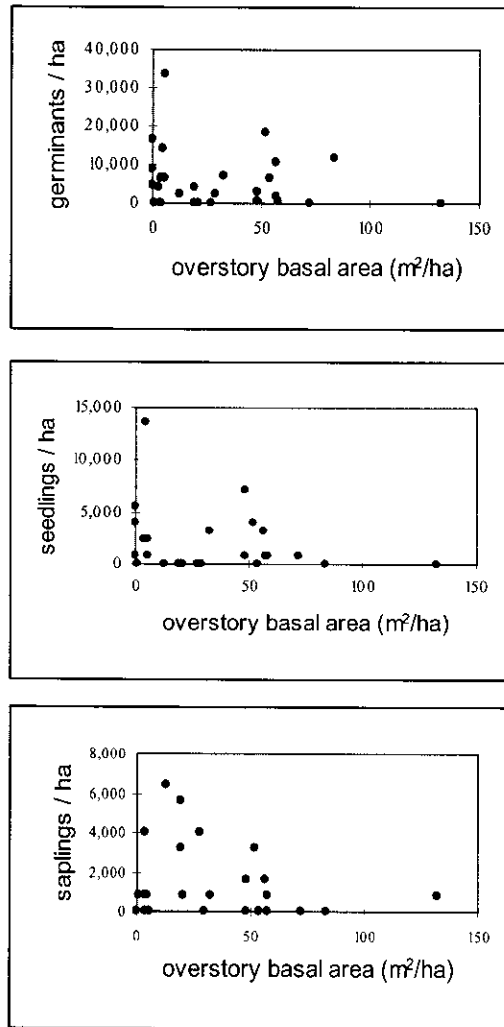


Figure 2. Regeneration stem density versus overstory basal area (m^2/ha) calculated with a 5-m radius.

was not significant. However, 15-m overstory basal area per hectare was not significant with percent shrub cover in the model.

Spatial Patterns

The quadrat-based spatial pattern analyses consistently indicated that all three size classes of regeneration were aggregated (Table 3). Variance/mean ratios were greater than 1, and the Index of Dispersion showed that these were highly significant ($P<0.005$) when compared to the Chi-square distribution (Greig-Smith 1983). This result was

TABLE 3. Results of quadrat-based spatial pattern analysis indicating aggregation among all three regeneration size classes. Values for Index of Dispersion all have P -values < 0.005 . Values for Standardized Morisita's Index are statistically significant at $\alpha=0.05$.

	Variance/ Mean	Index of Dispersion	Standardized Morisita's Index
Germinants	12.10	314.6	.526
Seedlings	5.52	143.5	.529
Saplings	3.26	84.9	.519

corroborated by significant values for standardized Morisita's Index. Because the stand lacks any obvious topographic heterogeneity, the spatial distribution may have been influenced by the spatial patterns of overstory trees and shrubs. The magnitude of the variance/mean ratio was inversely related to size class, showing that aggregation was stronger among seedlings than saplings, and strongest among germinants.

The trend from germinants to saplings offers evidence at a fine scale that the spatial patterns of ponderosa pine stems develop toward regularity over time, most likely as a result of spatially-influenced, competition-induced mortality patterns. The transformation of tree spatial distributions from a clustered pattern to a more regular pattern was observed in larger stems by Kenkel (1988) in a juvenile, even-aged boreal stand of jack pine, and by Moeur (1993) in old-growth mixed-conifer stands in the Rocky Mountains. Our results suggest that ponderosa pine stands may experience density-dependent mortality—and the associated trend toward a more regular spatial pattern—at a very early stage.

Conclusion

This study found that important relationships exist between ponderosa pine regeneration and adjacent vegetation. The presence of overstory trees had a negative impact on regeneration density of smaller size classes; this influence diminished as regeneration became larger. The overstory effect was present at a small spatial scale (5-m radius), but was not present at a larger scale (15-m). Like overstory trees, saplings also adversely impacted

the occurrence of germinants and seedlings. Shrub cover was negatively related to saplings, but was positively related to germinants and seedlings. Quadrat-based spatial analyses revealed that regeneration in each size class was aggregated, and that aggregation was greatest at smaller regeneration sizes. Taken together, these findings suggest that regeneration is particularly sensitive to the influences of adjacent vegetation; that the relationships between regeneration and adjacent vegetation change as stems become larger; and that these relationships are borne out in regeneration spatial patterns that begin as highly aggregated and gradually transform during stand development toward a more regular pattern.

The specific mechanisms that produced these results were not identified. Amelioration of microenvironmental conditions and competition for site resources are hypothesized as the primary agents, but other potential factors include site litter and nutrient heterogeneity, seed-caching animals, or seedling-clipping and seedling-browsing animals. To develop a more robust understanding of ponderosa pine seedling recruitment processes in this region, a larger dataset with more explanatory factors and replication across site and stand conditions is necessary. A data-intensive study is currently underway in central Oregon to better address the relationships of overstory trees and shrubs to seedling emergence, survival, and growth (Keyes and Maguire 2000). Although that study is based in disturbed stands, it may provide a more comprehensive basis for clarifying shrub and overstory influences on regeneration dynamics.

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