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# The Effects of Aboveground and Belowground Competition on Understory Species Composition in a *Pinus ponderosa* Forest

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**ABSTRACT.** The objective of this research was to test the hypothesis that water and nutrients, and not light, control understory plant species composition in a *Pinus ponderosa* forest in northeastern Oregon. The experiment was conducted as a split-plot experimental design with a  $2 \times 2$  factorial analysis. To assess the effects of root competition of overstory trees on understory species composition, 20 plots ( $4 \times 4$  m) were trenched approximately 1.0 m in depth, and compared to 24 nontrenched plots. To increase light levels to understory vegetation, trees were thinned from 345 to 148 trees  $\text{ha}^{-1}$  in half of each block (2.5 ha) during the winter and early spring of 1986. Canonical discriminant analysis indicated that light accounted for the greatest environmental resource response among the treatments. The number of species (8) that increased in cover and density was 60% greater when tree root competition was reduced in the root-reduction treatment, versus 5 when tree canopy influences were reduced in the canopy-reduction treatment. Simple correlation showed that changes in species composition were significantly ( $P \leq 0.05$ ) related to both changes in aboveground attributes (light, midday air temperature, and soil temperature) and belowground attributes (soil water potential, pH, and nitrogen). Competition for limited resources, light, water, and nutrients, does affect understory species composition as evidenced by the response of individual species to increasing availability of these resources. FOR. SCI. 41(4):864-889.

**ADDITIONAL KEY WORDS.** Competition, understory, thinning, trenching, *Pinus ponderosa*.

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**C**OMPOSITION OF FOREST UNDERSTORY SPECIES ARE CONTROLLED by overstory trees which filter light, moderate understory air and soil temperature, and directly compete for soil water and nutrients (Spurr and Barnes 1980). In previous studies we have demonstrated that understory production in *Pinus ponderosa* forests in northeastern Oregon is limited by water and nitrogen (Riegel 1989, Riegel et al. 1991, Riegel et al. 1992). However, it is unclear how individual species respond to limited water and nitrogen. Increasing resources which control or limit understory species may alter plant species composition. Tilman (1985) proposed the resource-ratio hypothesis, which states that plant species are specialized on different proportions or ratios of limiting resources and that composition of a plant community should change whenever the relative availability of the limiting resources changes. Determining which resources contribute to understory species response may allow for the prediction of changes after disturbance such as fire, logging, and grazing (Tilman 1982, 1985, 1988).

Land managers are currently testing the performance of partial canopy removals (e.g., shelterwood and two-aged silvicultural systems) in the interior forests of the Pacific Northwest. By testing these "non-clearcutting" systems, managers are attempting to address public criticism over clearcutting, as well as the need to provide forage and habitat for domestic and wild ungulates, and maintain biologic diversity. *Carex geyeri* and *Calamagrostis rubescens*, both rhizomatous graminoids, are the dominant understory species in many of these interior forests (Franklin and Dyrness 1973). After logging, conifer reforestation efforts are often hampered by the aggressive and competitive ability of *Carex* and *Calamagrostis*, for they respond positively to the removal of the overstory which increases light, water, and nutrients to the understory and the residual overstory (Sloan and Ryker 1986). On a *P. ponderosa* site in western Montana, foliage density of *Carex*, *Calamagrostis*, and associated forbs and shrubs were directly related to a linear decrease in soil water content in late summer (Petersen and Maxwell 1987). Decreasing density of *Calmagrostis* was found to increase the mean size of young *Pinus* and also to modify the shape and distribution of individual trees which may affect subsequent stand dynamics (Petersen 1988).

Forest understory species are comprised of a variety of life forms, physiologic tolerances, and reproductive strategies which allow them to live and reproduce under numerous abiotic and biotic conditions. As a *Pinus* stand grows, understory species composition responds to changes in the quality and quantity of light (Chazdon 1988) and less abundant belowground resources (Barrett and Youngberg 1965). Early seral understory species grow rapidly, taking advantage of the abundance of resources. As the canopy closes, these species are replaced by midseral plants which have a wider range of tolerance to competition, and are more responsive to repeated low intensity disturbance such as fire and grazing (Hall 1976, 1977, Johnson and Simon 1987). Finally, late seral species successfully compete in stand conditions that midseral and especially early seral species cannot tolerate: low light and tightly cycled nutrients (Tilman 1982, 1985, 1988). After life cycle completion, many understory species not present in the current vegetation remain dormant in the seed bank until their germination requirements are met (Archibold 1989).

Our interest in conducting this research was to quantify how cover and density of individual understory species respond to increased levels of light, water, and nutrients. This research complements our understory production study (Riegel 1989, Riegel et al. 1991, Riegel et al. 1992) which was conducted simultaneously on the same experimental plots. Our research demonstrated that water and nitrogen were the dominant environmental factors governing understory production. We found no relationship between light and biomass production.

The objectives of this research were: (1) to test the hypothesis that belowground resources and not aboveground resources have a differential effect on cover and density of understory plant species in a *P. ponderosa* forest in north-eastern Oregon, and (2) to evaluate the relationship of life form and species response to increasing light, soil, water, nitrogen, and related variables.

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## STUDY AREA

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The study was conducted on the Hall Ranch of the Eastern Oregon Agricultural Research Center, located approximately 19 km southeast of Union, Oregon (lat-

itude 43°12' and longitude 117°53'). The Hall Ranch is within the southwestern foothills of the Wallowa Mountains in the northeastern corner of the state at an elevation of 1060 m.

The climate is continental with cold wet winters, and hot dry summers with occasional thunderstorms. Mean monthly air temperatures vary from a minimum of -19.2°C in December to 1.1°C in July; from a maximum of 8.5°C in December to 36.9°C in July (29 yr mean of minimum and maximum temperatures; file data, Eastern Oregon Agricultural Research Center, Union). The majority of precipitation on the Hall Ranch occurs between November and May as snow. Mean annual precipitation for 1963-1987 was 605 mm (Williams 1989).

The research was conducted in a *Pinus ponderosa*/*Symphoricarpos albus* community type (midseral) similar to Johnson and Simon's (1987) *Pseudotsuga menziesii*/*Symphoricarpos albus* plant association of the Wallowa-Snake Province of northeastern Oregon. *Pinus ponderosa* dominates 97% of the overstory with *P. menziesii* and *Larix occidentalis* found as infrequent associates. *Pinus ponderosa* and *P. menziesii* codominate the reproduction. *Symphoricarpos albus*, *Carex geyeri*, *Calamagrostis rubescens*, and *Arnica cordifolia* dominate the understory. Sites were selectively logged (i.e., "high graded") before 1936; since then there has been no logging.

Three major soil series occur within the research site: Hall Ranch, fine-loamy, mixed, frigid, Ultic Haploxerolls (block 1 nonthin and thin; block 2 thin); Klicker, loamy skeletal, mixed frigid Ultic Argixerolls (blocks 2 and 3 nonthin); and Tolo, medial over loamy, mixed frigid Typic Vitrandepts (block 3 thin) (Dyksterhuis and High 1985). Surface soil texture ranges from silt loam to silty clay loam, and soil depth varies from 38 cm to greater than 92 cm.

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## METHODS

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To evaluate the effects of above- and belowground overstory competition of commercial sized trees (>15.24 cm top on 487.68 and 975.36 cm logs and >20.32 cm on odd sized logs) on understory plants we used a split-plot experimental design with three replications. This design separated the effects of tree canopy and tree roots on understory plants. Three 5.0 ha blocks, located within 1.0 km of each other, were selected. Stands were relatively homogeneous in overstory species composition and stand structure; however, understory vegetation differed slightly among blocks. To increase light levels within the understory, overstory trees were commercially thinned in the canopy-reduction treatment (Figure 1). A consultant professional forester (Mountain Timber Forest Consultants, La Grande, Oregon) selected and marked the trees for a residual mean tree spacing of 8.23 m. Half of each block was commercially thinned from a density of 345 to 148 trees ha<sup>-1</sup> during the winter and spring of 1986. In both thinned and nonthinned sites, tree diameters at breast height (dbh) ranged from 0.3 to 135.6 cm with a mean of 31.8 cm. Thinning decreased canopy cover by 52% (60.61 to 28.99%) and basal area by 59% (22.1 to 10.2 m ha<sup>-1</sup>) (Riegel 1989, Riegel et al. 1992).

Competition between the overstory and understory for soil water and nutrients was reduced when tree roots were severed by trenching in the root-reduction treatment (Figure 1). Forty-eight, 4.0 × 4.0 m plots (16/block) were subjectively

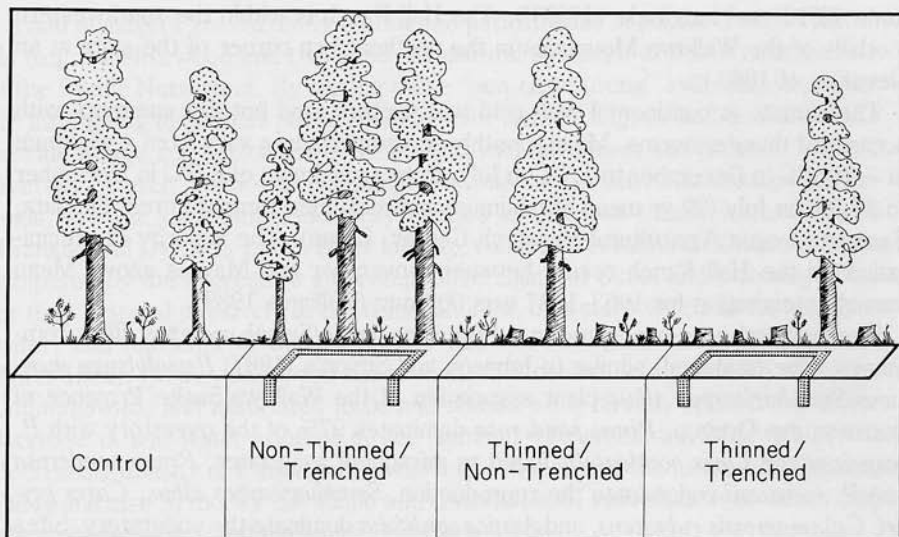
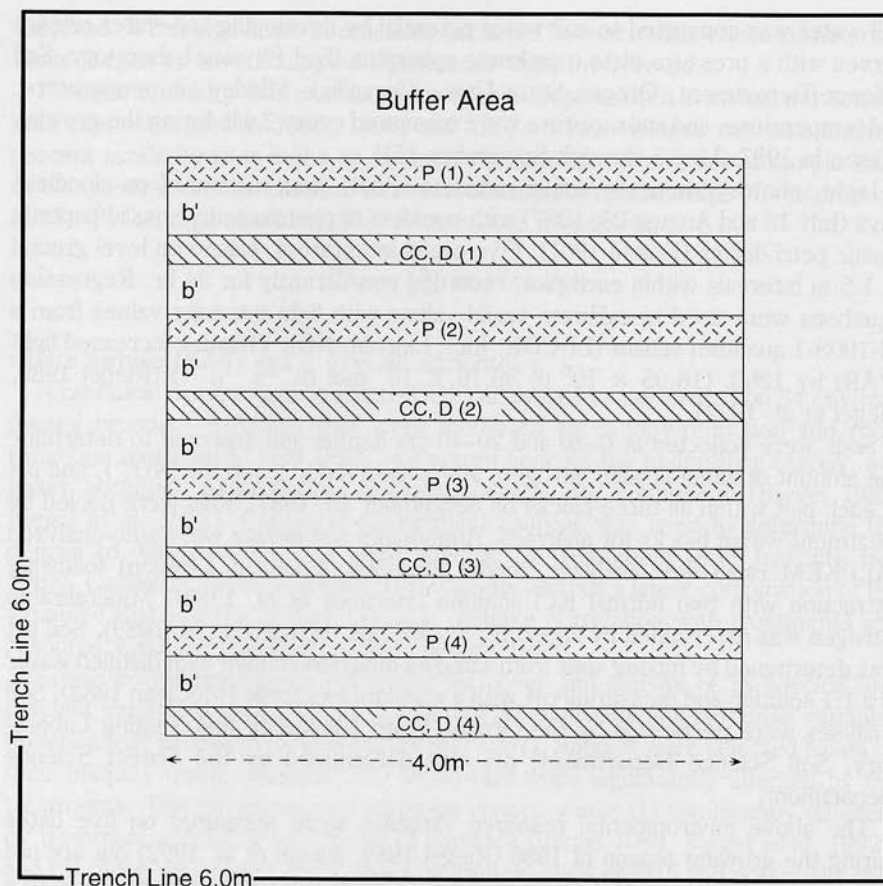


FIGURE 1. Layout of the canopy-control, canopy-reduction, root-control, and root-reduction treatments.

established to ensure adequate representation of the variation in canopy cover (Figure 2). Four trench and four nontrench plots were randomly assigned in both thinned and nonthinned treatments within each of the three blocks prior to logging. Perimeters of 24 plots ( $6.0 \times 6.0$  m) were trenched 20 to 30 cm wide and to a depth of 1 m unless the presence of large rocks and boulders prohibited trenching to that depth (Figure 2). Plots were trenched using a four wheel drive Ditch Witch (Charles Machine Works, model R60, Perry, Oklahoma) in September of 1985. Backfill was replaced to allow subsurface water movement. We randomly selected one of the four perimeters, in each trench plot, and re-excavated the trench in an area  $0.20 \times 0.30 \times 100$  cm deep for evidence of root growth in the trench in late September of 1986 and 1987. We found no evidence of roots in 1986 or 1987. Four plots were destroyed during logging operations in block 3; one nontrench and three trench. The effect of logging, using conventional rubber tire skidders, on understory vegetation was not assessed within this study as disturbance was minimal. Hereafter, treatments are referred to as canopy-reduction, canopy-control (nonthinned), root-reduction, and root-control (non-trenched) treatments.

#### UNDERSTORY VEGETATION MEASUREMENTS

Density of individual species was measured in four,  $4.0 \times 0.10$  cm microplots within each plot (Figure 2) (Pieper 1978). Cover was ocularly estimated by cover class (Riegel 1989) for all species within a  $0.20 \times 0.50$  m plot frame, at four points, spaced at 1.0 m intervals along each 4.0 m transect (16/plot). Cover classes for ocular estimates were: (1)  $<0.1$ , (2) 0.1–1, (3) 1–2, (4) 3–5, (5) 6–10, (6) 11–20, (7) 21–30, (8) 31–40, (9) 41–50, (10) 51–60, (11) 61–70, (12) 71–80, (13) 81–90, and (14) 91–100%. For statistical analyses, classes were converted to the mean value within each cover category. Cover and density were measured in



**Transect Sizes:**

- P = Production - 4.0m x 0.20m/transect x 4 transects
- CC = Canopy Cover - 0.20m x 0.50m plots read every 1.0m  
- 4 plots/transect x 4 transects
- D = Density - 4.0m x 0.10m/transect x 4 transects
- b' = Buffer Area - 4.0m x 0.3428m area of undisturbed vegetation

FIGURE 2. Production, canopy cover, and density transects within a plot.

1985 prior to canopy and root reduction and in 1986 and 1987 after canopy reduction. Measurements were recorded during the growing season (July and August) in all 3 yr. Vascular plant nomenclature and taxonomy follows Hitchcock and Cronquist (1973).

**ENVIRONMENTAL RESOURCE VARIABLES**

Air temperature at midday (1300 hr) was measured with a Princo sling psychrometer (Southampton, Pennsylvania). Soil temperature was measured with a Reotemp soil thermometer (San Diego, California) at three depths; 15, 30, and 45 cm per plot. Soil moisture was measured gravimetrically: one soil moisture core was collected at three depths; 0-20, 20-40, and 40-60 cm in each plot. Percent

soil water was converted to soil water potential by developing soil water release curves with a pressure plate membrane apparatus (Soil Physics Laboratory, Soil Science Department, Oregon State Univ., Corvallis). Midday air temperature, soil temperature, and soil moisture were measured every 2 wk during the growing season in 1987 (May 5 through September 15).

Light, photosynthetically active radiation (PAR), was measured on cloudless days (July 18 and August 28, 1987) with booklets of photosensitive ozalid paper in plastic petri dishes (Friend 1961). Five ozalid integrators, placed on level ground at 1.5 m intervals within each plot, recorded concurrently for 24 hr. Regression equations were used to calibrate ozalid values with light intensity values from a LI-190S-1 quantum sensor (LI-COR, Inc., Lincoln, NE). Thinning increased light (PAR) by 126% ( $16.05 \times 10^6$  to  $36.16 \times 10^6$  mol m<sup>-2</sup>s<sup>-1</sup>d<sup>-1</sup>) (Riegel 1989, Riegel et al. 1992).

Soils were collected at 0–20 and 20–40 cm depths and analyzed to determine the amount of mineralizable nitrogen, ammonium (NH<sub>4</sub><sup>+</sup>), nitrate (NO<sub>3</sub><sup>-</sup>), and pH in each plot within all three blocks on September 15, 1987. Soils were pooled by treatment within blocks for analyses. Ammonium and nitrate were auto-analyzed (ALPKEM rapid flow analyzer, model RFA-300, Portland, Oregon) following extraction with two normal KCl solution (Horneck et al. 1989). Mineralizable nitrogen was determined by anaerobic incubations (Horneck et al. 1989). Soil pH was determined by mixing soils from samples described above with distilled water in a 1:1 solution and measuring pH with a standard electrode (McClellan 1982). Soil analyses were performed by the Oregon State University Soil Testing Laboratory, Soil Science Department; pH was determined by the Forest Science Department.

The above environmental resource variables were measured on five dates during the growing season of 1986 (Riegel 1989, Riegel et al. 1992) but are not discussed in this paper. Results of analyses utilizing 1986 environmental resource variables were similar to 1987.

#### EXPERIMENTAL DESIGN AND DATA ANALYSIS

The experiment was conducted as a split-plot design with a 2 × 2 factorial analysis. To meet the assumptions of analysis variance, all zeros were converted to 0.1, then a log<sub>10</sub> transformation of the data was performed. Analysis was carried out only for species that occurred in plots of every treatment combination. The general linear model procedure was used to test differences in canopy and root treatments because the experimental design was not balanced (SAS Institute Inc. 1987). The effects of overstory canopy on understory vegetation are emphasized in the canopy-reduction versus the canopy-control treatments by averaging across both root-reduction and root-control treatments. Belowground effects on understory vegetation are emphasized in the root-reduction versus the root-control treatments which are averaged across canopy-reduction and canopy control-treatments. Variables tested were understory cover and density by life-form and species within each year. To determine differences between years, cover and density values by life-form and species were subtracted by plot of 1 yr from that of another year. For example, a cover or density value by plot was subtracted from the same plot value of another year; 1987 from 1986, 1987 from 1985, and 1986 from 1985. A probability value of  $P \leq 0.05$  was used throughout the analyses to test significance of F values. Only significant differences are

reported. When significant interactions occurred between main effect means, only those judged to have ecological significance were interpreted.

Percent similarity was calculated for species represented in cover and density data sets measured in 1985, 1986, and 1987. A resemblance measure such as percent similarity is an index or distance calculated for every pair of sample-units or composites used to examine between community relationships (Overton et al. 1987). Percentage similarity (*PS*) is calculated as follows;

$$PS_{jl} = \sum_i \min(p_{ij}, p_{il}),$$

where sample units *j* and *l*, over all attributes *i*.

A canonical discriminant function (CDF) analysis was performed on 34 environmental resource variables that were increased by canopy-reduction and root-reduction treatments; light (PAR) measured beneath the understory canopy, soil water potential, mineralizable nitrogen, nitrate, and ammonium (Riegel 1989, Riegel et al. 1992). Canonical discriminant analysis was used to determine the degree to which resource(s) were affected by treatments (SAS Institute Inc. 1987). Canonical discriminant function analysis derives a linear combination of the variables that has the highest possible multiple correlation with treatments and resource variables (Legendre and Legendre 1983).

Simple correlations were performed on cover and density of 14 species (dependent variables) with a selected group of 30 environmental response variables (independent variables) (SAS Institute Inc. 1987). Species were selected based on their ubiquity (most common) and those that were significantly affected by the treatments. The environmental variables chosen were: (1) significantly different by treatment according to analysis of variance (Riegel 1989, Riegel et al. 1992), and (2) those we believe had a direct bearing on plant growth and potentially able to influence species composition. A correlation coefficient table was used (with 42 degrees of freedom;  $n-2$ ) to determine significance of each correlation (Little and Hills 1978). Only significant differences with a probability of  $P \leq 0.05$  are reported in the text.

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## RESULTS

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### WITHIN YEAR DIFFERENCES

#### Cover

Prior to treatment establishment, there were no differences in cover of life forms (graminoids, forbs, and shrubs) in 1985. There were differences, however, by species (Table 1).

In 1986, the first season following treatment, graminoid and forb cover increased 75%, while shrub cover increased 54% in the root-reduction versus root-control treatments (Table 2). *Calamagrostis rubescens* increased in the root reduction treatment (Table 1). In the canopy-reduction versus canopy-control treatments shrub cover was 45% lower (Table 2). *Lathyrus nevadensis* and *Calamagrostis* also decreased after canopy reduction. *Taraxacum officinale* was the only species that increased after canopy reduction. Canopy-reduction  $\times$  root-reduction interactions were observed for *Poa pratensis* and *Achillea millefolium*.

TABLE 1.

Cover (%) of species that were significant ( $P \leq 0.05$ ) by treatments (means and standard deviations) for 1985, 1986, and 1987. Significant effects were for A = canopy-control and canopy-reduction treatments; B = root-control and root-reduction treatments; and A  $\times$  B = control  $\times$  root interaction.

Species/year	Canopy-reduction Root-control		Canopy-reduction Root-reduction		Canopy-control Root-control		Canopy-control Root-reduction		$P$ ( $\leq 0.05$ )
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	
<b>1985</b>									
<i>Achillea millefolium</i>	1.3	1.1	1.3	1.1	0.6	1.00	0.8	1.2	A
<i>Aster occidentalis</i>	1.9	2.2	2.4	2.6	0.9	1.4	0.9	1.6	A
<i>Poa pratensis</i>	7.3	8.6	12.1	12.1	1.5	2.4	2.9	4.6	B
<i>Rosa gymnocarpa</i>	2.7	3.8	0.4	0.7	0.9	1.9	0.9	1.4	A $\times$ B
<i>Trisetum canescens</i>	4.4	3.4	6.4	2.8	4.3	4.0	3.5	4.3	A $\times$ B
<b>1986</b>									
<i>Achillea millefolium</i>	1.3	0.8	3.4	2.4	0.3	0.6	2.8	3.4	A $\times$ B
<i>Calamagrostis rubescens</i>	0.4	0.8	0.7	0.9	0.5	0.9	2.8	2.9	A,B
<i>Lathyrus nevadensis</i>	3.9	3.6	3.3	2.8	3.5	3.3	4.1	5.0	A
<i>Poa pratensis</i>	6.1	5.7	10.6	8.7	1.4	2.0	6.6	9.6	A $\times$ B
<i>Taraxacum officinale</i>	0.6	0.9	1.9	1.5	0.0	0.0	1.2	2.3	A
<b>1987</b>									
<i>Achillea millefolium</i>	2.4	1.2	2.7	1.2	0.1	0.3	1.3	1.3	A
<i>Aster occidentalis</i>	2.1	2.4	5.7	6.3	0.9	1.8	0.9	1.3	A,B
<i>Carex geyeri</i>	1.5	6.2	13.5	5.1	8.8	5.8	17.3	11.4	B
<i>Calamagrostis rubescens</i>	0.7	1.0	1.4	1.4	1.4	1.7	3.9	3.8	B
<i>Galium boreale</i>	1.7	1.4	1.9	1.7	0.2	0.5	0.4	1.0	A
<i>Lathyrus nevadensis</i>	3.0	3.0	1.3	1.9	1.2	1.8	2.1	3.7	A $\times$ B
<i>Luzula campestris</i>	1.3	1.3	1.3	2.0	0.4	0.8	1.3	1.3	A
<i>Poa pratensis</i>	8.5	8.4	20.2	20.0	1.4	2.5	7.2	8.5	B
<i>Taraxacum officinale</i>	1.3	1.3	1.2	1.4	0.1	0.3	0.5	1.0	A,B
<i>Tragopogon dubius</i>	0.1	0.3	0.3	0.5	0.0	0.2	1.0	1.2	A,B
<i>Trisetum canescens</i>	2.3	1.7	6.8	6.9	1.5	1.3	10.0	9.9	A $\times$ B



TABLE 2.

Cover (%) and density (# of individuals/m<sup>2</sup>) by life forms that were significant ( $P \leq 0.05$ ) by treatments (means and standard deviations) for 1986 and 1987. Significant effects were for A = canopy-control and canopy-reduction treatments; B = root-control and root-reduction treatments; and A × B = canopy × root interaction.

	Canopy-reduction Root-control		Canopy-reduction Root-reduction		Canopy-control Root-control		Canopy-control Root-reduction		$P \leq 0.05$
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	
1986									
<i>Cover</i>									
Forbs	0.6	0.4	0.9	0.5	0.5	0.3	1.0	0.3	B
Graminoids	1.8	0.9	2.2	1.0	1.5	0.5	3.4	1.5	B
Shrubs	1.3	0.9	1.6	1.0	2.0	1.3	3.1	2.0	A,B
1987									
Forbs	0.7	0.2	1.0	0.3	0.5	0.3	0.8	0.2	B
Graminoids	2.5	1.1	4.3	0.9	1.4	0.5	4.4	1.3	B
Shrubs	1.3	0.8	1.6	0.8	2.0	1.2	2.7	1.4	B
<i>Density</i>									
1986									
Forbs	266.6	74.4	348.3	90.5	189.8	49.8	390.4	70.1	B
Graminoids	1133.2	279.9	1357.5	278.2	1030.8	203.9	1866.5	322.5	B
1987									
Forbs	530.2	81.4	617.8	106.4	239.2	48.5	443.1	55.5	B
Graminoids	2365.9	309.5	2939.7	345.3	1276.1	236.1	2526.7	318.7	B
Shrubs	87.1	30.5	113.9	38.1	96.9	26.2	132.1	30.5	B

Interactions appear to be a function of increased light and soil resources in the canopy-reduction/root-reduction treatment. The combination of increased light from canopy reduction and soil water and nutrients from root reduction produced higher cover values as compared to the controls.

In 1987, graminoids increased 124%, forbs 57%, and shrubs 33% in the root-reduction treatment (Table 2). Within the root-reduction treatment *Carex geyeri*, *Poa*, *Calamagrostis*, *Taraxacum*, *Aster occidentalis*, and *Tragopogon dubius* increased over the root control (Table 1). Canopy reduction had no effect on life form cover in 1987. *Tragopogon* decreased in cover in the canopy-reduction versus the canopy-control treatments while *Galium boreale*, *Luzula campestris*, *Achillea*, *Taraxacum*, and *Aster* increased. A canopy-reduction  $\times$  root-reduction interaction was observed for *Trisetum canescens* and *Lathyrus*. The interaction observed in *Trisetum* appears to be a function of higher cover values in the root-reduction treatment from increased soil resources. Increasing soil resources from root reduction without canopy reduction yielded the highest cover; however, *Trisetum* also responded to increased light levels in the canopy-reduction treatments as compared to the controls. Interaction in *Lathyrus* occurred due to variation among treatment means.

### Density

There were no differences in density by life form between treatments in 1985. There were differences, however, in individual species by treatment (Table 3).

In 1986, within the root-reduction treatment, density of graminoids increased 53% and forbs 64% (Table 2). *Calamagrostis*, *Silene menziesii*, and *Taraxacum* increased in the root-reduction over the root-control treatment (Table 3). Canopy reduction increased *Aster* and *Achillea*. A canopy-reduction  $\times$  root-reduction interaction was observed for *Trisetum*. *Trisetum* density in the canopy-control/root-reduction treatment was twice that of the canopy-reduction/root-reduction treatment. Interactions may have occurred as *Trisetum* responded to increased soil resources and to a lesser degree increased light levels in the canopy-reduction treatments.

In 1987, graminoids increased 50%, and forbs and shrubs 35% within the root-reduction versus root-control treatments (Table 2). *Tragopogon*, *Calamagrostis*, and *Taraxacum* increased in the root-reduction versus root-control treatments (Table 3). *Achillea*, *Aster*, and *Taraxacum* also increased in the canopy-reduction treatment.

Although tree seedling cover and density were measured in all 3 yr there were no significant differences between treatments, either collectively tested as a life form or as individual species.

## BETWEEN YEAR DIFFERENCES

### Cover

Within the root-reduction treatment, forbs increased from 1985 to 1986 while graminoids increased from 1986 to 1987 (Table 4). Over the 2-yr period, from 1985 to 1987, graminoids and forbs both increased. In all 3 yr, plant cover by life form did not increase in the canopy-reduction treatment.

*Achillea* cover increased in the root-reduction treatment from 1985 to 1986 (Table 5). *Tragopogon* increased in cover in the root-reduction treatment from

TABLE 3.

Density (# of individuals/m<sup>2</sup>) of species that were significant ( $P \leq 0.05$ ) by treatments (means and standard deviations) for 1985, 1986, and 1987. Significant effects were for A = canopy-control and canopy-reduction treatments; B = root-control and root-reduction treatments; and A × B = canopy × root interaction.

Species/year	Canopy-reduction Root-control		Canopy-reduction Root-reduction		Canopy-control Root-control		Canopy-control Root-reduction		$P$ ( $P \leq 0.05$ )
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	
<b>1985</b>									
<i>Fragaria virginiana</i>	62.0	56.9	89.7	40.3	44.3	40.1	27.5	27.3	A
<i>Symphoricarpos albus</i>	36.5	32.1	86.6	77.0	55.2	53.6	47.3	52.2	A × B
<i>Trisetum canescens</i>	166.0	166.9	214.4	90.8	149.2	128.6	163.6	268.0	A × B
<i>Viola adunca</i>	4.0	33.4	5.3	4.9	4.2	10.7	2.5	5.3	A
<b>1986</b>									
<i>Achillea millefolium</i>	19.6	17.6	32.2	32.7	6.1	8.3	23.8	32.2	A
<i>Aster occidentalis</i>	33.9	54.2	61.4	73.3	15.6	25.0	67.3	144.6	A
<i>Calamagrostis rubescens</i>	9.6	19.9	23.3	28.2	16.1	28.8	127.7	161.1	B
<i>Silene menziesii</i>	21.6	66.0	10.3	26.3	3.6	9.4	23.6	48.7	B
<i>Taraxacum officinale</i>	3.4	5.5	13.6	20.5	1.1	3.6	5.6	10.5	B
<i>Trisetum canescens</i>	87.1	73.2	141.1	138.3	59.2	88.3	286.6	330.3	A × B
<b>1987</b>									
<i>Achillea millefolium</i>	41.4	22.5	57.2	41.9	5.0	9.5	22.9	35.2	A
<i>Aster occidentalis</i>	65.2	85.2	104.2	90.8	22.5	38.0	26.3	56.3	A
<i>Calamagrostis rubescens</i>	37.7	58.6	45.3	48.3	31.3	42.0	154.6	191.6	B
<i>Taraxacum officinale</i>	8.2	9.9	13.1	11.6	1.9	3.9	4.0	6.1	A,B
<i>Tragopogon dubius</i>	0.2	0.8	2.0	2.7	0.8	2.2	9.0	13.4	B

TABLE 4.

Changes in life forms cover (%) and density (# of individuals/m<sup>2</sup>) that were significant ( $P \leq 0.05$ ) between years, by treatments (means and standard deviations). Significant effects were for A = canopy-control and canopy-reduction treatments; B = root-control and root-reduction treatments; and A × B = control × root interaction.

	Canopy-reduction Root-control		Canopy-reduction Root-reduction		Canopy-control Root-control		Canopy-control Root-reduction		$P \leq 0.05$
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	
<i>Cover</i>									
1985-1986									
Forbs	-0.1	0.5	0.2	0.7	0.0	0.2	0.4	0.3	B
1986-1987									
Graminoids	0.7	0.8	2.1	1.1	-0.1	0.8	1.0	1.1	B
1985-1987									
Forbs	0.0	0.3	0.4	0.4	0.0	0.2	0.3	0.3	B
Graminoids	-0.3	1.2	1.5	1.4	-0.7	0.5	2.3	1.8	B
<i>Density</i>									
1985-1986									
Forbs	-53.9	93.1	-23.0	115.8	-7.6	28.3	69.0	55.6	A, B
1986-1987									
Forbs	105.5	73.5	107.8	83.5	19.8	29.2	21.1	79.6	A
Graminoids	493.1	133.4	632.9	241.1	98.1	216.1	264.1	157.4	A
1985-1987									
Forbs	51.6	70.0	84.8	72.3	12.2	31.7	90.1	68.8	B
Graminoids	385.9	300.5	517.4	204.7	-108.5	180.4	484.1	307.8	A × B

TABLE 5.

Changes in species over (%) that were significant ( $P \leq 0.05$ ) between years, by treatments (means and standard deviations). Significant effects were for A = canopy-control and canopy-reduction treatments; B = root-control and root-reduction treatments; and A  $\times$  B = control  $\times$  root interaction.

Species/year	Canopy-reduction Root-control		Canopy-reduction Root-reduction		Canopy-control Root-control		Canopy-control Root-reduction		$(P \leq 0.05)$
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	
<b>1985-1986</b>									
<i>Achillea millefolium</i>	0.1	1.3	2.3	2.7	-0.3	1.0	2.0	2.4	B
<b>1986-1987</b>									
<i>Achillea millefolium</i>	1.1	1.4	-0.8	2.2	-0.1	0.7	-1.4	2.9	A
<i>Berberis repens</i>	-0.4	3.0	0.5	2.7	-1.0	2.0	0.5	2.9	A $\times$ B
<i>Carex geyeri</i>	3.5	4.3	5.4	5.5	-1.7	7.4	3.3	5.1	A
<i>Taraxacum officinale</i>	0.7	1.1	0.0	1.8	0.1	0.3	-0.6	1.7	B
<i>Tragopogon dithius</i>	0.1	0.3	0.3	0.5	0.0	0.2	0.8	1.1	B
<b>1985-1987</b>									
<i>Arrhenatherum elatius</i>	0.0	0.0	0.0	0.1	-0.1	0.4	0.3	0.7	A
<i>Aster occidentalis</i>	0.4	2.3	3.5	4.2	0.0	1.0	-0.1	0.7	A,B
<i>Carex geyeri</i>	-2.6	7.6	-0.4	8.8	-4.8	5.5	5.6	10.8	B
<i>Taraxacum officinale</i>	1.2	1.3	1.8	1.2	0.1	0.2	0.5	1.0	B

1986 to 1987. Though *Taraxacum* decreased in cover in the root-reduction treatment from 1986 to 1987, 2 yr after treatment establishment (1985 to 1987) there was a net increase in cover. *Carex* and *Aster* both increased in cover within the root-reduction treatment between 1985 and 1987. A canopy-reduction  $\times$  root-reduction interaction was observed in 1986 to 1987 for *Berberis repens*. This interaction appears to be a function of the canopy-reduction/root-control treatment having the least change in cover from 1986–1987 while cover in the canopy-control/root-control treatment was higher.

*Achillea* and *Carex* increased in cover from 1986 to 1987 and *Aster* and from 1985 to 1987 in the canopy-reduction treatment (Table 5). *Arrhenatherum* was the only species that decreased in cover from 1985 to 1987 in the canopy-reduction versus canopy-control treatments.

### Density

Two years after treatment establishment (1985 to 1987), forbs had increased in the root-reduction versus root-control treatments (Table 4). From 1985 to 1986, density of forbs decreased in canopy-reduction versus canopy-control treatments but increased in root-reduction versus root-control treatments. However, from 1986 to 1987, graminoids and forbs increased in canopy-reduction versus canopy-control treatments. A canopy-reduction  $\times$  root-reduction interaction was observed for graminoids in 1985–1987. Interaction appears to be a function of increased density in the root-reduction and canopy-reduction/root-control treatments with a decline in the canopy-control/root-control treatment.

*Achillea*, *Silene*, and *Taraxacum* increased density from 1985 to 1986 in the root-reduction versus root-control treatment (Table 6). *Lathyrus* was the only species to decrease in density the first year after root-reduction (1985 to 1986). Two years (1985 to 1987) after the root-reduction treatment was established, *Carex*, *Taraxacum*, and *Tragopogon* increased in density.

The first year after canopy reduction, 1985 to 1986, density of *Potentilla gracilis* and *Rosa gymnocarpa* increased, but *Carex* decreased (Table 6). *Carex* did, however, increase in density in the canopy-reduction treatment over the 2 yr (1985 to 1987) period. From 1986 to 1987, density of *Achillea*, *Aster*, *Galium*, and *Poa* increased within canopy-reduction versus canopy-control treatments. *Achillea*, *Luzula*, and *Taraxacum* increased in the canopy-reduction versus canopy-control treatment from 1985 to 1987. Canopy-reduction  $\times$  root-reduction interactions were observed for *Symphoricarpos albus* and *Trisetum* from 1985 to 1986 and for *Poa*, *Spiraea*, and *Trisetum* from 1985 to 1987. Though *Symphoricarpos* and *Trisetum* density increased in the canopy-control/root-reduction treatment between 1985–1986 it was the variation among the means of all treatments that produced the interaction. Interaction in *Poa* appears to be a function of higher density in the canopy-reduction treatment, the highest in the canopy-reduction/root-reduction treatment, with essentially no change in the control. The interaction for *Spiraea* appears to be caused by decreases in density in the canopy-control treatment with a great amount of variation, while canopy reduction only slightly decreased density. Interaction for *Trisetum* is a function of increased density in the canopy-control/root-reduction treatment with little response in the canopy-reduction treatment, all with tremendous variation.

TABLE 6.

Changes in species density (# of individual/m<sup>2</sup>) that were significant ( $P \leq 0.05$ ) between years, by treatments (means and standard deviations). Significant effects were for A = canopy-control and canopy-reduction treatments; B = root-control and root-reduction treatments; and A × B = control × root interaction.

Species/year	Canopy-reduction Root-control		Canopy-reduction Root-reduction		Canopy-control Root-control		Canopy-control Root-reduction		$(P \leq 0.05)$
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	
<b>1985-1986</b>									
<i>Achillea millefolium</i>	-0.5	7.9	13.3	31.9	-2.9	6.0	14.2	19.0	B
<i>Carex geyeri</i>	-276.3	614.8	-388.3	484.5	-410.2	772.2	92.1	436.7	A
<i>Lathyrus nevadensis</i>	-8.2	59.2	-23.3	29.5	10.0	26.3	-5.8	29.0	B
<i>Potentilla gracilis</i>	2.3	6.9	0.0	5.0	-1.1	2.3	-1.3	3.3	A
<i>Rosa gymnocarpa</i>	-2.3	4.9	-2.2	5.2	-1.1	13.6	9.8	46.6	A
<i>Silene menziesii</i>	-29.8	52.7	4.7	14.9	-1.1	13.6	9.8	46.6	B
<i>Symphoricarpos albus</i>	0.2	1.8	-4.7	14.9	-1.1	13.6	9.8	46.6	A × B
<i>Taraxacum officinale</i>	1.1	29.8	-9.5	47.4	-20.8	50.9	20.4	45.0	B
<i>Trisetum canescens</i>	3.0	5.1	11.7	18.6	-3.6	9.9	5.0	10.6	A × B
<b>1986-1987</b>									
<i>Achillea millefolium</i>	21.8	17.4	25.0	24.8	-1.1	10.7	-0.8	20.6	A
<i>Aster occidentalis</i>	6.4	58.5	42.8	58.2	6.9	19.6	-41.1	88.5	A
<i>Galium boreale</i>	19.6	20.2	12.2	17.2	0.4	1.0	4.2	13.1	A
<i>Poa pratensis</i>	320.7	293.7	611.1	548.7	32.9	103.6	90.2	108.2	A
<b>1985-1987</b>									
<i>Achillea millefolium</i>	21.4	14.8	38.3	37.0	-4.0	14.1	13.3	23.2	A
<i>Canex geyeri</i>	400.8	504.8	327.8	413.8	-225.4	439.6	403.3	657.7	A,B
<i>Luzula compestris</i>	25.2	44.6	0.8	18.8	-4.4	12.9	29.0	36.0	A
<i>Poa pratensis</i>	413.0	443.2	714.5	571.5	13.6	76.4	236.3	283.4	A × B
<i>Spiraea betulifolia</i>	-0.9	3.2	-0.8	2.5	-2.7	22.5	-9.8	42.7	A × B
<i>Taraxacum officinale</i>	7.7	10.0	11.1	10.8	-2.7	7.6	3.3	6.6	A,B
<i>Tragopogon dubius</i>	0.2	0.8	1.1	2.8	0.8	2.2	7.9	10.5	B
<i>Trisetum canescens</i>	36.1	166.0	128.6	272.8	-73.3	75.9	359.8	580.3	A × B

## PERCENTAGE SIMILARITY

Prior to treatment establishment in 1985, there was nearly 90% similarity in species cover and density between root-control and root-reduction treatments. Percent similarity dropped 11% for cover (79%) and density (80%) in 1986 and remained unchanged in 1987. There was approximately 80% similarity of species cover and density in 1985 between canopy-control versus canopy-reduction treatments. In 1986, species cover similarity dropped 5% (75%) with an additional 2% decline (73%) in 1987. Species density similarity dropped 2% (78%) in 1986 but increased 1% (79%) in 1987.

## CANONICAL DISCRIMINANT FUNCTION ANALYSIS

Light (PAR) was by far the best discriminator of treatments having a canonical structure value (0.96) over twice that of the second highest discriminator, soil water potential (-0.41) (40-60 cm), measured on June 3. Other resource variables which contributed to the spatial separation between treatments were: nitrate (0-20 cm), soil water potential (0-20 cm) on August 27, (40-60 cm) and (20-40 cm) on May 20, (40-60 cm) on June 22, and ammonium (0-20 cm). A graph of resource variables displayed in canonical space exhibits these individuals grouped by treatment (Figure 3). CDF 1 and CDF 2 explained 97% of the variation in treatments. Canopy-reduction and canopy-control treatments are separated primarily on the basis of the amount of light the understory receives, whereas the root-reduction treatments are separated based on soil water potential, nitrate, and ammonium.

## CORRELATION ANALYSIS

Correlation analyses were performed on cover and density of 14 plant species and 30 environmental variables. Results of the analyses using cover and density were similar. Only correlations of density and environmental variables are reported in Table 7. *Achillea*, *Aster*, *Galium*, *Poa*, and *Taraxacum* were positively correlated with canopy attributes that increased by canopy reduction: light, and midday air, and soil temperatures. *Carex*, *Calamagrostis*, *Trisetum*, and *Tragopogon* were correlated positively with soil attributes that increased within the root-reduction treatments. *Carex* was positively correlated with ammonium and mineralizable nitrogen while *Tragopogon* was positively correlated with nitrate, pH, and soil water potential. *Calamagrostis* was positively correlated with soil water potential. *Trisetum* was positively correlated with soil water potentials, nitrate, mineralizable nitrogen, and ammonium. *Symphoricarpos* was positively correlated with nitrate, soil temperature, mineralizable nitrogen, and pH. Correlations of environmental variables with *Arnica*, *Lathyrus*, *Luzula*, and *Silene* did not indicate a discernable trend.

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## DISCUSSION

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Species composition of understory plants responded to increased levels of light (PAR), water, or nutrients, or some combination of these three, following canopy and root reduction of overstory trees. Canopy influences generally did not affect



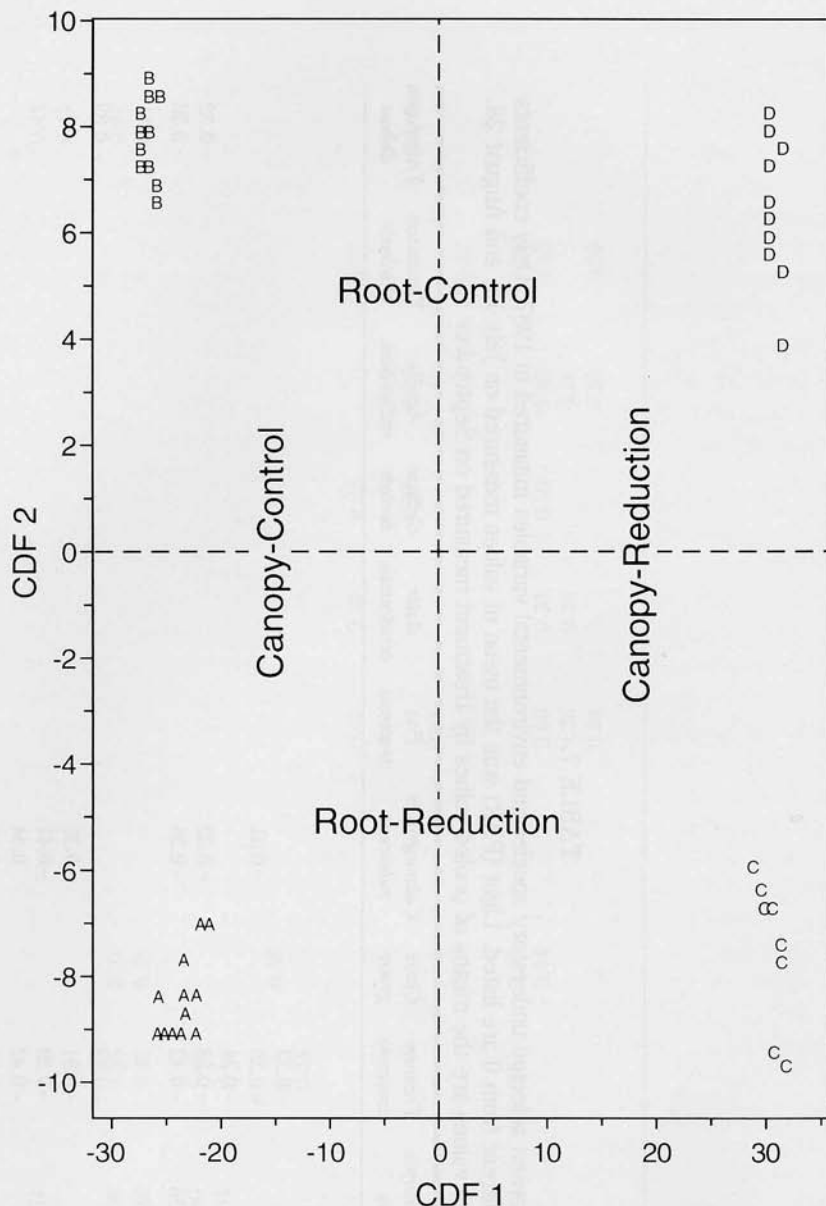


FIGURE 3. Plot of canonical discriminant functions (CDF) 1 and 2 for resource variables. Letters represent (A) Nonthinned/trenched, (B) nonthinned/nontrenched, (C) thinned/trenched, and (D) thinned/nontrenched plots. Of the 44 plots, 3 are hidden.

composition of life forms, although species composition within life forms changed. It appears that the reduction of tree root competition, however, consistently influenced both life form and species composition. We are uncertain which resource, water, nutrients, or some combination of the two, caused these responses. The number of species (8) that increased in cover and density was 60% greater when tree root competition was reduced, versus (5) when tree canopy influences alone were reduced. We found understory aboveground biomass increased after

TABLE 7.

Correlation coefficients between selected understory species and environmental variables measured in 1987. Only coefficients significantly ( $P \leq 0.05$ ) different from 0 are listed. Light (PAR) was the mean of values measured on July 18, and August 28. Soil nitrogen values are the means of pooled values by treatment measured on September 15.

	<i>Symphoricarpos albus</i>	<i>Trisetum canescens</i>	<i>Carex geyeri</i>	<i>Calamagrostis rubescens</i>	<i>Poa pratensis</i>	<i>Aster occidentalis</i>	<i>Galium boreale</i>	<i>Achillea millefolium</i>	<i>Taraxicum officinale</i>	<i>Tragopogon dubius</i>
<i>Soil water potential</i>										
20 cm										
May 6		-0.32								
June 3		-0.35		-0.31						
June 22		-0.34								
July 12		-0.38		-0.32						-0.32
September 13		-0.43		-0.36						-0.36
40 cm										
May 6		-0.33								
June 3		-0.51		-0.36						
June 22		-0.39		-0.41						
July 12		-0.42		0.34						
August 15		-0.53		-0.40						
September 13										-0.33

<i>Light</i>									
<i>Soil pH</i>									
20 cm	0.31								0.42
40 cm									0.44
<i>Mineralizable nitrogen</i>									
20 cm	0.39	0.33	0.37						0.47
40 cm	0.36	0.42	0.35						0.51
$NO_3$									
20 cm	0.50	0.50							
40 cm	0.51	0.51							
$NH_4$									
20 cm		0.38							
40 cm		0.38							
<i>Midday air temperature</i>									
May 6				0.49	0.39	0.32			0.47
June 3									
July 12				0.34	0.37	0.37	0.49	0.49	0.42
August 15							0.32		
September 13									
<i>Soil temperature</i>									
May 6	0.44	0.31	-0.37	0.66	0.33	0.50	0.43	0.33	0.36
June 3			-0.44	0.36	0.30		0.36	0.43	0.43
July 12				0.34			0.50	0.36	0.36
August 15								0.50	0.50
September 13									

reducing root competition while increased light levels had little effect (Figure 4) (Riegel 1989, Riegel et al. 1992).

Increasing light by an average of 126% in the canopy-reduction treatment was the resource altered by the greatest magnitude in the canopy-reduction versus canopy-control understory environments. The reduction of tree root competition in the upper 1 m significantly increased soil water potentials (less negative) (10–15%), mineralizable nitrogen (48%), and soil pH (Riegel 1989, Riegel et al. 1992). This was reflected in the growth of *Carex*, the dominant graminoid, in which xylem potentials and nutrient concentrations and accumulations significantly increased when tree root competition was reduced (Riegel 1989, Riegel et al. 1992).

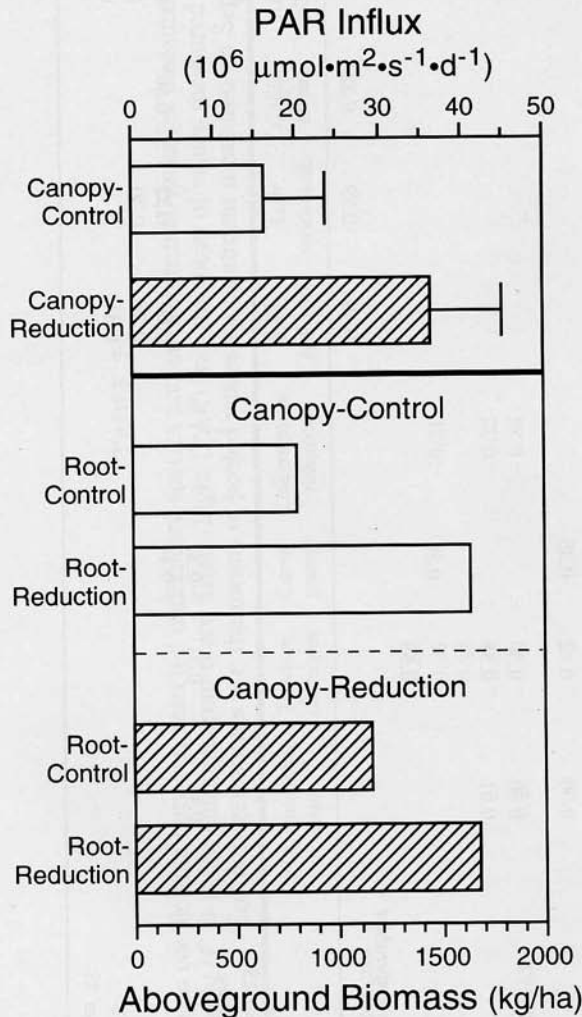


FIGURE 4. Treatment effects on light (photosynthetic active radiation (PAR)) and understory aboveground biomass response averaged for 1986 and 1987 (Riegel 1989, Riegel et al. 1992). Canopy-reduction significantly ( $P < 0.05$ ) increased light reaching the forest floor. Understory aboveground biomass significantly increased in the root-reduction treatments. Aboveground biomass standard error = 372.1.

Correlation of plant density and selected environmental variables measured in 1987 demonstrated that species response to treatment effects can be correlated to a change in either canopy-affected attributes (light, midday air temperature, and soil temperature) or root-competition-affected attributes (soil water potential, pH, and nitrogen). *Poa*, *Achillea*, *Aster*, *Galium*, and *Taraxacum* had the highest correlations with light and other related tree canopy variables. However, *Trisetum*, *Carex*, *Calamagrostis*, *Tragopogon*, and *Symphoricarpos albus*, a midseral rhizomatous shrub, were also correlated with soil variables.

Of the 103 understory species growing on the plots (graminoids, forbs, shrubs, and tree seedlings) only 14 responded to treatment effects in at least one of the 2 yr after study establishment. The greatest change in percent similarity of species among treatments was within the first year after treatment establishment. The fact that fewer species changed during the second growing season probably was a function of greater resource competition among understory species. Though species composition changed between years, the number of species within a treatment were not different. A longer time interval after treatment establishment is necessary before generalizations can be made about long-lived perennials.

We believe the majority of species that increased in cover or density in the canopy-reduction treatment did so because of increased light. This is supported by the canonical discriminant function and correlation analyses. *Achillea* and *Aster*, both rhizomatous forbs, increased in density in 1986 and 1987, and cover in 1987 after light was increased in the canopy-reduction treatment. *Achillea millefolium* increased between years more consistently than any other species. This native early seral species increases with disturbance such as fire (Volland and Dell 1981) and is more often associated with plant communities that have higher light intensities than those found in the understory of *Pinus ponderosa* forests (Franklin and Dyrness 1973, Johnson and Simon 1987). McConnell and Smith (1965) measured a 27% increase in *Achillea* biomass 3 yr after thinning *P. ponderosa* in north-central Washington. Other native species that increased in cover included two midseral plants, *Potentilla gracilis* and *Galium boreale*, rhizomatous forbs, and *Luzula campestris*, a tufted perennial graminoid. *Taraxacum officinale*, a widely distributed and plastic ruderal perennial forb (Dennis 1980), also increased in the canopy-reduction treatment.

Increasing light decreased shrub cover in 1986, but had no effect on cover of other life forms in 1987, or density in either year. Shrubs showed a general nonsignificant initial response in a canopy-reduction *Pinus ponderosa* stand in north central Washington (McConnell and Smith 1965, 1970). Young et al. (1967) reported that *Symphoricarpos albus* and *Rosa gymnocarpa* growing in the mixed conifer forest at slightly higher elevations than our study site on the Hall Ranch were found predominantly under low density tree canopies. In our experiment, shrub species such as *Symphoricarpos*, *Berberis*, and *Spiraea* may not have been able to respond to the additional light as quickly as graminoids or forbs. These shrubs may also have been more limited by nutrients than certain species of graminoids or forbs (Gleeson and Tilman 1990). *Rosa*, the only shrub species to respond to canopy reduction, did increase 96% in density from 1985 to 1986.

Herbaceous species decreased in the canopy-reduction treatment; *Calamagrostis*, *Lathyrus*, and *Tragopogon dubius* (within year differences) and *Arrhenatherum* (between year differences). *Tragopogon*, a ruderal biennial forb that

thrives on disturbance and commonly increases after thinning (Dennis 1980), increased following root reduction. These species probably either declined because they were resource limited as evidenced by lack of response to the additional resources provided (i.e., midseral plants that would not respond to additional resources as much as pioneer and early seral species); or simply were out-competed by more aggressive species as resources were depleted. Pioneer species respond more quickly to increased light, water, and nutrients than mid to late seral species that exist under lower light requirements and tolerate higher water and nutrient stress (Grime 1977, 1979).

*Carex* and *Calamagrostis* increased in the root-reduction treatment in 1986 and 1987 and decreased in the canopy-reduction treatment the first year after treatment, which suggests that they were responding to belowground rather than aboveground resources. *Carex*, however, increased the second year in the canopy-reduction treatment. Increases in *Calamagrostis* following thinning appears to primarily be due to a change in the belowground rather than the aboveground processes. McConnell and Smith (1965) reported a 42% yield increase of *Calamagrostis* 3 yr after thinning a *Pinus ponderosa* stand. On the Hall Ranch near our study site, *Calamagrostis* biomass increased 13 to 33% 4 yr after a sanitation cut in a mixed conifer stand (Young et al. 1967). *Calamagrostis* biomass, however, did not increase in the first or second year after canopy reduction (Riegel 1989, Riegel et al. 1992). Biomass accumulation is proportional to the quantity of resources which have been assimilated by a species in the past (Bonham 1989). It is also possible that species growing in association with *Calamagrostis*, such as *Carex*, the dominant understory species in *P. ponderosa* stands on the Hall Ranch, are more competitive. Young et al. (1967) noted *Calamagrostis* responded favorably to moderate amounts of soil disturbance associated with logging activities. Of the species we measured, only *Calamagrostis* biomass significantly increased in the root-reduction treatment (Riegel 1989, Riegel et al. 1992). This may have been caused by a nutrient flush as soil microbes mineralized nutrient rich fine roots of thinned trees and other vegetation that were killed from logging disturbance. Biomass of *Calamagrostis* has been reported to increase when fertilized with ammonium-nitrate alone and in combination with sulfur (Freyman and van Ryswyk 1969). In 1989, 4 yr after treatment establishment, *Calamagrostis* flowered profusely only in the root-reduction treatment (Riegel 1989, unpublished data). It appears that water and/or nutrients limit both flowering and biomass production of *Calamagrostis* and not additional light received after thinning.

When tree root competition was reduced, cover and density of graminoids, forbs, and shrubs increased in 1986 and 1987, with the exception of shrub density in 1986. The ability of rhizomatous graminoids such as *Calamagrostis*, *Carex*, and *Poa* to reproduce vegetatively may allow these species to respond quickly to additional soil water and nutrients (McConnell and Smith 1965, 1970). Some species present in our understory were limited by water and nutrients rather than light. For example, *Silene menziesii* apparently was only water- and nutrient-limited, as it increased in the root-reduction but not in the canopy-reduction treatments.

Several forbs that increased following removal of overstory root competition include *Achillea*, *Aster*, and *Taraxacum*. These same forbs also increased after light levels were increased in the canopy-reduction treatment. *Poa pratensis*, a widely distributed nonnative grass, also increased in the canopy-reduction and

root-reduction treatments. Apparently these species were limited by light, water, and nutrients.

*Lathyrus nevadensis*, an early seral rhizomatous forb, was the only species to decline in both canopy and root-reduction treatments, apparently from enhanced growth of more competitive species. *Lathyrus* may have also declined because it is a legume, and fixation could have been limited with higher levels of available soil nitrogen (Waring and Schlesinger 1985).

Of the species that responded to increasing limited resources, 57% were rhizomatous. Only one species, *Poa*, was nonnative. These species characterize an early and midsuccessional understory. Prior to fire suppression in these *Pinus ponderosa* communities, a natural fire frequency of approximately 10 yr promoted the selection of rhizomatous species. These plants could withstand repeated low intensity fires by having their vegetative buds buried below the soil surface, protecting them from heat and consumption by fire (Hall 1976, 1977). Plants that were best able to compete and colonize the site after fire became dominant. Periodic burning has equipped these plants with the ability to withstand defoliation by wild herbivores and more recently domestic livestock. Increasing any of the limiting resources will promote growth of the more competitive rhizomatous plants. Aboveground shoots of *Carex* and *Calamagrostis* constitute a small proportion of the biomass as compared to rhizomes (Svejcar and Vavra 1983). Propagating by rhizomes means potentially faster resource acquisition and site domination. Vegetative reproduction is most advantageous when the chance of disturbance is frequent or predictable and environmental conditions are relatively stable (Radosevich and Holt 1984). Early successional species often have greater maximal rates of vegetative growth than later successional species (Bazzaz 1979, Tilman and Cowan 1989). Propagating vegetatively with rhizomes appears to be of value during the early and midsuccessional stage of forest development where early site occupancy following disturbance is essential (Radosevich and Holt 1984).

Competition theory has stirred considerable debate among ecologists (Thompson 1987, Thompson and Grime 1988, Tilman 1987a, Goldberg 1990, Grace 1990, Tilman 1990, Goldberg and Barton 1992). Different definitions of competition and semantics appear to be the basis of this dispute (Grace and Clark 1990). The experimental design (split-plot, 2 × 2 factorial analysis) used in our study demonstrates that aboveground and belowground competition can be partitioned from below-ground, which Thompson (1987) previously disputed Tilman's (1987b) claim as unsubstantiated. Results from our study suggest understory species response to the reduction of overstory competition was conditional on the levels of resource addition. Understory species that favorably respond and dominate a site can be labeled "uptake specialists" (Grace and Clark 1990) which are not necessarily superior competitors as stated by Grime (1979). However, persistence of understory species competing for resources at the lowest physiologic requirements or without altering resources through disturbance is also a trait of competitive superiority (Tilman 1988). Competitive abilities of understory species change along resource gradients depending on the physiologic and morphologic attributes of a given species. Prudent land managers should consider how their activities (e.g., logging and grazing) change resource gradients and affect understory species.

It is apparent that no single resource controls species density or cover in an early to midseral understory *Pinus ponderosa* forest in northeastern Oregon.

Pioneer, early, and midsuccessional species are promoted by various combinations of higher light intensities and soil moisture and nutrients. Although light does not appear to limit understory biomass in these communities (Riegel 1989, Riegel et al. 1991, Riegel et al. 1992), light, water, and nutrients do affect the cover, density, and species composition of the understory as evidenced by the response to increasing these resources.

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