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Understory Vegetation Response to Increasing Water and Nitrogen Levels in a *Pinus ponderosa* Forest in Northeastern Oregon

Abstract

Competition for soil moisture has been proposed as the dominant environmental resource governing understory production in pine forests of eastern Oregon. Other studies have demonstrated that light and nitrogen may also be limiting understory growth. The objective of this research was to test the hypotheses that both water and nitrogen and/or their interaction limit understory biomass production in a *Pinus ponderosa* (ponderosa pine) forest in northeastern Oregon. The experiment was a completely randomized block design with three blocks and four treatments: 1) control, 2) water (irrigated biweekly), 3) nitrogen (NH_4 NO_3, 32 percent N; 50 kg N ha^{-1}), and 4) water + nitrogen. At peak standing crop (June 26 through July 7) the water + nitrogen treatment produced 16 and 18 percent greater aboveground dry weight biomass than the nitrogen and water treatments and 36 percent more than the control treatments. Nitrogen and water treatments were 17 and 15 percent more productive than the control treatment. There was no relationship between light (PAR), measured at the center of each plot with light sensitive ozalid paper, and biomass production. Understory vegetation is significantly limited by both water and nitrogen in *P. ponderosa* forests of northeastern Oregon.

Introduction

Competition for limited resources, such as light, water, and nutrients governs forest understory vegetation production. Light is often the limiting environmental variable controlling understory plant communities in mesic forests (Christy 1986). Water or competition for soil moisture has been proposed as the dominant environmental factor governing understory production in more xeric pine forests in eastern Oregon (Krueger 1980). In a previous study we investigated the effect of resource limitation on understory growth in a *Pinus ponderosa* forest in northeastern Oregon (Riegel 1989). Competition for resources was separated into above ground and below ground components by commercially thinning to increase light to the understory and by trenching the perimeters of plots to sever tree roots growing inside. Understory biomass significantly increased when overstory root competition was reduced for belowground resources, regardless of light levels on the plot. We were uncertain, however, if understory growth increased due to increased levels of soil moisture, nutrients, or a synergistic effect.

The concept of resource limitation was developed in agriculture to refer to the limitation of productivity (Chapin 1980, Chapin *et al.* 1986). The more resource-limited an individual or community is, the more its production increases in response to an addition of the limiting resource. This relationship between resource availability and productivity provides objective criterion for evaluating the extent of resource limitation to the production of individual plants or a community. If specific resources are limiting, their addition will increase productivity.

We designed an experiment to test the effect of increasing limited resources, soil moisture and nitrogen, on understory vegetation biomass production in a *P. ponderosa* forest in northeastern Oregon. Our objectives were to test the hypotheses that both water and nitrogen and/or their interaction limit understory biomass production in this ecosystem.

Study Area

The study was conducted on the Hall Ranch of the Eastern Oregon Agricultural Research Center, located approximately 19 km southeast of Union, Oregon (Figure 1). The Hall Ranch is within the southwestern foothills of the Wallowa Mountains in the northeastern corner of the state at an elevation of approximately 1060 m.

The climate is continental with cold wet winters, and hot dry summers with occasional thunderstorms. Mean monthly air temperature extremes vary from a minimum of −19.2°C in December

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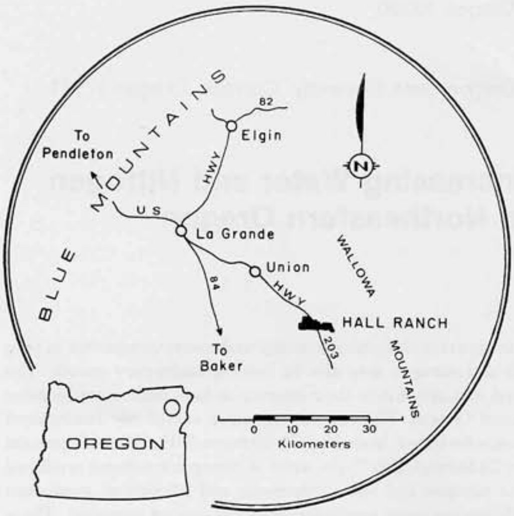

Figure 1. The Hall Ranch, location of the study area.

to 1.1°C in July; from a maximum of 8.5°C in December to 36.9°C in July (file data; Eastern Oregon Agricultural Research Center, Union). The majority of precipitation on the Hall Ranch occurs between November and June in the form of snow during the winter. Mean annual precipitation for 1963-1987 was 605 mm (Williams 1988).

The experiment was conducted in a *Pinus ponderosa/Symphoricarpos albus* (white snowberry) community type similar to Johnson and Simon's (1987) *Pseudotsuga menziesii* (Douglas-fir)/*Symphoricarpos albus* plant association of the Wallowa-Snake Province of northeastern Oregon. *Pinus* dominates the overstory and codominates reproduction with *Pseudotsuga menziesii*. Density of the overstory was 345 trees ha^{-1}, basal area 22 $m^2\ ha^{-1}$, and tree diameters at breast height (dbh) ranged from 0.3 to 135.6 cm with a mean of 31.8 cm. *Symphoricarpos*, *Carex geyeri* (elk sedge), *Calamagrostis rubescens* (pinegrass), and *Arnica cordifolia* (heartleaf arnica) dominate the understory. Sites were selectively logged before 1936; since then there has been no logging.

Three major soil series occur within the research site: the Hall Ranch series, fine-loamy, mixed, frigid, Ultic Haploxerolls (block 1 non-thin and thin; block 2 thin); the Klicker series, loamy skeletal, mixed frigid Ultic Agrixerolls (blocks 2 and 3 non-thin); and the Tolo series, 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 to greater than 92 cm.

Methods

On April 15, 1987, 120, 1 x 1 m plots were established in the understory of a *Pinus* forest. The experiment was a completely randomized block design. Three 5.0 ha stands or blocks were selected for this study. Stands were considered to be relatively homogeneous in species composition and stand structure, however, understory species composition varied slightly among blocks. Four treatments: 1) control, 2) water, 3) nitrogen, and 4) water + nitrogen were randomly assigned to each plot by block. There were 10 plots per treatment within each of the three blocks.

Nitrogen (NH_4, NO_3, 32 percent N) was applied by hand at 50 kg N ha^{-1} on each nitrogen plot on April 15th, prior to spring growth. The amount of nitrogen applied to the forest floor was supplemented to approximate mineralization of tree roots and subsequent fertilization response in trenched plots, where tree root competition was removed, from our earlier study (Riegel 1989). We calculated the additional nitrogen requirement by taking the 1986 biomass production from the non-thinned/trenched plots, 1711.99 kg ha^{-1} x 1.5 percent nitrogen in plant tissue (Marschner 1986) = 25.68 kg ha^{-1}, then doubled that value to insure a response (Timothy L. Righetti, personal communication). Approximately 85.02 mm of precipitation (John D. Williams, personal communication) was received from the date of fertilization through the last day biomass was harvested (July 7).

Water treatments were irrigated biweekly from May 6 through June 18 to simulate the increase in soil water after tree roots growing in trenched plots had been severed (Riegel 1989). Our objective was to ameliorate the amount of soil water the understory received after tree root competition had been reduced after trenching, a difference of 10-15 percent between trenched and non-trenched treatments. The amount of water required to simulate higher soil water content was calculated for a soil volume of 100 x 100 x 50 cm (depth) = 500,000 cm^3. To increase soil water by 10 percent in the 0-20 cm depth, we measured bulk density 0.9 gm/cm^3 x 500,000 cm^3 = 45,000 gm soil, which is approximately 22.5 L of water, assuming 50 percent porosity. As the season progressed we increased the amount of water to 30 L on May 21, and 40 L June 3 and 18. Soil moisture was measured gravimetrically at three depths (0-20, 20-40, and 40-60 cm) both inside and adjacent to each plot 24 hours after watering on May 21 and June 4. To construct the soil water release curves, gravimetric soil moisture was converted to volumetric soil moisture content. A representative soil water release curve for the 0-20 cm depth is shown in Figure 2. Soil water retentivity was determined on a pressure plate membrane apparatus (Soil Physics Laboratory, Soil Science Department, Oregon State Univ., Corvallis).

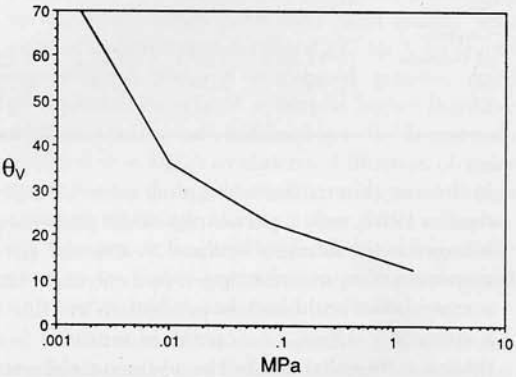

Figure 2. Representative soil water release curve of the 0-20 cm depth from block 1, the Hall Ranch soil series. The x axis is soil water potential (MPa) and the y axis, percent volumetric soil moisture (Θ_v).

Plots were clipped at peak standing crop beginning June 26 through July 7. Immediately prior to clipping, each plot was photographed to assist with interpreting results. *Carex* was clipped and bagged separately. Biomass was dried for 48 hours at 60°C and weighed.

Carex biomass samples were pooled by treatment within blocks for nitrogen analysis. Nitrogen concentration was determined with a semimicro-Kjeldahl apparatus (Bremner 1965). Nitrogen total accumulation of biomass is defined as the total quantity of nitrogen in the above ground portion of the plant per unit area (kg ha^{-1}), derived by multiplying the nitrogen concentration of *Carex* x total biomass (kg ha^{-1}) of each plot (Jarrell and Beverly 1981).

Light, photosynthetic active radiation (PAR), was quantified for each plot with ozalid integrators; booklets of light sensitive ozalid paper in plasic petri dishes (Friend 1961). One integrator was placed on a leveled area in the center of each plot for 24 hours on 6 September 1987.

Analysis of variance was used to test treatment differences in biomass production, nitrogen concentration and nitrogen total accumulation, and quantity of light. Comparisons of treatment means were tested using Waller-Duncan K-ratio. A probability value of $P < 0.05$ was used throughout the analyses to test significance of F values. Probability levels were calculated in the SAS Institute Inc. (1987) program. Only significant differences are reported in the text. A simple linear regression was used to examine the relationship of biomass production and quantity of light. Due to inadequate and uneven sample size, statistical analysis of soil moisture data were not performed.

Results and Discussion

This research supports the hypothesis that water and nitrogen are limiting environmental variables that control understory production in *P. ponderosa* forests of northeastern Oregon. The greatest response occurred when water + nitrogen were added to the forest floor (Figure 3). Water + nitrogen produced (1031.2 kg ha^{-1}) 16 and 18 percent greater biomass than nitrogen (888.6 kg ha^{-1}) and water (870.6 kg ha^{-1}) treatments and 36 percent more than the control (756.7 kg ha^{-1}). However, the addition of water and nitrogen in separate treatments produced only 15 and 17 percent more understory biomass, respectively, than the control treatment. In the water + nitrogen treatment, addition of water facilitated the uptake of nitrogen to understory plants. This synergistic effect of nitrogen uptake enhanced by higher soil moisture has been documented in a competition

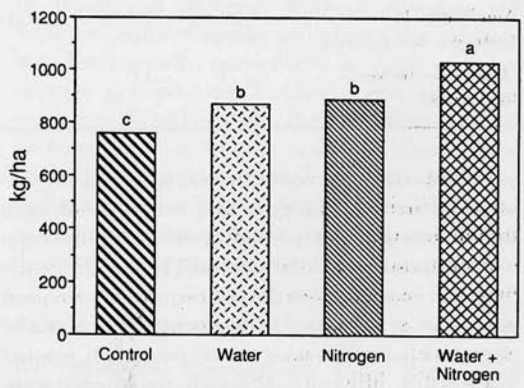

Figure 3. Understory biomass (kg ha^{-1}) response to treatments. Means with the same letter are not significantly different. Standard error of treatment means is ±14.74 kg ha^{-1}.

study using trenches conducted in the same experimental blocks of this study (Riegel 1989).

Irrigating plots increased soil moisture by 41 percent (seven percent difference between watered and non-watered treatments) in the upper third of the profile (0-20 cm depth) where the greatest root competition occurs (Snider and Miller 1985, Svejcar 1986) (Table 1). Addition of soil water increased soil water content to similar levels measured in trenched plots (Riegel 1989) in the 0-20 cm depth. In the mid (20-40 cm) and lower third (40-60 cm) soil depths, adding water also increased soil moisture, but generally less than in the upper third of the profile.

TABLE 1. Volumetric soil moisture (%) (means and standard deviations) measured 24 hours after irrigation within water and non-water treatments.

Treatments	Soil Depths (cm)		
	0-20	20-40	40-60
May 21, 1987 (n = 22)			
Watered (water and water + nitrogen)	23 (5)	20 (3)	19 (3)
Non-Watered (nitrogen and control)	15 (2)	18 (6)	18 (4)
Differences between treatments	8	2	1
June 4, 1987 (n = 5)			
Watered (water and water + nitrogen)	29 (8)	30 (18)	20 (3)
Non-Watered (nitrogen and control)	22 (3)	19 (8)	20 (1)
Differences between treatments	7	11	0

Carex nitrogen concentrations significantly increased in both nitrogen and water + nitrogen treatments with 35 percent more tissue nitrogen concentration than the control (Table 2). Tissue nitrogen concentration did not respond to increased soil water as compared to the control. Nitrogen total accumulation of biomass among treatments was not statistically different, although treatments were higher than the control. *Carex* uptake of nitrogen in the trench treatment (Riegel 1989) produced a similar response. Nitrogen concentrations of *Carex*

TABLE 2. Total nitrogen tissue concentration (%) of *Carex geyeri* foliage and content (kg ha^{-1}) of biomass (means, standard deviations, and standard errors) by treatments. Means with the same letter are not significantly different ($P < 0.05$).

	Nitrogen	Water	Water + Nitrogen	Control
Nitrogen Concentration of *Carex geyeri*	1.33 a	1.04 b	1.32 a	0.98 b
SD	0.15	0.23	0.12	0.24
SE	0.04			
Nitrogen Content of Biomass	11.82 a	9.05 a	13.61 a	7.42 a
SD	5.14	3.30	1.74	2.75
SE	1.50			

in the non-thinned/trenched plots were 1.31 percent in 1987, only 2 percent less than plant tissue nitrogen in the nitrogen fertilized treatments. These responses of increased nitrogen concentration, total accumulation and biomass production are due to a synergistic effect, i.e., uptake of nutrients from the soil were enhanced by the additional soil water in the water + nitrogen and trenched treatments (Jarrell and Beverly 1981, Riegel 1989). However, tissue N concentrations were nearly equal in both nitrogen treatments, but the addition of water in the water + nitrogen treatment promoted more growth. Increased biomass production in the nitrogen treatments may have been aided by increased nitrogen availability early in the growing season, when water was not limiting. Plants growing in fertilized plots appeared darker green and also regrew faster after defoliation than the water or control treatments.

Information on the effect of irrigating and fertilizing herbaceous wild land plants is limited. In an agroecosystem, Singh *et al.* (1979) reported unirrigated *Triticum aestivum* (wheat) did not respond to a nitrogen application greater than 80 kg N ha^{-1}, whereas on irrigated plots response to nitrogen was linear up to 120 kg N ha^{-1}. In our experiment, where water and nitrogen treatments had nearly equal biomass production, the addition of water decreased soil moisture limitation but apparently increased the nitrogen requirement. When plant growth and yield are limited by available moisture the nitrogen requirement is relatively low. If water is applied and growth is increased, the nitrogen requirement may also increase. Protein synthesis is typically reduced by water stress (Hsiao 1973, Hsiao and Acevedo 1974) and the activities of some enzymes involved in nitrogen metabolism are decreased although others are increased (Todd 1972).

Pumphrey's (1980) findings reinforce our results, that the effect of a nitrogen addition to this system is enhanced when soil moisture is not limiting for plant uptake. When soil moisture is low, nutrient movement to the root surface and uptake are reduced (Marschner 1986). In a study conducted adjacent to our research area, Pumphrey found that spring precipitation correlated most closely with yield of both nitrogen fertilized (67 kg N ha^{-1}) and non-fertilized plots of introduced grasses. April precipitation correlated with yield higher than any other month, for both fertilized ($r = 0.74$) and non-fertilized ($r = 0.42$) treatments. Utilization of water and nutrients during the early growing season takes optimum advantage of this weather pattern. Reducing nitrogen deficiency by fertilizing allowed the grass to be more responsive to precipitation and subsequent higher soil moisture levels.

Other research has demonstrated that sulfur and phosphorus may also limit understory biomass production in this region (Freyman and van Ryswyk 1969; Geist 1971, 1974, 1976a, 1976b, 1977; Geist and Strickler 1978; Klock *et al.* 1975). *Calamagrostis rubescens* fertilized with ammonium and nitrate applied at 100 and 200 kg N ha^{-1} increased biomass production by factors of 1.25 and 2.25 during the year of application (Freyman and van Ryswyk 1969). This response was increased when S (gypsum) was applied with nitrogen. A *Dactylis glomerata* (orchard grass) stand fertilized with ammonium sulfate at a rate of 92 kg N ha^{-1} produced four times more biomass than ammonium nitrate treated plots at the same rate and seven times the unfertilized yield of 213 kg ha^{-1} in the first year (Geist 1976a). Though we did not measure S and P concentration in the soil, *Carex* tissue concentrations of these nutrients were reported higher in plots where tree root competition had been reduced (Riegel 1989).

Light (PAR) does not appear to be limiting understory production in these forests as there was no relationship to light quantity and biomass production. Correlation between biomass and light (PAR), measured on each plot, were not significant ($r^2 = 0.01$). Differences in light levels between treatments were also not significant (Table 3). Plots were distributed in a random stratified procedure which accounted for a 13 percent range in quantity of light that understory vegetation receives. Though we did not increase light as we did with water and nitrogen, results from our thinning study where light was increased demonstrated that the understory biomass did not respond to higher light intensities caused by opening the stand from commercial thinning (Riegel 1989).

TABLE 3. Light, photosynthetic active radiation-PAR (μmol m^{-2} day x 10^6) (means, standard deviations, and standard errors), measured at ground level. There were no significant differences between treatments.

Nitrogen	Water	Water + Nitrogen	Control
12.82 x 10^6	12.22 x 10^6	11.65 x 10^6	12.81 x 10^6
SD 39.34 x 10^6	38.24 x 10^6	7.40 x 10^6	64.30 x 10^6
SE 2.69 x 10^6			

It is doubtful that adding water and nitrogen fertilizer had the same effect as trenching, thus limiting the comparisons of these studies. Severing tree roots decreased soil water depletion rates in the trenched plots throughout the growing season, as compared to non-trenched plots. Besides increasing nitrate and mineralizable nitrogen from the addition of severed tree roots following trenching, many other belowground processes were altered (Riegel 1989). Also, within trenched plots there were no tree roots competing for water and nitrogen. In this experiment, however, tree roots were competing for nitrogen and water which may explain why the response was not as great as in the trenched plots.

Understory vegetation, composed primarily of native herbaceous species, is primarily limited both by water and nitrogen. Without adequate soil moisture, nutrient uptake and plant water relations may limit growth, particularly in years of below average precipitation. Prudent forest and range managers should consider the role overstory competition plays in limiting resources that control understory vegetation growth to insure sustained multiple-resource productivity. Continual resource extraction in nitrogen limited systems may lead to decreased long term productivity.

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Literature Cited

Bremner, J. M. 1965. Nitrogen availability indexes. *In:* C. A. Black (ed.), Methods of soil analysis, Vol. 2, Amer. Soc. Agron., Madison, WI. Pp. 1324-1345.

Chapin, F. S., III. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:233-260.

Chapin, F. S., III, P. M. Vitousek, and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. Amer. Midl. Nat. 127:48-58.

Christy, E. J. 1986. Effect of root competition and shading on growth of suppressed western hemlock (*Tsuga heterophylla*). Vegetatio. 65:21-28.

Dyksterhuis, E. L., and C. T. High. 1985. Soil survey of Union County area, Oregon. USDA Soil Conserv. Serv., in cooperation with Oregon State Univ. Agr. Exp. Sta.

Freyman, S., and A. L. van Ryswyk. 1969. Effect of fertilization on pinegrass in southern British Columbia. J. Range Manage. 22:390-395.

Friend, D. T. C. 1961. A simple method of measuring integrated light values in the field. Ecol. 42:577-580.

Geist, J. M. 1971. Orchardgrass responses to fertilization of seven surface soils from the central Blue Mountains of Oregon. USDA Forest Service, Pac. Northw. For. Range Exp. Sta. Res. Pap. PNW-122.

__________. 1974. Chemical characteristics of some forest and grassland soils of northeastern Oregon; II. Progress in defining variability in Tolo and Klicker soils. USDA Forest Service Pac. Northwest For. Range Exp. Sta. Res. Note PNW-217.

__________. 1976a. Orchardgrass growth on nitrogen and sulfur fertilized volcanic ash soil. J. Range Manage. 29:415-418.

__________. 1976b. Forested range fertilization in Eastern Oregon and Washington. Rangeman's J. 3:116-118.

__________. 1977. Nitrogen response relationships of some volcanic ash soils. Soil Sci. Soc. Amer. J. 41:996-1000.

Geist, J. M., and G. S. Strickler. 1978. Physical and chemical properties of some Blue Mountain soils in northeastern Oregon. USDA Forest Service Pac. Northwest For. Range Exp. Sta. Res. Pap. PNW-236.

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Hsiao, T. C. 1973. Plant responses to water stress. Ann. Rev. Plant. Physiol. 24:519-570.

Hsiao, T., and E. Acevedo. 1974. Plant response to water deficits, water use efficiency and drought resistance. Agric. Meterol. 14:59-84.

Jarrell, W. M., and R. B. Beverly. 1981. The dilution effect in plant nutrition effects. Adv. Agron. 34:197-223.

Johnson, C. G., and S. A. Simon. 1987. Plant associations of the Wallowa-Snake Province. USDA Forest Service, PNW Region R-6 ECOL-TP-225A-86.

Klock, G. O., J. M. Geist, and A. R. Tiedemann. 1975. Response of orchardgrass to sulphur in sulphur-coated urea. Sulphur Institute J. 11:4-8.

Krueger, W. C. 1980. How a forest affects a forage crop. Oregon State Univ. Agr. Sta. Spec. Rep. 583. May 1980. Corvallis, Oregon.

Marschner, H. 1986. Mineral nutrition of higher plants. Academic Press, London, England.

Pumphrey, F. V. 1980. Precipitation, temperature, and herbage relationships for a pine woodland site in northeastern Oregon. J. Range Manage. 33:307-310.

Riegel, G. M. 1989. Understory competition for resources in *Pinus ponderosa* forests of northeastern Oregon. Ph.D. thesis, Oregon State Univ., Corvallis.

SAS Institute Inc. 1987. SAS/STAT Guide for personal computers, version 6 ed., Gary, NC.

Singh, N. T., A. C. Vig, R. Singh, and M. R. Chaudhury. 1979. Influence of different levels of irrigation and nitrogen on yield and nutrient uptake by wheat. Agron. J. 71:401-404.

Snider, M. D., and R. F. Miller. 1985. Effects of tractor logging on soils and vegetation in eastern Oregon. Soil Sci. Soc. Amer. J. 49:1280-1282.

Svejcar, T. 1986. Comparative water relations of *Carex geyeri* and *Calamagrostis rubescens*. Bot. Gaz. 147:71-77.

Todd, G. W. 1972. Water deficits and enzyme activity. *In:* T. T. Kozlowski (ed.), Water deficits and plant growth Vol. 3, Academic Press, New York. Pp. 177-216.

Williams, J. D. 1988. Overland flow and sediment potentials in logged and unlogged sites of a ponderosa pine forest in northeastern Oregon. Master's thesis, Oregon State Univ., Corvallis.