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The objective of this research was to determine which environmental resources, light, water, and nutrients, control understory plant production and composition in a *Pinus ponderosa* forest in northeastern Oregon. A split-plot experimental design, with three blocks, four treatments, and 44 plots, was established in the summer of 1985. Twenty plots (4 x 4 m) were trenched approximately one meter in depth, and 24 non-trenched plots were used to assess the effects of root competition of overstory trees on understory plants. Trees were commercially thinned in the winter and spring 1986 from a density of 345 to 148 trees/ha^{-1} to increase light levels to the understory.

Thinning significantly increased light, decreased midday relative humidity and increased midday air temperatures and soil temperatures. Xylem potential of the dominant graminoid, *Carex geyeri*, soil water potential, mineralizable nitrogen, and pH were significantly increased within the trenched treatment in comparison to the non-trenched plots. Micro and macro nutrients in *C. geyeri* and *Symphoricarpos albus*, the dominant shrub, significantly increased in both treatments.

Controlling root competition for soil water and nutrients did significantly increase understory aboveground biomass, whereas increasing light had no effect. A supplemental experiment during the third year of this study indicated that water and nitrogen had a synergistic effect in improving production. Species composition, cover and density, however, were significantly effected by light, water, and nutrients.

This research demonstrated that belowground resources were the primary controlling factors of understory production in *P. ponderosa* forests in northeastern Oregon. However, belowground and aboveground resources influenced species composition.

Understory Competition for Resources in *Pinus ponderosa* Forests of Northeastern Oregon

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UNDERSTORY COMPETITION FOR RESOURCES IN *PINUS PONDEROSA* FORESTS OF NORTHEASTERN OREGON

INTRODUCTION

Pinus ponderosa forests are widely distributed within the interior mountain ranges of the Northwest (Franklin and Dyrness 1973). These forests provide timber, forage for livestock and wild herbivores, and contribute to highly desired scenic beauty. In the Blue Mountains of northeastern Oregon *P. ponderosa* forests comprise much of the economic land base where timber and forage resources are managed as dual or multiple uses of a single ecosystem. Often these resources are managed independently, rather than simultaneously. Integration of forestry and grazing management objectives has the potential to improve returns from both livestock grazing and timber yields on the same unit of land.

Forest grazing describes the utilization of forest understory vegetation by herbivores, especially livestock (Doescher et al. 1987). Understory production can be increased and species composition changed through thinning, clearcutting or other methods of harvesting the overstory. Commercial thinning of *P. ponderosa* cover allows for light of greater intensity and duration to reach the forest floor and increases soil moisture by reducing overstory competition and canopy interception of precipitation. Nutrient cycling is also changed as competition for soil nutrients from the overstory is reduced, nutrients are removed off site in logs, and mineralization of organic residues from dead roots and associated mycorrhizae alter microbial populations. Interspecific competition above ground takes the form of competition for available light that has filtered through the overstory canopy (Harper 1977, Schoener 1983). Competition below ground involves root competition for available water and nutrients necessary for plant development. It has been proposed that moisture or competition for moisture is the dominant environmental resource controlling yield of understory vegetation in forested ranges in eastern Oregon (Krueger 1980). Response to increased levels of light, water, and nutrients will vary depending upon the physiologic tolerances and competitive ability of understory species.

This research consisted of two separate studies which are part of a larger, long-term ecosystem investigation of understory response to overstory thinning and livestock grazing. The purpose of this research was to increase our knowledge of what resources control understory vegetation competing with a second growth _P. ponderosa_ overstory.

Relatively little research has been conducted examining the effect of overstory on understory vegetation in the coniferous forests of the Pacific northwest. Many of the relationships previously described have been from forests of the northeast (Toumey 1929, Toumey and Kienholz 1931), southeast (Horn 1985), north central (Shirley 1945, Anderson et al. 1969), southwest (Clary 1969, Ffolliott and Clary 1975), and Rocky Mountain states (Evenson et al. 1980, Wilcox et al. 1981, McCune 1986). What is known are general relationships, but research defining which resources light, water, and nutrients, that govern understory vegetation is very limited, including the P. ponderosa forests of the Pacific northwest (Moir 1966). The following is a summary of the available knowledge.

This introduction consists of a review of the literature specific to: 1) overstory/understory relationships: light versus water and nutrients, 2) understory response to grazing and logging, and 3) understory dominants of P. ponderosa in northeastern Oregon.

Overstory/Understory relationships: Light versus Water and Nutrients.

Understory biomass production in P. ponderosa communities is a function of climate, soils, disturbance (fire and management history), and density of the overstory (Clary 1975). As tree density (both stem and canopy) increases, shading, interception of precipitation and competition for water and nutrients reduces productivity of the herbaceous understory (Moir 1966).

The relationship of canopy density and understory production in P. ponderosa forests has been shown to be linear by Arnold (1950), Cooper (1960), McConnell and Smith (1965), Moir (1966) and Mitchell et al. (1987), while Pearson (1964), Jameson (1967), Clary (1969) and Ffolliott and Clary (1975) reported a curvilinear relationship. Understory production in P. ponderosa forests of northeastern Oregon decreased approximately 5 lbs./acre with a 1.6% annual crown cover increase (Skovlin 1976).

Light, at sufficient levels in the understory, is available for a net gain in plant weight through photosynthesis. Sunflecks, the chief form of light in the understory, move over the ground as the angle of the sun is changed by the rotation of the earth and as wind moves the foliage of the overstory (Chazdon 1988).

Water reaching the understory may be largely restricted to current precipitation through direct fall and partially through stem flow and drip from the overstory trees (Spurr and Barnes 1980). Understory plants utilize as much as 45% of available soil moisture in pumice soils of central Oregon (Barrett and Youngberg 1965). Here, P. ponderosa and understory vegetation compete primarily for available soil moisture.

Nutrient supply in the soil is strongly influenced by the water supply. As water becomes more limited, 1) reduced mass flow of nutrients to the roots results from decreased soil water movement, 2) shrinkage causes reduced contact between soil particles and roots that consequently reduces nutrient diffusion, 3) general concentrations, or dilutions can effect the chemistry of many soil nutrients, and 4) mineralization and decomposition rates decrease thus reducing the rate of nutrients re-entering the soil solution (Bloom et al. 1985). Nitrogen is an essential nutrient which frequently limits ecosystem production and is often the main limiting soil resource, particularly in mesic forests of the west (Harvey et al. 1987).

Primary environmental resources governing understory vegetation are the availability of light and water (Young and Smith 1979 1980 1982 1983), and nutrients (Moir 1966, Freyman and Ryswyk 1969, Geist 1971 1974 1976a 1976b 1977 1978, Klock et al. 1975). Limiting environmental resources of P. ponderosa understory in the White Mountains of Arizona appear to be a combination of light and throughfall moisture (McLaughlin 1978). In most cases it is difficult to separate the interaction of canopy shading and soil moisture competition to determine which resource may limit understory production.

Toumey (1929) and Toumey and Kienholz (1930) were the first North American's to attempt to separate the effects of canopy shading and soil moisture competition on understory plants. Under a canopy of P. strobus a series of plots, one 9 x 9 feet in size, trenched three feet deep and one foot wide, and two 4.5 x 9 feet non-trenched plots, one on each side of the trenched plot, were established to remove the effects of overstory root competition for soil moisture. No stems of overstory trees were within the plots. Three years after trenching soil moisture increased by an average of 16.4% and the number of species and density of individuals had doubled. A few xeric species were replaced while many of the new species that established in the trenched plots were considered mesic.

More recent overstory/understory research has focused on the affect of light levels and moisture competition on conifer reproduction. In the spruce-pine forests of north central Minnesota, Shirley (1945) concluded that competition for shade and soil moisture were "intertwined" and a single factor could not be pinpointed as the most important factor. In the Piedmont forests of North Carolina, tree seedling aboveground and belowground competition was differentiated by planting in recent windthrow clearings and under forest canopies and controlling overstory roots competition by trenching (Horn 1985). Controlling overstory roots in low elevation Abies grandis forests in western Montana increased understory vegetation cover by 48% over a five year period (McCune 1986). Growth of suppressed Tsuga heterophylla was increased when root competition was controlled by trenching (Christy 1986). Though light was increased 30 to 40% by pruning the overstory canopy, there was no synergistic effect. When shrub root competition was controlled, soil moisture availability was found to be the primary factor limiting *A. concolor* growth in the northern Sierra Nevada (Conard and Radosevich 1982). However, adding artificial shade and eliminating root competition produced the greatest growth increase, probably by improving the water balance of shaded trees.

In a *P. ponderosa* woodland in Utah, understory species were correlated with environmental variables (Evenson et al. 1980, Wilcox et al. 1981). Shrubs and grasses were found to be more common in understory communities whereas forbs and annuals were more common in open environments. Correlations suggested that shrubs and grasses were water limited, but not nutrient limited; in contrast, forbs and annuals were nutrient limited, but not water limited.

In desert ecosystems competition for shade and soil moisture are more acute. Elimination of *Prosopis juliflora* shade and root competition increased cover of understory vegetation growing in the canopy zone by 5% (Tiedemann and Klemmedson 1977). Jameson (1970) found the basal area of *Bouteloua gracilis* had the greatest gain when both root competition and shade of *Juniperus monosperma* were removed.

Understory Response to Grazing and Logging.

Research on livestock grazing in forested ranges in northeastern Oregon has focused on grazing in mixed conifer forest plantations (Krueger 1983). Miller and Krueger (1976) compared the production and utilization by cattle, of understory species for similar habitat types in unlogged sites to seeded forage on clearcuts. Of the total forage utilized by cattle, only eight percent was from the forest although these accounted for 41% of the study area. Given a choice, cattle preferred the open, cut blocks to the denser adjoining forests.

Skovlin et al. (1976) studied the effects of cattle stocking levels and grazing systems on a ponderosa pine-bunchgrass range at the Starkey Experimental Forest in northeastern Oregon. Their results showed that in all herbage categories, production declined over the 11 years of grazing treatments compared to non-grazed sites. Shrubs maintained near original production, graminoids declined 33% while forbs declined approximately 70%. Changes in graminoid production were directly proportional to intensity of livestock stocking. Proper stocking levels are critical for maintenance of Carex geyeri and Calamagrostis rubescens, however, Calamagrostis is the more sensitive of the two (Skovlin et al. 1976).

Herbage production in logged mixed conifer stands on the Hall Ranch near Union, Oregon, varied depending on the degree of disturbance (Young et al. 1967). Thinning of P. ponderosa forests in eastern Washington increased Calamagrostis production (McConnell and Smith 1965, 1970). However, it is not known if this response was a function of increased light or water availability. The ability of Calamagrostis to respond to disturbance has been attributed to its dense rhizomes which provide a competitive advantage over grasses and forbs which reproduce from seed.

Understory Dominants of Pinus ponderosa in northeastern Oregon.

Of the two understory dominants in *P. ponderosa* forests in northeastern Oregon (Franklin and Dyrness 1973, Hall 1975, Johnson and Simon 1987), *Carex* has been found to be better physiologically adapted to cope with limited soil moisture than *Calamagrostis* (Svejcar 1983, 1986). This greater level of drought avoidance of *Carex* over *Calamagrostis* was attributed to: 1) more negative xylem potentials, 2) more negative osmotic potentials, 3) high bound water fraction, 4) more rigid cell walls, and 5) maintenance of low diffusive resistance to more negative xylem potentials.

Allocation of biomass to rhizomes of *Carex*, *Calamagrostis*, and *Arnica cordifolia*, is greater than allocation to above ground organs (Svejar and Vavra 1983). *Calamagrostis* rhizome length can be as much as four times longer per unit weight than that of *Arnica* and *Carex* respectively. Svejar and Vavra (1983) hypothesized the longer rhizome of *Calamagrostis* per unit weight may be a compensation for the lack of sexual reproduction observed in most stands.

The ability of the understory to respond to thinning is important for maintaining a forage base for livestock and wild ungulates. Both *Carex* and *Calamagrostis* distribution and production are known to decline with increasing tree stand density and canopy cover (Skovlin et al. 1976, Young et al. 1967). However, it is unknown if these species are responding to decreased light levels from shade or limited water and/or nutrients from increased competition of trees. All species have specific light, soil moisture, and nutrient requirements which regulate physiologic processes. Understanding the response of understory plants to increased light, water, and nutrient levels may help land managers predict optimum forage production for a given overstory stocking level and understory plant succession as the tree canopy increases.

The objectives of this research were to:

1) test the hypothesis that belowground resources as effected by tree root competition, are the primary factors limiting understory production, and that light does not limit understory production in *P. ponderosa* forests of northeastern Oregon,

2) if the above hypothesis is true, are water and/or nitrogen the primary factors limiting understory vegetation production,

3) evaluate the effect of tree root competition on plant uptake of macro and micronutrients by understory vegetation,

4) test the hypothesis that belowground resources, and not above ground, control density and cover of understory species, and

5) evaluate the relationship of life-form and species response to increasing light, soil water, nitrogen, and related environmental variables.

CHAPTER II.

COMPETITION FOR RESOURCES BETWEEN UNDERSTORY VEGETATION AND OVERSTORY PINUS PONDEROSA IN NORTHEASTERN OREGON

ABSTRACT

The objective of this research was to determine which environmental resources, light, water, and/or nutrients, control understory plant production in a *Pinus ponderosa* forest in northeastern Oregon. A split-plot experimental design, with three blocks 5.0 ha, four treatments, and 44 plots, was established in the summer of 1985. Twenty plots (4 x 4 m) were trenched approximately one meter in depth, and 24 non-trenched plots were used to assess the effects of root competition of overstory trees on understory plants. Trees were commercially thinned in the winter and spring 1986 from a density of 345 to 148 trees/ha^{-1} to increase light levels to the understory. Thinning significantly increased light (PAR), decreased midday relative humidity and increased midday air temperatures and soil temperatures. Xylem potential of the dominant graminoid, *Carex geyeri*, soil water potential, mineralizable nitrogen, and pH were significantly increased within the trenched versus the non-trenched treatments. Micro and macro nutrients in *C. geyeri* and *Symphoricarpos albus*, the dominant shrub, were significantly influenced in both treatments. Increasing light did not increase understory biomass production. Reducing root competition for soil water and nutrients significantly increased understory aboveground dry weight biomass 53 and 94% in 1986 and 1987, respectively. This

research demonstrated that belowground resources were the primary controlling factors of understory production in *P. ponderosa* forests in northeastern Oregon.

INTRODUCTION

Pinus ponderosa forests are widely distributed within the interior mountain ranges of the northwestern United States (Franklin and Dyrness 1973). When timber is thinned or clear cut understory production is increased (McConnell and Smith 1965 1970, Young et al. 1967). The ability of the understory to respond to overstory removal is critical for maintaining a forage base for livestock and wild ungulates (Skovlin et al. 1976). Commercially thinning *Pinus* allows more light to reach the forest floor and increases soil moisture by reducing overstory competition and canopy interception of precipitation. Nutrient cycling also changes as: 1) competition for soil nutrients from the overstory is reduced, 2) nutrients are removed off site in logs, and 3) organic residues from dead roots with high C:N ratios and associated mycorrhizae, alter microbial populations.

In the understory, interspecific competition aboveground is for available light that has filtered through the overstory canopy (Harper 1977, Schoener 1983). Competition belowground involves root competition for available water and nutrients necessary for plant development. Krueger (1980) proposed understory vegetation in forested ranges east of the Cascades in Oregon is limited primarily by water. In a stand of *Pinus* saplings, in pumice soils of central Oregon, water use of plots where the understory was undisturbed was 45% greater than on plots where the understory was removed (Barrett and Youngberg 1965). Competition from understory vegetation had a highly significant effect on growth of *Pinus* throughout the 20 year period (Barrett 1982).

Most forests in the Inland Northwest tend to be nitrogen limited (Harvey et al. 1987). Competition for nitrogen also plays an important role in determining plant growth and species composition (Tilman 1982 1985 1988). Responses of understory species to increased levels of light, water, and nutrients will vary depending upon their physiologic tolerances and competitive ability. It is important we understand how environmental variables limit understory vegetation to predict understory responses to forest harvesting and further our knowledge of overstory and understory competition.

The objective of this research was to: 1) test the hypothesis that belowground resources as effected by tree root competition, is the factor limiting understory production and that the tree canopy which effects light does not limit understory production in *P. ponderosa* forests of northeastern Oregon, 2) if belowground resources are limited by tree root competition, are water and/or nitrogen the primary factors limiting understory vegetation production, and 3) evaluate the effect of tree root competition on plant uptake of other macro and micronutrients by understory vegetation.

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 southern 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 $-19.2^{o}C$ in December to $1.1^{o}C$ in July; from a maximum of $8.5^{o}C$ in December to $36.9^{o}C$ in July (file data; Eastern Oregon Agricultural Research Center, Union). The majority of precipitation on the Hall ranch occurs between November and May in the form of snow. Mean annual precipitation for 1963-1987 was 605 mm (Williams 1989).

The research was conducted in the *Pinus ponderosa*/ *Symphoricarpos albus* community type similar to Johnson and Simon's (1987) *Pseudotsuga menziesii*/*Symphoricarpos albus* plant association of the Wallowa-Snake Province of northeastern Oregon. *Pinus* dominates the overstory and codominates the reproduction with *Pseudotsuga menziesii*. *Symphoricarpos*, *Carex geyeri*, *Calamagrostis rubescens*, and *Arnica cordifolia* 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: Hall Ranch, fine-loamy, mixed, frigid, Ultic Haploxerolls (block 1 non-thin and thin; block 2 thin), Klicker, loamy skeletal, mixed frigid Ultic Agrixerolls

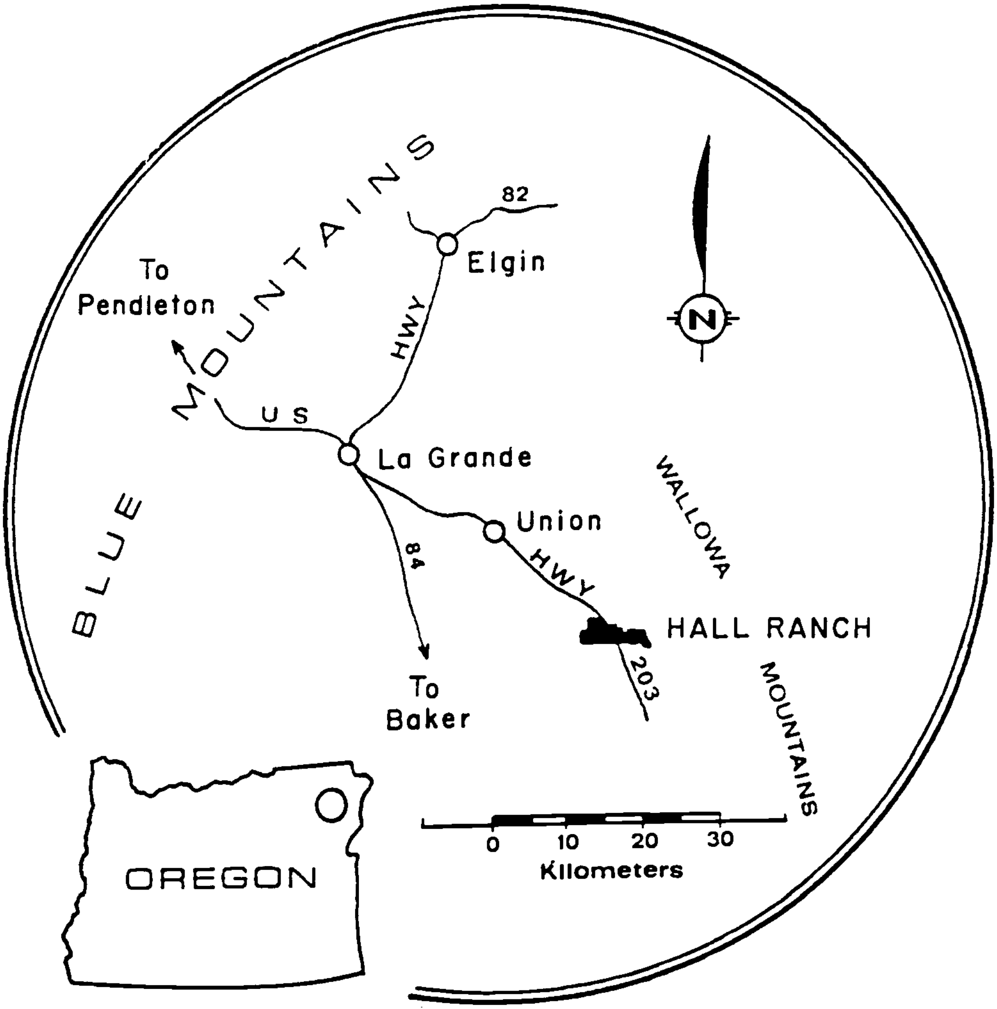


Figure 1. The Hall Ranch, location of the study area.

(blocks 2 and 3 non-thin), and Tolo, medial over loamy, mixed frigid Typic Vitrandepts (block 3 thin) (Dyksterhuis and High 1985). Surface soil texture from silt loam to silty clay loam and soil depth varies from 38 to greater than 92 cm. All series especially the Tolo, originated from pumicite parent material ejected from Mt. Mazama 6,500 years ago.

METHODS

Three 5.0 ha blocks, located within 1.0 km of each other, were selected for this study. Half of each block (2.5 ha) was commercial thinned in the winter of 1986 and the remaining half left undisturbed (control). Stands were relatively homogeneous in overstory species composition and stand structure, however, understory vegetation differs slightly among blocks. Stands were thinned from a density of 345 to 148 trees/ha^{-1} during the winter and spring of 1986. Tree diameters at breast height (dbh) ranged from 0.3 to 135.6 cm with a mean of 31.8 cm.

A total of 48, 4.0 x 4.0 m, macro plots (16/block) were subjectively established to insure adequate representation of the variation in canopy cover. Four trench and four non-trench plots, were randomly assigned in both thin and non-thin treatments within each of the three blocks prior to logging. Perimeters of twenty four plots (6.0 x 6.0 m) were trenched to a depth of 1 m unless the presence of large rocks and boulders prohibited trenching to that depth (Figure 2). Plots were trenched in September of 1985 using a four wheel drive Ditch Witch, model R60. Backfill was replaced to allow sub-surface water movement. Four plots were destroyed during logging operations in block three; (three thinned/trenched and one thinned/non-trenched).

Trenching has been used as an experimental technique to separate the effects of overstory canopy shading and soil resource competition on the understory (Toumey 1929, Toumey and Kienholz 1931, Coile 1937, Shirley 1945, Horn 1985, Christy 1986, and McCune 1986). Trenching has also

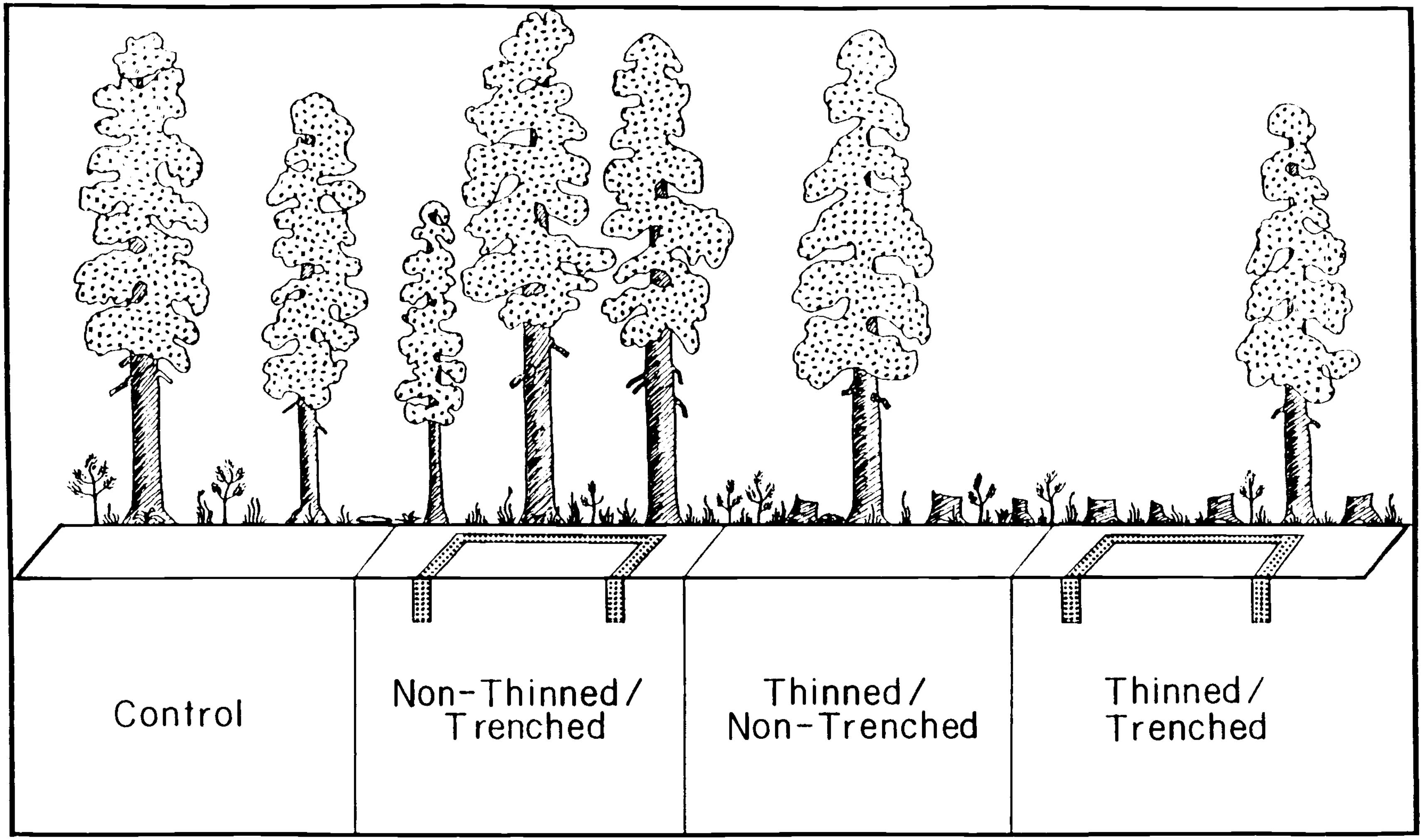


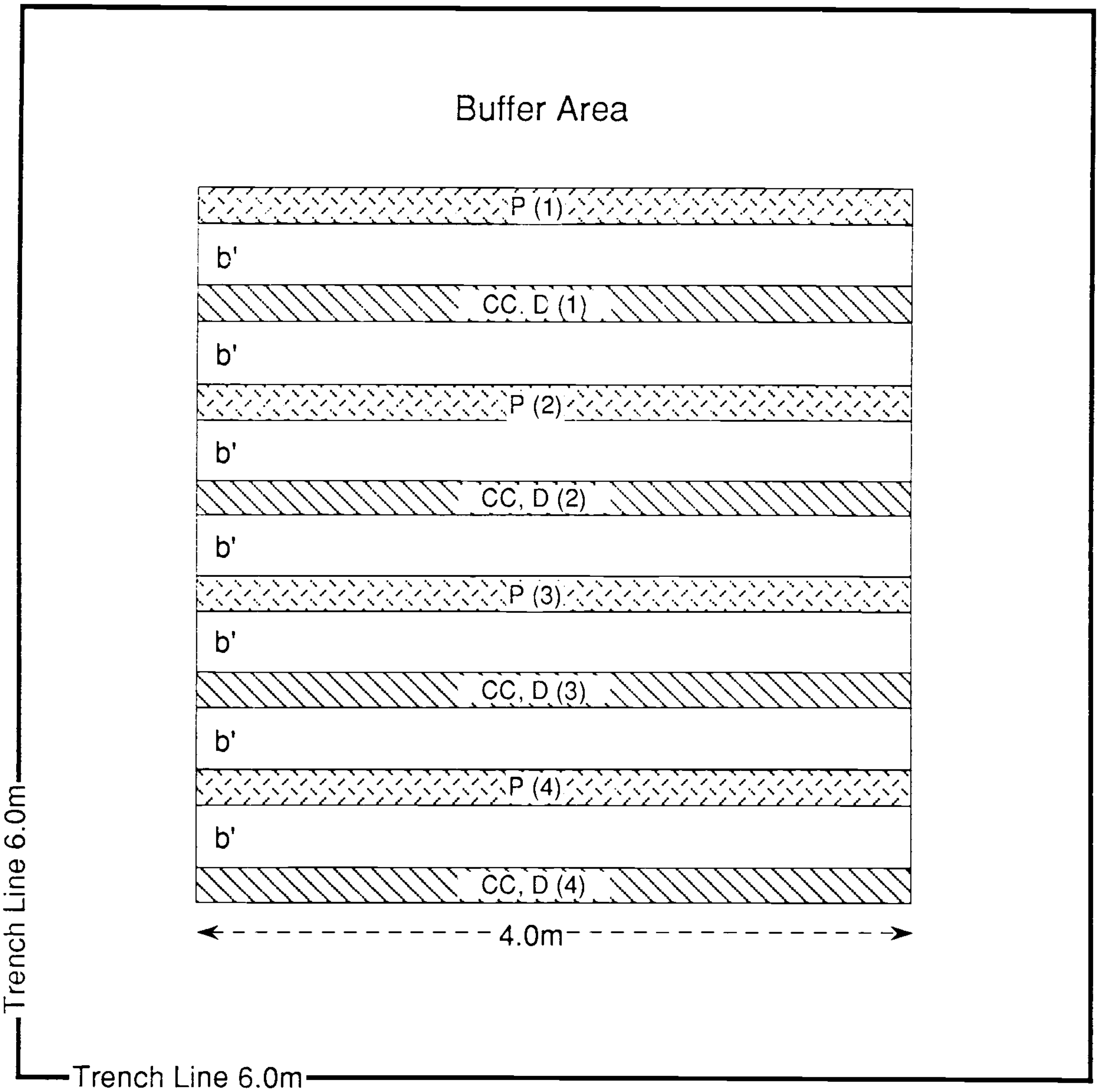
Figure 2. Plot layout within the Non-Thinned, Thinned, Non-Trenched, and Trenched treatments.

been used to intentionally simulate the effect of clear cutting on soil nitrogen mineralization, ammonium, and nitrate production (Vitousek et al. 1982).

Understory Vegetation Measurements

Understory standing crop biomass was clipped at peak standing crop (seasonal maximum biomass) within each of the 4.0 x 4.0 m macro plots (late June through July of 1986 and 1987). Plants were clipped to the top of the litter surface within two, 4.0 x 0.2 m production transects (Figure 3). Each transect was divided into four, 1.0 x 0.2 m micro plots. Within the production transect one of the four micro plots was randomly selected to be harvested by species and forage classes. Plants were clipped as they approached senescence to minimize physiologic impact and competition from associated species. Transects one and three were harvested in 1986 and two and four were harvested in 1987 to avoid clipping the same transect. Individual species clipped were community dominants Carex geyeri, Calamagrostis rubescens, Poa pratensis, and Symphoricarpos albus. Forage classes included other perennial grasses, perennial forbs, annuals and biennials, and other shrubs. Herbage was dried 48 hours at 60°C and weighed.

Water status of Carex was determined by measuring xylem potential with a pressure chamber (PMS Instrument Company; Model 1000; Corvallis, OR) (Scholander et al. 1965, Waring and Cleary 1967). Predawn and midday measurements were made biweekly during the growing season on five dates in 1986 and nine dates in 1987. Two randomly selected tillers of Carex were sampled from each macro plot. The most recently expanded leaf blade was



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 3. Production, canopy cover, and density transects within a macro plot.

used for each measurement. A moist paper towel was placed in the pressure chamber to limit vapor loss and samples were pressurized at 0.025 MPa s^{-1}. Relative humidity and air temperature were measured concurrently with a Princo sling psychrometer (Southampton, PA) when xylem potential measurements were recorded. Phenology of key understory species was also recorded on days xylem potential was measured.

Soil moisture was measured gravimetrically on the same dates xylem potential was measured. One soil moisture core was collected at three depths; 0-20, 20-40, and 40-60 cm, in each macro plot. Soils were dried at $100^{o}C$ for 48 hours and weighed to attain percent water content. Percent soil water was converted to soil water potential by developing soil water release curves. To construct soil water release curves soils were sampled for bulk density to convert soil moisture into volumetric soil moisture content. Soil water retentivity was determined on a pressure plate (Soil Physics Laboratory, Soil Science Department OSU, Corvallis OR).

Soil temperature was measured with a Reotemp soil thermometer (San Diego, CA; model 4) on the same dates and approximately the same time midday xylem potentials were recorded. Temperatures were sampled at three depths 15, 30, and 45 cm per macro plot.

Overstory canopy was photographed with a fisheye lens on a 35 mm camera to determine cover. Cover was photographed during August, 1985 prior to thinning and in August, 1986 after thinning. Slides from black and white negatives were projected on a plotter and proportions of sky and cover were calculated using the analysis procedure of Chan et al. (1986).

Light, photosynthetic active radiation (PAR), was measured on cloudless days (8 August 1986; 18 July and 28 August 1987) with booklets of photosensitive ozalid paper in plastic petri dishes (Friend 1961). Five ozalid integrators recorded concurrently at 1.5 m intervals within each macro plot (two in the buffer area above production transect 2 and two in the buffer area above production transect 4 approximately 1.5 m and 3.0 m from the left boarder, and one in the middle approximately 3.0 m from the left boarder). Integrators were placed on leveled ground in an opening beneath the understory canopy during the evening and collected 24 hours latter. Booklets were kept in the dark until they were developed in ammonia fumes. Regression equations were used to calibrate ozalid values by exposing a series of integrators to sunlight for various time intervals at EOARC in Union the same day integrators were in the field (Appendix Table 1). Calibration measurements were made each year with a LI-190S-1 quantum sensor (LICOR, Inc., Lincoln, Nebraska). The number of bleached sheets was equated to micromoles per square meter per second (μ mol m^{-2} s^{-1}). Exposures were made at increasing time intervals from 1 minute to 8 hours.

Ozalid paper is only sensitive to a small portion of the light spectrum (400 to 700 nm), however, it integrates light into a single value. This technique is appropriate as an index of overall light levels (Emmingham and Waring 1973, Christy 1986). Comparisons with instantaneous light measurements for photosynthesis should not be made (Sam Chan, personal communication).

Nutrient Analysis

Soils were collected and analyzed to determine the amount of mineralizable nitrogen, ammonium (NH_4), and nitrate (NO_3) in each macro plot within blocks one and two in September of 1986, and all three blocks in September of 1987. Soils were pooled by treatment within blocks for analyses. Ammonium and nitrate were auto analyzed 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 soil from samples described above with distilled water in a 1:1 solution and measuring pH with a standard electrode (McClean 1982). Soil analyses were performed by the Oregon State University Soil Testing Lab, Soil Science Department; pH was determined by the Forest Science Department.

Carex and Symphoricarpos samples of current years growth, collected for biomass measurements, were ground in a Wiley mill (20-mesh screen) for tissue nutrient analysis. Nitrogen concentration was determined with a semimicro-Kjeldahl apparatus (Bremner 1965). Samples were analyzed for P, K, Mg, Ca, S, Mn, Fe, Cu, B, and Zn by ICP emission spectroscpy after dry-ashing at 500^{o}C and being dissolved in 5 ml of 20% HNO_3 diluted to 5% before analysis (Isaac and Johnson 1985). Nutrient total accumulation of Carex and Symphoricarpos is defined as the total quantity of a nutrient in the aboveground portion of the plant per unit area (kg/ha^{-1}). Nutrient total accumulation was calculated as nutrient concentration x biomass of Carex and Symphoricarpos (Jarrell and Beverly 1981).

Descriptive Measurements

Prior to thinning in September, 1985, basal area of trees adjacent to the center of each macro plot was measured using a CRUZ ALL angle gauge (Jackson, MS) (Hursch et al. 1972). Basal area of thinned stands were measured in September, 1986.

Experimental Design and Data Analysis

The experiment was conducted as a split plot design with a 2 x 2 factorial analysis. Hereafter, treatments are referred to as thinned, non-thinned, trenched, and non-trenched; and plots (treatment combinations) as non-thinned/non-trenched (control), non-thinned/trenched, thinned/non-trenched and thinned/trenched. Analysis of variance was used to test differences in thinning and trenching treatments. Variables tested were biomass production, xylem potential, soil water potential, light, air and soil temperature, relative humidity, soil pH, and soil and plant nutrients. A probability value of $P<0.05$ was used throughout the analysis 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 repeated measures analysis of variance was used (general linear models procedure) to test treatment differences of xylem potential, soil water potential, air and soil temperature, and relative humidity (SAS Institute Inc. 1987).

RESULTS

Environmental Response

Light

Thinning decreased canopy cover by 52% and basal area by 59% (Table 1). Light (PAR) reaching the understory was 126% greater in thinned versus non-thinned treatments (Table 2). Light values were higher in 1987 than the previous year. The first measurement of 1987 was measured on 18 July (second date; 28 August 1987) yielding higher light quantity due to longer day length than August 8, 1986.

Air Temperature

Thinning influenced air temperatures in the thinned treatment. Predawn temperatures were not different within treatments in 1986 (Figure 4a; Appendix Table 2). In 1987, however, predawn temperatures were lower in the thinned treatments on 5 of the 9 dates measured (Figure 5a; Appendix Table 3). Air temperatures at midday were higher in the thinned treatment on July 13, August 12, and September 10, 1986 and August 15 and 27 in 1987 (Figures 6a and 7a; Appendix Tables 2 and 3). There was a time x thinned interaction in 1987 (Appendix Table 4).

Relative Humidity

Predawn relative humidities were not significantly different within treatments in either years (Figures 4b and 5b; Appendix Tables 5 and 6). Midday relative humidity, however, was lower in the thinned treatment (Figures 6b and 7b; Appendix Tables 5 and 6). There was a time x thinned interaction for relative humidity at

Table 1. Basal area (m^2/ha^{-1}) and canopy cover (%) (means and standard errors) by treatments for 1985 and 1986. P = Probability level.

Treatments	Basal Area		Canopy Cover	
	1985	1986	1985	1986
Non-Thinned	22.1	22.1	56.41	56.41
Thinned	24.9	10.2	60.61	28.99
SE	4.3	22.8	5.14	33.59
P	0.2081	0.0010	0.1703	0.0001

Table 2. Light, photosynthetic active radiation-PAR (μ mol m^{-2} s^{-1}/day 10^6), from ozalid integrators by treatments for 1986 and 1987. Values for 1986 are based on one measurement (8 August) and 1987 on two measurements (18 July and 28 August). Standard error (SE) A = Non-Thinned and Thinned, SE B = on-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

Treatments	1986	1987
Non-Thinned	$15.00X10^6$	$17.10X10^6$
Thinned	$30.45X10^6$	$41.93X10^6$
Non-Trenched	$21.25X10^6$	$28.42X10^6$
Trenched	$22.86X10^6$	$28.42X10^6$
SE A	1.84E+20	3.06E+20
P	0.0231	0.0098
SE B	2.87E+06	1.48E+19
P	0.1661	0.1599
SE AB	1.90E+19	1.68E+19
P	0.4729	0.2385

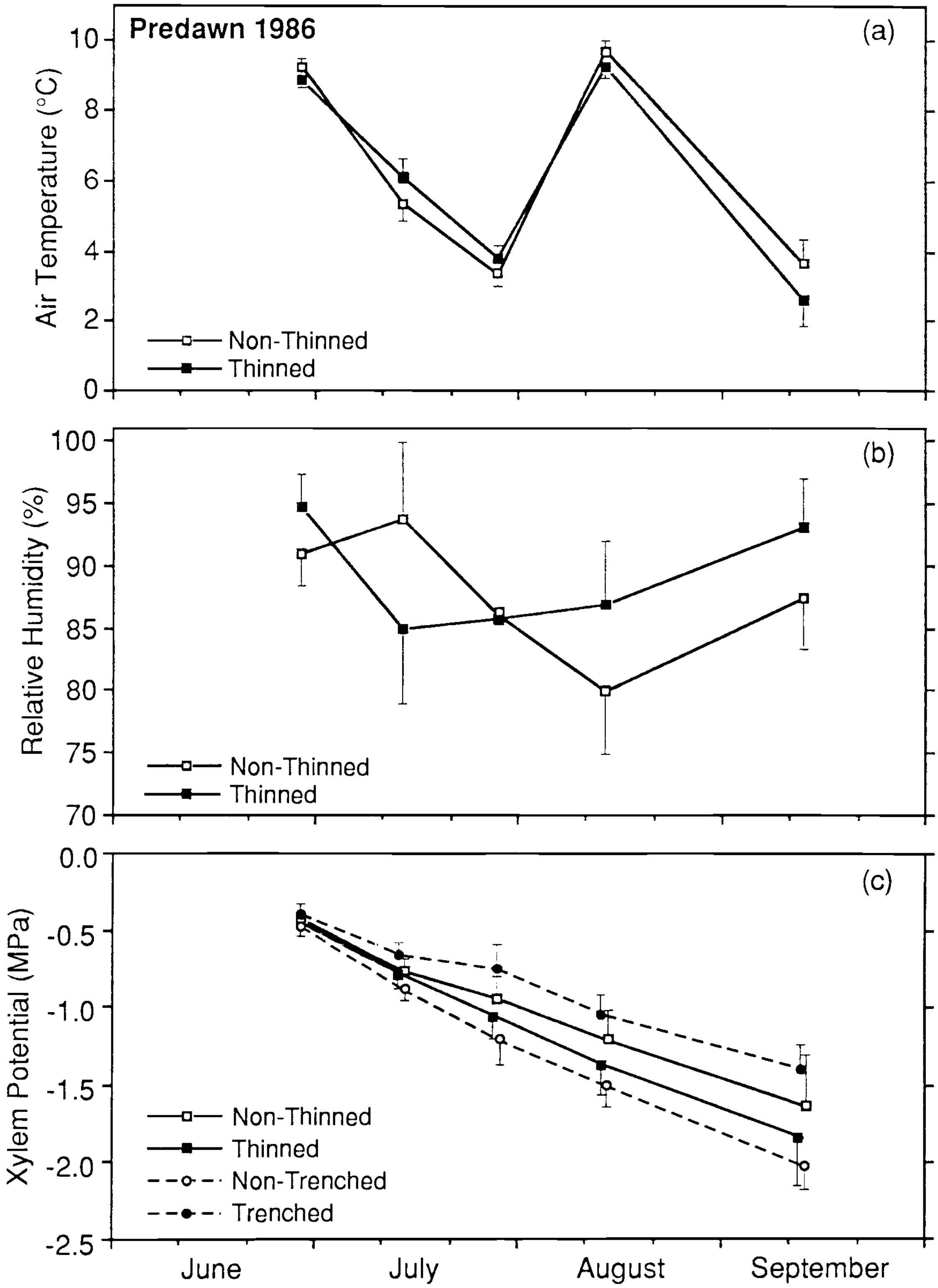


Figure 4. Predawn (a) air temperature, (b) relative humidity, (c) xylem potential (means and standard errors) by date in 1986.

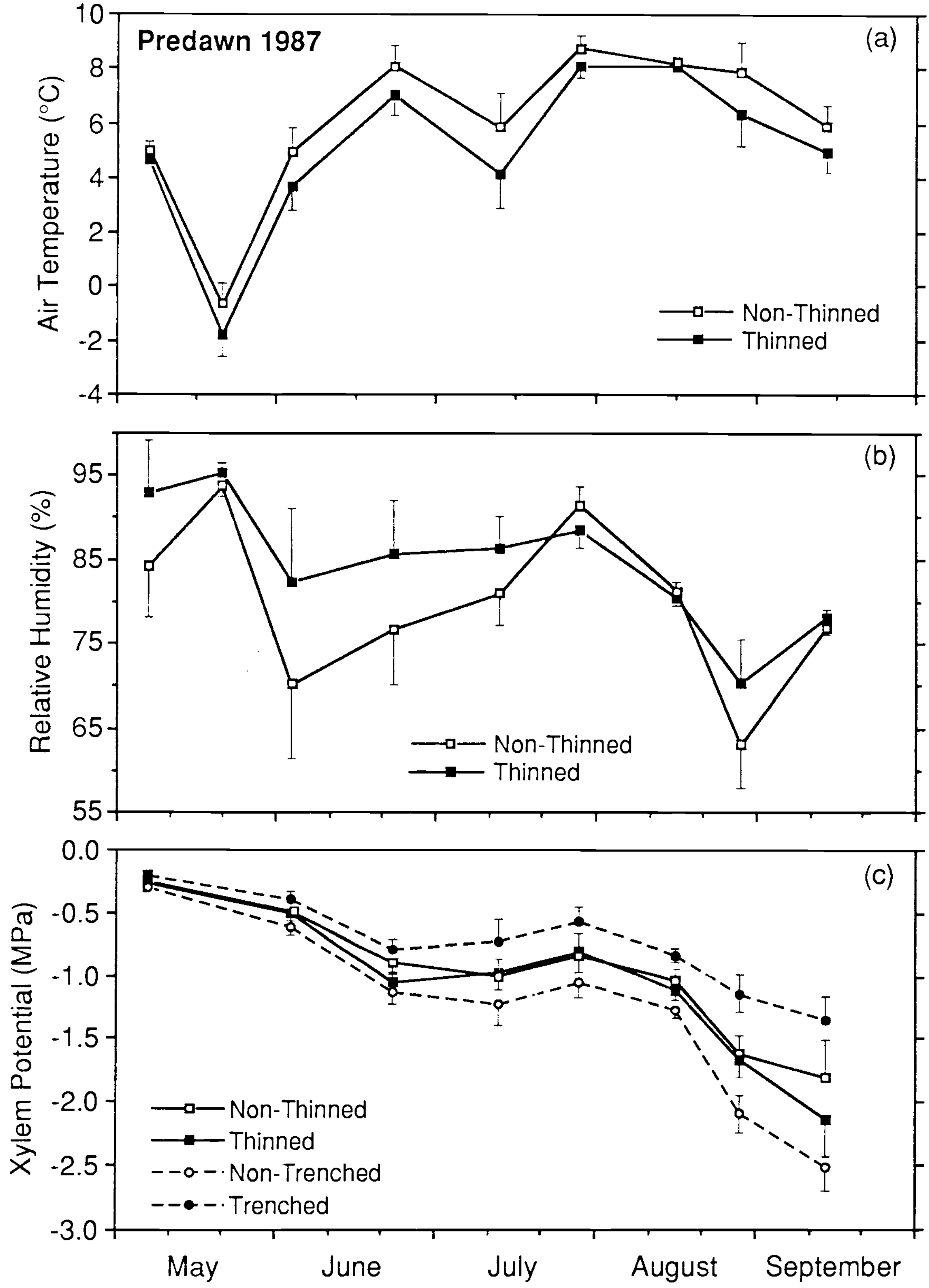


Figure 5. Predawn (a) air temperature, (b) relative humidity, (c) xylem potential (means and standard errors) by date in 1987.

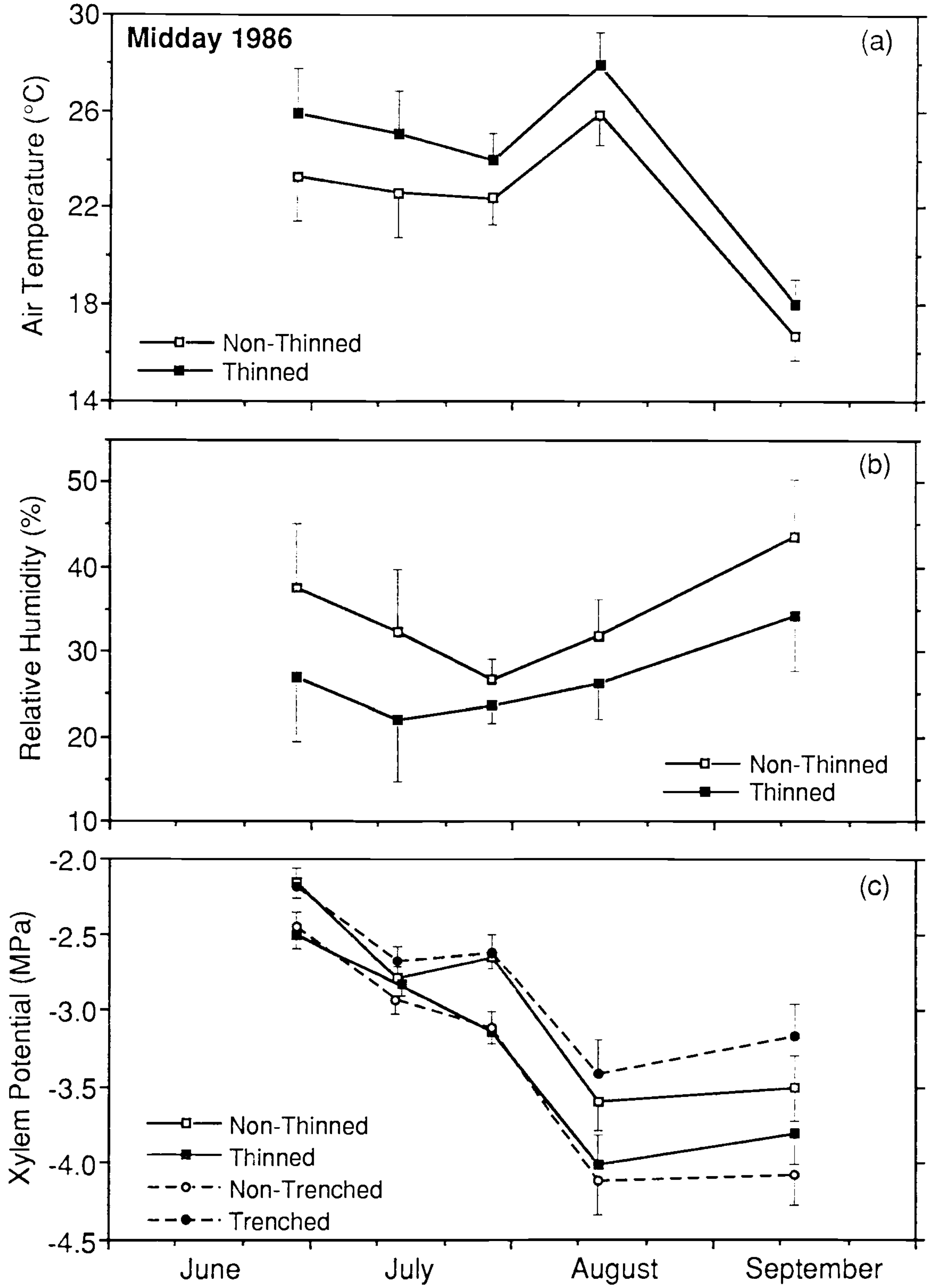


Figure 6. Midday (a) air temperature, (b) relative humidity, (c) xylem potential (means and standard errors) by date in 1986.

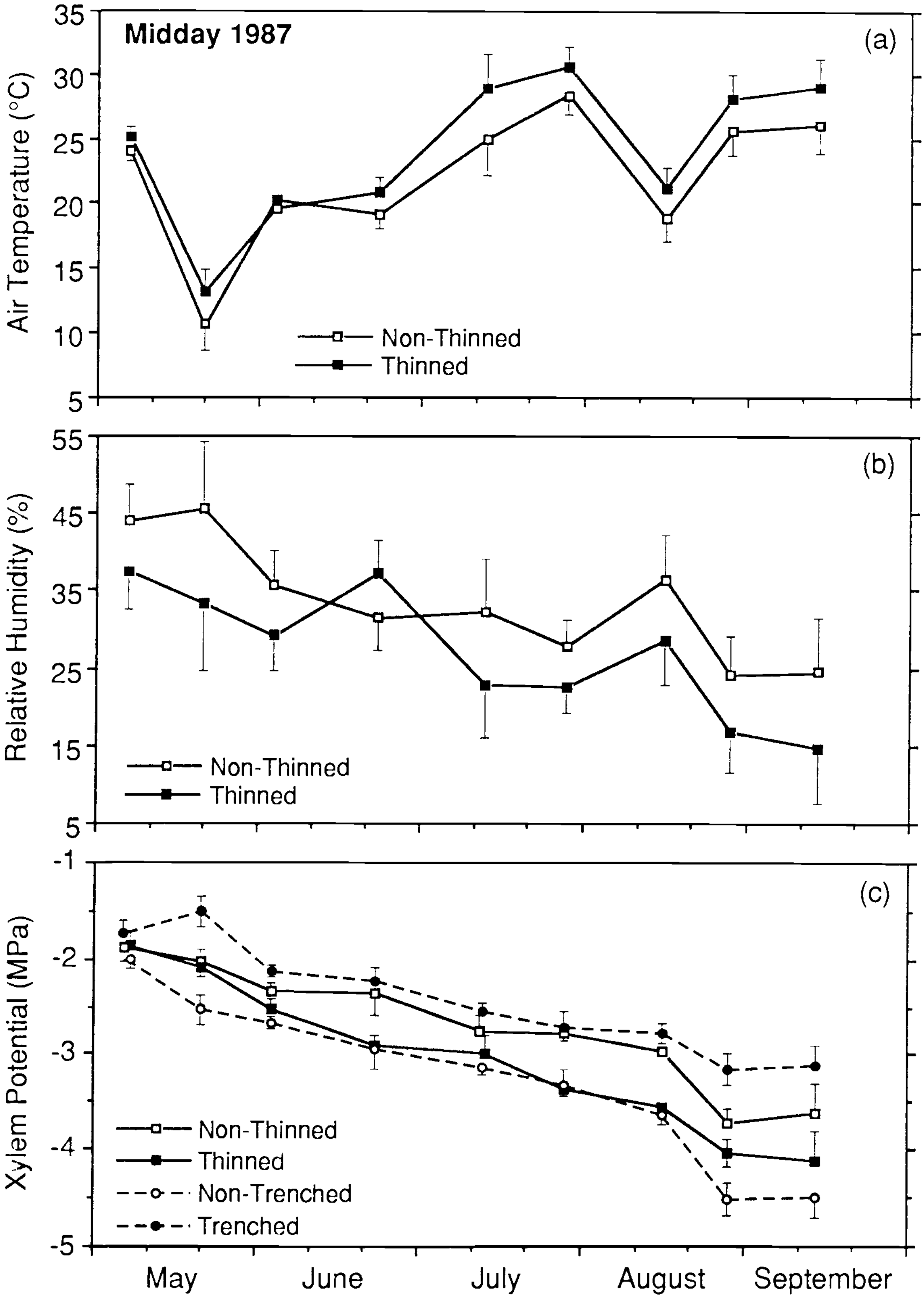


Figure 7. Midday (a) air temperature, (b) relative humidity, (c) xylem potential (means and standard errors) by date in 1987.

both predawn and midday in 1986 and a time x thinned interaction at midday in 1987 (Appendix Table 4).

Soil Temperature

Thinning did not effect soil temperature in 1986, however, trenching, did increase soil temperature on September 10 at the 45 cm depth (Figure 8; Appendix Tables 7 and 8). There was a thinned x trenched interaction on August 12, 1986. In 1987, soil temperatures were higher in the thinned treatment at 15 and 30 cm depths on both June 3 and 22. In the trenched treatment, soil temperatures were lower in the 15 and 30 cm depths on August 27, 1987 (Figure 9; Appendix Tables 9 and 10). In 1987, soil temperature had a time x thinned interactions in the 15 and 30 cm depths, and time x thinned x trenched interactions for the 45 cm depth (Appendix Table 4).

Soil Water Potential

In 1986, soil water potentials in the 0-20 cm depth within the thinned treatment were more negative than on the non-thinned on July 13; and less negative in trenched treatment versus non-trenched on August 12 (Figure 10; Appendix Tables 11 and 12). The trenched treatment had less negative soil water potentials than non-trenched in the 20-40 cm depth from June 28 through the 1986 growing season. Though there were thinned x trenched interactions from July 13 through the growing season, differences between trenched versus non-trenched plants were highly significant. Soil water potentials were not effected by the thinned treatment in either the 20-40 or 40-60 cm depths in 1986. In the trenched treatment soil water potentials were consistently less negative than the

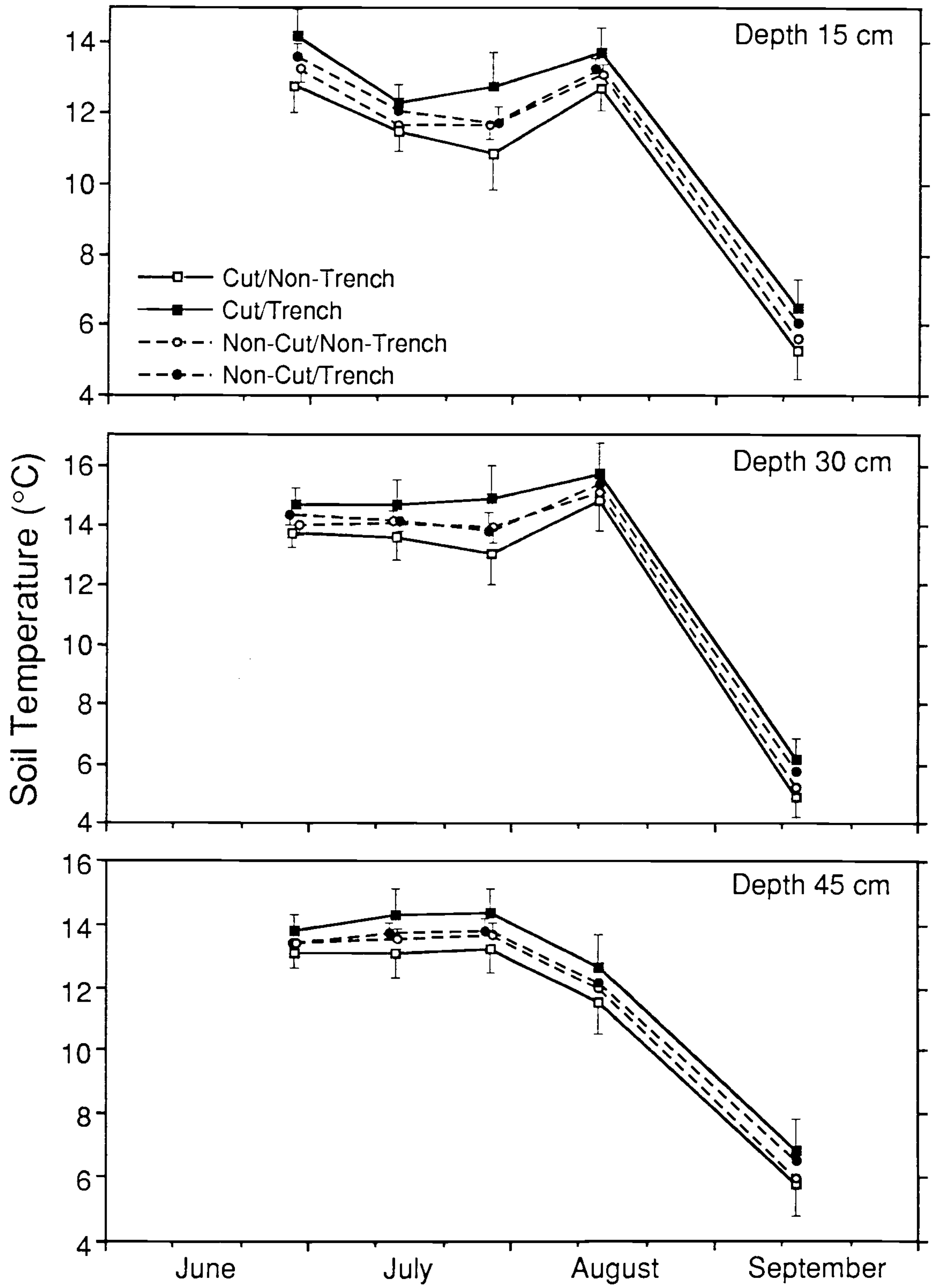


Figure 8. Soil temperatures (means and standard errors) by depth and date in 1986.

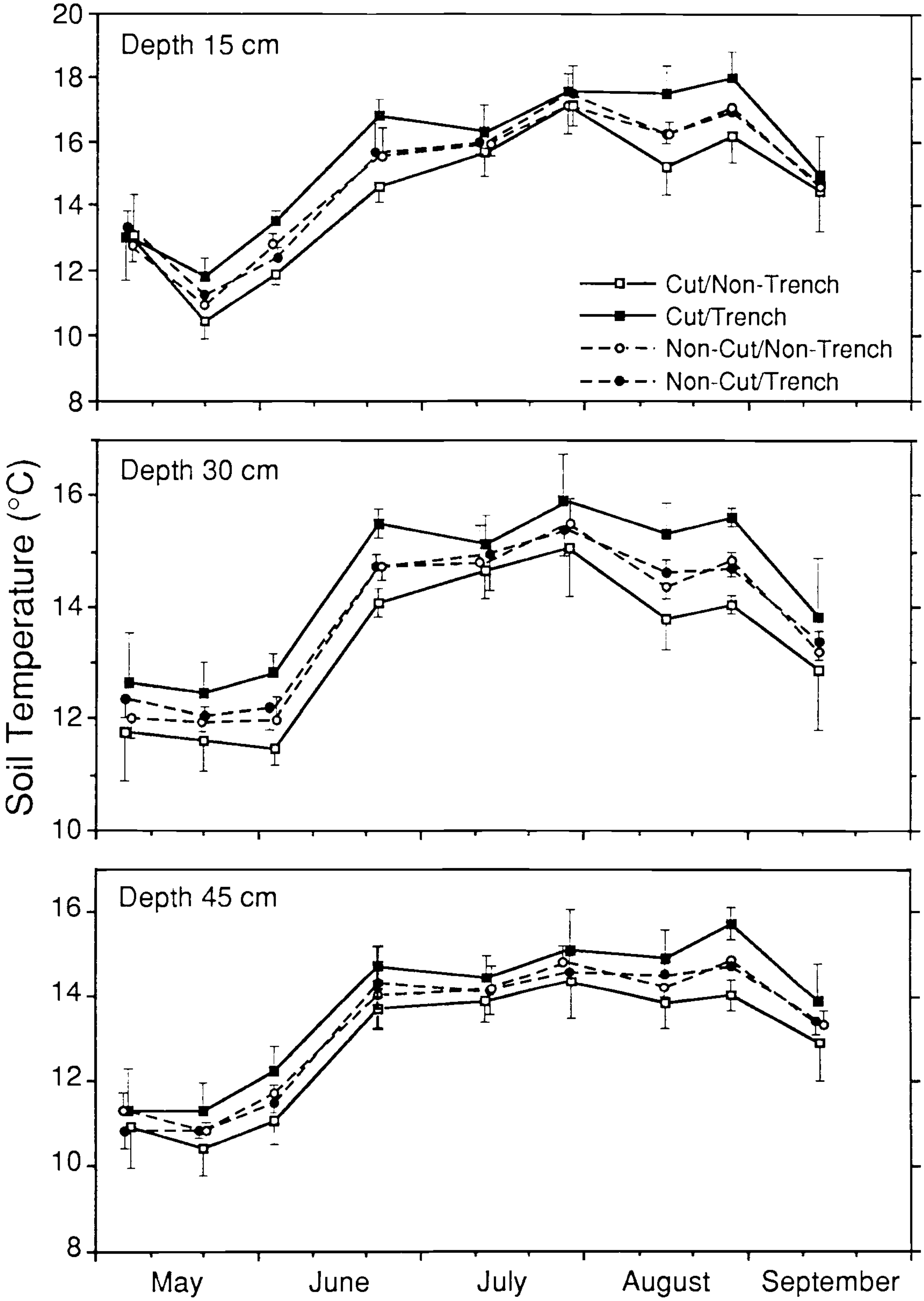


Figure 9. Soil temperatures (means and standard errors) by depth and date in 1987.

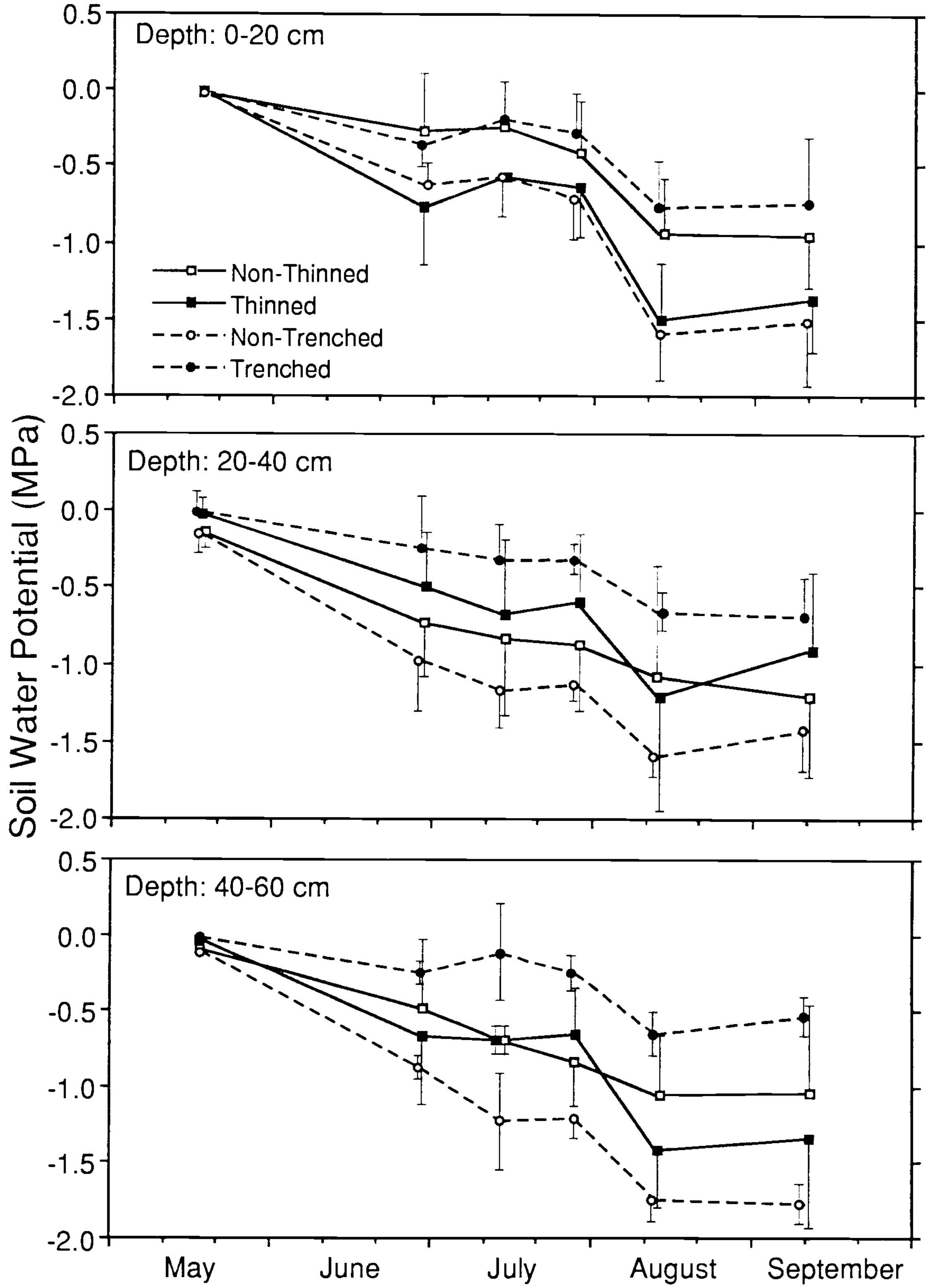


Figure 10. Soil water potentials (means and standard errors) by depth and date in 1986.

non-trenched in the 40-60 cm depth through the entire season of 1986. There were thinned x trenched interactions but differences between trenched treatments were highly significant. Soil water potentials in 1986 had a time x thinned interaction in the 0-20 cm depth and a time x thinned x trenched interaction in the 20-40 and 40-60 cm depths (Appendix Table 4).

In 1987, thinning did not affect soil water potentials in the 0-20 cm depth in 1987 (Figure 11; Appendix Tables 13 and 14). The trenched treatment, however, had less negative soil water potentials than non-trenched treatment in the 0-20 cm depth during the later part of the growing season. Trenched x thinned interactions occurred on May 20, August 27 and September 13, 1987, but only on the later date were differences between trenched versus non-trenched highly significant. Soil water potential in the 20-40 cm depth was not affected by thinning, in 1987, while the trenched treatment was consistently less negative than the non-trenched treatment. Thinned x trenched interactions occurred on all but the first date, however, all trenched treatments were highly significant. The thinned treatment was less negative than non-thinned in the 40-60 cm depth. Trenched plots were consistently less negative than non-trenched plots, throughout the growing season of 1987. Although thinned x trenched interactions occurred on June 3 through August 27, trenched treatments were highly significant on all but August 5. Soil water potentials in 1987 had time x thinned x trenched interactions at all three depths (Appendix Table 4).

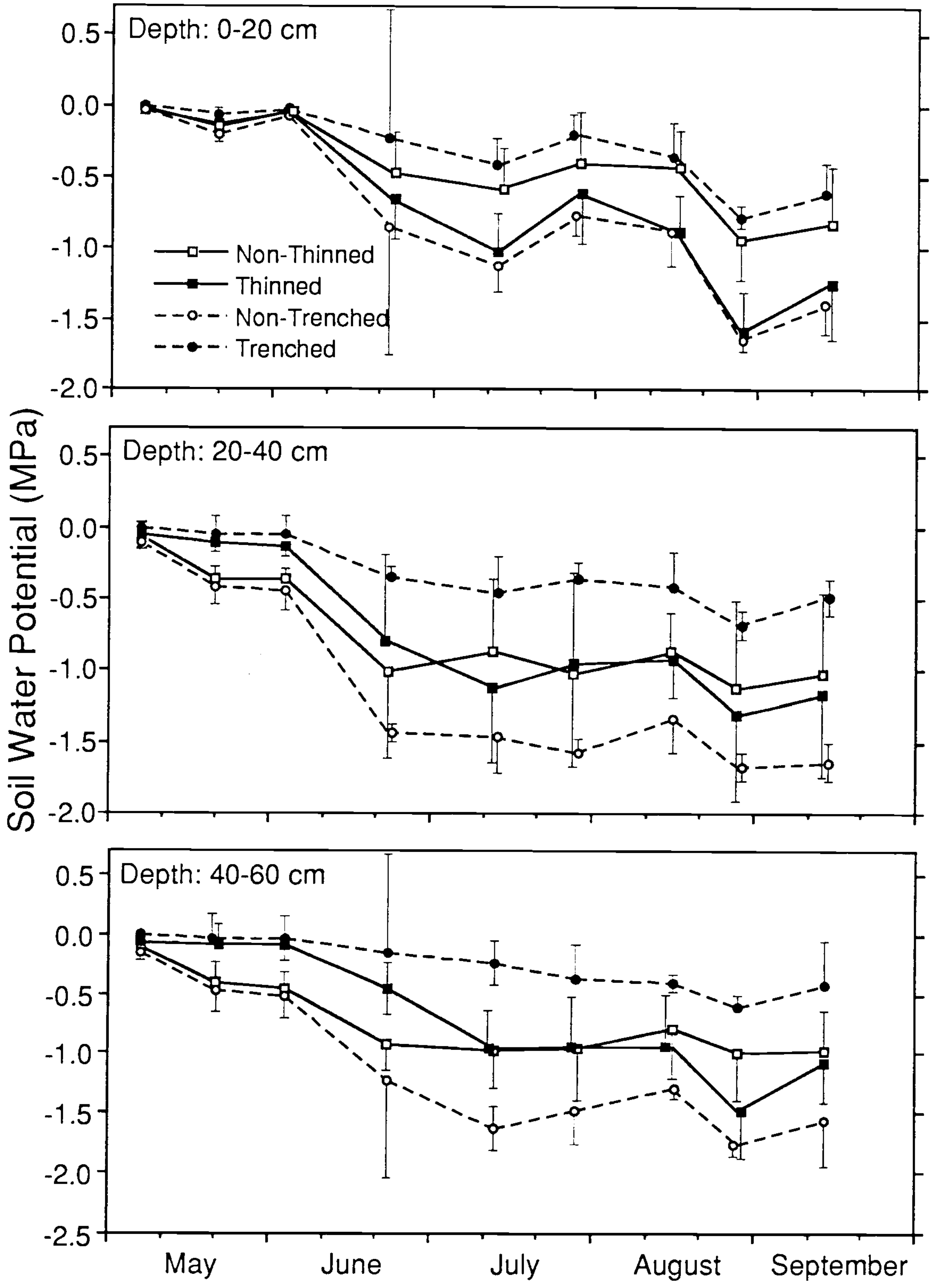


Figure 11. Soil water potentials (means and standard errors) by depth and date in 1987.

Soil pH and Nitrogen

Soil pH in the 0-20 cm depth was higher in the trenched treatment as compared to the non-trenched treatment in 1986 (Table 3, Appendix Table 15). There was a thinned x trenched interaction in the 20-40 cm depth in 1987; the trenched treatment had the highest ph levels measured.

Mineralizable nitrogen, ammonium, and nitrate concentrations were not different among treatments in either year. Mineralizable nitrogen in 1987 had a thinned x trenched interaction in the 0-20 cm depth, though the trenched (non-thinned/trenched plots) treatment had the highest concentrations (Table 4, Appendix Tables 16, 17, and 18).

Plant Response

Biomass

Understory dry weight biomass was 53 and 94% greater in 1986 and 1987, respectively, in the trenched plots compared to non-trenched plots (Figures 12 and 13; Appendix Tables 19 and 20). Trenching increased perennial graminoids in 1986 (Figure 12; Appendix Tables 21 and 22). Perennial forbs increased in response to both thinned and trenched treatments (Figure 13). In 1987, both perennial graminoids (forage class) and *Calamagrostis* increased in percent composition in the trenched treatment though there were thinned x trenched interactions.

Xylem Water Potential

Predawn xylem potentials in *Carex* were not different between thinned treatments in either years (Figures 4c and 5c; Appendix Tables 23, 24, 25, and 26). Predawn

Table 3. Soil pH by treatments and depths (cm) means and standard errors) for 1986 and 1987. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

	1986 Depth (cm)		1987 Depth (cm)	
Treatments	0-20	20-40	0-20	20-40
Non-Thinned	6.07	6.22	6.18	6.44
Thinned	5.92	5.57	6.00	6.23
Non-Trenched	5.90	5.89	6.06	6.27
Trenched	6.09	5.90	6.12	6.40
SE A	0.04	0.22	0.03	0.04
P	0.2807	0.3336	0.2649	0.6560
SE	0.02	0.09	0.02	0.02
P	0.0303	0.9886	0.1695	0.0308
SE AB	0.03	0.13	0.03	0.02
P	0.5065	0.6214	0.7797	0.0368

Table 4. Soil mineralizable nitrogen, nitrate, and ammonium (ppm) by treatments and depths (means and standard deviations) for 1986 and 1987.

	1986				1987			
	Depth (cm)							
	0-20		20-40		0-20		20-40	
Treatments	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
	Mineralizable Nitrogen							
Non-Thinned	40.68	21.91	18.85	5.87	57.70	25.41	57.87	21.09
Thinned	31.94	11.56	17.49	7.27	56.05	12.65	52.35	12.05
Non-Trenched	34.13	13.44	14.62	2.96	52.88	13.64	47.63	10.02
Trenched	38.49	21.58	21.71	7.14	60.87	24.15	62.58	19.34
	Nitrate							
Non-Thinned	0.54	0.48	0.45	0.17	1.02	1.85	0.97	1.78
Thinned	0.38	0.22	0.36	0.17	0.20	0.00	0.22	0.04
Non-Trenched	0.36	0.21	0.39	0.16	0.22	0.04	0.20	0.00
Trenched	0.55	0.48	0.43	0.19	1.00	1.86	0.98	1.77
	Ammonium							
Non-Thinned	41.44	19.86	15.95	19.50	35.98	16.85	47.70	16.30
Thinned	19.54	6.71	35.86	24.53	40.48	5.72	41.74	15.72
Non-Trenched	36.31	18.71	24.55	17.81	35.97	11.25	39.78	8.78
Trenched	24.66	16.90	27.26	29.83	40.50	13.79	49.66	19.96

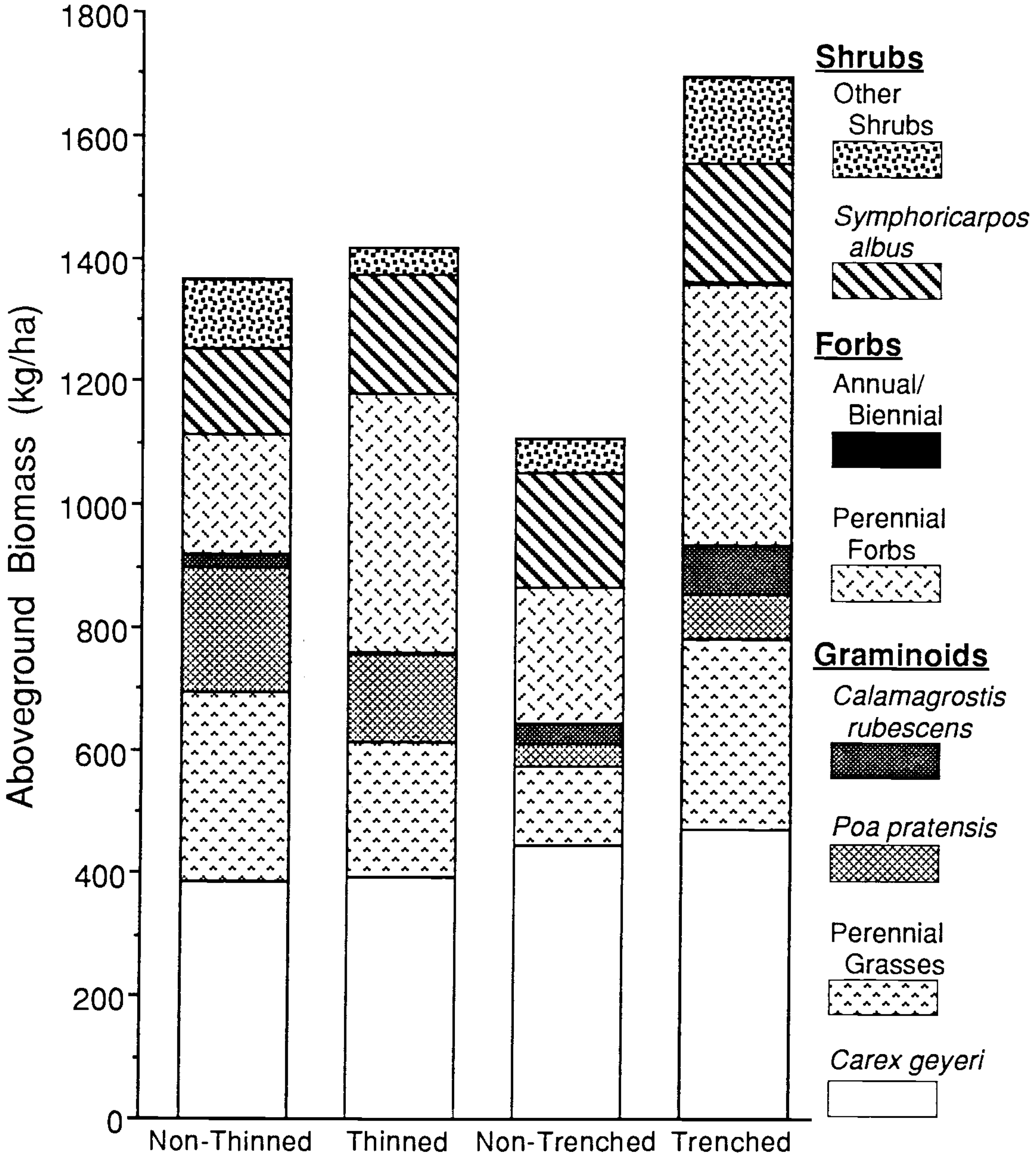


Figure 12. Understory biomass by species, life-form, and total by treatments in 1986.

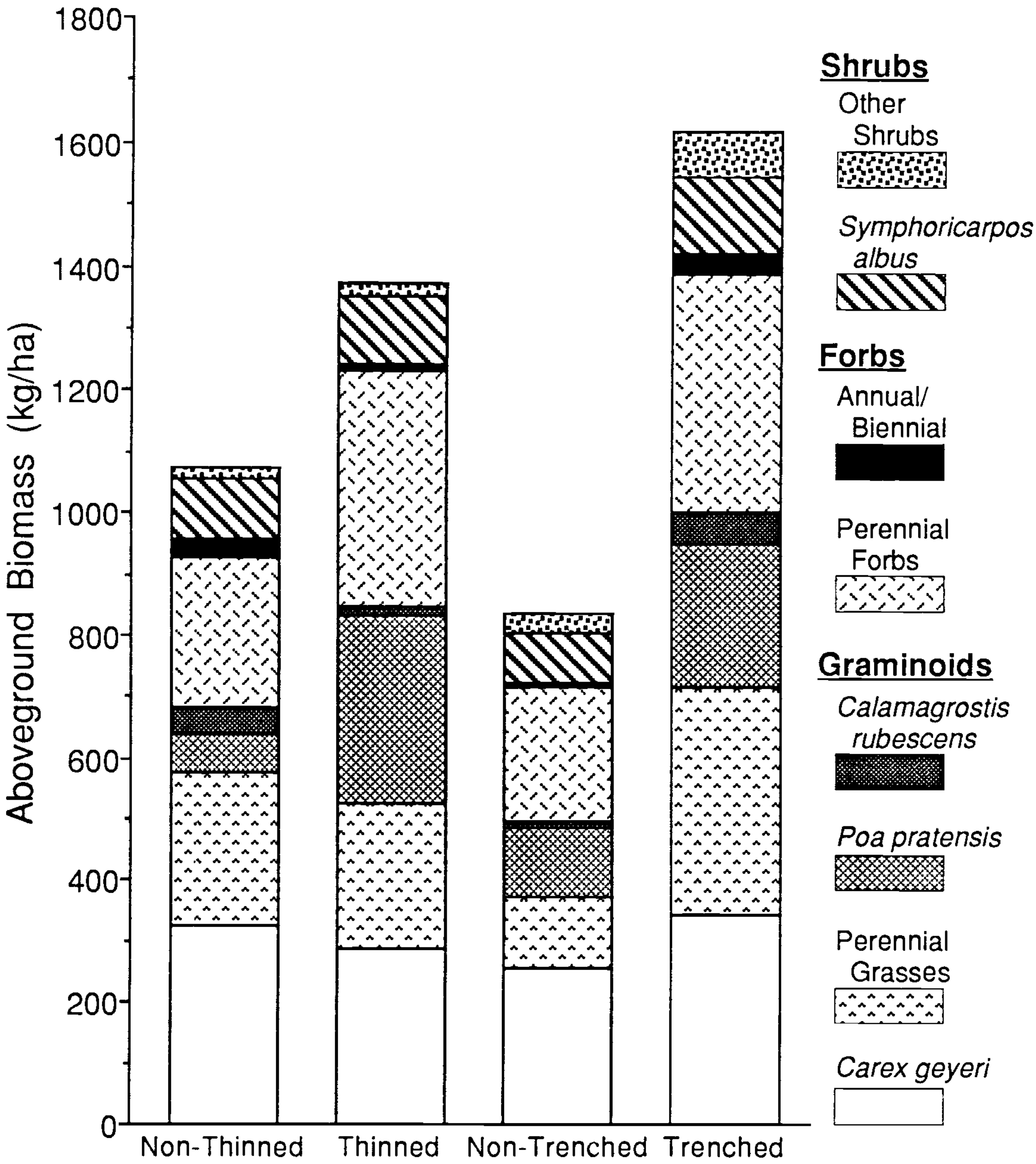


Figure 13. Understory biomass by species, life-form, and total by treatments in 1987.

xylem potentials, however, were less negative in trenched treatments versus non-trenched in 1986 and 1987, except on June 28, 1986. Predawn xylem potentials had a time x trenched interaction in 1986 and a time x thinned x trenched interaction for 1987 (Appendix Table 4).

Midday xylem potentials in Carex were only different on three dates in the thinned versus non-thinned treatments during the two growing seasons (Figures 6c and 7c; Appendix Tables 23, 24, 25 and 26). Midday xylem potentials were less negative in trenched versus non-trenched treatments in 1986 and 1987. Within the trenched treatment, the non-thinned plots were usually less negative than the thinned treatment in both years. In 1986, a thinned x trenched interaction occurred on July 27, though the trenched treatment was less negative than the non-trenched. Although there were thinned x trenched interactions in 1987 for both predawn and midday xylem potentials on June 3, and midday on August 27, and September 13, trenched treatments were also less negative than non-trenched. Within these interactions the thinned treatment had more negative midday xylem potential than the non-thinned, while the trenched treatment was less negative than non-trenched only on July 27, and August 15, 1987. Midday xylem potentials had a time x thinned interaction in 1986 and a time x thinned x trenched interaction in 1987 (Appendix Table 4).

Plant Nutrients

Both the thinned and trenched treatments influenced concentrations of several plant nutrients in Carex (Table 5, Appendix Table 27). Thinning decreased K in both years, Mn in 1986 and Zn in 1987, while trenching increased concentrations of both K and Zn in 1987.

Table 5. Nutrient concentrations of *Carex geyeri* foliage by treatments (means and standard errors) for 1986 and 1987. N, P, K, S, Ca, and Mg are reported in % dry wt; other micronutrients are reported in ppm dry wt. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

Treatments	N	P	K	S	Ca	Mg	Mn	Fe	Cu	B	Zn	Al
	%						ppm					
1986												
Non-Thinned	1.10	0.19	2.08	0.11	0.43	0.16	760.83	266.17	2.33	8.33	66.50	240.67
Thinned	1.08	0.17	1.43	0.10	0.42	0.15	439.67	241.17	2.33	8.00	41.72	190.17
Non-Trenched	0.95	0.17	1.73	0.09	0.37	0.16	633.83	207.83	2.33	8.67	52.22	139.50
Trenched	1.23	0.20	1.78	0.11	0.47	0.16	566.67	299.50	2.33	7.67	56.00	291.33
SE A	0.01	0.02	0.47	0.01	0.01	0.01	227.10	17.68	0.00	0.47	35.04	71.42
P	0.9375	0.3311	0.0549	0.4226	0.8352	0.4639	0.0165	0.6067	1.0000	0.6349	0.1913	0.5199
SE B	0.20	0.02	0.04	0.01	0.07	0.00	47.49	64.82	0.00	1.41	5.34	214.72
P	0.0273	0.0626	0.8068	0.1318	0.0002	0.9367	0.4391	0.0032	1.0000	0.1841	0.7369	0.0147
SE AB	0.02	0.01	0.15	0.00	0.02	0.03	18.83	6.00	0.00	0.33	2.11	40.83
P	0.8201	0.6355	0.5200	0.7247	0.0697	0.2737	0.8216	0.7013	1.0000	0.6231	0.8503	0.3305
1987												
Non-Thinned	1.31	0.22	2.12	0.12	0.38	0.15	518.83	177.83	5.17	6.83	79.83	90.67
Thinned	1.21	0.22	1.79	0.11	0.40	0.16	431.83	131.33	3.67	5.67	40.67	58.83
Non-Trenched	1.14	0.21	1.72	0.10	0.38	0.15	501.17	159.67	3.67	7.67	52.00	80.83
Trenched	1.38	0.23	2.19	0.12	0.40	0.16	449.50	149.50	5.17	4.83	68.50	68.67
SE A	0.08	0.00	0.23	0.01	0.01	0.00	61.52	32.88	2.12	1.65	55.39	45.02
P	0.3581	0.7157	0.0503	0.2079	0.3414	0.7510	0.2502	0.1789	0.0955	0.4825	0.0118	0.2284
SE B	0.17	0.02	0.33	0.02	0.02	0.00	36.53	7.19	2.12	4.01	23.33	17.21
P	0.0021	0.0647	0.0347	0.0006	0.4397	0.4685	0.4357	0.3895	0.0399	0.0721	0.0401	0.1537
SE AB	0.14	0.04	0.16	0.02	0.06	0.01	60.67	15.50	1.50	0.17	14.50	38.42
P	0.0146	0.0147	0.3418	0.0011	0.0619	0.1848	0.3671	0.2154	0.0399	0.8933	0.0580	0.0172

Carex contained greater total N concentrations in the trenched treatment than the non-trenched in 1986, though there were thinned x trenched interactions in 1987. In the trenched treatment Carex also had greater concentrations of Ca, Fe, Cu, and Al in 1986 and P and S in 1987 though there were thinned x trenched interactions. There were also thinned x trenched interactions of S, Cu, and Al in 1987.

Thinning did not influence nutrient total accumulation (kg/ha^{-1}) of Carex in either years (Table 6, Appendix Table 28). Total accumulation of Ca in Carex, however, increased in trenched plots. There were thinned x trenched interactions of Mn total accumulation in 1986 and P, S, Ca total accumulations in 1987.

There was considerable variation in Symphoricarpos nutrient response to treatments (Table 7, Appendix Table 29). In 1986, concentrations of P were reduced in the thinned treatment, while higher in the trenched treatment. The thinned treatment had higher concentrations of Mn in 1986, but lower Mg in 1987. Trenching increased Cu concentration in 1986. A thinned x trenched interaction occurred in 1987 for N concentrations.

Neither thinned nor trenched treatments changed nutrient total accumulations (kg/ha^{-1}) in Symphoricarpos in either year (Table 8, Appendix Table 30).

Table 6. Nutrient total accumulations (kg/ha^{-1}) of *Carex geyeri* foliage by treatments (means and standard errors) for 1986 and 1987. N, P, K, S, Ca, and Mg are reported in % dry wt.; other micronutrients are reported in ppm dry wt. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level; T = Trace (<0.005 kg/ha^{-1}).

Treatments	Nutrients											
	N	P	K	S	Ca	Mg	Mn	Fe	Cu	B	Zn	Al
	%						ppm					
	1986											
Non-Thinned	11.29	1.98	20.73	1.10	4.01	1.54	0.31	0.13	T	T	0.03	0.10
Thinned	7.78	1.23	10.35	0.70	2.96	1.12	0.17	0.09	T	T	0.01	0.08
Non-Trenched	7.35	1.28	13.48	0.72	2.78	1.19	0.21	0.11	T	T	0.02	0.10
Trenched	11.73	1.94	17.61	1.08	4.19	1.47	0.26	0.11	T	T	0.02	0.08
SE A	2.80	0.45	4.42	0.25	0.57	0.25	0.05	0.02	-	-	0.01	0.01
P	0.4690	0.3574	0.2386	0.3832	0.3222	0.3616	0.1866	0.3049	-	-	0.3624	0.3971
SE B	1.42	0.26	2.07	0.16	0.29	0.18	0.01	0.02	-	-	0.00	0.03
P	0.0947	0.1519	0.2313	0.1949	0.0275	0.3101	0.0679	0.9628	-	-	0.5185	0.7438
SE AB	2.01	0.37	2.93	0.23	0.42	0.25	0.02	0.03	-	-	0.00	0.04
P	0.2341	0.3271	0.3507	0.3645	0.1432	0.6673	0.0068	0.4463	-	-	0.1012	0.5906
	1987											
Non-Thinned	8.52	1.44	13.62	0.78	2.34	0.94	0.15	0.06	T	T	0.03	0.03
Thinned	6.87	1.25	10.43	0.60	2.32	0.91	0.12	0.04	T	T	0.01	0.02
Non-Trenched	6.03	1.12	9.39	0.55	1.99	0.83	0.13	0.04	T	T	0.02	0.02
Trenched	9.36	1.57	14.66	0.84	2.66	1.03	0.15	0.05	T	T	0.03	0.02
SE A	1.49	0.23	1.65	0.13	0.27	0.12	0.03	0.01	-	-	0.00	0.01
P	0.5145	0.6102	0.3060	0.4158	0.9569	0.8909	0.4929	0.4274	-	-	0.1567	0.5101
SE B	0.91	0.18	1.71	0.06	0.29	0.12	0.02	0.01	-	-	0.00	0.00
P	0.0611	0.1461	0.0957	0.0263	0.1796	0.3024	0.5935	0.4734	-	-	0.0705	1.0000
SE AB	1.29	0.25	2.42	0.08	0.41	0.17	0.03	0.01	-	-	0.00	0.00
P	0.0651	0.0546	0.1197	0.0199	0.0529	0.1021	0.1374	0.4734	-	-	0.0705	0.4216

Table 7. Nutrient concentrations of <u>Symphoricarpos albus</u> foliage by treatments (means and standard errors) for 1986 and 1987. N, P, K, S, Ca, and Mg are reported in % dry wt.; other micronutrients are reported in ppm dry wt. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

Treatments	Nutrients											
	N	P	K	S	Ca	Mg	Mn	Fe	Cu	B	Zn	Al
	%						ppm					
	1986											
Non-Thinned	1.16	0.75	2.92	0.32	1.69	0.50	556.67	203.67	7.67	58.00	50.83	130.50
Thinned	1.16	0.59	2.61	0.34	1.54	0.48	285.17	178.17	7.00	47.83	46.50	97.83
Non-Trenched	1.05	0.58	2.68	0.28	1.55	0.49	380.17	179.00	6.00	50.00	39.33	101.50
Trenched	1.27	0.75	2.85	0.38	1.68	0.50	461.67	202.83	8.67	55.83	58.00	126.83
SE A	0.00	0.11	0.21	0.01	0.11	0.01	191.98	18.03	0.47	7.19	3.06	23.10
P	0.9777	0.0193	0.4706	0.7552	0.5941	0.7270	0.0346	0.6515	0.7315	0.1631	0.6735	0.4167
SE B	0.16	0.12	0.12	0.07	0.09	0.01	57.63	16.85	1.89	4.12	13.20	17.91
P	0.0699	0.0278	0.5577	0.3610	0.4367	0.8388	0.4464	0.4339	0.0020	0.2332	0.0878	0.3688
SE AB	0.05	0.09	0.10	0.05	0.22	0.05	5.50	54.83	0.00	4.83	5.67	63.67
P	0.6242	0.1257	0.7123	0.6050	0.2179	0.4496	0.9573	0.1162	1.0000	0.3096	0.5324	0.0638
	1986											
Non-Thinned	1.64	0.43	2.64	0.19	0.99	0.35	244.33	128.83	7.50	35.33	40.17	47.00
Thinned	1.30	0.34	1.95	0.13	0.88	0.32	222.33	90.33	5.17	27.83	27.33	30.00
Non-Trenched	1.19	0.38	2.16	0.14	0.87	0.30	207.83	92.67	5.33	31.00	27.17	31.00
Trenched	1.76	0.40	2.43	0.18	1.01	0.36	258.83	126.50	7.33	32.17	40.33	46.00
SE A	0.01	0.01	0.16	0.02	0.06	0.03	10.44	10.28	0.95	0.11	3.69	5.38
P	0.9763	0.4262	0.5054	0.3737	0.1466	0.0124	0.8323	0.5278	0.1982	0.9764	0.2201	0.5391
SE BP	0.14	0.03	0.10	0.01	0.04	0.01	7.91	7.33	0.74	4.11	3.90	4.11
P	0.0807	0.2658	0.5440	0.6185	0.6073	0.6902	0.7221	0.2872	0.1328	0.3170	0.5210	0.4942
SE AB	0.25	0.04	0.01	0.03	0.20	0.06	19.23	9.02	1.04	2.24	7.30	6.71
P	0.0485	0.3456	0.9614	0.1645	0.1345	0.1887	0.5498	0.3429	0.1328	0.6763	0.4080	0.4365

Table 8. Nutrient total accumulations (kg/ha^{-1}) of *Symphoricarpos albus* foliage by treatments (means and standard errors) for 1986 and 1987. N, P, K, S, Ca, and Mg are reported in % dry wt; other micronutrients are reported in ppm dry wt. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level; T = Trace (<0.005 kg/ha^{-1}).

Treatments	Nutrients											
	N	P	K	S	Ca	Mg	Mn	Fe	Cu	B	Zn	Al
	%						ppm					
	1986											
Non-Thinned	4.39	2.20	10.20	1.07	4.59	1.43	0.09	0.04	T	T	0.01	0.02
Thinned	3.61	1.55	7.35	0.83	4.63	1.40	0.04	0.02	T	T	0.01	0.01
Non-Trenched	3.40	1.47	7.57	0.69	3.97	1.23	0.06	0.02	T	T	0.01	0.01
Trenched	4.60	2.28	9.98	1.21	5.25	1.59	0.06	0.04	T	T	0.01	0.02
SE A	0.62	0.36	2.00	0.17	0.39	0.07	0.03	0.01	-	-	0.00	0.01
P	0.4632	0.3286	0.4190	0.4153	0.9577	0.8093	0.4233	0.3727	-	-	0.4226	0.4987
SE B	0.87	0.45	1.18	0.31	0.71	0.20	0.00	0.01	-	-	0.00	0.01
P	0.3812	0.2527	0.2210	0.3035	0.2685	0.2641	0.7676	0.3696	-	-	0.2302	0.2720
SE AB	1.23	0.64	1.66	0.44	1.00	0.28	0.01	0.02	-	-	0.00	0.01
P	0.4555	0.5362	0.9624	0.4561	0.6248	0.7320	0.0913	0.5727	-	-	1.0000	0.5185
	1987											
Non-Thinned	3.41	0.83	5.45	0.40	1.71	0.64	0.03	0.01	T	T	T	0.01
Thinned	3.33	0.85	4.75	0.33	2.13	0.78	0.03	0.01	T	T	T	0.01
Non-Trenched	2.48	0.76	4.13	0.29	1.68	0.59	0.02	0.01	T	T	T	0.00
Trenched	4.26	0.92	6.07	0.44	2.16	0.83	0.03	0.01	T	T	T	0.01
SE A	0.87	0.13	1.35	0.10	0.18	0.08	0.01	0.00	-	-	-	0.00
P	0.7122	0.5199	0.9710	0.9448	0.1066	0.1644	0.8127	0.7500	-	-	-	0.7257
SE B	0.69	0.10	0.91	0.07	0.20	0.09	0.01	0.00	-	-	-	0.00
P	0.3830	0.9181	0.4838	0.4394	0.7802	0.5341	0.6684	0.2234	-	-	-	0.4950
SE AB	0.98	0.14	1.29	0.09	0.29	0.12	0.01	0.01	-	-	-	0.00
P	0.4865	0.3284	0.6410	0.4178	0.2343	0.3659	0.3744	0.5367	-	-	-	0.4950

DISCUSSION

The herb-shrub understory biomass significantly responded to the reduction of tree root competition, supporting the hypothesis that competition for belowground resources is a primary limiting factor in P. ponderosa forests. Increased light levels (PAR), however, appeared to have little effect on understory vegetation biomass suggesting light is not a limiting factor in these forests.

With tree roots removed, understory biomass increased 53 to 94% in the trenched treatment during the two years as compared to the non-trenched treatment. We believe the primary reason for an increase in understory biomass production in the trenched treatment was due to more favorable soil-plant water relations. This allowed for a longer period of plant growth and contributed to greater mineralization of organic matter in trenched plots. A secondary response, which is more difficult to partition, maybe the affect of greater nutrient availability in the trenched treatment.

Opening up the overstory alone, which increased light levels by 126%, did not significantly increase understory biomass. The combination of increasing light and soil resources did not show a synergistic effect (Figure 14). Understory biomass production was nearly equal in either the thinned/trenched plots, where light and soil resources were increased, or non-thinned/trenched plots where only soil resources were increased. Large increases in understory biomass production in these plots would indicate light is not the primary limiting factor. The control versus thinned/non-

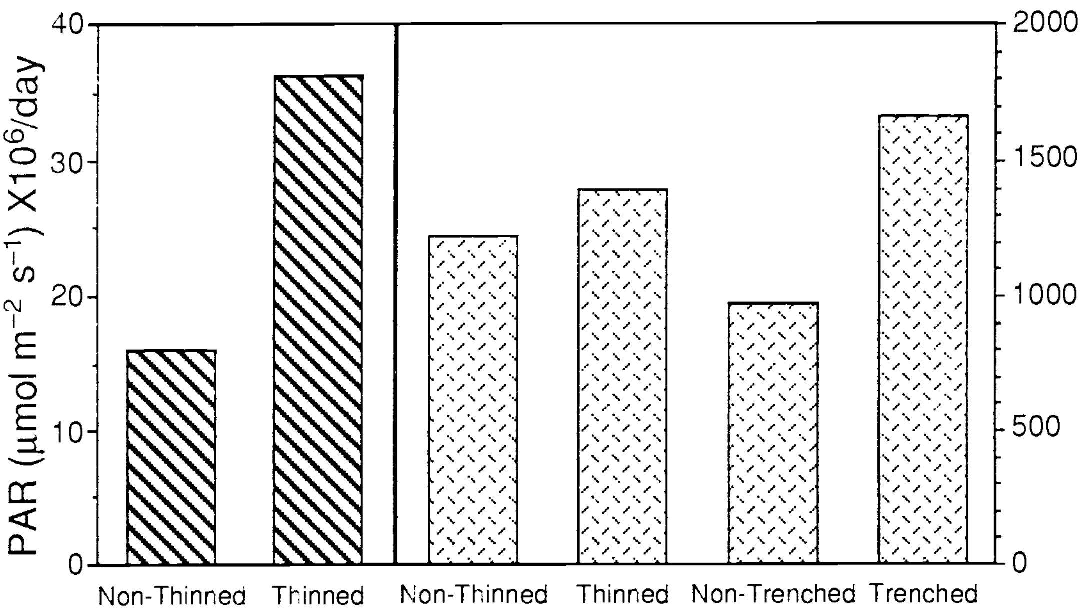


Figure 14. Treatment effects on light (photosynthetic active radiation (PAR)) and understory biomass response averaged for 1986 and 1987.

trenched plots are not directly comparable as thinning removes a portion of the overstory thus increasing light to the understory, and decreases root competition for soil water and nutrients. Other research has reported an increase in understory biomass after thinning (McConnell and Smith 1965 1970, Moir 1966, Young et al. 1967).

Water played a major role in effecting understory biomass response. When overstory root competition was removed Carex predawn xylem potentials were less negative indicating increased available soil water. Predawn water potentials are considered an accurate measure of soil water availability in the immediate vicinity of the roots (Ritchie and Hinkley 1975). A consistent pattern of predawn xylem potentials, occurred from mid to the later part of the growing season when soil moisture became limiting. Carex in the non-thinned/trenched plots were always less negative than the thinned/trenched, thinned/non-trenched, and control, respectively. Biomass response of the different plots can also be ranked in a similar order in 1986, but in 1987 there was higher production in the thinned/trenched versus the non-thinned/trenched.

Removal of tree root competition by trenching and thinning affected soil water potentials. Non-thinned/trenched plots remained the least negative in all three depths in both years. As the growing season progressed and soil became drier, there were larger differences with greater variation between the thinned and non-thinned treatments. The largest differences occurred at a soil depth of, 40-60 cm, where tree roots would have absorbed water in trenched plots later in the season after most of the understory species were senescent. Greater water utilization and transpiration from the overstory in non-trenched plots is probably the reason for these differences. In all three depths, (0-20, 20-40, 40-60 cm), the control had the most negative soil water potentials by the end of the growing season. In thinned treatments, soil water potentials were generally less negative in the 20-40 and 40-60 cm depths than the non-thinned during the early to mid part of the growing season. This was probably due to less interception of precipitation by the tree canopy in the thinned treatment (Williams 1989) and the reduction of transpiration from the overstory as fewer trees occupied the site. Reducing tree root competition did not greatly effect soil water content at the 0-20 cm depth, although soil water content increased below 20 cm. Based on the response of xylem potentials and biomass in understory species, however, available water in the 0-20 cm depth was probably increased. Roots of *Carex geyeri* and *Berberis repens* have been reported to grow to a depth of 2 m, however, the majority of roots at lower depths are those of overstory trees (Nimlos et al. 1968). Tree and understory rooting patterns, understory plant response, and soil water depletion patterns in our study suggest competition for below ground resources is greatest in the 0-20 cm soil depth. Other research has demonstrated that the majority of tree roots are in the upper 50 cm of soil, however, the absorbing roots are within top 20 cm (Berndt and Gibbons 1958, Hermann and Petersen 1969, Hermann 1977). Seasonal water use patterns of a deep rooted plant, *Artemisia tridentata*, had a similar effect on shallower rooted herbaceous plants (Sturges 1977). Soil water content in a *Artemisia*-bunchgrass stand did not increase in the upper soil profile when *Artemisia* was removed, however, grass biomass did increase. Soil water content did, however, increase in the lower soil profile when sagebrush was removed indicating less effective water use by the herbaceous component at the lower depth. Though thinned/trenched plots did not have root competition from trees, greater evaporation due to less overstory shade may have caused soil water potentials to be more negative than the non-thinned/trenched plots.

Growth of understory plants in trenched plots was prolonged through August with Arnica, Aster occidentalis, Hieracium albertinum, and Lupinus leucophyllus var. tenuispicus flowering well into September. Without overstory root competition for water in trenched plots, the understory did not become water limited until late August adding two months to the growing season in these plots.

Midday xylem potentials are more difficult to interpret but generally support predawn xylem and soil water potentials. Midday xylem potentials were generally less negative in the non-thinned treatments presumably because of the affect of shade from the overstory. The more shaded non-thinned treatments had lower midday temperatures and higher relative humidities than the thinned, from the mid to later part of the growing season. Understory plants growing in sunflecks of the non-thinned or in the more sunlit areas within the thinned treatments are also exposed to greater windspeeds and fluctuation in soil temperature throughout the day (Young and Smith 1980). Greater evaporative demands and higher light at midday in the thinned treatment may have affected transpiration, stomatal conductance, and xylem potential. However, as soil water potentials were less negative in the trenched versus non-trenched treatment, conductance of Carex at midday was a third to twice that of the control (file data; Eastern Oregon Agricultural Research Center, Burns). Vogel (1985) reported *Carex geyeri* conductance declined and xylem potential became more negative in stands of *Pseudotsuga menziesii*-*Pinus ponderosa* as soil water potentials became more negative.

Soil nitrogen was also effected by the reduction of overstory competition. Non-thinned/trenched plots had higher levels of nitrate in both years and ammonium in 1987 compared with other treatments, though they were not statistically significant due to the inability to test significance between all plot combinations, we believe they are biologically significant. By 1987, higher levels of mineralizable nitrogen were measured in the 0-20 cm depth in the trenched treatment. Incorporating new organic residues with high C:N ratios, such as tree roots, probably immobilized mineral N in microbes during decomposition until the ratio was approximately 30:1 (Geist 1974). Other researchers have reported similar nutrient flushes following trenching. Rommel (1938) first noted the increased grass growth and darker color of vegetation, suggesting a fertilization effect from severing tree roots and their associated mycorrhizae. Two years after trenching plots in *P. ponderosa* forests in New Mexico, Vitousek et al. (1982) measured low net nitrogen mineralization in both the forest floor and mineral soil while nitrate was produced after a delay in the soil but not at all in the forest floor. They concluded the delay in nitrate response was caused by a low gross rate of nitrogen mineralization.

An increase in soil pH, from 5.90 in 1986 to 6.40 in 1987, in the upper 20-40 cm depth in the trenched treatment, may have favored nitrate as the dominant form of nitrogen over ammonium (Haynes 1986). Grass species may have been enhanced as they preferentially absorb nitrate (Elliot and White 1987). An increase in soil moisture, by reducing tree root competition, could also have made phosphorus more available, depending on it's elemental form, as it became more desorbed from clay lattices (Mengel and Kirby 1982). Concentration of phosphorus in soil solution increases with high soil moisture or flooding. Soil pH in wet or flooded acid soils increases because of the release of OH^- ions when $Fe(OH)_3$ and similar compounds are reduced to $Fe(OH)_2$ of $Fe_3(OH)_8$ (Sanchez 1976). In acid soils, increasing pH to between 6 and 7 causes greater mineralization of organic phosphorus (Sanchez 1976).

Root soil contact was also enhanced when soil moisture was increased by removal of tree root competition which allowed for greater nutrient absorption (Barber 1984). Nutrient turnover may have been accelerated as graminoids and other understory herbs cycle nutrients faster than overstory trees (Yarie 1980).

When tree roots were removed Carex and Symphoricarpos generally had higher nutrient concentrations of nitrogen and phosphorus, but lower nutrient total accumulations. These responses are due to a synergistic effect, i.e. uptake of nutrients from the soil was enhanced due to higher soil nutrient concentrations and soil moisture (Jarrell and Beverly 1981). Determining total nutrient accumulations is important for interpretating growth response from nutrient uptake and concentration. In trenched treatments nutrient concentrations were higher, and nutrient total accumulations and Carex biomass production also increased though not significantly. This may also have caused luxury consumption when nutrient concentrations and total accumulations increased but growth did not, presumably a response to higher soil nutrient concentrations. Slow growing species such as Carex and Symphoricarpos that absorb nutrients in excess of immediate growth requirements may use these reserves to support growth after soil reserves are exhausted (Chapin 1980). Luxury consumption occurs when there is only a limited change in root absorption capacity in compensation for changing plant nutrient status (Chapin 1980). Soil water potential in trenched treatments increased presumably making root absorption of water and nutrients easier (Marschner 1986).

Nitrogen and phosphorus do not appear to strongly limit growth of Carex and Symphoricarpos. Both are native species and do well in a variety of soil types (Franklin and Dyrness 1973). They do not appear to be strong competitors for these nutrients, i.e they did not respond as quickly to the additional nutrients and gain biomass as other species. Native species from relatively infertile soils apparently reach their near maximum metabolic rates at low nutrient tissue concentrations and have no large reductions in respiration, photosynthesis or root absorption activity and are able to maintain these concentrations under normal field conditions (Chapin 1980). Nutrient concentrations in Symphoricarpos were generally higher than in Carex, but we are not certain if this is a function of longer lived plant having greater time to accumulate nutrients.

When overstory root competition was removed biomass production of perennial graminoids and forbs increased in both years. These plants may have been nutrient or water deficient or simply more responsive to nutrient additions. Carex geyeri and Symphoricarpos begin vegetative growth later than dominant perennial graminoids, Trisetum canadense, and Carex rossii, and forbs, Arnica cordifolia and Lathyrus nevadensis (Riegel and Miller 1989). Calamagrostis, which initiates growth early in the spring (Stubbendieck et al. 1986), and often increases in response to overstory thinning (McConnell and Smith 1965 1970), increased biomass production in trenched plots only in 1987. Plants that begin growth early have the potential to be more successful in competing for limited nutrients. Since we did not measure nutrient concentrations in other plants we can only speculate that species which significantly increased biomass, were responding to additional nutrients that were mineralized or no longer utilized by the overstory, and/or the result of the interaction of increased soil moisture.

Thinning decreased concentrations of several nutrients in Carex in 1986 and 1987. Phosphorus concentration and total accumulation in Symphoricarpos decreased in 1986, though the latter was not significant. A concurrent decrease in both concentration and total accumulation with either no change or an increase in biomass production is due to a dilution effect (Jarrell and Beverly 1981). We speculate that soil microbes and/or other plants that we did not measure such as perennial graminoids or forbs which did increase in biomass, may have been more effective in competing for these nutrients.

We conclude that belowground resources are the limiting factors of understory plant biomass in a P. ponderosa forest. Light does not appear to be the limiting factor of understory plant biomass. Primary belowground limiting factors appear to be water and nitrogen. Response of understory species to increased levels of water and nutrients appears to be synergistic. However, additional research needs to be conducted to better separate out the belowground controlling factors.

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CHAPTER III.

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* forest in northeastern Oregon. The experiment was a completely randomized block design with three 5.0 ha blocks. Four treatments: 1) control, 2) water, 3) nitrogen, and 4) water + nitrogen, were randomly assigned to each plot by block, with 10 plots per treatment within each of the three blocks for a total of 120 (1 x 1 m) plots. Nitrogen (NH_4-NO_3, 32% N) was applied by hand at 50 kg/ha^{-1} on each nitrogen plot on April 15, 1987. Water treatments were irrigated biweekly from May 6 through June 18. Light (PAR) was measured at center of each plot with light sensitive ozalid paper on September 6. At peak standing crop (June 26 through July 7) the water + nitrogen treatment produced 16 and 18% greater aboveground dry weight biomass than the nitrogen and water treatments and 36% more than the control treatments. Biomass from nitrogen and water treatment

were nearly equal in production and were 17 and 15% more productive than the control treatment. Light does not appear to be limiting understory production in these forests as there was no relationship to light quantity and biomass production. Understory vegetation, composed primarily of native herbaceous species, is primarily limited by both water and nitrogen in P. ponderosa forests of northeastern Oregon.

INTRODUCTION

Competition for limited resources, 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 and Miller 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 by definition.

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 southern 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^{o}C in December to 1.1^{o}C in July; from a maximum of 8.5^{o}C in December to 36.9^{o}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 1989).

The experiment was conducted in the _Pinus ponderosa_/_Symphoricarpos albus_ community type similar to Johnson and Simon's (1987) _Pseudotsuga menziesii_/_Symphoricarpos albus_ plant association of the Wallowa-Snake Province of northeastern Oregon. _Pinus_ dominates the overstory and codominates reproduction with _Pseudotsuga menziesii_. _Symphoricarpos_, _Carex geyeri_, _Calamagrostis rubescens_, and _Arnica cordifolia_ 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: Hall Ranch, fine-loamy, mixed, frigid, Ultic Haploxerolls (block 1 non-thin and thin; block 2 thin), Klicker, loamy skeletal, mixed frigid Ultic Agrixerolls

(blocks 2 and 3 non-thin), 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 to greater than 92 cm. All series especially the Tolo, originated from pumicite parent material ejected from Mt. Mazama 6,500 years ago.

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 (NH4-NO3, 32% N) was applied by hand at 50 kg/ha^{-1} on each nitrogen plot in April, 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 from our earlier study (Riegel and Miller 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% nitrogen in plant tissue (Marschner 1986) = 25.68 kg/ha^{-1}, then doubled that value to insure a response (Dr. Timothy L. Righetti, personal communication).

Water treatments were irrigated biweekly from May 6 through June 18 to simulate the increase in soil water in trenched plots (Riegel and Miller 1989). 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. We estimated bulk density (Dr. J. Michael Geist, personal communication) to be between 1.0 to 1.5

gm/cm^3 x 500,000 cm^3 = 650,000 gm soil, which is approximately 65 l of water. As we were only interested in increasing soil water content in the upper 1/3 of the profile where the greatest root competition occurs (Snider and Miller 1985, Svejcar 1986), we calculated that the addition of 20 l as reasonable to start. 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 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.

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^oC 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 plastic 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

Irrigating plots increased soil moisture by 47% in the upper third of the profile (0-20 cm depth) on both dates of measurement (Table 9). In the mid (20-40 cm) and lower third (40-60 cm) soil depths, adding water also increased soil moisture, but generally less than the upper third of the profile.

Water + nitrogen treatment produced greater dry weight than the nitrogen, water, and control treatments (Figure 15; Appendix Table 31). Water + nitrogen produced 16 and 18% greater biomass than nitrogen and water treatments and 36% more than the control. Biomass from nitrogen and water treatments were nearly equal in production and were 17 and 15% more productive respectively, than the control treatment (Figure 15).

Both nitrogen and water + nitrogen treatments had 35% more tissue nitrogen concentration than the control (Table 10). Tissue nitrogen concentration did not respond to increased soil water as compared to the control. There was no difference in nitrogen total accumulation of biomass between treatments (Table 10).

Correlation between biomass and light (PAR), measured on each plot, were not significant (r^2 = 0.01) (Appendix Table 32). Differences in light levels between treatments were not significant (Table 11).

Table 9. Gravimetric 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)	25 (5)	22 (3)	21 (3)
Non-Watered (nitrogen and control)	17 (2)	20 (6)	20 (4)
Differences between treatments	8	2	1
June 4, 1987 (n=5)			
Watered (water and water + nitrogen)	32 (8)	33 (18)	22 (3)
Non-Watered (nitrogen and control)	24 (3)	21 (8)	22 (1)
Differences between treatments	8	12	0

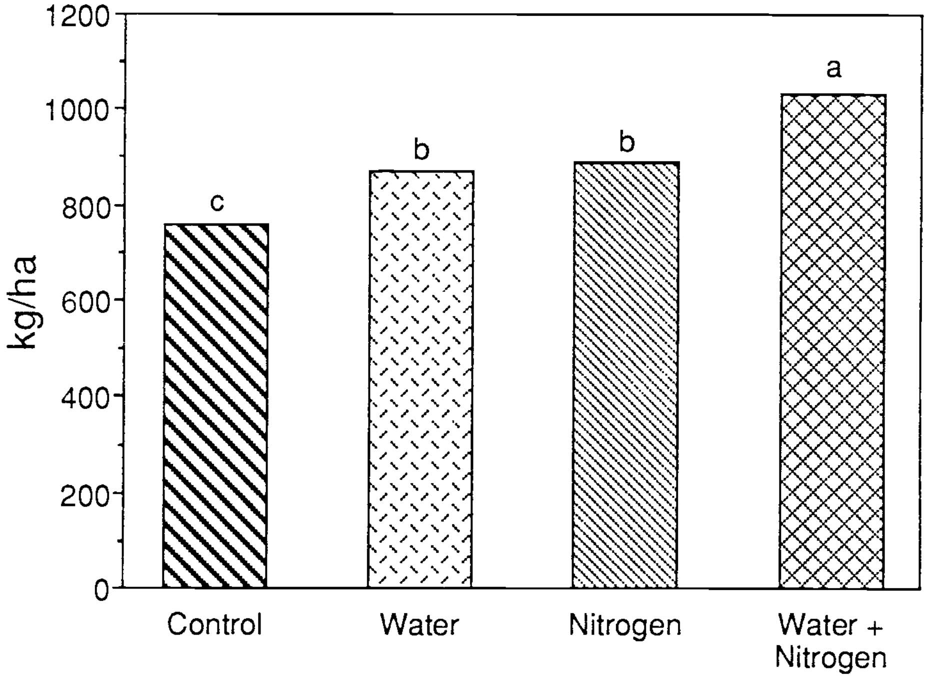

Figure 15. Understory biomass response to treatments. Means with the same letter are not significantly different.

Table 10. 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
SE0.04				
Nitrogen Content of Biomass	1391.52 a	940.29 a	1053.81 a	862.33 a
SD	514.27	330.10	174.21	274.79
SE	149.98			

Table 11. Light, photosynthetic active radiation-PAR (μ mol m^{-2} s^{-1} day x 10^6) (means, standard deviations, and standard errors), measured at ground level. There was no significant ($P<0.05$) differences between treatment means.

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			

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

The addition of water and nitrogen in separate treatments produced a similar increase in understory biomass production over the control. Addition of soil water increased soil water content to similar levels measured in trenched plots (Riegel and Miller 1989) in the 0-20 cm depth.

Carex nitrogen concentrations significantly increased in both nitrogen and water + nitrogen treatments. Nitrogen total accumulation of biomass among treatments, were not statistically different, although they were higher than the control. Carex uptake of nitrogen in the trench treatment (Riegel and Miller 1989) produced a similar response. Nitrogen concentrations of Carex in the non-thinned/trenched plots were 1.31% in 1987, only 2% 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 and Miller 1989). However, 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 did not respond to a nitrogen application greater than 80 kg/ha^{-1}, whereas on irrigated plots response to nitrogen was linear up to 120 N kg/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 addition of nitrogen 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/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 S and P may also limit understory biomass production in this region (Freyman and van Ryswk 1969, Geist 1971 1974 1976a 1976b 1977 1978, Klock et al. 1975). _Calamagrostis_ 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 Ryswk 1969). This response was increased when S (gypsum) was applied with nitrogen. A _Dactylis_ _glomerata_ 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 higher in the non-thinned/trenched plots where tree root competition had been reduced (Riegel and Miller 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. Plots were distributed in a random stratified procedure which accounted for a 13% 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 was not responding to higher light intensities caused by opening the stand from commercial thinning (Riegel and Miller 1989).

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 mineralizable nitrogen and nitrate from the addition of severed tree roots following trenching, many other belowground processes were altered (Riegel and Miller 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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CHAPTER IV.

RESPONSE OF UNDERSTORY SPECIES COMPOSITION TO RESOURCE COMPETITION IN A PINUS PONDEROSA FOREST

ABSTRACT

The objective of this research was to determine which environmental resources, light, water, and/or nutrients, control understory plant composition in a Pinus ponderosa forest in northeastern Oregon. A split-plot experimental design, with three blocks 5.0 ha, four treatments, and 44 plots, was established in the summer of 1985. Twenty plots (4 x 4 m) were trenched approximately one meter in depth, and 24 non-trenched plots were used to assess the effects of root competition of overstory trees on understory plants. Trees were commercially thinned in the winter and spring 1986 from a density of 345 to 148 trees/ha^{-1} to increase light levels to the understory. Increasing light (PAR) significantly increased species composition, cover, and density. Density of graminoids and forbs significantly increased, while shrub cover significantly decreased. Controlling root competition for soil water and nutrients did significantly increase species composition, cover and density in the trenched treatment. Cover and density of graminoids, forbs and shrubs increased when soil moisture and nutrient competition with the overstory was controlled. Canonical discriminant analysis indicated that light accounted for the greatest environmental resource response among the treatments. Use of simple correlation found that changes in species composition

were significantly related to changes in canopy attributes (light, midday, air temperature, and soil temperature) or root competition effected attributes (soil water potential, pH, and nitrogen). The greatest change in percent similarity of species by treatment was within the first year after treatment establishment. Lack of a second year response probably was a function of greater resource competition than the first year after treatment establishment. Early and mid seral rhizomatous species contributed the most to understory response. Competition for limited resources, light, water, and nutrients does effect cover, density and species composition of the understory as evidenced by the response to increasing these resources.

INTRODUCTION

Cover and density 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. Previous studies have demonstrated that understory production in _Pinus ponderosa_ forests in northeastern Oregon are water and nitrogen limited (Riegel and Miller 1989a 1989b). It is unclear, however, if water and nitrogen are the dominant resources that control understory species composition, density, and cover. Increasing resources which control or limit understory species may alter cover and density. This shift may encourage site dominance by species which were previously resource limited. Tilman (1985) proposed the resource-ratio hypothesis which states that plant species are specialized on different proportions, 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 successional trends after a disturbance such as fire, logging, and grazing (Tilman 1982 1985 1988).

Carex geyeri and _Calamagrostis rubescens_, both rhizomatous graminoids, are the dominant understory species in many of the interior forests of the Pacific Northwest (Franklin and Dyrness 1973). The ability of these species to respond to logging is important to maintaining a forage base for livestock and wild ungulates. After logging, reforestation efforts are often hampered by the aggressive competitive ability of

C. geyeri and Calamagrostis, as removal of the overstory increases light, water, and nutrients to the understory and the residual overstory (Sloan and Ryker 1986). In western Montana, foliage density of C. geyeri, Calamagrostis, and associated forbs and shrubs linearly decreased soil water content in late summer in a Pinus site (Petersen and Maxwell 1987). Competition with the rhizomatous understory species that dominate the understory of Pinus forests in northeastern Oregon presents a major problem to forest managers (Johnson and Simon 1987). Our interest in conducting this research was to quantify how cover and density of understory species respond to increased levels of light, water, and nutrients.

The objective of this research was to: 1) test the hypothesis that below ground resources, control cover and density of understory species in a P. ponderosa forest in northeastern Oregon, and 2) evaluate the relationship of life-form and species response to increasing light, soil water, nitrcgen, and related environmental variables.

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 southern 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^{o}C in December to 1.1^{o}C in July; from a maximum of 8.5^{o}C in December to 36.9^{o}C in July (file data; Eastern Oregon Agricultural Research Center, Union). The majority of precipitation on the Hall ranch occurs between November and May in the form of snow. Mean annual precipitation for 1963-1987 was 605 mm (Williams 1989).

The research was conducted in the *Pinus ponderosa*/*Symphoricarpos albus* community type similar to Johnson and Simon's (1987) *Pseudotsuga menziesii*/*Symphoricarpos albus* plant association of the Wallowa-Snake Province of northeastern Oregon. *Pinus* dominates the overstory and codominates the reproduction with *Pseudotsuga menziesii*. *Symphoricarpos*, *C. geyeri*, *Calamagrostis*, and *Arnica cordifolia* 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: Hall Ranch, fine-loamy, mixed, frigid, Ultic Haploxerolls (block 1 non-thin and thin; block 2 thin), Klicker, loamy skeletal, mixed frigid Ultic Agrixerolls

(blocks 2 and 3 non-thin), 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 to greater than 92 cm. All series especially the Tolo, originated from pumicite parent material ejected from Mt. Mazama 6,500 years ago.

METHODS

Three 5.0 ha stands or blocks, located within 1.0 km from each other, were selected for this study. Half of each block (2.5 ha) was commercially thinned in the winter of 1986 and the remaining half left undisturbed representing the control. Stands were considered to be relatively homogeneous in overstory species composition and stand structure, however, understory vegetation among blocks was heterogeneous in species composition. Stands were thinned from a density of 345 to 148 trees/ha^{-1} during the winter and spring of 1986. Tree diameters at breast height (dbh) ranged from 0.3 to 135.6 cm with a mean of 31.8 cm.

A total of 48, 4.0 x 4.0 m, macro plots were subjectively established to insure adequate representation of the variation in canopy cover. Four trench and four non-trench plots, were randomly assigned in both thin and non-thin treatments within each of the three blocks prior to logging. Twenty four plots had their perimeters (6.0 x 6.0 m) trenched to a depth of 1 m unless the presence of large rocks and boulders prohibited trenching to that depth. Perimeters of plots were trenched to sever roots entering the plots (Figure 2). Trenching was performed in September of 1985 with the use of a four wheel drive Ditch Witch, model R60. Backfill was replaced to enable sub-surface water movement. Four plots were destroyed during logging operations in block three; (three thinned/trenched and one thinned/non-trenched).

Understory Vegetation Measurements

Density was measured by counting all individuals by species along four, 4.0 x 0.10 m transects within each macro plot (Pieper 1978) (Figure 3). Cover was ocularly estimated by cover class for all species within a 0.20 x 0.50 m plot frame, at four points (spaced 1.0 m apart along each, 4.0 m transect (16/macro plot) (Figure 3). Cover classes are in Appendix Table 33. Cover and density were measured in 1985 prior to thinning and in 1986 and 1987 after thinning. Measurements were made during the growing season (July and August) in all three years. Vascular plant nomenclature and taxonomy follows Hitchcock and Cronquist (1973). A species list of understory species found in the study area during 1985 through 1987 is presented in Appendix Table 34.

Environmental Response

Response of environmental resources to treatment effects from this study are reported and discussed in Chapter II.

Experimental Design and Data Analysis

The experiment was conducted as a split plot design with a 2 x 2 factorial analysis. Hereafter, treatments are referred to as thinned, non-thinned, trenched, and non-trenched; and plots (treatment combinations) as non-thinned/non-trenched (control), non-thinned/trenched, thinned/non-trenched and thinned/trenched. To meet the assumptions of analysis of variance a log 10 transformation of the data was performed. Analysis of variance was used to test differences in thinning and trenching treatments. Variables tested were cover and density by life-form, species within each year. To determine differences between years, cover and density data by life-form and species were subtracted by plot of one year 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 $P<0.05$ was used throughout the analysis to test significance of F values. Probability levels were calculated in the SAS Institute Inc. (1987) program. Only significant differences are reported.

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 (Overton et al. 1987). Percentage similarity (PS) is calculated as follows;

$PS_{jl} = \min (p_{ij}, p_{il})$, where sample units j and l, over all attributes i.

A canonical discriminant function analysis was performed on the resource variables that we increased in our thinning and trenching treatments; light (photosynthetic active radiation, PAR) measured beneath the understory canopy, soil water potential (measured at 0-20, 20-40, and 40-60 cm), mineralizable nitrogen, nitrate, and ammonium (measured at 0-20 and 20-40 cm) (Riegel and Miller 1989a). Canonical discriminant analysis was used to determine which resource(s) had the greatest impact on the 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 species cover and density (dependent variables) with a selected group of environmental variables (independent variables). Species were selected based on their ubiquity (most common) and those that were significantly effected by the treatments. The environmental variables chosen were those that were: 1) significantly different by treatment according to analysis of variance (Riegel and Miller 1990a), 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) to determine significance of each correlation (Little and Hills 1978). Only significant differences with a probability of $P<0.05$ are reported in the text.

RESULTS

Within Year Differences

Cover

There were no differences in cover of life-forms (graminoids, forbs, and shrubs) in 1985, prior to treatment establishment, between treatments. There were differences, however, by species. In the thinned treatment, Achillea millefolium ssp. lanulosa and Aster occidentalis had 65 and 99% greater cover, respectively, than the non-thinned treatment (Table 12). Poa pratensis had 59% more cover in the trenched versus the non-trenched treatment (Table 12). There were thinned x trenched interactions of Trisetum canescens and Rosa gymnocarpa.

In 1986, shrub cover was 45% lower in thinned versus non-thinned treatments. Graminoid and forb cover increased 75%, while shrub cover increased 54% in trenched versus non-trenched treatments (Table 13). Thinning decreased Lathyrus nevadensis ssp. cusickii and Calamagrostis 8 and 64%, respectively (Table 12). Trenching, however, increased Calamagrostis 297%. Taraxacum officinale was the only species that increased (82%) from thinning. Though Poa and Achillea had thinned x trenched interactions, they also had a highly significant increase in cover in trenched versus non-trenched treatments (Table 12).

Though thinning had no effect on life-form cover, in 1987, trenching increased graminoids by 124, forbs 57, and shrubs 33% (Table 13). Tragopogon dubius decreased in cover by 53% in thinned versus non-treatments (Table 12). Thinning increased Luzula campestris by 48%,

Table 12. Cover (%) of species that were significant (P<0.05) by treatments (means and standard deviations) for 1985, 1986, and 1987.

Species/Year	Non-Thinned		Thinned		Non-Trenched		Trenched	
1985	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Achillea millefoilum	0.72	1.06	1.19	1.08	0.92	1.04	0.95	1.15
Aster occidentalis	0.97	1.46	1.93	2.28	1.32	1.79	1.50	2.08
Poa pratensis	2.27	3.65	8.50	10.12	3.98	6.47	6.33	9.21
Rosa gymnocarpa	0.98	1.60	1.55	2.62	1.69	2.67	0.75	1.50
Trisetum canescens	3.91	4.05	4.76	3.44	4.15	3.67	4.46	3.95
1986								
Achillea millefolium	1.55	3.00	2.25	1.95	0.79	0.85	3.05	2.94
Calamagrostis rubescens	1.64	2.37	0.59	0.79	0.48	0.82	1.91	2.41
Lathyrus nevadensis	3.85	4.06	3.63	3.14	3.71	3.29	3.79	4.06
Poa pratensis	4.05	7.26	8.15	7.34	3.70	4.75	8.34	9.19
Taraxacum officinale	0.67	1.67	1.22	1.36	0.35	0.65	1.54	1.97
1987								
Achillea millefolium	0.77	1.06	2.49	1.18	1.22	1.38	1.92	1.36
Aster occidentalis	0.91	1.47	3.74	4.77	1.52	2.09	2.94	4.75
Carex geyeri	13.07	9.84	12.40	5.70	10.09	6.02	15.70	9.24
Calamagrostis rubescens	2.67	3.11	1.06	1.20	1.08	1.37	2.89	3.17
Galium boreale	0.36	0.75	1.82	1.48	0.95	1.24	1.10	1.47
Lathyrus nevadensis	1.69	2.87	2.30	2.61	2.09	2.51	1.83	3.02
Luzula campestris	0.92	1.12	1.36	1.60	0.90	1.10	1.36	1.60
Poa pratensis	4.35	6.77	13.75	15.52	4.83	6.93	12.78	15.56
Stellaria longipes	0.18	0.21	1.07	3.61	0.16	0.16	1.05	3.52
Taraxacum officinale	0.40	1.31	1.60	1.67	0.73	1.03	1.19	1.31
Trisetum canescens	5.75	8.14	4.30	5.16	1.85	1.48	8.64	8.66
Tragopogon dubius	0.60	0.92	0.28	0.34	0.17	0.00	0.78	0.45

Table 13. Cover (%) and density (# of individuals/m^2 ha^{-1}) by life-forms that were significant ($P<0.05$) by treatments (means and standard errors) for 1986 and 1987. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched and Trenched, and SE AB = A x B interaction. P = Probability level.

	Non-Thinned	Thinned	Non-Trenched	Trenched	SE A	P	SE B	P	SE A x B	P
COVER										
1986										
Forbs	0.73	0.74	0.54	0.94	0.14	0.7287	0.11	0.1033	0.16	0.2232
Graminoids	2.47	1.99	1.66	2.90	0.55	0.493	0.45	0.0301	0.64	0.1177
Shrubs	2.56	1.40	1.62	2.49	0.10	0.0047	0.23	0.0131	0.33	0.0821
1987										
Forbs	0.62	0.82	0.56	0.88	0.09	0.094	0.08	0.0065	0.11	0.853
Graminoids	2.92	3.33	1.95	4.37	0.45	0.2335	0.39	0.0013	0.54	0.1565
Shrubs	2.33	1.43	1.66	2.21	0.33	0.0776	0.23	0.0495	0.32	0.5165
DENSITY										
1986										
Forbs	290.10	303.37	226.53	372.38	99.30	0.4469	64.63	0.0234	91.40	0.7698
Graminoids	1448.65	1234.12	1079.78	1648.33	452.32	0.7035	146.02	0.0088	206.51	0.076
1987										
Forbs	341.15	569.63	378.38	517.97	114.10	0.0778	84.26	0.0345	119.16	0.9079
Graminoids	1901.35	2624.13	1797.28	2703.70	469.97	0.1663	156.55	0.0016	221.39	0.0716
Shrubs	114.48	99.13	92.18	124.28	47.99	0.5975	11.71	0.0526	16.56	0.3592

Achillea 223%, Taraxacum, and Aster nearly 300%. Galium boreale increased 406%, the largest increase in thinned versus non-thinned treatments. Within the trenched treatment C. geyeri, Poa, and Calamagrostis increased 56 to 168% over the non-trenched (Table 12). Forbs that increased in the trenched versus the non-trenched treatments include Taraxacum 63%, Aster 93%, and Tragopogon 359%. Trisetum had a thinned x trenched interaction, however, there was a highly significant increase in cover (367%), the largest cover increase in the two years after the trenched treatment was established (Table 12). There were thinned x trenched interactions of Lathyrus and Stellaria longipes (Table 12).

Density

There were no differences in density by life-form between treatments in 1985. There were differences, however, in individual species by treatment; Fragaria virginiana var. platypetala and Viola adunca were 21 and 90% greater, respectively, greater in thinned stands prior to treatment establishment (Table 14). There were thinned x trenched interactions of Trisetum and Symphoricarpos.

In 1986, within the trenched treatment density of graminoids increased 53 and forbs 64% (Table 13). Thinning increased Aster and Achillea 11 and 69%, respectively (Table 14). In the trenched treatment Calamagrostis increased 535% over the non-trenched. Silene menziesii and Taraxacum also increased in the trenched treatment by 58 and 289%, respectively. Trisetum had a thinned x trenched interaction, however,

Table 14. Density (# of individuals/m^2 ha^{-1}) of species that were significant ($P<0.05$) by treatments (means and standard deviations) for 1985, 1986, and 1987.

Species/Year	Non-Thinned		Thinned		Non-Trenched		Trenched	
1985	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Fragaria virginiana	35.25	34.43	66.93	53.15	49.38	48.25	49.93	45.08
Symphoricarpos albus	51.25	51.88	52.90	59.85	44.68	45.13	60.00	64.25
Trisetum canescens	156.40	205.63	168.78	141.78	150.02	144.20	175.18	211.15
Viola adunca	3.50	4.53	4.25	8.23	4.07	9.25	3.60	5.05
1986								
Achillea millefolium	14.95	24.65	25.30	25.55	12.55	14.85	27.45	31.83
Aster occidentalis	41.58	104.83	46.33	63.25	24.45	41.58	64.82	116.85
Calamagrostis rubescens	71.95	126.68	15.88	24.25	13.08	24.55	83.03	131.83
Silene menziesii	13.70	35.75	16.70	51.10	11.38	45.88	18.00	40.28
Taraxacum officinale	3.53	7.93	8.08	14.78	2.35	15.58	9.15	7.80
Trisetum canescens	172.98	263.43	111.40	107.80	72.55	80.80	224.33	270.33
1987								
Achillea millefolium	14.08	26.78	48.50	32.70	22.48	24.83	37.68	41.03
Aster occidentalis	24.53	46.93	82.80	87.60	43.05	66.98	59.73	81.15
Calamagrostis rubescens	92.98	149.55	41.20	52.85	34.43	49.43	107.78	155.53
Stellaria longipes	3.13	7.60	13.13	28.23	3.88	8.48	11.83	27.65
Taraxacum officinale	3.08	5.00	10.43	10.65	5.03	7.80	7.93	9.70
Tragopogon dubius	5.05	10.18	1.20	1.95	0.75	1.60	6.05	10.63

it had a highly significant increase in cover, 209%, in trenched versus non-trenched treatments (Table 14).

Thinning did not increase life-form density in 1987 but trenching did increase graminoids by 50%, and forbs and shrubs by 35% in the trenched versus non-trenched treatments (Table 13). Thinning increased Achillea, Aster, and Taraxacum approximately 240% (Table 14). Calamagrostis increased 213% in trenched versus non-trenched treatments (Table 14). Trenching increased Taraxacum 58% and Tragopogon 707%, the largest increase in density the two years after treatment establishment. Stellaria had a thinned x trenched interaction.

Though tree seedling cover and density were measured in all three years there were no significant differences between treatments, either collectively tested as a life-form or as individual species.

[Cover and density means and standard deviations of life-forms by plots are presented in Appendix Table 35. Treatment means and standard errors of log 10 transformed cover and density data are in Appendix Tables 36 and 37, respectively. Plot means and standard deviations of log 10 cover and density by species are in Appendix Tables 38 and 39, respectively. Plot means and standard deviations of cover and density by species are in Appendix Tables 40 and 41, respectively.]

Between Year Differences

Cover

Thinning did not increase plant cover by life-form between all three years. Within the trenched treatment, however, forbs increased from 1985 to 1986 while graminoids increased from 1986 to 1987 (Table 15). Over

Table 15. Changes in life-forms cover (%) and density (# of individuals/m^2 ha^{-1}) (log 10) that were significant ($P<0.05$) between years, by treatments (means and standard errors). Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched and Trenched, and SE AB = A x B interaction. P = Probability level.

	Non-Thinned	Thinned	Non-Trenched	Trenched	SE A	P	SE B	P	SE A x B	P
COVER										
1985-986										
Forbs	0.23	0.07	-0.03	0.35	0.17	0.282	0.14	0.047	0.20	0.388
1986-1987										
Graminoids	0.46	1.34	0.29	1.47	0.34	0.0685	0.23	0.002	0.32	0.3732
1985-1987										
Forbs	0.12	0.14	-0.02	0.29	0.19	0.8945	0.07	0.009	0.10	0.8924
Graminoids	0.81	0.52	-0.47	1.94	0.87	0.8913	0.78	0.017	1.11	0.4622
DENSITY										
1985-1986										
Forbs	76.78	-1.00	-74.35	73.93	7.36	0.0012	54.37	0.028	76.90	0.3563
1986-1987										
Forbs	51.05	266.28	151.85	145.60	31.50	0.0115	72.77	0.6575	102.91	0.6955
Graminoids	452.70	1390.00	717.50	1055.35	21.71	0.0003	233.63	0.1062	330.40	0.8924
1985-1987										
Forbs	127.83	166.25	77.50	219.53	36.12	0.1481	78.90	0.0509	111.58	0.7581
Graminoids	469.48	1112.75	319.90	1245.95	162.58	0.037	111.48	0.0005	157.66	0.0033

the two year period, from 1985 to 1987, graminoids and forbs increased.

Thinning increased cover of Achillea and C. geyeri from 1986 to 1987 and Aster from 1985 to 1987 (Table 16). Arrhenatherum elatius was the only species that decreased in cover from 1985 to 1987 in the thinned versus non-thinned treatments.

Trenching increased the cover of Achillea and Taraxacum from 1985 to 1986 and Berberis repens and Tragopogon from 1986 to 1987 (Table 16). Though Taraxacum decreased in cover in the trenched treatment from 1986 to 1987, two years after treatment establishment (1985 to 1987) there was a net increase in cover. Carex geyeri and Aster both increased in cover within the trenched treatment between 1985 and 1987. Arrhenatherum and Berberis had thinned x trenched interactions in 1986 to 1987 but had highly significant increases in trenched versus non-trenched treatments.

Density

From 1985 to 1986, density of forbs decreased in thinned versus non-thinned treatments, but increased in trenched versus non-trenched treatments (Table 15). However, from 1986 to 1987 graminoids and forbs increased in thinned versus non-thinned treatments. Two years after treatment establishment (1985 to 1987), forbs had increased in the trenched versus non-trenched treatments. Though graminoids had a thinned x trenched interaction, they also had a highly significant increase in density in trenched versus non-trenched treatments.

The first year after thinning, 1985 to 1986, density of Potentilla gracilis and Rosa increased but C. geyeri and C. rossii decreased (Table 17). Carex geyeri did,

Table 16. Changes in species cover (%) that were significant (P<0.05) between years, by treatments (means and standard deviations).

Species/Years	Non-Thinned		Thinned		Non-Trenched		Trenched	
1985-1986	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Achillea millefolium	0.83	2.15	1.06	2.29	-0.14	1.11	2.11	2.49
Taraxacum officinale	0.53	1.72	1.10	1.30	0.22	0.70	1.42	1.96
1986-1987								
Achillea millefolium	-0.78	2.17	0.26	1.95	-0.14	1.21	-1.13	2.58
Arrehenatherum elatius	0.06	0.65	0.01	0.04	0.00	0.00	0.07	0.70
Berberis repens	-0.77	2.43	0.46	2.79	-0.36	2.55	-0.05	2.79
Carex geyeri	0.80	6.73	4.36	4.84	0.76	6.56	4.23	5.22
Taraxacum officinale	-0.25	1.27	0.40	1.41	0.40	0.79	-0.35	1.73
Tragopogon dubius	0.40	0.87	0.21	0.38	0.08	0.24	0.57	0.91
1985-1987								
Arrehenatherum elatius	-0.06	0.86	1.82	3.57	0.19	1.75	1.46	3.26
Aster occidentalis	0.08	0.57	0.01	0.04	-0.06	0.29	0.17	0.52
Carex geyeri	0.44	9.94	-1.61	8.00	-3.72	6.52	3.05	10.23
Taraxacum officinale	0.29	0.74	1.50	1.26	0.62	1.07	1.07	1.25

Table 17. Changes in species density (# of individuals/m^2 ha^{-1}) that were significant ($P<0.05$) between years, by treatments (means and standard deviations).

Species/Years	Non-Thinned		Thinned		Non-Trenched		Trenched	
1985-1986	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Achillea millefolium	5.63	16.30	5.75	22.60	-1.75	6.93	13.80	24.60
Carex geyeri	-159.08	658.05	-326.70	548.68	-346.15	681.93	-113.80	508.08
C. rossii	38.22	239.45	-27.13	153.33	-56.85	163.85	80.12	225.30
Lathyrus nevadensis	2.08	28.25	-15.00	47.63	1.30	45.00	-13.33	29.78
Potentillia gracilis	-0.63	1.53	-1.25	6.10	-1.63	4.93	-0.13	3.20
Rosa gymnocarpa	-1.15	2.75	-2.25	4.93	-1.63	3.75	-1.68	4.12
Senecio canus	-2.93	9.80	-2.00	9.63	-2.83	9.83	-2.15	9.60
Silene menziesii	4.38	34.00	-14.25	43.18	-14.78	39.63	7.63	35.88
Symphoricarpos albus	-0.20	51.48	-3.63	38.00	-10.33	42.73	7.63	47.35
Taraxacum officinale	0.73	10.93	6.88	13.40	-0.43	8.48	7.85	14.55
Trisetum canescens	16.58	326.63	-57.38	121.65	-77.50	111.70	49.18	342.35
1986-1987								
Achillea millefolium	-0.95	16.08	23.25	20.53	9.90	18.23	10.25	25.50
Aster occidentalis	-17.08	67.25	36.50	57.13	18.58	43.55	-5.13	86.45
Festuca rubra	16.15	36.28	54.00	68.45	23.93	54.90	43.70	56.73
Galium boreale	2.30	9.27	16.25	18.80	9.58	16.78	7.63	15.13
Lupinus leucophyllus	-2.40	4.20	0.25	3.80	-0.33	1.90	-2.15	5.65
Poa pratensis	61.58	107.63	451.25	440.60	170.53	257.25	313.45	443.43
Stellaria longipes	1.98	7.88	11.50	26.95	2.93	8.55	10.00	26.53
1985-1987								
Achillea millefolium	4.70	20.73	29.00	27.68	8.15	19.13	24.05	31.68
Carex geyeri	88.95	634.38	367.93	455.60	74.07	561.00	370.95	554.85
Luzula campestris	12.30	31.45	14.25	35.18	9.78	34.87	16.90	32.53
Melca bulbosa	-0.33	1.53	-5.38	18.63	-2.83	10.55	-2.37	14.95
Poa pratensis	124.90	232.65	548.62	514.38	204.55	365.83	441.20	483.33
Spirea betulifolia	-6.25	33.58	-0.88	2.85	-1.85	16.08	-5.95	32.05
Stellaria longipes	2.40	7.73	10.12	28.70	2.18	7.80	10.00	27.98
Taraxacum officinale	0.33	7.60	9.25	10.28	2.28	10.15	6.68	9.30
Trisetum canescens	143.23	461.28	77.75	219.25	-20.98	136.15	260.73	478.28
Tragopogon dubius	4.38	8.25	0.63	1.98	0.55	1.68	5.00	8.70

however, increase in density in the thinned treatment over the two year (1985 to 1987) period. From 1986 to 1987 density of Achillea, Aster, Galium, and Poa increased within thinned versus non-thinned treatments. Achillea, Luzula, and Taraxacum increased in the thinned versus non-thinned treatment from 1985 to 1987.

Trenching increased density of Achillea, Carex rossii, Silene, and Taraxacum from 1985 to 1986 (Table 17). Lathyrus was the only species to decrease in density the first year after thinning (1985 to 1986). Two years (1985 to 1987) after the trenched treatment was established, C. geyeri, Taraxacum, and Tragopogon increased in density.

Thinned and trenched interactions occurred for C. rossii (from 1985 to 1986) and Poa (from 1985 to 1987) though both had highly significant increases in trenched versus non-trenched treatments. Species that had interactions include; Senecio canus and Symphoricarpos from 1985 to 1986, Festuca rubra and Lupinus leucophyllus from 1986 to 1987, and Melica bulbosa and Spiraea betulifolia from 1985 to 1987. Trisetum had an interaction from 1985 to 1986 and from 1985 to 1987, while Stellaria had an interaction from 1986 to 1987 and from 1985 to 1987.

[Cover and density means and standard deviations of life-forms by plots are presented in Appendix Table 42. Treatment means and standard errors of log 10 transformed cover and density data are in Appendix Tables 43 and 44, respectively. Plot means and standard deviations of log 10 cover and density by species are in Appendix Tables 45 and 46, respectively. Plot means and standard deviations of cover and density by species are in Appendix Tables 47 and 48, respectively.]

Percentage Similarity

Cover

Prior to treatment establishment in 1985, there was an 80% similarity of species cover between non-thinned and thinned treatments. In 1986, percent similarity dropped 6.0% (75.2%) with an additional 2.9% decline (73.0%) in 1987.

There was 89.9% similarity in species cover in 1985 between non-trenched and trenched treatments. Percent similarity dropped 12.1% (79.0%) in 1986 and an additional 0.4% (78.7%) in 1987.

Density

In 1985, there was 81.4% similarity of species density between non-thinned versus thinned treatments. Similarity dropped 3.9% (78.2%) in 1986 but increased 0.5% (78.6%) in 1987.

Percent similarity was 91.2% in 1985 between non-trenched versus trenched treatments. In 1986, similarity declined 12.3% (80.0%) but increased 0.4% (80.3%) by 1987.

Canonical Discriminant Function Analysis

Canonical discriminant function (CDF) analysis separated the treatments by resource variables. The analysis was run on 42 resource variables measured in 1986 and 1987. Results of the analysis for 1986 were similar to 1987; only the later year is reported (Appendix Table 49). The values of total canonical structure are the correlations between resource variables within the four treatments.

Light (PAR) was by far the best discriminator of treatments (Table 18) having a canonical structure value (0.960262) over twice that of the second highest discriminator, soil water potential (-0.411032) (40-60 cm) measured on June 3. Other resource variables which contributed to the spatial separation 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 16). CDF 1 and CDF 2 explained 97.03% of the variation in treatments. Thinned and non-thinned treatments are separated primarily on the basis of the amount light the understory receives whereas the trenched treatments are separated based on soil water potential, nitrate, and ammonium.

Correlation Analysis

Correlation analyses were run on cover and density of 16 plant species and 26 environmental variables measured in 1986 and 1987. Results of the analyses for 1986 were similar to 1987, only correlations of density and environmental variables measured in 1987 are reported in Table 18. *Achillea*, *Aster*, *Galium*, *Poa*, and *Taraxacum* positively correlated with canopy attributes that were increased by thinning; light, midday air and soil temperatures. *Carex geyeri*, *Calamagrostis*, *Trisetum*, and *Tragopogon* correlated positively with soil attributes that increased within the trenched treatments. Ammonium and mineralizable nitrogen were positively correlated with *C. geyeri* while nitrate, pH and soil water potential were positively correlated with *Tragopogon*. *Calamagrostis* positively correlated with soil water

Table 18. Correlation coefficients between selected understory species and environmental variables measured in 1987. Only coefficients significantly different from 0 ($P<0.05$) are listed.

	Berberis repens	Symphoricarpos albus	Trisetum canescens	Carex geyeri	Carex rossii
Soil Water Potential					
20 cm					
May 6			-0.3243		
June 3			-0.346		
June 22			-0.3384		
July 12			-0.3771		
September 13			-0.4253		
		-0.3609			
40 cm					
May 6					-0.2969
June 3			-0.3252		
June 22			-0.5104		-0.4161
July 12			-0.3927		-0.4076
August 15			-0.4208		-0.3764
September 13			-0.5337		-0.4498
Light					
Soil pH					
20 cm		0.3104			
40 cm	0.3931				
Mineralizable Nitrogen					
20 cm		0.3888	0.3307	0.3683	
40 cm		0.3573	0.4185	0.3496	
NO_3					
20 cm		0.5002	0.4989		
40 cm		0.5098	0.5057		
NH_4					
20 cm				0.3749	
40 cm			0.3754		
Midday Air Temperature					
May 6					-0.3965
June 3					-0.4974
July 12	0.2966				
August 15					
September 13					
Soil Temperature					
May 6		0.4377	0.3114	-0.3697	
June 3				-0.4368	
July 12					
August 15					
September 13					

Table 18. (continued)

	Calamagrostis rubescens	*Poa pratensis*	*Luzula campestris*	*Arnica cordifolia*	*Aster occidentalis*
Soil Water Potential					
20 cm					
May 6					
June 3	-0.3079				
June 22					
July 12	-0.3208				
September 13	-0.3609				
40 cm					
May 6			-0.3305		
June 3			-0.3615	-0.3161	
June 22	-0.359		-0.4429	-0.4121	
July 12	-0.4101		-0.395	-0.3443	
August 15	0.3371				
September 13	-0.4043		-0.4116		
Light		0.4892			0.3965
Soil pH					
20 cm				-0.5599	
40 cm				-0.384	
Mineralizable Nitrogen					
20 cm				-0.3085	
40 cm					
NO_3					
20 cm				-0.3085	
40 cm					
NH_4					
Midday Air Temperature					
May 6		0.4905			0.385
June 3			-0.3825	-0.7087	
July 12					
August 15				0.4793	
September 13		0.3437			
Soil Temperature					
May 6			-0.4627	-0.5342	
June 3		0.6586		-0.3377	0.3296
July 12		0.3596			0.3011
Aug. 15		0.3373			
Sept. 13					

Table 18. (continued)

	Silene menziesii	*Galium boreale*	*Lathyrus nevadensis*	*Achillea millefolium*	*Taraxicum officinale*	*Tragopogon dubius*
Soil Water Potential						
20 cm						
May 6						
June 3						
June 22						
July 12						-0.3199
September 13						-0.3576
40 cm						
May 6						-0.3305
June 3						
June 22						
July 12						
August 15						
September 13						
Light		0.4346		0.5761	0.4243	
Soil pH						
20 cm						
40 cm			0.3068			
NO_3						
20 cm						0.4739
40 cm						0.5129
NH_4						
20 cm						
40 cm						

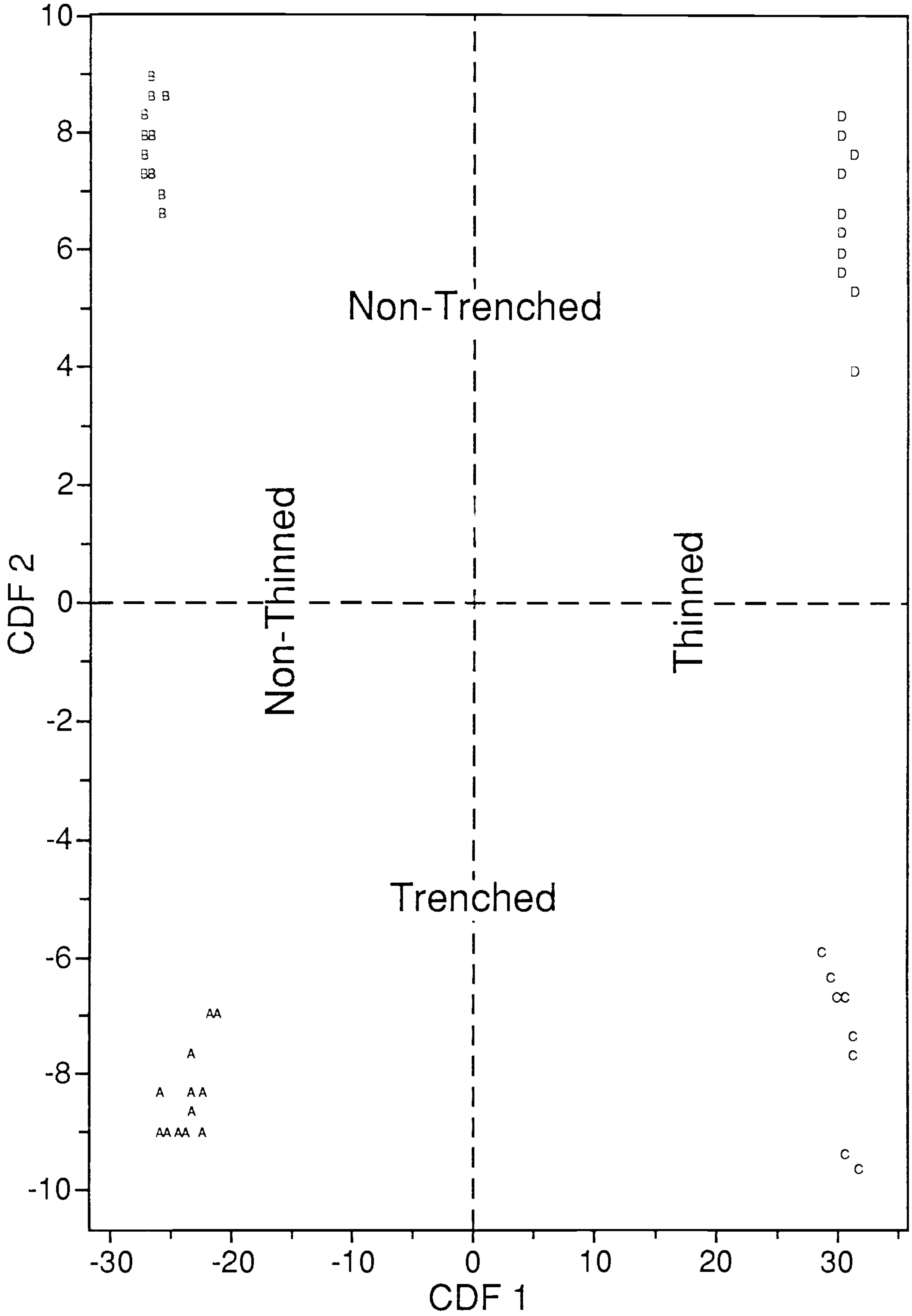

Figure 16. Plot of canonical discriminant functions (CDF) 1 and 2 for resource variables. Letters represent: (A) Non-Thinned/Trenched, (B) Non-Thinned/ Non-Trenched, (C) Thinned/Trenched, and (D) Thinned/Non-Trenched plots. Of the 44 plots, three are hidden.

potential. Trisetum also positively correlated with soil water potentials, nitrate, mineralizable nitrogen, and ammonium. Symphoricarpos positively correlated with nitrate, soil temperature, mineralizable nitrogen, and pH. Correlations of environmental variables with Berberis, C. rossii, Lathyrus, Luzula, Arnica, and Silene did not indicate a discernable trend.

DISCUSSION

Cover and density of understory vegetation responded to increased levels of light (PAR), water, and nutrients. The number of species that increased in cover and density was 80% greater in the trenched treatment versus the thinned treatment. This trend is similar to the understory biomass response, which increased more when root competition was controlled by trenching, than when light was increased from thinning (Riegel and Miller 1989a).

Increasing light 126% by thinning the overstory was the primary factor responsible for differences between thinned versus non-thinned understory environments. Trenching controlled root competition for soil water and nutrients and significantly increased soil water potentials, xylem potentials and nutrient concentrations and accumulations in _C_. _geyeri_, and increased mineralizable nitrogen and soil pH within the trenched treatment (Riegel and Miller 1989a).

Correlation of plant density and selected environmental variables measured in 1987 demonstrates that species response to treatment effects can be correlated to a change in either canopy effected attributes (light, midday air temperature, and soil temperature) or root competition effected attributes (soil water potential, pH, and nitrogen). _Poa_, _Achillea_, _Aster_, _Galium_, and _Taraxacum_ which significantly increased or decreased in either cover or density when light increased from thinning had the highest correlations with light and related variables. Species correlated with environmental variables that were altered when root competition was removed were Trisetum, C. geyeri, Calamagrostis, and Tragopogon. Symphoricarpos, a mid seral rhizomatous shrub that dominated the shrub layer, also correlated with soil variables.

Of the 103 understory species (graminoids, forbs, shrubs, and tree seedlings) only 17 responded to treatment effects in the two years after study establishment. The greatest change in percent similarity of species by treatment was within the first year after treatment establishment. Lack of a second year response probably was a function of greater resource competition than the first year after treatment establishment, i.e. no new resources were added in the second year and greater interspecific competition existed among understory species.

Increasing light in the thinned treatment decreased shrub cover in 1986, but had no effect on other life-form cover in 1987, or density in either year. Shrubs showed a general non-significant initial response in a thinned Pinus stand in north central Washington (McConnell and Smith 1965 1970). Young et al. (1967) reported that Symphoricarpos and Rosa growing in the mixed conifer forest above our study site were found predominantly in low density tree canopy cover. 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 the graminoids or forbs. Rosa, the only species to respond to thinning, did increase 96% in density from 1985 to 1986.

Achillea and Aster, both rhizomatous forbs, increased in density in 1986 and 1987, and cover in 1987 after light was increased in the thinned treatment. Achillea, a widely distributed native early seral species, increases with disturbance and is more often associated in plant communities with higher light intensities than found in the understory of Pinus forests (Franklin and Dyrness 1973, Johnson and Simon 1987). McConnell and Smith (1965) measured a 27% increase in Achillea biomass three years after thinning Pinus in north-central Washington. Other native species that increased in cover the second year after treatment include two mid seral plants, Galium, a rhizomatous forb, and Luzula, a tufted perennial. Taraxacum, a widely distributed and plastic ruderal perennial forb (Dennis 1980) also increased in the thinned treatment.

We believe the majority of the species that increased in the thinned treatment did so because of increased light. This is supported by the canonical discriminant function and correlation analyses. Though thinning also decreases competition for soil water and nutrients, understory plants soon utilize the additional resources until they have become limiting (Riegel and Miller 1989a).

Three species decreased in cover or density within the thinned treatment; Calamagrostis, Lathyrus, and Tragopogon. Tragopogon, a ruderal biennial forb that thrives on disturbance, (Dennis 1980) commonly increases after thinning. Calamagrostis has also been reported to increase after thinning (McConnell and Smith 1965 1970, Young et al. 1967). On the Hall Ranch near our study site, Calamagrostis biomass increased 13 to 33% four years after a sanitation cut in a mixed conifer stand (Young et al. 1967). McConnell and Smith (1965) reported a 42% yield increase of Calamagrostis three years after thinning a Pinus stand. Calamagrostis biomass, however, did not increase in the first or second year after our stands were thinned (Riegel and Miller 1989a). The lack of increase we saw in *Calamagrostis* growing in the thinned treatment, may have also been a function of fewer individual plants growing on these sites prior to establishment of treatments. It is also possible that species growing in association with *Calamagrostis*, such as *C. geyeri* the dominant understory species in *Pinus* stands on the Hall Ranch, are more competitive.

With root competition controlled in the trenched treatment, cover and density of graminoids, forbs, and shrubs increased in 1986 and 1987, with the exception of shrub density in 1986. Graminoids which contributed to the increase were *Calamagrostis*, *C. geyeri*, *Poa*, and *Trisetum*. The ability of *Calamagrostis*, *C. geyeri* and *Poa*, to reproduce with rhizomes may allow these species to quickly respond to the additional soil water and nutrients (McConnell and Smith 1965 and 1970). Of species measured, only *Calamagrostis* biomass significantly increased in the trenched treatment (Riegel and Miller 1989a). Species present in our understory may have not been as light limited as others were, but instead water and nutrient limited.

Reports of *Calamagrostis* increasing after thinning may be primarily due to a change in the belowground rather than the aboveground processes. Young et al. (1967) noted *Calamagrostis* responds favorably to moderate amounts of soil disturbance associated with logging activities. 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* also increased when fertilized with ammonium-nitrate alone and in combination with sulfur (Freyman and van Ryswyk 1969).

Poa, a non-native early seral rhizomatous grass, and Trisetum a native, early seral caespitose perennial grass, apparently are water and nitrogen limited as they increased in the trenched but not in the thinned treatments.

Forbs that increased following removal of overstory root competition include Achillea, Aster, Taraxacum, Tragopogon, and Silene. These same forbs with the exception of Silene, also increased after light levels were increased in the thinned treatment. Apparently these species are controlled by a combination or ratio of limited resources (Tilman 1985 1988). Lathyrus, an early seral rhizomatous forb, was the only species to decline in the trenched treatment apparently from water and nutrient enhanced growth of more competitive species. Lathyrus may have declined because it is a legume and not nitrogen limited.

Between year differences of cover in the thinned treatment were subtle compared with differences in density. There were no life-form differences in cover, however, density of forbs decreased from 1985 to 1986 while graminoids and forbs increased in 1986 and 1987. Achillea increased in cover and density between years more consistently than any other species. Thinning also promoted the density of Poa between 1986 and 1987 and from 1985 to 1987. Trenching affected Taraxacum more than any other species increasing it's cover from 1985 to 1986 and collectively from 1985 to 1987, though between 1986 to 1987 it decreased in cover. Other species, that consistently increased were Achillea, C. geyeri, and Tragopogon.

A few species, Potentilla and Rosa, increased in density the first year after thinning (1985 to 1986); and

Achillea, C. rossii, and, Silene in cover, but did not increase after that. In the first year after thinning C. geyeri and C. rossii decreased while Lathyrus decreased the first year after trenching. These species either declined because they were resource limited as evidenced by lack of response to the additional resources provided, i.e. mid seral 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. Pioneer and early successional species respond quicker to increased light, water, and nutrients than mid to late seral and climax species that exist under lower light requirements and tolerate higher water and nutrient stress (Tilman 1982 1985 1988).

Arrhenatherum, a non-native forage grass that was probably seeded in the meadow adjacent to block one, declined in cover from 1985 to 1987 within the thinned treatment presumably because it was out competed by other species.

Of the species that increased in response to increasing limited resources, 77% were rhizomatous. Only one species, Poa, is non-native. These species characterize an early and mid successional understory. Prior to fire suppression, a natural fire frequency of approximately ten years in these Pinus communities promoted the selection of rhizomatous plants which 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 1977a 1977b). Plants that were best able to compete and colonize the site after fire became dominant. Periodic burning has facilitated these plants with the ability to withstand defoliation by wild herbivores and more recently domestic livestock. Logging or thinning is another disturbance that impacts the understory. Increasing any of the limiting resources will promote growth of the more competitive rhizomatous plants. Shoots of C. geyeri, Calamagrostis, and Arnica 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 environmental conditions are relatively stable and the chance of disturbance is frequent or predictable (Radosevich and Holt 1984). Propagating vegetatively with rhizomes appears to be of value during the early and mid successional stage of forest development where early site capture following disturbance is essential (Radosevich and Holt 1984).

It is apparent that no single resource controls species density or cover in a early to mid seral understory in a P. ponderosa forest. Pioneer, early, and mid successional species are promoted by various combinations of higher light intensities and soil moisture and nutrients. Competition for limited resources, light, water, and nutrients, does effect the cover, density and species composition of the understory as evidenced by the response to increasing these resources.

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CHAPTER V.

CONCLUSIONS

The overall objective of this research was to define those environmental resources that control understory plant composition and production in a *Pinus ponderosa* forest in northeastern Oregon. The primary factors we evaluated were light, plant-soil water relations, soil nitrogen, and macro and micronutrients of the dominant understory species, *Carex geyeri* and *Symphoricarpos albus*. Other environmental variables measured were: understory air temperature and relative humidity at predawn and midday, soil temperature, and pH.

Opening up the overstory canopy to increase light did not significantly increase understory biomass production. Species composition, cover and density, however, did significantly change as a result of increased light levels. Density of graminoids and forbs, significantly increased while shrub cover significantly decreased.

Controlling root competition of *Pinus* roots for soil water and nutrients did significantly increase understory biomass. Species composition, cover and density of graminoids, forbs, and shrubs significantly increased when the availability of soil moisture and nutrients were increased.

Species response to treatment effects can be correlated to a change in either canopy effected attributes (light, midday air temperature, and soil temperature) or root competition effected attributes (soil water potential, pH, and nitrogen). The greatest change in percent similarity of species by treatment was within the first year after treatment establishment. Lack of a second year response probably was a function of greater resource competition than the first year after treatment establishment

We were unable to separate out the effects of water and nutrients, in the trenched treatments, on understory growth. Results from our trenched treatment were inconclusive as to which belowground resource, water or nutrients, contributed the most to increasing understory growth. Our second experiment, in which water and nitrogen were supplemented to the understory, indicated that water and nitrogen had a synergistic effect in improving growth.

In conclusion this research demonstrated that belowground resources were the primary controlling factors of understory production in P. ponderosa forests in northeastern Oregon. Competition for limited resources, light, water, and nutrients does effect cover, density and species composition of the understory as evidenced by the response to increasing these resources. Early and mid seral rhizomatous species contributed the most to understory response.

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APPENDIX

Appendix Table 1. Regression analysis of ozalid paper exposed to light and calibration to photosynthetic active radiation-PAR (μ mol m^{-2} s^{-1}/day x 10^6) measured in 1986 and 1987.

	1986	1987
Constant	-2.13372	-2.08700
Standard Error of Y Estimate	0.149451	0.156983
r^2	0.987513	0.979774
Number of Observations	14	30
Degrees of Freedom	12	28
X Coefficient	0.521839	0.595636
Standard Error of Coefficient	0.016939	0.016173

Appendix Table 2. Air temperatures (°C) at predawn and midday by treatments (means and standard errors) through the growing season of 1986. P = Probability levels.

Treatments	June 28	July 13	July 27	August 12	September 10
			Predawn		
Non-Thinned	9.26	5.37	3.33	9.72	3.61
Thinned	8.89	6.11	3.80	9.26	2.59
SE	0.26	0.53	0.33	0.33	0.72
P	0.4226	0.3808	0.3703	0.3727	0.3816
			Midday		
Non-Thinned	23.33	22.59	22.41	25.92	16.67
Thinned	25.93	25.09	23.98	27.87	18.06
SE	1.83	1.77	1.11	1.38	0.98
P	0.2497	0.0494	0.0606	0.0068	0.0129

Appendix Table 3. Air temperatures (°C) at predawn and midday by treatments (means and standard errors) through the growing season of 1987. P = Probability levels.

Treatments	May 6	May 20	June 3	June 22	July 12	July 27	August 15	August 27	September 13
					Predawn				
Non-Thinned	5.04	-0.69	4.95	8.06	5.83	8.75	8.15	7.87	5.93
Thinned	4.68	-1.81	3.70	6.99	4.12	8.09	8.06	6.30	4.91
SE	0.26	0.79	0.88	0.75	1.21	0.47	0.07	1.11	0.72
P	0.6081	0.0197	0.0042	0.4114	0.0299	0.5381	0.8075	0.0769	0.0263
					Midday				
Non-Thinned	22.93	10.51	19.54	19.21	24.91	28.38	18.80	25.56	26.02
Thinned	25.05	13.10	20.17	20.79	28.80	30.60	21.11	28.15	29.03
SE	0.79	1.83	0.43	1.12	2.75	1.57	1.64	1.83	2.13
	0.2259	0.0603	0.6164	0.0619	0.0925	0.0201	0.0460	0.0198	0.0506

Appendix Table 4. Probability values of repeated measures analysis of variance, general linear models procedure.

	Air Temperature			
	1986		1987	
	Predawn	Midday	Predawn	Midday
Time	0.0001	0.0001	0.0001	0.0001
Time X Cut	0.3187	0.7576	0.2575	0.0238

	Relative Humidity			
	1986		1987	
	Predawm	Midday	Predawn	Midday
Time	0.0009	0.0001	0.0003	0.0001
Time X Cut	0.0026	0.0589	0.3583	0.0166

	Soil Temperature					
	1986			1987		
	Depth (cm)					
	15	30	45	15	30	45
Time	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Time X Cut	0.3670	0.1200	0.3376	0.0001	0.0005	0.0001
Time X Trench	0.4238	0.5548	0.8980	0.7857	0.6780	0.0440
Time X Trench X Cut	0.5761	0.5462	0.4996	0.3138	0.1071	0.0018

	Soil Water Potential					
	1986			1987		
	Depth (cm)					
	20	40	60	20	40	60
Time	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Time X Cut	0.0009	0.2103	0.0007	0.0196	0.0078	0.0001
Time X Trench	0.0005	0.0026	0.0001	0.0009	0.0001	0.0001
Time X Trench X Cut	0.0584	0.0081	0.0001	0.0003	0.0001	0.0001

	Xyelm Potential			
	1986		1987	
	Predawn	Mid-Day	Predawn	Mid-Day
Time	0.0001	0.0001	0.0001	0.0001
Time X Cut	0.8515	0.1782	0.1891	0.0006
Time X Trench	0.0005	0.0545	0.0001	0.0001
Time X Trench X Cut	0.9771	0.2979	0.0536	0.0055

Appendix Table 5. Relative humidities (%) at predawn and midday by treatments (means and standard errors) through the growing season of 1986. P = Probability level.

Treatments	June 28	July 13	July 27	August 12	September 10
			Predawn		
Non-Thinned	91.00	93.67	86.00	79.83	87.33
Thinned	94.67	85.00	85.67	86.92	93.00
SE	2.59	6.13	0.24	5.01	4.01
P	0.4226	0.0796	0.7418	0.2562	0.0848
			Midday		
Non-Thinned	37.67	32.33	26.83	32.00	43.67
Thinned	27.00	22.00	23.67	26.17	34.33
SE	7.54	7.31	2.24	4.12	6.60
P	0.0785	0.0010	0.1846	0.0334	0.0013

Appendix Table 6. Relative humidities (%) at predawn and midday by treatments (means and standard errors) through the growing season of 1987. P = Probability level.

Treatments	May 28	May 13	June 3	June 22	July 12	July 27	August 15	August 27	September 13
					Predawn				
Non-Thinned	84.30	93.66	70.00	76.58	81.00	91.50	81.50	63.00	77.00
Thinned	93.00	95.33	82.33	85.67	86.33	88.50	80.33	70.33	78.17
SE	6.13	1.18	8.72	6.42	3.77	2.12	0.82	5.19	0.82
P	0.2022	0.4226	0.2425	0.2954	0.1835	0.4568	0.8864	0.3681	0.5616
					Midday				
Non-Thinned	44.00	45.58	35.50	31.33	32.33	27.67	36.50	24.00	24.42
Thinned	37.33	33.25	29.17	37.25	22.75	22.67	28.50	16.75	14.58
SE	4.71	8.72	4.48	4.18	6.78	3.54	5.66	5.13	6.95
P	0.0634	0.0757	0.0628	0.3229	0.0726	0.1194	0.0239	0.0406	0.0700

Appendix Table 7. Soil temperatures (°C) by treatments and depths (means and standard errors) through the growing season of 1986. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

Treatments	June 28	July 13	July 27	August 12	September 10
			15 cm		
Non-Thinned	12.78	11.46	10.85	12.70	5.28
Thinned	14.17	12.29	12.73	13.74	6.48
Non-Trenched	13.25	11.65	11.67	13.11	5.61
Trenched	13.59	12.04	11.74	13.25	6.05
SE A	0.75	0.53	1.03	0.66	0.81
P	0.1876	0.1699	0.1776	0.1979	0.4804
SE B	0.35	0.28	0.43	0.31	0.11
P	0.3296	0.1090	0.9819	0.5301	0.1121
SE AB	0.50	0.40	0.61	0.43	0.16
P	0.8569	0.9031	0.8559	0.7706	0.1388
			30 cm		
Non-Thinned	13.72	13.61	13.07	14.81	4.89
Thinned	14.71	14.69	14.90	15.70	6.18
Non-Trenched	14.00	14.04	13.97	15.07	5.23
Trenched	14.35	14.17	13.83	15.38	5.74
SE A	0.49	0.78	1.07	1.03	0.71
P	0.1171	0.3090	0.1916	0.4697	0.2976
SE B	0.33	0.38	0.59	0.15	0.16
P	0.2120	0.9135	0.7501	0.0602	0.0834
SE AB	0.46	0.53	0.83	0.21	0.23
P	0.5742	0.6678	0.4034	0.0602	0.5771
			45 cm		
Non-Thinned	13.10	13.09	13.25	11.56	5.75
Thinned	13.78	14.29	14.35	12.66	6.80
Non-Trenched	13.42	13.55	13.67	11.96	5.97
Trenched	13.40	13.73	13.83	12.18	6.50
SE A	0.52	0.81	0.78	1.03	1.02
P	0.2341	0.2570	0.2728	0.3588	0.4723
SE B	0.19	0.31	0.37	0.14	0.11
P	0.7390	0.7808	0.9110	0.1336	0.0338
SE AB	0.27	0.43	0.53	0.20	0.15
P	0.9020	0.5098	0.8593	0.0284	0.7939

Appendix Table 8. Soil temperatures (°C) by plots and depths (means and standard errors) through the growing season of 1986.

Plots	June 28	July 13	July 27	August 12	September 10
			15 cm		
Thinned/Non-Trenched	13.90	12.09	12.60	13.60	5.98
Thinned/Trenched	14.50	12.53	12.88	13.91	7.08
Non-Thinned/Non-Trenched	12.65	11.24	10.82	12.66	5.27
Non-Thinned/Trenched	12.91	11.68	10.89	12.75	5.28
SE	0.71	0.56	0.86	0.61	0.22
			30 cm		
Thinned/Non-Trenched	14.61	14.57	14.66	15.34	5.73
Thinned/Trenched	14.83	14.83	15.19	16.14	6.72
Non-Thinned/Non-Trenched	13.44	13.56	13.33	14.81	4.78
Non-Thinned/Trenched	13.99	13.67	12.81	14.81	5.00
SE	0.66	0.75	1.17	0.30	0.32
			15 cm		
Thinned/Non-Trenched	13.81	14.00	14.18	12.30	6.38
Thinned/Trenched	13.74	14.64	14.56	13.11	7.30
Non-Thinned/Non-Trenched	13.06	13.15	13.20	11.65	5.60
Non-Thinned/Trenched	13.13	13.04	13.29	11.48	5.89
SE	0.38	0.61	0.74	0.28	0.21

Appendix Table 9. Soil temperatures (°C) by treatments and depths (means and standard errors) through the growing season of 1987. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

Treatments	May 6	May 20	June 3	June 22	July 12	July 27	August 15	August 27	September 13
					15 cm				
Non-Thinned	13.06	10.48	11.88	14.58	15.68	17.08	15.23	16.14	14.44
Thinned	13.03	11.84	13.53	16.82	16.31	17.54	17.50	17.99	14.95
Non-Trenched	12.80	10.93	12.84	15.55	15.92	17.10	16.26	17.02	14.61
Trenched	13.31	11.27	12.40	15.64	16.01	17.50	16.26	16.93	14.74
SE A	1.31	0.57	0.31	0.47	0.77	0.60	0.90	0.81	1.20
P	0.8753	0.1132	0.0171	0.0283	0.4228	0.8475	0.0968	0.1001	0.7380
SE B	0.51	0.23	0.33	0.89	0.41	0.87	0.35	0.22	0.23
P	0.2557	0.1654	0.5359	0.5060	0.8884	0.8887	0.9812	0.8410	0.8019
SE AB	0.72	0.32	0.47	0.93	0.58	1.22	0.49	0.32	0.32
P	0.9025	0.9840	0.0690	0.9762	0.1333	0.4941	0.9065	0.0719	0.9731
					30 cm				
Non-Thinned	11.77	11.60	11.48	14.06	14.65	15.04	13.79	14.04	12.85
Thinned	12.65	12.45	12.83	15.50	15.13	15.90	15.31	15.62	13.80
Non-Trenched	12.00	11.93	11.98	14.72	14.80	15.48	14.35	14.84	13.20
Trenched	12.36	12.04	12.21	14.71	14.93	15.38	14.63	14.68	13.38
SE A	0.87	0.54	0.31	0.26	0.52	0.85	0.55	0.17	1.06
P	0.4965	0.2214	0.0332	0.0218	0.3610	0.4589	0.0882	0.0070	0.4423
SE B	0.36	0.16	0.40	0.23	0.65	0.47	0.20	0.13	0.18
P	0.4224	0.4159	0.3774	0.9722	0.8617	0.4952	0.1923	0.4810	0.3374
SE AB	0.51	0.23	0.57	0.33	0.93	0.67	0.29	0.18	0.25
P	0.1293	0.9592	0.2369	0.5199	0.1647	0.9005	0.6201	0.1710	0.1188
					40 cm				
Non-Thinned	10.90	10.41	11.04	13.69	13.90	14.38	13.85	14.04	12.92
Thinned	11.28	11.30	12.25	14.75	14.46	15.13	14.95	15.73	13.91
Non-Trenched	11.30	10.83	11.70	14.04	14.16	14.83	14.20	14.86	13.34
Trenched	10.82	10.81	11.48	14.31	14.14	14.60	14.52	14.75	13.40
SE A	0.99	0.67	0.56	0.48	0.51	0.92	0.62	0.37	0.89
P	0.9877	0.3039	0.1520	0.1143	0.3320	0.5801	0.1796	0.0285	0.3559
SE B	0.43	0.16	0.22	0.34	0.60	0.38	0.22	0.13	0.33
P	0.1369	0.8235	0.2055	0.2342	0.9082	0.2235	0.1312	0.9235	0.9303
SE AB	0.61	0.23	0.31	0.48	0.85	0.54	0.30	0.19	0.46
P	0.1997	0.1593	0.6076	0.1368	0.1104	0.9419	0.3076	0.2153	0.7011

Appendix Table 10. Soil temperatures (^{o}C) by plots and depths (means and standard errors) through the growing season of 1987.

Plots	May 13	May 6	June 20	June 22	July 12	July 27	August 15	August 27	September 13
					15 cm				
Thinned/Non-Trenched	12.79	11.60	13.44	16.73	15.89	16.90	17.36	17.77	14.82
Thinned/Trenched	13.30	12.13	13.63	16.92	16.83	18.33	17.67	18.25	15.11
Non-Thinned/Non-Trenched	12.82	10.33	12.30	14.48	15.96	17.29	15.25	16.33	14.42
Non-Thinned/Trenched	13.30	10.63	11.47	14.68	15.40	16.88	15.21	15.94	14.46
SE	1.01	0.46	0.66	0.96	0.81	1.73	0.69	0.45	0.45
					30 cm				
Thinned/Non-Trenched	12.09	12.36	12.45	15.36	14.55	15.77	15.05	15.57	13.50
Thinned/Trenched	13.33	12.56	13.28	15.67	15.83	16.06	15.64	15.69	14.17
Non-Thinned/Non-Trenched	11.92	11.54	11.54	14.13	15.04	15.21	13.71	14.17	12.92
Non-Thinned/Trenched	11.63	11.65	11.42	14.00	14.25	14.88	13.88	13.92	12.79
SE	0.72	0.33	0.80	0.47	1.31	0.94	0.40	0.26	0.35
					45 cm				
Thinned/Non-Trenched	11.68	11.14	12.32	14.36	13.89	15.10	14.64	15.66	13.75
Thinned/Trenched	10.78	11.50	12.17	15.22	15.17	15.17	15.33	15.81	14.11
Non-Thinned/Non-Trenched	10.96	10.54	11.13	13.75	14.42	14.58	13.79	14.13	12.96
Non-Thinned/Trenched	10.85	10.29	10.96	13.63	13.38	14.17	13.92	13.96	12.88
SE	0.86	0.33	0.44	0.68	1.20	0.77	0.43	0.27	0.65

Appendix Table 11. Soil water potentials (MPa) by treatments and depths (means and standard errors) through the growing season of 1986. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

Treatments	May 17	June 28	July 13	July 27	August 12	September 10
			0-20 cm			
Non-Thinned	-0.02	-0.27	-0.25	-0.41	-0.94	-0.95
Thinned	-0.01	-0.77	-0.57	-0.64	-1.50	-1.37
Non-Trenched	-0.02	-0.63	-0.57	-0.72	-1.59	-1.51
Trenched	-0.01	-0.36	-0.20	-0.29	-0.77	-0.74
SE A	0.01	0.38	0.04	0.33	0.36	0.34
P	0.8788	0.2501	0.0132	0.5556	0.1663	0.1962
SE B	0.01	0.15	0.26	0.26	0.30	0.43
P	0.0789	0.0930	0.1191	0.0914	0.0530	0.1354
SE AB	0.01	0.22	0.37	0.37	0.42	0.60
P	0.5086	0.2816	0.9931	0.5575	0.0758	0.4650
			20-40 cm			
Non-Thinned	-0.14	-0.73	-0.84	-0.87	-1.09	-1.21
Thinned	-0.02	-0.50	-0.68	-0.60	-1.22	-0.92
Non-Trenched	-0.16	-0.98	-1.17	-1.14	-1.60	-1.43
Trenched	-0.01	-0.24	-0.33	-0.32	-0.66	-0.69
SE A	0.10	0.36	0.49	0.44	0.73	0.52
P	0.2694	0.4156	0.5688	0.4001	0.9638	0.4540
SE B	0.13	0.33	0.24	0.10	0.12	0.25
P	0.2443	0.0532	0.0122	0.0005	0.0007	0.0184
SE AB	0.19	0.47	0.34	0.14	0.17	0.35
P	0.3290	0.0601	0.0155	0.0005	0.0026	0.0147
			40-60 cm			
Non-Thinned	-0.09	-0.48	-0.69	-0.84	-1.06	-1.05
Thinned	-0.02	-0.67	-0.69	-0.65	-1.42	-1.34
Non-Trenched	-0.10	-0.87	-1.23	-1.22	-1.75	-1.78
Trenched	-0.01	-0.2	-0.11	-0.25	-0.65	-0.53
SE A	0.02	0.45	0.09	0.30	0.39	0.59
P	0.0571	0.5863	0.7556	0.4508	0.4334	0.4877
SE B	0.02	0.08	0.32	0.12	0.14	0.13
P	0.0083	0.0008	0.0170	0.0006	0.0008	0.0006
SE AB	0.03	0.11	0.45	0.17	0.20	0.19
P	0.0099	0.0037	0.5145	0.0022	0.0021	0.0015

Appendix Table 12. Soil water potentials (MPa) by plots and depths (means and standard errors) through the growing season of 1986.

Plots	May 17	June 28	July 13	July 27	August 12	September 10
			0-20 cm			
Thinned/Non-Trenched	-0.02	-0.78	-0.69	-0.73	-1.63	-1.62
Thinned/Trenched	-0.01	-0.76	-0.42	-0.52	-1.35	-1.05
Non-Thinned/Non-Trenched	-0.03	-0.48	-0.46	-0.71	-1.55	-1.40
Non-Thinned/Trenched	-0.01	-0.06	-0.04	-0.11	-0.34	-0.50
SE	0.02	0.31	0.53	0.52	0.59	0.85
			20-40 cm			
Thinned/Non-Trenched	-0.03	-0.49	-0.65	-0.53	-1.28	-0.80
Thinned/Trenched	-0.01	-0.53	-0.72	-0.68	-1.15	-1.06
Non-Thinned/Non-Trenched	-0.27	-1.44	-1.66	-1.71	-1.89	-2.00
Non-Thinned/Trenched	-0.01	-0.03	-0.03	-0.04	-0.29	-0.42
SE	0.27	0.66	0.49	0.20	0.25	0.50
			40-60 cm			
Thinned/Non-Trenched	-0.02	-0.78	-1.08	-0.73	-1.49	-1.53
Thinned/Trenched	-0.02	-0.55	-0.22	-0.55	-1.33	-1.10
Non-Thinned/Non-Trenched	-0.17	-0.95	-1.37	-1.66	-1.98	-2.00
Non-Thinned/Trenched	-0.01	-0.02	-0.02	-0.02	-0.15	-0.12
SE	0.04	0.15	0.64	0.24	0.28	0.27

Appendix Table 13. Soil water potentials (MPa) by treatments and depths (means and standard errors) through the growing season of 1987. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

Treatments	May 6	May 20	June 3	June 22	July 12	July 27	August 15	August 27	September 13
					0-20 cm				
Non-Thinned	-0.03	-0.14	-0.05	-0.48	-0.58	-0.40	-0.43	-0.94	-0.83
Thinned	-0.02	-0.15	-0.05	-0.65	-1.03	-0.62	-0.88	-1.59	-1.25
Non-Trenched	-0.04	-0.21	-0.08	-0.86	-1.13	-0.77	-0.89	-1.65	-1.39
Trenched	-0.01	-0.07	-0.03	-0.23	-0.41	-0.20	-0.36	-0.78	-0.61
SE A	0.01	0.07	0.01	0.29	0.27	0.35	0.25	0.28	0.40
P	0.9523	0.4759	0.4082	0.5601	0.1380	0.4266	0.0938	0.0873	0.2339
SE B	0.02	0.05	0.02	0.90	0.18	0.14	0.24	0.08	0.21
P	0.1290	0.0584	0.0886	0.0770	0.0116	0.0082	0.1288	0.0004	0.0192
SE AB	0.02	0.07	0.03	0.93	0.26	0.19	0.35	0.12	0.29
P	0.3312	0.0298	0.0674	0.9223	0.0637	0.1774	0.0958	0.0002	0.0240
					20-40 cm				
Non-Thinned	-0.07	-0.36	-0.36	-1.01	-0.87	-1.03	-0.87	-1.12	-1.03
Thinned	-0.05	-0.10	-0.14	-0.80	-1.13	-0.96	-0.93	-1.31	-1.17
Non-Trenched	-0.11	-0.41	-0.45	-1.44	-1.46	-1.58	-1.34	-1.68	-1.64
Trenched	-0.01	-0.05	-0.05	-0.34	-0.46	-0.36	-0.41	-0.68	-0.49
SE A	0.04	0.08	0.07	0.61	0.51	0.64	0.27	0.60	0.57
P	0.4114	0.0559	0.0505	0.5719	0.7947	0.7707	0.9852	0.9003	0.9651
SE B	0.04	0.13	0.13	0.06	0.26	0.11	0.23	0.10	0.13
P	0.0484	0.0262	0.0205	0.0001	0.0076	0.0001	0.0068	0.0003	0.0003
SE AB	0.06	0.18	0.18	0.08	0.37	0.15	0.32	0.14	0.18
P	0.3359	0.0289	0.0361	0.0001	0.0415	0.0010	0.0172	0.0006	0.0021
					40-60 cm				
Non-Thinned	-0.11	-0.40	-0.46	-0.93	-0.97	-0.96	-0.79	-0.99	-0.98
Thinned	-0.07	-0.09	-0.08	-0.46	-0.96	-0.95	-0.95	-1.47	-1.07
Non-Trenched	-0.16	-0.47	-0.53	-1.23	-1.63	-1.48	-1.29	-1.76	-1.56
Trenched	-0.01	-0.03	-0.03	-0.16	-0.24	-0.38	-0.40	-0.61	-0.43
SE A	0.06	0.17	0.14	0.22	0.32	0.43	0.42	0.41	0.34
P	0.5042	0.1583	0.0731	0.1012	0.9094	0.7848	0.4400	0.2379	0.8612
SE B	0.06	0.19	0.18	0.82	0.19	0.29	0.08	0.10	0.38
P	0.0363	0.0471	0.0314	0.0007	0.0007	0.0168	0.0004	0.0002	0.0202
SE AB	0.08	0.27	0.26	0.85	0.26	0.41	0.12	0.14	0.53
P	0.2317	0.0724	0.0401	0.0024	0.0254	0.0218	0.0002	0.0003	0.0784

Appendix Table 14. Soil water potentials (MPa) by plots and depths (means and standard errors) through the growing season of 1987.

Plots	May 6	May 20	June 3	June 22	July 12	July 27	August 15	August 27	September 13
					0-20 cm				
Thinned/Non-Trenched	-0.03	-0.15	-0.06	-0.91	-1.17	-0.79	-0.95	-1.58	-1.34
Thinned/Trenched	-0.01	-0.14	-0.05	-0.34	-0.86	-0.41	-0.80	-1.60	-1.14
Non-Thinned/Non-Trenched	-0.05	-0.26	-0.10	-0.81	-1.09	-0.76	-0.83	-1.72	-1.43
Non-Thinned/Trenched	-0.01	-0.02	-0.01	-0.14	-0.07	-0.05	-0.03	-0.16	-0.22
SE	0.03	0.10	0.05	0.96	0.37	0.28	0.49	0.17	0.41
					20-40 cm				
Thinned/Non-Trenched	-0.07	-0.09	-0.17	-0.87	-1.21	-1.11	-0.95	-1.32	-1.29
Thinned/Trenched	-0.01	-0.10	-0.11	-0.71	-1.02	-0.78	-0.91	-1.29	-1.02
Non-Thinned/Non-Trenched	-0.14	-0.71	-0.72	-1.96	-1.69	-2.00	-1.70	-2.00	-1.97
Non-Thinned/Trenched	-0.01	-0.01	-0.01	-0.07	-0.04	-0.05	-0.04	-0.23	-0.09
SE	0.09	0.26	0.26	0.11	0.52	0.21	0.46	0.20	0.25
					40-60 cm				
Thinned/Non-Trenched	-0.10	-0.12	-0.10	-0.57	-1.31	-1.08	-0.98	-1.55	-1.18
Thinned/Trenched	-0.02	-0.05	-0.06	-0.33	-0.54	-0.79	-0.91	-1.38	-0.93
Non-Thinned/Non-Trenched	-0.21	-0.79	-0.92	-1.83	-1.92	-1.84	-1.57	-1.96	-1.91
Non-Thinned/Trenched	-0.01	-0.01	-0.01	-0.03	-0.02	-0.08	-0.01	-0.03	-0.05
SE	0.11	0.38	0.37	0.88	0.37	0.58	0.17	0.20	0.75

Appendix Table 15. Soil pH by plots and depths (means and standard errors) for 1986 and 1987.

	1986		1987	
	Depth (cm)		Depth (cm)	
Plots	0-20	20-40	0-20	20-40
Thinned/Non-Trenched	5.84	5.61	6.02	6.34
Thinned/Trenched	6.00	5.52	6.12	6.35
Non-Thinned/Non-Trenched	5.97	6.18	6.14	6.22
Non-Thinned/Trenched	6.18	6.27	6.21	6.54
SE	0.03	0.13	0.03	0.02

Appendix Table 16. Soil mineralizable nitrogen, nitrate, and ammonium (ppm; log 10) by treatments and depths (means and standard errors) for 1986 and 1987. Standard error (SE) A = Non-Thinned and Thinned, and SE B = Non-Trenched-Trenched. P = Probability level.

	1986		1987	
	Depth (cm)		Depth (cm)	
Treatments	0-20	20-40	0-20	20-40
	Mineralizable Nitrogen			
Non-Thinned	1.56	1.26	1.73	1.74
Thinned	1.49	1.22	1.74	1.71
Non-Trenched	1.51	1.16	1.71	1.67
Trenched	1.54	1.32	1.76	1.78
SE A	0.07	0.01	0.04	0.02
P	0.6535	0.3507	0.9896	0.3336
SE B	0.05	0.03	0.02	0.05
P	0.7694	0.0793	0.0381	0.2323
SE AB	0.07	0.04	0.02	0.07
P	0.6596	0.4980	0.0315	0.5033
	Nitrate			
Non-Thinned	-0.41	-0.38	-0.38	-0.42
Thinned	-0.49	-0.48	-0.70	-0.67
Non-Trenched	-0.50	-0.44	-0.67	-0.70
Trenched	-0.40	-0.41	-0.41	-0.39
SE A	0.05	0.01	0.20	0.17
P	0.5000	0.0950	0.4283	0.5000
SE B	0.07	0.04	0.15	0.20
P	0.4723	0.7135	0.3115	0.3792
SE AB	0.10	0.06	0.21	0.28
P	0.3832	0.1465	0.3115	0.4789
	Ammonium			
Non-Thinned	1.56	0.74	1.52	1.66
Thinned	1.27	1.47	1.61	1.60
Non-Trenched	1.50	1.12	1.54	1.59
Trenched	1.32	1.09	1.59	1.66
SE A	0.10	0.11	0.06	0.02
P	0.3524	0.9764	0.9357	0.2477
SE B	0.08	0.18	0.03	0.10
P	0.3378	0.6855	0.1344	0.5583
SE AB	0.12	0.25	0.04	0.13
P	0.3686	0.5407	0.0789	0.4892

Appendix Table 17. Soil mineralizable nitrogen, nitrate, and ammonium (ppm; log 10) by plots and depths (means and standard errors) for 1986 and 1987.

Treatments	1986 Depth (cm)		1987 Depth (cm)	
	0-20	20-40	0-20	20-40
	Mineralizable Nitrogen			
Thinned/Non-Thinned	1.49	1.16	1.78	1.70
Thinned/Trenched	1.48	1.28	1.77	1.78
Non-Thinned/Non-Trenched	1.52	1.16	1.62	1.70
Non-Thinned/Trenched	1.59	1.35	1.93	1.91
SE	0.10	0.05	0.03	0.10
	Nitrate			
Thinned/Non-Thinned	-0.47	-0.41	-0.70	-0.70
Thinned/Trenched	-0.50	-0.55	-0.70	-0.61
Non-Thinned/Non-Trenched	-0.52	-0.47	-0.61	-0.70
Non-Thinned/Trenched	-0.29	-0.28	0.08	-0.02
SE	0.13	0.08	0.30	0.40
	Ammonium			
Thinned/Non-Thinned	1.27	1.45	1.61	1.63
Thinned/Trenched	1.26	1.50	1.57	1.61
Non-Thinned/Non-Trenched	1.73	1.61	1.45	1.58
Non-Thinned/Trenched	1.38	1.35	1.75	1.83
SE	0.17	0.36	0.06	0.19

Appendix Table 18. Soil mineralizable nitrogen, nitrate, and ammonium (ppm) by plots and depths (means and standard deviations) for 1986 and 1987.

	1986				1987			
	Depth (cm)				Depth (cm)			
	0-20		20-40		0-20		20-40	
Plots	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
	Mineralizable Nitrogen							
Thinned/Non-Trenched	33.70	16.90	14.53	2.39	62.03	5.76	49.67	11.85
Thinned/Trenched	30.18	4.20	20.45	9.71	50.07	16.11	55.03	14.19
Non-Thinned/Non-Trenched	34.55	11.62	14.72	3.84	43.73	13.46	45.60	9.90
Non-Thinned/Trenched	46.80	29.75	22.97	4.51	71.67	29.13	70.13	23.73
	Nitrate							
Thinned/Non-Trenched	0.40	0.28	0.43	0.21	0.20	0.00	0.20	0.00
Thinned/Trenched	0.35	0.17	0.30	0.12	0.20	0.00	0.23	0.06
Non-Thinned/Non-Trenched	0.33	0.15	0.35	0.10	0.23	0.06	0.20	0.00
Non-Thinned/Trenched	0.75	0.64	0.55	0.17	1.80	2.60	1.73	2.48
	Ammonium							
Thinned/Non-Trenched	18.90	1.87	28.48	7.02	44.07	6.57	42.37	12.98
Thinned/Trenched	20.18	10.02	43.25	34.76	36.90	0.00	41.11	21.35
Non-Thinned/Non-Trenched	53.73	2.15	20.63	25.50	27.87	8.73	37.20	3.46
Non-Thinned/Trenched	29.15	22.64	11.28	13.63	44.10	20.89	58.20	17.92

Appendix Table 19. Total biomass production (kg/ha^{-1}) by treatments (means and standard errors) for 1986 and 1987. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

Treatments	1986	1987
Non-Thinned	1364.15	1074.35
Thinned	1414.72	1372.00
Non-Trenched	1106.39	835.44
Trenched	1694.62	1619.50
SE A	159.16	188.09
P	0.96	0.13
SE B	200.10	172.01
P	0.03	0.00
SE AB	282.99	243.26
P	0.38	0.39

Appendix Table 20. Total biomass production (kg/ha^{-1}) by plots (means and standard errors) for 1986 and 1987.

Plots	1986	1987
Thinned/Non-Trenched	1204.66	1111.88
Thinned/Trenched	1671.46	1689.93
Non-Thinned/Non-Trenched	1016.30	582.03
Non-Thinned/Trenched	1711.99	1566.67
SE	400.21	344.02

Appendix Table 21. Biomass production (kg/ha^{-1}) by treatments of selected species and forage classes (means and standard errors) for 1986 and 1987. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

Treatments	Species or Forage Class							
	Carex geyeri	*Calamagrostis rubescens*	*Poa pratensis*	*Symphoricarpos albus*	Perennial grasses	Perennial forbs	Annual/ Biennial	Other shrubs
	1986							
Non-Thinned	475.83	27.78	251.11	168.75	379.72	235.83	2.40	139.90
Thinned	357.50	5.23	128.18	176.38	199.55	380.50	0.88	37.38
Non-Trenched	79.02	27.92	30.42	155.87	112.08	189.24	0.43	49.89
Trenched	469.17	79.17	71.88	190.12	308.13	424.64	3.10	140.83
SE A	135.57	26.92	98.72	14.76	100.12	17.30	3.94	46.00
P	0.3897	0.2117	0.2573	0.3920	0.7107	0.0074	0.6497	0.0987
SE B	71.21	20.75	34.57	40.65	51.45	53.91	3.39	78.66
P	0.2390	0.1022	0.0564	0.4868	0.0219	0.0041	0.4454	0.2996
SE AB	100.70	29.35	48.89	57.48	72.76	76.24	4.80	111.24
P	0.1761	0.3836	0.3107	0.6080	0.3234	0.1874	0.4085	0.2704
	1987							
Non-Thinned	304.17	40.52	59.06	92.60	234.27	228.23	27.29	15.00
Thinned	283.38	16.00	300.00	107.38	237.25	378.50	12.65	20.45
Non-Trenched	258.59	11.30	112.71	81.74	119.02	221.52	7.30	32.92
Trenched	334.29	49.17	229.76	118.57	363.33	378.69	35.24	74.79
SE A	70.89	19.32	166.47	13.13	117.00	96.98	32.61	28.20
P	0.7543	0.2372	0.1642	0.4414	0.8001	0.1598	0.6007	0.2334
SE B	68.66	9.51	102.68	31.51	55.92	66.47	36.39	15.73
P	0.2817	0.0119	0.0950	0.2007	0.0098	0.0250	0.4708	0.2624
SE AB	97.10	13.45	145.21	44.56	79.08	94.00	51.46	22.25
P	0.1873	0.0380	0.3415	0.9011	0.0538	0.4672	0.38	0.1126

Appendix Table 22. Biomass production (kg/ha^{-1}) by plots of selected species and forage classes (means and standard errors) by plots or 1986 and 1987.

Plots	Species or Forage Class							
	Carex geyeri	*Calamagrostis rubescens*	*Poa pratensis*	*Symphoricarp albus*	Perennial grasses	Perennial forbs	Annual/ Biennial	Other shrubs
Thinned/Non-Trenched	367.27	5.23	128.18	165.23	199.55	240.23	0.91	36.36
Thinned/Trenched	345.56	27.78	251.11	190.00	379.72	551.94	0.83	38.61
Non-Thinned/Non-Trenched	389.79	27.92	30.42	147.29	112.08	142.50	0.00	62.29
Non-Thinned/Trenched	561.88	79.17	71.88	190.21	308.13	329.17	4.79	217.50
SE	142.41	41.50	69.15	81.29	102.90	107.82	6.78	157.32
Thinned/Non-Trenched	293.64	10.23	220.45	89.09	172.05	292.27	13.68	20.45
Thinned/Trenched	270.83	23.06	397.22	129.72	316.94	483.89	11.39	15.00
Non-Thinned/Non-Trenched	226.46	12.29	13.96	75.00	70.42	156.67	1.46	32.92
Non-Thinned/Trenched	381.88	68.75	104.17	110.21	398.13	299.79	53.13	74.79
SE	137.32	19.02	205.36	63.02	111.83	132.94	72.78	31.46

Appendix Table 23. Xylem potentials (MPa) at predawn and midday of Carex geyeri by treatments (means and standard errors) through the growing season of 1986. Standard errors (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

Treatments	June 28	July 13	July 27	August 12	September 10
			Predawn		
Non-thinned	-0.42	-0.76	-0.94	-1.21	-1.63
Thinned	-0.44	-0.79	-1.06	-1.38	-1.84
Non-Trenched	-0.47	-0.88	-1.21	-1.51	-2.03
Trenched	-0.39	-0.65	-0.75	-1.05	-1.40
SE	0.03	0.08	0.14	0.19	0.32
P	0.6641	0.7610	0.4367	0.6043	0.7363
SE B	0.07	0.08	0.16	0.14	0.15
P	0.1347	0.0239	0.0303	0.0112	0.0062
SE AB	0.10	0.11	0.23	0.19	0.21
P	0.8620	0.2472	0.7921	0.6335	0.9560
			Midday		
Non-Thinned	-2.16	-2.78	-2.64	-3.60	-3.51
Thinned	-2.50	-2.83	-3.14	-4.01	-3.80
Non-Trenched	-2.44	-2.93	-3.11	-4.12	-4.08
Trenched	-2.18	-2.67	-2.61	-3.42	-3.16
SE A	0.09	0.07	0.08	0.19	0.21
P	0.0736	0.3328	0.0161	0.1995	0.3136
SE B	0.09	0.09	0.11	0.22	0.20
P	0.0147	0.0329	0.0067	0.0142	0.0044
SE AB	0.12	0.13	0.15	0.32	0.28
P	0.3480	0.8129	0.0359	0.8195	0.1257

Appendix Table 24. Xylem potentials (MPa) at predawn and midday of Carex geyeri by plots (means and standard errors) through the growing season of 1986.

Plots	June 28	July 13	July 27	August 12	September 10
	Predawn				
Thinned/Non-Trenched	-0.46	-0.86	-1.25	-1.54	-2.10
Thinned/Trenched	-0.42	-0.71	-0.82	-1.20	-1.51
Non-Thinned/Non-Trenched	-0.48	-0.91	-1.17	-1.48	-1.95
Non-Thinned/Trenched	-0.36	-0.61	-0.70	-0.94	-1.31
SE	0.14	0.15	0.32	0.27	0.30
	Midday				
Thinned/Non-Thinned	-2.55	-2.95	-3.23	-4.26	-4.04
Thinned/Trenched	-2.44	-2.69	-3.03	-3.70	-3.52
Non-Thinned/Non-Trenched	-2.33	-2.91	-3.00	-4.00	-4.13
Non-Thinned/Trenched	-1.98	-2.65	-2.29	-3.20	-2.89
SE	0.17	0.18	0.22	0.45	0.40

Appendix Table 25. Xylem potentials (MPa) at predawn and midday of *Carex geyeri* by treatments (means and standard errors) through the growing season of 1987. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched-Trenched, and SE AB = A x B interaction. P = Probability level.

Treatments	May 6	June 3	June 22	July 12	July 27	August 15	August 27	September 13
	Predawn							
Non-Thinned	-0.25	-0.49	-0.90	-1.00	-0.84	-1.03	-1.62	-1.81
Thinned	-0.27	-0.51	-1.06	-0.98	-0.80	-1.12	-1.66	-2.13
Non-Trenched	-0.30	-0.61	-1.13	-1.23	-1.06	-1.28	-2.09	-2.51
Trenched	-0.21	-0.39	-0.79	-0.72	-0.56	-0.84	-1.14	-1.35
SE A	0.02	0.05	0.07	0.12	0.14	0.08	0.15	0.30
P	0.5181	0.9659	0.1923	0.3064	0.8124	0.6028	0.9292	0.5687
SE B	0.02	0.06	0.09	0.17	0.11	0.06	0.15	0.19
P	0.0041	0.0121	0.0076	0.0156	0.0052	0.0009	0.0112	0.0015
SE AB	0.03	0.09	0.12	0.24	0.16	0.09	0.21	0.27
P	0.9803	0.5356	0.0527	0.2032	0.3200	0.0927	0.0763	0.1568

	May 6	May 20	June 3	June 22	July 12	July 27	August 15	August 27	September 13
	Midday								
Non-Thinned	-1.89	-2.02	-2.34	-2.36	-2.76	-2.78	-2.97	-3.72	-3.61
Thinned	-1.86	-2.08	-2.52	-2.91	-2.98	-3.36	-3.55	-4.04	-4.11
Non-Trenched	-2.00	-2.53	-2.68	-2.95	-3.14	-3.33	-3.64	-4.52	-4.50
Trenched	-1.73	-1.51	-2.13	-2.24	-2.55	-2.72	-2.78	-3.16	-3.11
SE A	0.14	0.12	0.09	0.24	0.17	0.07	0.03	0.15	0.30
P	0.5372	0.5827	0.3275	0.1050	0.7610	0.0134	0.0020	0.1047	0.1578
SE B	0.12	0.16	0.06	0.16	0.08	0.17	0.11	0.16	0.20
P	0.0280	0.0014	0.0003	0.0054	0.0239	0.0110	0.0006	0.0005	0.0014
SE AB	0.17	0.22	0.08	0.22	0.11	0.23	0.15	0.22	0.28
P	0.8506	0.1748	0.0418	0.3977	0.2472	0.3647	0.3090	0.0438	0.0479

Appendix Table 26. Xylem potentials (MPa) at predawn and midday of <u>Carex geyeri</u> by plots (means and standard errors) through the growing season of 1987.

Plots	May 6	June 3	June 22	July 12	July 27	August 15	August 27	September 13
	Predawn							
Thinned/Non-Trenched	-0.31	-0.59	-1.09	-1.08	-0.98	-1.26	-1.93	-2.49
Thinned/Trenched	-0.22	-0.41	-1.01	-0.84	-0.58	-0.94	-1.33	-1.70
Non-Thinned/Non-Trenched	-0.30	-0.62	-1.17	-1.37	-1.14	-1.30	-2.25	-2.53
Non-Thinned/Trenched	-0.20	-0.37	-0.63	-0.63	-0.54	-0.76	-1.00	-1.10
SE	0.04	0.13	0.18	0.33	0.22	0.12	0.30	0.38

	May 6	May 20	June 3	June 22	July 12	July 27	August 15	August 27	September 15
	Midday								
Thinned/Non-Thinned	-1.95	-2.67	-2.68	-3.28	-3.13	-3.54	-3.87	-4.49	-4.55
Thinned/Trenched	-1.75	-1.35	-2.32	-2.46	-2.79	-3.13	-3.16	-3.49	-3.58
Non-Thinned/Non-Trenched	-2.05	-2.41	-2.69	-2.64	-3.14	-3.14	-3.43	-4.54	-4.46
Non-Thinned/Trenched	-1.72	-1.63	-1.99	-2.07	-2.38	-2.41	-2.50	-2.90	-2.75
SE	0.24	0.31	0.12	0.32	0.15	0.33	0.21	0.32	0.40

Appendix Table 27. Nutrient concentrations of *Carex geyeri* foliage by plots (means and standard errors) for 1986 and 1987. N, P, K, S, Ca, and Mg are reported in % dry wt; other micronutrients are reported in ppm dry wt.

Plots	N	P	K	S	Ca	Mg	Mn	Fe	Cu	B	Zn	Al
	%						ppm					
	1986											
Thinned/Non-Trenched	0.95	0.15	1.32	0.09	0.36	0.14	482.67	192.33	2.33	8.33	38.78	134.67
Thinned/Trenched	1.21	0.19	1.53	0.11	0.47	0.17	396.67	290.00	2.33	7.67	44.67	245.67
Non-Thinned/Non-Trenched	0.95	0.18	2.13	0.10	0.39	0.17	785.00	223.33	2.33	9.00	65.67	144.33
Non-Thinned/Trenched	1.25	0.21	2.04	0.11	0.46	0.15	736.67	309.00	2.33	7.67	67.33	337.00
SE	0.02	0.01	0.15	0.00	0.02	0.03	18.83	6.00	0.00	0.33	2.11	40.83
	1987											
Thinned/Non-Thinned	1.15	0.22	1.64	0.10	0.42	0.16	488.00	128.67	3.67	7.00	39.67	51.33
Thinned/Trenched	1.26	0.21	1.95	0.11	0.38	0.15	375.67	134.00	3.67	4.33	41.67	66.33
Non-Thinned/Non-Trenched	1.12	0.19	1.80	0.10	0.34	0.14	514.33	190.67	3.67	8.33	64.33	110.33
Non-Thinned/Trenched	1.51	0.26	2.43	0.14	0.43	0.16	523.33	165.00	6.67	5.33	95.33	71.00
SE	0.14	0.04	0.16	0.02	0.06	0.01	60.67	15.50	1.50	0.17	14.50	38.42

Appendix Table 28. Nutrient total accumulations (kg/ha^{-1}) of Carex geyeri foliage by plots (means and standard errors) for 1986 and 1987. N, P, K, S, Ca, and Mg are reported in % dry wt; other micronutrients are reported in ppm dry wt. T = Trace (<0.005 kg/ha^{-1}).

Plots	N	P	K	S	Ca	Mg	Mn	Fe	Cu	B	Zn	Al
	%						ppm					
1986												
Thinned/Non-Trenched	7.00	1.11	9.83	0.64	2.64	1.04	0.19	0.10	T	0.01	0.02	0.10
Thinned/Trenched	8.57	1.35	10.87	0.76	3.29	1.21	0.14	0.08	T	T	0.01	0.06
Non-Thinned/Non-Trenched	7.70	1.44	17.12	0.80	2.93	1.33	0.24	0.11	T	T	0.02	0.09
Non-Thinned/Trenched	14.89	2.52	24.35	1.40	5.09	1.74	0.38	0.14	T	T	0.04	0.10
SE	2.01	0.37	2.93	0.23	0.42	0.25	0.02	0.03	T	T	0.00	0.04
1987												
Thinned/Non-Trenched	6.83	1.36	10.19	0.61	2.54	0.99	0.14	0.04	T	T	0.01	0.02
Thinned/Trenched	6.90	1.13	10.67	0.58	2.09	0.83	0.10	0.04	T	T	0.01	0.02
Non-Thinned/Non-Trenched	5.23	0.87	8.59	0.48	1.45	0.66	0.12	0.05	T	T	0.02	0.03
Non-Thinned/Trenched	11.81	2.00	18.64	1.09	3.23	1.22	0.19	0.06	T	T	0.04	0.03
SE	1.29	0.25	2.42	0.08	0.41	0.17	0.03	0.01	T	T	0.00	0.00

Appendix Table 29. Nutrient concentrations of *Symphoricarpos albus* foliage by plots (means and standard errors) for 1986 and 1987. N, P, K, S, Ca, and Mg are reported in % dry wt; other micronutrients are reported in ppm dry wt.

Plots	N	P	K	S	Ca	Mg	Mn	Fe	Cu	B	Zn	Al
	%						ppm					
1986												
Thinned/Non-Trenched	1.07	0.55	2.58	0.32	1.58	0.50	241.67	193.67	5.67	47.33	40.00	117.00
Thinned/Trenched	1.25	0.62	2.64	0.36	1.49	0.47	328.67	162.67	8.33	48.33	53.00	78.57
Non-Thinned/Non-Trenched	1.03	0.62	2.78	0.25	1.51	0.47	518.67	164.33	6.33	52.67	38.67	86.00
Non-Thinned/Trenched	1.30	0.87	3.05	0.39	1.86	0.53	594.67	243.00	9.00	63.33	63.00	176.00
SE	0.05	0.09	0.10	0.05	0.22	0.05	5.50	54.83	0.00	4.83	5.67	63.57
1987												
Thinned/Non-Thinned	1.48	0.48	2.41	0.17	1.24	0.43	282.50	101.00	6.50	37.00	32.00	33.00
Thinned/Trenched	1.62	0.37	2.30	0.15	0.94	0.35	256.33	113.33	6.00	31.00	33.33	38.00
Non-Thinned/Non-Trenched	1.39	0.44	2.71	0.16	0.91	0.32	227.33	118.00	6.33	37.33	33.00	40.00
Non-Thinned/Trenched	1.90	0.43	2.56	0.21	1.07	0.37	261.33	139.67	8.67	33.33	47.33	54.00
SE	0.25	0.04	0.01	0.03	0.20	0.06	19.23	9.02	1.04	2.24	7.30	6.71

Apppendix Table 30. Nutrient total accumulations (kg/ha^{-1}) of Symphoricarpos albus foliage by plots (means and standard errors) for 1986 and 1987. N, P, K, S, Ca, and Mg are reported in % dry wt.; other micronutrients are reported in ppm. dry wt. T = Trace (0<0.005/kg/ha^{-1}).

Plots	Nutrients											
	N	P	K	S	Ca	Mg	Mn	Fe	Cu	B	Zn	Al
	%						%					
	1986											
Thinned/Non-Trenched	3.51	1.35	6.18	0.75	4.25	1.27	0.03	0.02	T	0.01	0.00	0.01
Thinned/Trenched	3.70	1.75	8.51	0.90	5.00	1.53	0.04	0.02	T	0.01	0.01	0.01
Non-Thinned/Non-Trenched	3.28	1.58	8.96	0.62	3.68	1.19	0.09	0.03	T	0.01	0.01	0.01
Non-Thinned/Trenched	5.50	2.81	11.45	1.51	5.50	1.66	0.08	0.05	T	0.01	0.01	0.03
SE	1.23	0.64	1.66	0.44	1.00	0.28	0.01	0.02	T	0.01	0.00	0.01
	1987											
Thinned/Non-Trenched	3.81	1.18	5.65	0.41	2.91	1.01	0.04	0.01	T	0.01	0.01	0.01
Thinned/Trenched	4.12	0.91	5.74	0.38	2.32	0.90	0.03	0.01	T	T	0.00	0.01
Non-Thinned/Non-Trenched	2.42	0.73	4.50	0.30	1.42	0.51	0.02	0.01	T	T	0.00	0.00
Non-Thinned/Trenched	4.40	0.93	6.40	0.49	2.00	0.76	0.03	0.02	T	T	0.00	0.01
SE	0.98	0.14	1.29	0.09	0.29	0.12	0.01	0.01	T	T	T	0.00

Appendix Table 31. Understory biomass response (means, standard deviations, and standard error) to treatments. Means with the same letter are not significantly different (P<0.05).

Nitrogen	Water	Water + Nitrogen	Control
888.60 b	870.6 b	1031.20 a	756.70 c
SD 294.85	236.16	344.88	230.18
SE 14.74			

Appendix Table 32. Relationship of light, photosynthetic active radiation-PAR (μ mol m^{-2} s^{-1}/day x 10^6), measured at ground level, and understory biomass production.

Constant	94.48
Standard Error of Y Estimate	26.03
r^2	0.01
Number of Observations	120
Degrees of Freedom	118
X Coefficient	0.00
Standard Error of Coefficient	0.00

Appendix Table 33. Cover classes used to ocularly estimate understory species.

Code	Cover
1	.1
2	.55
3	1.5
4	4
5	8
6	15.5
7	25.5
8	35.5
9	45.5
10	55.5
11	65.5
12	75.5
13	85.5
14	95.5

Appendix 34. List of species found in the study area. Alpha codes follow Garrison et al. (1976); nomenclature follows Hitchcock and Cronquist 1973.

Coniferophyta

Pinaceae

ABGR	_Abies_ _grandis_ (Dougl.) Lindl.
LAOC	_Larix_ _occidentalis_ Nutt.
PIPO	_Pinus_ _ponderosa_ Dougl. ex Loud.
PSMS	_Psuedotsuga_ _menziesii_ (Mirbel) Franco

Anthrophyta

Dicotyledoneae

Apiaceae

LOTR	_Lomatium_ _triternatum_ (Pursh) Coulter & Rose
OSCH	_Osmorhiza_ _chilensis_ Hook. & Arn.
OSOC	_O_. _occidentalis_ (Nutt.) Torr.
PEGA2	_Perideridia_ _gairdneri_ (H. & A.) Math.

Apocynaceae

APAN	_Apocynum_ _androsaemifolium_ L.

Asteraceae

ACMI	_Achillea_ _millefolium_ L. ssp. _lanulosa_ (Nutt.) Piper
AGGL	_Agoseris_ _glauca_ (Pursh) Raf.
ANRO	_Antennaria_ _rosea_ Greene
ANRA	_A_. _racemosa_ Greene
ARCO	_Arnica_ _cordifolia_ Hook.
ARLO	_A_. _longifloia_ D.C. Eat.
ARSO	_A_. _sororia_ Greene
ASOC	_Aster_ _occidentalis_ (Nutt.) T.& G.
CIAR	_Cirsium_ _arvense_ (L.) Scop.
ERPU	_Erigeron_ _pumilus_ Nutt.
ERSUC	_E_. _subtrinervis_ Rybd. var. _conspicuus_ (Rydb.) Cronq.

Asteraceae (continued)

HACAC *Haplopappus carthamoides* (Hook.) Gray
var. *cusickii* Gray
HICY *Hieracium cynoglossoides* Arv-Tour.
HIAL *H. albiflorum* Hook.
HIAL2 *H. albertinum* Farr.
LASE *Lactuca serriola* L.
MAEX *Madia exigua* (Smith) Gray
MAGR *M. gracilis* (Smith) Keck
SECA *Senico canus* Hook.
SEPS *S. pseudaureus* Rybd.
SOMIE *Solidago missouriensis* Nutt. var. *extraria* Gray
TAOF *Taraxacum officinale* Weber
TRDU *Tragopogon dubius* Scop.

Berberidaceae

BERE *Berberis repens* Lindl.

Boraginaceae

PLSC2 *Plagiobothrys scouleri* (H. & A.) Johnst.
LIRU *Lithospermum ruderale* Dougl.

Caprifoliaceae

SYAL *Symphoricarpos albus* (L.)

Caryophylaceae

STLO *Stellaria longipes* Goldie
STNI *S. nitens* Nutt.
SIME *Silene menziesii* Hook. var. *viscosa* (Greene) Hitch
& Maguire

Crassulaceae

SEST *Sedum stenopetalum* Pursh

Ericaceae

ARUV *Arctostaphylos uva-ursi* (L.) Spreng.
VASC *Vaccinium scoparium* Leib.

Fabaceae

LANEC Lathyrus nevadensis Wats. ssp. cusickii (Wats.) C. L. Hitchc.
LULE Lupinus leucophyllus Doug. var. tenuispicus (A. Nels.) C. P. Sm.
TRRE Trifolium repens L.
VIAM Vicia americana Muhl.

Gentaceae

GEVI Gentiana oregana Engelm. ex Gray

Geraniaceae

GEVI Geranium viscosissium F. & M.

Grossulariaceae

RICE Ribes cereum Dougl.

Hydrophylaceae

PHHA Phacelia hastata Doug ex Lehm.

Lamiaceae

PRVU Prunella vulgaris L.

Malvaceae

SIOR Sidalcea oregana (Nutt.) Gray

Monotropaceae

PTAN Pterospora andromeda Nutt.

Onagraceae

CLRH *Clarkia rhomboidea* Dougl. ex Hook.
EPAN *E. angustifolium* L.
EPPA *Epilobium paniculatum* Nutt. ex T. & G.

Polemoniaceae

COGR2 *Collomia grandiflora* Dougl.
COLI2 *C. linearis* Nutt.

Polygonaceae

ERCO5 *Eriogonum compositum*
RUAC *Rumex acetosella* L.

Portulacaceae

CLPE *Claytonia perfoliata* Donn var. *depresa* (Gray) Jeps.

Pyrolaceae

CHUM *Chimaphila umbellata* (L.) Bart.

Ranunculaceae

DENU3 *Delphinium nuttallianum* Gray
THFE2 *Thalictrum fendleri* Engelm.

Rosaceae

AMAL *Amelanchier alnifolia* Nutt.
CRCOP *Crataegus columbiana* Howell var. *piperi* (Britt.) Eggleston
FRVI *Fragaria virginiana* Duchesne var. *platypetala* (Rydb.) Hall
FRVE *F. vesca* L. *bracteata* (Heller) Davis
GETR *Geum trifolrum* Pursh
HODI *Holodiscus discolor* (Pursh) Maxim.
POGL *Potentillia glandulosa* Lindl.
POGR *P. gracilis* Dougl ex Hook.
PRVIM *Prunus virginiana* L. var. *melanocarpa* (A. Nels.) Sarg.

Rosaceae (continued)

ROGY   *Rosa gymnocarpa* Nutt.
SPBE   *Spiraea betulifolia* Pall.

Rubiaceae

GAAP   *Galium aparine* L.
GABO   *G. boreale* L.

Scrophulariaceae

CAHIH   *Castilleja hispida* Benth. var. *hispida* Benth.
VEAR   *Veronica arvensis* L.

Violaceae

VIAD   *Viola adunca* Sm.

Monocotyledoneae

Cyperaceae

CACO   *Carex concinnoides* Mack.
CAGE   *C. geyeri* Boot.
CARO   *C. rossii* Boot.

Iridaceae

IRMI   *Iris missouriensis* Nutt.

Juncaceae

LUCA2   *Luzula campestris* (L.) D.C.

Liliaceae

SMST   *Smilacina stellata* (L.) Desf.

Orchidaceae

GOOB Goodyeria oblongifolia Raf.
HAEL Habenaria elegans Nutt.

Poaceae

AGSP Agropyron spicatum (Pursh) Sribn. & Smith
AREL Arrhenatherum elatius L.
BRCA Bromus carinatus H. & A.
CARU Calamagrostis rubescens Buckl.
ELGL Elymus glaucus Buckl.
FEMI Festuca microstachys L.
FERU F. rubra L.
FESU F. sublata Trin.
KOCR Koeleria cristata (L.) Pers.
MEBU Melica bulbosa Geyer ex Porter & Coult.
PHPR Phelum pratense L.
POCO Poa compressa L.
POPR P. pratensis L.
STLE Stipa lettermanii Vasey
TRCA Trisetum canescens Buckl.

Appendix Table 35. Cover (%) and density (# of individuals/m^2 ha^{-1}) by life-forms that were significant ($P<0.05$) by plots (means and standard errors) for 1986 and 1987.

	Thinned/ Non-Trenched	Thinned/ Trenched	Non-Thinned/ Non-Trenched	Non-Thinned/ Trenched	SE
COVER					
1986					
Forbs	0.62	0.88	0.47	0.99	0.23
Graminoids	1.81	2.21	1.51	3.42	0.90
Shrubs	1.26	1.57	1.95	3.17	0.47
1987					
Forbs	0.67	1.00	0.45	0.80	0.16
Graminoids	2.54	4.29	1.41	4.44	0.77
Shrubs	1.27	1.63	2.01	2.65	0.45
DENSITY					
1986					
Forbs	266.60	348.33	189.80	390.43	129.26
Graminoids	1133.18	1357.50	1030.82	1866.45	292.04
1987					
Forbs	530.23	617.78	239.18	443.13	168.51
Graminoids	2365.90	2939.73	1276.05	2526.68	313.09
Shrubs	87.05	113.90	96.88	132.08	23.42

Appendix Table 36. Cover (%) (log 10) of species that were significant (P<0.05) by treatments (means and standard errors) for 1985, 1986, and 1987. Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched and Trenched, and SE AB = A x B interaction. P = Probability level.

Species/Year	Non-Thinned	Thinned	Non-Trenched	Trenched	SE A	P	SE9 B	P	SE A x B	P
1985										
Achillea millefolium	-0.55	-0.22	-0.38	-0.41	0.12	0.0438	0.08	0.1434	0.11	0.9082
Aster occidentalis	-0.50	-0.14	-0.29	-0.39	0.09	0.0244	0.18	0.3794	0.26	0.4456
Poa pratensis	-0.25	0.37	0.16	-0.08	0.51	0.2186	0.10	0.0167	0.13	0.3299
Rosa gymnocarpa	-0.53	-0.39	-0.59	-0.35	0.21	0.6575	0.11	0.0261	0.16	0.0237
Trisetum canescens	0.21	0.48	0.31	0.35	0.39	0.3924	0.08	0.5012	0.11	0.0186
1986										
Achillea millefolium	-0.31	0.08	0.20	-0.44	0.11	0.03	0.06	0.0001	0.08	0.0042
Calamagrostis rubescens	-0.29	-0.61	-0.15	-0.70	0.03	0.0144	0.27	0.0476	0.38	0.4844
Lathyrus nevadensis	0.02	0.20	0.06	0.15	0.05	0.0192	0.16	0.7105	0.23	0.4098
Poa pratensis	-0.05	0.55	0.40	0.06	0.53	0.2405	0.06	0.0008	0.08	0.0266
Taraxacum officinale	-0.80	-0.32	-0.32	-0.82	0.12	0.0305	0.34	0.0877	0.48	0.4897
1987										
Achillea millefolium	-0.55	0.34	0.05	-0.33	0.19	0.0298	0.23	0.1116	0.32	0.1012
Aster occidentalis	-0.51	0.17	-0.05	-0.35	0.21	0.0474	0.19	0.0512	0.27	0.1339
Carex geyeri	1.01	0.74	1.14	0.94	0.13	0.575	0.05	0.0058	0.07	0.0851
Calamagrostis rubescens	-0.02	-0.34	0.10	-0.40	0.29	0.3535	0.19	0.0351	0.27	0.4747
Galium boreale	-0.82	-0.04	-0.44	-0.49	0.25	0.0504	0.21	0.3731	0.29	0.9632
Lathyrus nevadensis	-0.42	-0.11	-0.36	-0.20	0.19	0.7443	0.09	0.0323	0.13	0.0317
Luzula campestris	-0.82	-0.28	-0.24	-0.49	0.03	0.0094	0.25	0.3527	0.35	0.1743
Poa pratensis	-0.05	0.79	0.58	0.11	0.48	0.135	0.21	0.0259	0.30	0.2353
Stellaria longipes	-0.87	-0.70	-0.65	-0.93	0.15	0.2535	0.15	0.058	0.21	0.0352
Taraxacum officinale	-0.72	-0.08	-0.33	-0.53	0.16	0.0353	0.08	0.0163	0.12	0.3471
Tragopogon dubius	-0.63	-0.77	-0.47	-0.90	0.03	0.0235	0.17	0.0538	0.24	0.1414
Trisetum canescens	0.27	-0.33	0.57	0.05	0.77	0.9333	0.12	0.0064	0.17	0.0475

Appendix Table 37. Density (# of individuals/m^2 ha^{-1}) (log 10) of species that were significant ($P<0.05$) by treatments (means and standard errors) for 1985, 1986, and 1987.

Species/Year	Non-Thinned	Thinned	Non-Trenched	Trenched	SE A	P	SE B	P	SE A x B	P
1985										
Fragaria virginiana	1.93	2.60	2.23	2.25	0.20	0.0354	0.43	0.4492	0.61	0.0599
Symphoricarpos albus	2.73	2.25	2.37	2.63	0.55	0.426	0.14	0.0631	0.19	0.0103
Trisetum canescens	2.88	3.70	3.33	3.15	1.44	0.4789	0.20	0.8894	0.29	0.0172
Viola adunca	-1.43	-0.68	-1.17	-1.00	0.26	0.0399	0.41	0.2137	0.59	0.0834
1986										
Achillea millefolium	0.50	1.40	0.65	1.17	0.24	0.024	0.71	0.2613	1.00	0.2913
Aster occidentalis	0.10	1.35	0.23	1.15	0.37	0.0324	0.59	0.0625	0.84	0.7686
Calamagrostis rubescens	1.20	-0.08	-0.55	1.90	0.75	0.2145	0.77	0.0171	1.09	0.4539
Silene menziesii	-0.83	-1.25	-1.48	-0.50	2.08	0.866	0.34	0.0066	0.48	0.844
Taraxacum officinale	-1.53	0.05	-1.50	-0.18	0.83	0.1222	0.72	0.0495	1.02	0.5463
Trisetum canescens	2.53	3.10	2.35	3.28	1.03	0.4783	0.20	0.003	0.28	0.019
1987										
Achillea millefolium	-0.10	2.98	0.90	1.73	0.53	0.0172	0.72	0.1709	1.02	0.3452
Aster occidentalis	-0.40	2.30	0.50	1.15	0.84	0.0509	0.76	0.1519	1.07	0.2271
Calamagrostis rubescens	1.98	1.23	0.78	2.58	1.01	0.5543	0.54	0.0175	0.76	0.1308
Stellaria longipes	-1.65	-0.38	-1.35	-0.73	1.00	0.2291	0.34	0.0384	0.48	0.009
Taraxacum officinale	-1.20	0.75	-0.73	0.15	0.60	0.0493	0.29	0.0093	0.41	0.3293
Tragopogon dubius	-0.98	-1.78	-2.13	-0.50	0.71	0.2468	0.36	0.008	0.50	0.1001

Appendix Table 38. Cover (%) (log 10) of species that were significant ($P<0.05$) by plots (means and standard errors) for 1985, 1986, and 1987.

Species/Year	Thinned/ Non-Trenched	Thinned/ Trenched	Non-Thinned/ Non-Trenched	Non-Thinned/ Trenched	SE
1985					
Achillea millefolium	-0.21	-0.22	-0.60	-0.50	13.66
Aster occidentalis	-0.25	-0.02	-0.52	-0.49	0.37
Poa pratensis	0.23	0.56	-0.36	-0.14	0.19
Rosa gymnocarpa	-0.15	-0.68	-0.54	-0.53	0.23
Trisetum canescens	0.40	0.57	0.31	0.12	0.15
1986					
Achillea millefolium	-0.06	0.25	-0.79	0.17	0.12
Calamagrostis rubescens	-0.72	-0.47	-0.68	0.09	0.53
Lathyrus nevadensis	0.20	0.22	0.10	-0.06	0.32
Poa pratensis	0.49	0.62	-0.34	-0.24	0.12
Taraxacum officinale	-0.63	0.05	-0.10	-0.60	0.68
1987					
Achillea millefolium	0.32	0.36	-0.92	-0.17	0.45
Aster occidentalis	-0.09	0.48	-0.58	-0.45	0.38
Carex geyeri	1.02	1.11	0.86	1.17	0.10
Calamagrostis rubescens	-0.49	-0.15	-0.32	0.28	0.38
Galium boreale	-0.04	-0.05	-0.90	0.74	0.41
Lathyrus nevadensis	0.03	-0.29	-0.42	-0.42	0.18
Luzula campestris	-0.25	-0.31	-0.72	-0.19	0.50
Poa pratensis	0.72	0.87	-0.46	0.36	0.42
Stellaria longipes	-1.02	-0.32	-0.84	-0.90	0.30
Taraxacum officinale	-0.21	0.07	-0.82	-0.63	0.24
Trisetum canescens	0.23	0.45	-0.12	0.67	0.16
Tragopogon dubius	-0.86	-0.66	-0.94	-0.32	0.34

Appendix Table 39. Density (# of individuals/m^2 ha^{-1}) (log 10) of species that were significant ($P<0.05$) by plots (means and standard errors) for 1985, 1986, and 1987.

Species/Year	Thinned/ Non-Trenched	Thinned/ Trenched	Non-Thinned/ Non-Trenched	Non-Thinned/ Trenched	SE
1985					
Fragaria virginiana	2.25	3.05	2.23	1.63	0.86
Symphoricarpos albus	1.90	2.65	2.83	2.60	0.27
Trisetum canescens	3.50	3.93	3.18	2.55	0.41
Viola adunca	-1.05	-0.23	-1.30	-1.58	0.83
1986					
Achillea millefolium	1.60	1.15	-0.20	1.23	1.42
Aster occidentalis	0.93	1.85	-0.45	0.63	1.18
Calamagrostis rubescens	-0.83	0.85	-0.28	2.68	1.54
Silene menziesii	-1.40	-1.03	-1.55	-0.10	0.67
Taraxacum officinale	-0.80	0.85	-2.13	0.93	1.44
Trisetum canescens	3.03	3.18	1.73	3.35	0.40
1987					
Achillea millefolium	2.88	3.10	-0.90	0.68	1.44
Aster occidentalis	1.63	3.13	-0.52	-0.30	1.52
Calamagrostis rubescens	0.85	1.70	0.73	3.23	1.08
Stellaria longipes	-1.30	0.78	-1.40	-1.88	0.68
Taraxacum officinale	0.23	1.40	-1.63	-0.78	0.58
Tragopogon dubius	-2.28	-1.17	-1.98	0.03	0.71

Appendix Table 40. Cover (%) of species that were significant (P<0.05) by plots (means and standard deviations) for 1985, 1986, and 1987.

Species/Year	Thinned/ Non-Trenched		Thinned/ Trenched		Non-Thinned/ Non-Trenched		Non-Thinned/ Trenched	
1985	x̄	SD	x̄	SD	x̄	SD	x̄	SD
Achillea millefolium	1.33	1.11	1.26	1.13	0.58	0.98	0.78	1.22
Aster occidentalis	1.87	2.20	2.41	2.62	0.89	1.44	0.94	1.62
Poa pratensis	7.25	8.60	12.13	12.10	1.52	2.43	2.94	4.61
Rosa gymnocarpa	2.66	3.83	0.42	0.73	0.93	1.87	0.92	1.44
Trisetum canescens	4.40	3.41	6.38	2.79	4.26	3.99	3.52	4.29
1986								
Achillea millefolium	1.29	0.84	3.39	2.38	0.25	0.61	2.77	3.41
Calamagrostis rubescens	0.37	0.79	0.71	0.89	0.46	0.94	2.75	2.88
Lathyrus nevadensis	3.85	3.55	3.30	2.80	3.52	3.25	4.09	4.95
Poa pratensis	6.14	5.72	10.57	8.69	1.42	2.02	6.63	9.58
Taraxacum officinale	0.56	0.93	1.93	1.54	0.00	0.00	1.16	2.30
1987								
Achillea millefolium	2.35	1.20	2.67	1.21	0.12	0.26	1.33	1.27
Aster occidentalis	2.14	2.36	5.65	6.31	0.85	1.76	0.86	1.28
Carex geyeri	1.48	6.22	13.54	5.12	8.82	5.79	17.32	11.38
Calamagrostis rubescens	0.68	0.98	1.44	1.44	1.36	1.68	3.93	3.76
Galium boreale	1.70	1.41	1.90	1.72	0.15	0.51	0.40	0.98
Lathyrus nevadensis	3.01	2.99	1.33	1.94	1.16	1.77	2.10	3.74
Luzula campestris	1.31	1.32	1.33	2.04	0.43	0.76	1.31	1.34
Poa pratensis	8.48	8.42	20.18	19.97	1.44	2.48	7.20	8.50
Stellaria longipes	0.06	0.19	2.20	5.33	0.11	0.20	0.10	0.29
Taraxacum officinale	1.25	1.30	1.96	1.38	0.14	0.26	0.52	0.99
Tragopogon dubius	0.13	0.31	0.32	0.45	0.04	0.15	1.03	1.16
Trisetum canescens	2.27	1.67	6.78	6.88	1.45	1.25	10.02	9.87

Appendix Table 41. Density (# of individuals/m^2 ha^{-1}) that were significant ($P<0.05$) of species by plots (means and standard deviations) for 1985, 1986, and 1987.

Species/Year	Thinned/ Non-Trenched		Thinned/ Trenched		Non-Thinned/ Non-Trenched		Non-Thinned/ Trenched	
1985	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Fragaria virginiana	62.00	56.85	89.70	40.25	44.28	40.08	27.50	27.30
Symphoricarpos albus	36.50	32.10	86.58	76.98	55.20	53.55	47.30	52.18
Trisetum canescens	166.00	166.90	214.38	90.78	149.18	128.60	163.55	267.95
Viola adunca	4.00	33.43	5.33	4.90	4.18	10.68	2.50	5.33
1986								
Achillea millefolium	19.55	17.58	32.23	32.72	6.05	8.30	23.75	32.18
Aster occidentalis	33.85	54.18	61.40	73.32	15.63	25.03	67.30	144.60
Carex concinnoides	9.55	19.92	23.33	28.15	16.05	28.80	127.70	161.08
Silene menziesii	21.60	66.03	10.28	26.30	3.55	9.38	23.55	48.73
Taraxacum officinale	3.40	5.50	13.60	20.48	1.05	3.60	5.63	10.45
Trisetum canescens	87.05	73.15	141.10	138.28	59.18	88.30	286.55	330.30
1987								
Achillea millefolium	41.38	22.50	57.23	41.85	5.00	9.48	22.93	35.22
Aster occidentalis	65.23	85.20	104.18	90.75	22.50	37.97	26.25	56.30
Calamagrostis rubescens	37.72	58.55	45.28	48.30	31.25	42.00	154.58	191.63
Stellaria longipes	2.95	6.70	25.28	39.20	4.38	10.23	1.45	3.78
Taraxacum officinale	8.18	9.88	13.05	11.58	1.88	3.85	3.95	6.08
Tragopogon dubius	0.23	0.75	1.95	2.73	0.83	2.23	8.95	13.38

Appendix Table 42. Changes in life-forms cover (%) and density (# of individuals/m^2 ha^{-1}) (log 10) that were significant ($P<0.05$) between years, by plots (means and standard errors).

	Thinned/ Non-Trenched	Thinned/ Trenched	Non-Thinned/ Non-Trenched	Non-Thinned/ Trenched	SE
COVER					
1985-1986					
Forbs	-0.08	0.24	0.01	0.44	0.28
1986-1987					
Graminoids	0.73	2.08	-0.11	1.02	0.45
1985-1987					
Forbs	-0.03	0.35	-0.01	0.25	0.14
Graminoids	-0.25	1.47	0.68	2.30	1.57
DENSITY					
1985-1986					
Forbs	-134.77	-57.50	-1.90	172.50	108.75
1986-1987					
Forbs	263.63	269.45	49.38	52.70	145.54
Graminoids	1232.73	1582.23	245.20	660.20	467.27

Appendix Table 43. Changes in species cover(%) (log 10) that were significant ($P<0.05$) between years, by treatments (means and standard errors). Standard error (SE) A = Non-Thinned and Thinned, SE B = Non-Trenched and Trenched and SE AB = A x B interaction. P = Probability level.

Species/Years	Non-Thinned	Thinned	Non-Trenched	Trenched	SE A	P	SEB	P	SE A x B	P
1985-1986										
Achillea millefolium	-0.08	0.14	0.24	-0.19	0.20	0.2807	0.17	0.033	0.24	0.5165
Taraxacum officinale	-0.61	-0.34	-0.33	-0.63	0.34	0.3312	0.18	0.462	0.26	0.0586
1986-1987										
Achillea millefolium	-0.53	-0.10	-0.27	-0.39	0.11	0.0471	0.17	0.6354	0.24	0.0775
Arrehenatherum elatius	-0.87	-0.99	-0.84	-1.00	0.04	0.0698	0.03	0.0066	0.05	0.0105
Berberis repens	-0.56	-0.43	-0.32	-0.67	0.10	0.2585	0.07	0.0036	0.10	0.0278
Carex geyeri	-0.02	0.43	0.30	0.08	0.05	0.007	0.37	0.3791	0.53	0.6831
Taraxacum officinale	-0.76	-0.27	-0.44	-0.63	0.18	0.0678	0.06	0.0116	0.09	0.103
Tragopogon dubius	-0.71	-0.77	-0.56	-0.90	0.13	0.4451	0.08	0.0119	0.12	0.063
1985-1987										
Arrehenatherum elatius	-0.86	-0.99	-0.96	-0.87	0.12	0.0406	0.12	0.4945	0.17	0.594
Aster occidentalis	-0.50	0.11	-0.33	-0.10	0.12	0.0412	0.12	0.0297	0.17	0.3226
Carex geyeri	-0.03	-0.15	-0.45	0.31	0.12	0.9024	0.31	0.0278	0.44	0.2941
Taraxacum officinale	-0.69	-0.10	-0.50	-0.34	0.12	0.0643	0.10	0.0449	0.14	0.2899

Appendix Table 44. Changes in species density (# of individuals/m^2 ha^{-1}) (log 10) that were significant (P<0.05) between years, by treatments (means and standard errors). Standard error (SE) A = Non-Thinned and Thinned; SE B = Non-Trenched and Trenched and SE AB = A x B interactions. P = Proability level.

Species/Years	Non-Thinned	Thinned	Non-Trenched	Trenched	SE A	P	SE B	P	SE A x B	P
1985-1986										
Achillea millefolium	-0.15	0.20	-0.78	-0.85	0.49	0.2873	0.30	0.0021	0.43	0.1785
Carex geyeri	-1.58	-3.05	-2.28	-2.20	0.26	0.012	1.21	0.819	1.71	0.088
C. rossii	0.05	-1.38	-1.75	0.65	0.28	0.0201	0.71	0.0239	1.00	0.0328
Lathyrus nevadensis	-0.55	-1.13	-0.15	-1.50	0.67	0.2642	0.66	0.0419	0.94	0.801
Potentillia gracilis	-2.15	-1.38	-1.75	-1.78	0.19	0.0504	0.71	0.8931	1.01	0.7324
Rosa gymnocarpa	-0.98	-1.83	-1.25	-1.48	0.22	0.0363	0.49	0.4383	0.69	0.6789
Senecio canus	-2.00	-2.25	-2.28	-1.93	0.12	0.1006	0.16	0.0835	0.22	0.002
Silene menziesii	-0.58	-1.95	-1.93	-0.40	0.88	0.3842	0.80	0.0352	1.13	0.1564
Symphoricarpos albus	-0.43	-0.65	-0.95	-0.05	1.33	0.8335	0.58	0.1937	0.81	0.0249
Taraxacum officinale	-1.73	0.00	-1.45	-0.40	0.65	0.0649	0.56	0.0425	0.79	0.4951
Trisetum canescens	-0.40	-1.28	-2.37	0.90	1.62	0.4364	1.00	0.0318	1.42	0.0132
1986-1987										
Achillea millefolium	-0.83	1.70	0.38	0.30	0.75	0.0539	0.46	0.9438	0.65	0.3235
Aster occidentalis	-1.52	1.45	-0.03	-0.40	0.85	0.044	0.99	0.9649	1.41	0.1857
Festuca rubra	0.60	2.15	0.60	2.08	1.41	0.3422	0.67	0.082	0.94	0.0522
Galium boreale	-1.70	0.65	-0.63	-0.65	0.42	0.0233	0.56	0.7164	0.79	0.1094
Lupinus leucophyllus	-1.65	-1.55	-1.75	-1.45	0.15	0.1454	0.16	0.0232	0.23	0.0056
Poa pratensis	1.25	4.88	2.43	3.43	0.68	0.0196	0.70	0.0822	0.98	0.2634
Stellaria longipes	-1.45	-0.43	-1.25	-0.70	1.14	0.3426	0.32	0.0476	0.46	0.0069
1985-1987										
Achillea millefolium	-0.50	2.18	0.28	1.17	0.62	0.032	0.71	0.1604	1.00	0.3894
Carex geyeri	0.50	3.08	0.48	2.95	0.56	0.0252	1.06	0.0389	1.50	0.0663
Luzula camestris	-0.60	0.05	-0.52	-0.05	0.09	0.0235	1.35	0.9938	1.91	0.0962
Meica bulbosa	-2.25	-1.95	-2.20	-2.03	0.26	0.4185	0.15	0.3415	0.21	0.0455
Poa pratensis	1.78	4.78	2.15	4.23	0.76	0.0337	0.64	0.0108	0.91	0.0435
Spirea betulifolia	-1.68	-2.13	-1.88	-1.90	0.79	0.4935	0.14	0.6001	0.20	0.046
Stellaria longipes	-1.50	-0.73	-1.43	-0.83	1.04	0.3839	0.37	0.0515	0.52	0.011
Taraxacum Officinale	-1.45	-0.80	-0.85	-0.05	0.25	0.0073	0.39	0.0234	0.55	0.8035
Tragopogon dubius	-1.00	-1.83	-2.13	-0.55	1.01	0.523	0.45	0.0101	0.64	0.4405
Trisetum canescens	0.23	1.00	-1.13	2.45	3.38	0.9903	0.80	0.0119	1.13	0.0044

Appendix Table 45. Changes in species cover (%) (log 10) that were significant (P<0.05) between years, by plots (means and standard errors).

Species/Years	Thinned/ Non-Trenched	Thinned/ Trenched	Non-Thinned/ Non-Trenched	Non-Thinned/ Trenched	SE
1985-1986					
Achillea millefolium	-0.02	0.33	-0.35	0.18	0.34
Taraxacum officinale	-0.63	0.02	-0.63	0.60	0.36
1986-1987					
Achillea millefolium	-0.03	-0.19	-0.73	-0.34	0.34
Arrehenatherum elatius	-1.00	-0.98	-1.00	-0.74	0.07
Berberis repens	-0.70	-0.11	-0.64	-0.48	0.15
Carex geyeri	0.42	0.45	-0.23	0.19	0.74
Taraxacum officinale	-0.42	-0.09	-0.82	-0.70	0.17
Tragopogon dubius	-0.86	-0.66	-0.44	-0.48	0.13
1985-1987					
Arrehenatherum elatius	-1.00	-0.98	-0.93	-0.80	0.25
Aster occidentalis	-0.03	0.30	-0.61	-0.40	0.24
Carex geyeri	-0.28	0.02	-0.60	0.53	0.62
Taraxacum officinale	-0.21	0.04	-0.76	-0.63	0.19

Appendix Table 46. Changes in species density (# of individuals/m^2 ha^{-1}) (log 10) that were significant (P<0.05) between years, by plots (means and standard errors).

Species/Years	Thinned/ Non-Trenched	Thinned/ Trenched	Non-Thinned/ Non-Trenched	Non-Thinned/ Trenched	SE
1985-1986					
Achillea millefolium	-0.30	0.78	-1.20	0.90	0.60
Carex geyeri	-2.00	-4.35	-2.53	-0.60	2.42
C. rossii	-1.60	-1.10	-1.88	1.95	1.42
Lathyrus nevadensis	-0.52	-1.85	0.18	-1.25	1.33
Potentillia gracilis	-1.63	-1.05	-2.00	-2.30	1.43
Rosa gymnocarpa	-1.65	-2.03	-0.90	-1.05	0.98
Senecio canus	-1.98	-2.58	-2.55	-1.45	0.31
Silene menziesii	-2.90	-0.78	-1.03	-0.15	1.60
Symphoricarpos albus	-0.28	-1.10	-1.58	0.75	1.15
Taraxacum officinale	-0.60	0.73	-2.23	-1.23	1.12
Trisetum canescens	-1.25	-1.33	-3.40	2.60	2.01
1986-1987					
Achillea millefolium	1.88	1.53	-1.00	-0.63	0.92
Aster occidentalis	1.08	1.93	-0.93	-2.15	1.99
Festuca rubra	2.08	2.25	-0.75	1.93	1.33
Galium boreale	0.98	0.25	-2.08	-1.33	1.12
Lupinus leucophyllus	-2.00	-1.03	-1.53	-1.75	0.33
Poa pratensis	4.80	4.98	0.25	2.25	1.39
Stellaria longipes	-1.33	0.68	-1.15	-1.75	0.65
1985-1987					
Achillea millefolium	1.98	2.40	-1.25	0.25	1.41
Carex geyeri	3.03	3.13	-1.85	2.83	2.12
Luzula campestris	0.83	-0.88	-1.75	0.58	2.70
Meica bulbosa	-2.25	-1.58	-2.15	-2.35	0.29
Poa pratensis	4.65	4.95	-0.13	3.75	1.28
Spirea betulifolia	-1.95	-2.35	-1.80	-1.55	0.29
Stellaria longipes	-1.63	0.40	-1.25	-1.75	0.74
Taraxacum officinale	0.45	1.28	-2.03	-0.85	0.77
Trisetum canescens	0.95	1.05	3.03	3.48	1.60
Tragopogon dubius	-2.28	-1.25	-1.98	-0.03	0.91

Appendix Table 47. Changes in species cover (%) that were significant (P<0.05) between years, by plots (means and standard deviations).

Species/Years	Thinned/ Non-Trenched		Thinned/ Trenched		Non-Thinned/ Non-Trenched		Non-Thinned/ Trenched	
1985-1986	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Achillea millefolium	0.07	1.28	2.27	2.72	-0.34	0.95	1.99	2.41
Taraxacum officinale	0.55	0.91	1.78	1.44	-0.09	0.17	1.16	2.30
1986-1987								
Achillea millefolium	1.07	1.39	-0.72	2.16	-0.13	0.66	-1.44	2.91
Arrehenatherum elatius	0.00	0.00	0.02	0.05	0.00	0.00	0.11	0.94
Berberis repens	-0.39	2.98	0.54	2.71	-1.04	1.97	0.49	2.88
Carex geyeri	3.48	4.32	5.44	5.47	-1.73	7.42	3.32	5.07
Taraxacum officinale	0.70	1.05	0.03	1.75	0.14	0.26	-0.63	1.73
Tragopogon dubius	0.13	0.31	0.32	0.45	0.04	0.15	0.75	1.13
1985-1987								
Arrehenatherum elatius	0.44	2.33	3.51	4.20	-0.04	1.02	-0.08	0.72
Aster occidentalis	0.00	0.00	0.02	0.05	-0.11	0.40	0.28	0.67
Carex geyeri	-2.58	7.57	-0.42	8.80	-4.77	5.53	5.64	10.81
Taraxacum officinale	1.24	1.30	1.80	1.21	0.05	0.17	0.52	0.99

Appendix Table 48. Changes in species density (# of individual/m^2 ha^{-1}) that were significant (P<0.05) between years, by plots (means and standard deviations).

Species/Years	Thinned/ Non-Trenched		Thinned/ Trenched		Non-Thinned/ Non-Trenched		Non-Thinned/ Trenched	
1985-1986	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Achillea millefolium	-0.45	7.90	13.33	31.93	-2.93	6.03	14.18	18.95
Carex geyeri	276.28	614.83	-388.33	484.50	-410.20	772.15	92.08	436.73
C. rossii	57.95	174.25	10.55	121.60	-55.83	161.10	132.30	273.15
Lathyrus nevadensis	-8.18	59.20	-23.33	29.45	10.00	26.33	-5.83	28.98
Potentillia gracilis	2.28	6.93	0.00	5.00	-1.05	2.25	-1.25	3.28
Rosa gymnocarpa	-2.28	4.93	-2.23	5.23	-1.05	13.63	9.80	46.58
Symphoricarpos albus	0.23	1.75	-4.73	14.88	-1.05	13.63	9.80	46.58
Taraxacum officinale	1.13	29.80	-9.45	47.43	-20.83	50.90	20.42	44.98
Trisetum canescens	2.95	5.10	11.68	18.63	-3.55	9.90	5.00	10.55
1986-1987								
Achillea millefolium	21.83	17.42	25.00	24.78	-1.05	10.73	-0.83	20.60
Aster occidentalis	6.38	58.45	42.78	58.15	6.88	19.58	-41.05	88.45
Festuca rubra	51.13	64.03	57.50	77.32	-1.05	29.65	33.33	35.05
Galium boreale	19.55	20.20	12.23	17.20	0.43	0.98	4.18	13.08
Lupinus leucophyllus	0.23	1.75	0.28	5.50	-0.83	1.95	-3.95	5.28
Poa pratensis	320.68	293.70	611.10	548.65	32.93	103.55	90.20	108.21
Stellaria longipes	2.50	5.25	22.50	38.00	3.33	11.00	0.63	2.18
1985-1987								
Achillea millefolium	21.38	14.78	38.33	37.00	-3.95	14.13	13.33	23.15
Carex geyeri	400.78	504.75	327.78	413.80	-225.43	439.63	403.33	657.68
Luzula campestris	25.23	44.63	0.83	18.75	-4.38	12.85	28.95	36.03
Meica bulbosa	-5.68	15.00	-5.00	23.28	-0.20	1.68	-0.43	1.45
Poa pratensis	412.95	443.23	714.45	571.50	13.55	76.35	236.25	283.37
Spirea betulifolia	-0.90	3.23	-0.83	2.50	-2.70	22.48	-9.80	42.73
Stellaria longipes	0.23	3.05	22.23	40.55	3.95	10.30	0.83	3.60
Taraxacum officinale	7.73	10.02	11.10	10.83	-2.70	7.58	3.33	6.60
Tragopogon dubius	0.23	0.75	1.10	2.83	0.83	2.23	7.93	10.50
Trisetum canescens	36.12	166.03	128.60	272.80	-73.32	75.93	359.80	580.33

Appendix Table 49. Total canonical structure values of selected environmental resource variables measured in 1987.

		CAN1	CAN2	CAN3	CAN4
Soil Water Potential					
May 6	0-20 cm	-0.12343	0.561846	0.108481	0.010498
	20-40 cm	-0.16661	0.557689	0.152078	0.009248
	40-60 cm	-0.17570	0.586049	0.188326	0.002825
May 20	0-20 cm	0.017209	0.452692	0.337111	-0.02494
	20-40 cm	-0.33695	0.47762	0.386211	0.016862
	40-60 cm	-0.35836	0.513969	0.351005	0.028847
June 3	0-20 cm	-0.02355	0.483325	0.269156	-0.01878
	20-40 cm	-0.28982	0.51917	0.359908	0.011783
	40-60 cm	-0.41103	0.54642	0.401124	0.014567
June 22	0-20 cm	0.128242	0.526033	0.006127	-0.02241
	20-40 cm	-0.15806	0.670928	0.455377	-0.01542
	40-60 cm	-0.33089	0.725207	0.441337	0.001537
July 12	0-20 cm	0.29897	0.536177	0.230922	-0.04651
	20-40 cm	0.117627	0.608339	0.38974	-0.02644
	40-60 cm	-0.03707	0.818844	0.262851	-0.00416
July 27	0-20 cm	0.178005	0.55068	0.123509	-0.03203
	20-40 cm	-0.06613	0.691869	0.395943	-0.01909
	40-60 cm	-0.03821	0.66144	0.381195	-0.01279
August 15	0-20 cm	0.286362	0.371585	0.205591	0.050408
	20-40 cm	0.004511	0.584635	0.449186	-0.03450
	40-60 cm	0.063664	0.557065	0.408201	-0.02826
August 27	0-20 cm	0.371999	0.583222	0.477472	-0.06769
	20-40 cm	0.081334	0.630912	0.488113	-0.05545
	40-60 cm	0.237635	0.693235	0.471522	0.059258
Sept. 13	0-20 cm	0.26982	0.57483	0.332622	-0.06674
	20-40 cm	0.045565	0.708076	0.428587	-0.02231
	40-60 cm	0.015947	0.680717	0.422744	-0.03693
Light		0.960262	-0.02256	-0.00375	-0.12696
Mineralizable Nitrogen					
	0-20 cm	0.155777	-0.36964	-0.46965	0.007663
	20-40 cm	-0.03296	-0.56646	-0.18515	0.024945
NH_4	20 cm	0.324119	-0.22658	-0.38413	-0.01089
	40 cm	-0.15981	-0.35263	-0.33718	0.048951
NO_3	20 cm	0.387991	-0.40655	-0.32691	0.0592
	40 cm	-0.28557	-0.47124	-0.28721	0.062326