

AN ABSTRACT OF THE THESIS OF

Suzanne W. Simard for the degree of Master of Science
in Forest Science presented on February 14, 1989
Title: Competition Among Lodgepole Pine Seedlings and Plant
Species in a Sitka Alder-Dominated Shrub Community
in the Southern Interior of British Columbia

Abstract approved: Signature redacted for privacy.
Dr. Steven R. Radosevich

Sitka alder (*Alnus sinuata* (Regel) Rydb.) dominates many lodgepole pine (*Pinus contorta* ssp. *latifolia* Dougl.) sites following clearcutting in the Montane Spruce zone of the southern interior of British Columbia. The objectives of this study were to examine the effects of the sitka alder-dominated shrub community on the performance of lodgepole pine and levels of environmental resources and conditions. Competitive interactions were examined in two studies: (1) among two year-old planted seedlings and plant species in various experimentally created shrub densities (0 to 2514 clumps/ha) and herb covers (0 to 100%), and (2) among eight year-old naturally regenerated saplings and plant species in an undisturbed community.

In the first study, survival of seedlings among the experimentally created competition levels was 86% two years after planting. The main causes of mortality were drought and browsing by hares (*Lepus* sp.). Survival rate was not significantly affected by shrub and herb densities; however, survival was lowest where all vegetation had been removed. Seedling mortality in the total removal treatment may have been the result of high radiation loads and low moisture availability immediately following planting.

Mean seedling size in the plantation was negatively affected by shrub and herb density. Stem diameter was the most responsive performance measure, smaller on average by 25% when seedlings were growing among maximum shrub and herb densities as compared with those growing free of competition. Height, in contrast, increased as shrub and herb densities increased. The decrease in diameter and increase

in height in response to increasing vegetative competition reflected patterns in resource (particularly carbon) allocation.

Several environmental factors were important to the enhancement of seedling water uptake and growth when competing vegetation was removed. Significant increases in seedling water uptake did not coincide with increases in soil water potential, but rather with increases in soil temperatures. Increases in seedling diameter corresponded with increased soil and air temperatures, light availability and mineralizable $\text{NO}_3\text{-N}$.

Individual seedling size in the plantation decreased with increasing amounts of neighboring plants. Visual estimates of percent cover of neighboring plants (extensive interspecific competition indices) explained more variation in pine size than did the more detailed measurements of alder size and proximity (intensive indices). Percent cover of all shrubs and herbs accounted for 16% of the variation in height:diameter ratio while angular dispersion and distance to neighboring sitka alder accounted for only 9%. A competition threshold, i.e. the amount of neighboring vegetation at which competition began and growth was limited, was not identified. Seedlings with the largest stem diameters, however, occurred in neighborhoods with less than 10% cover of herbs and shrubs each. The best multiple regression models developed explained 22% of the variation in pine diameter and 43% of the variation in height. The independent variables were initial height, seedling vigour, browsing damage and percent cover of all shrubs. Light and, to a lesser degree, soil water available to seedlings were reduced by neighboring vegetation.

Within the experimentally created competition levels, sitka alder clumps sprouted to a mean height of 70 cm and mean diameter of 73 cm two growing seasons after manual cutting. The tallest stems (125 cm) reached 42% of the pre-treatment height (3 m). The density of sprouting alder clumps had a significant effect on the development of most neighboring shrub and herb species. Percent cover of alder, thimbleberry (*Rubus parviflorus*), fireweed (*Epilobium angustifolium*) and pinegrass (*Calamagrostis rubescens*) was greatest in the intermediate density range of 1258 to 1886 clumps/ha. Within this

density range, threshold levels of environmental resources and conditions may have been reached which resulted in the greatest vegetative cover. Two growing seasons after planting, all neighboring species except grouseberry (*Vaccinium scoparium*) were overtopping pine seedlings.

In the second study of a 10 year-old undisturbed sitka alder-dominated community, two vegetation types were identified. Type I was dominated by lodgepole pine and pinegrass while type II was dominated by sitka alder, thimbleberry and black huckleberry (*Vaccinium membranaceum*). The size of individual pine saplings was more negatively affected by neighboring plants in type II than I. Sitka alder, of all the dominant species in the undisturbed community, had the greatest competitive effect on pine size. The extensive competition index, percent cover of sitka alder, explained 45% of the variation in stem diameter. In contrast, the intensive indices, height of and distance to neighboring sitka alders, together explained 40% of the variation in stem diameter. A clearly defined competition threshold was not identified. Rather, pine size increased linearly as sitka alder densities decreased. Sitka alder had a negative effect on light availability to pine, particularly in type II.

Competition Among Lodgepole Pine Seedlings and Plant
Species in a Sitka-Alder Dominated Shrub Community
in the Southern Interior of British Columbia

by
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A THESIS
submitted to
Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed February 14, 1989

Commencement June, 1989

ACKNOWLEDGEMENTS

I am grateful to the many people who provided support and encouragement during my post-graduate endeavors.

I was attracted to Oregon State University by the progressive thinking on forest vegetation management of my major professor, Dr. Steven Radosevich. Steve provided direction and counsel during my research, but allowed me the independence I needed to satisfy my curiosity. I thank the rest of my committee, Dr.'s Mark Wilson, Dave Hibbs and Neil Christensen, for their advise during the preparation of my thesis. I am grateful to Dave Coates for the suggestions, outlook and friendship he offered during the formative stages of the project.

Funding for the project was graciously provided by the British Columbia Ministry of Forests and Forestry Canada through the Federal Resource Development Agreement (FRDA). I thank Mr. Alan Vyse, Forest Science Officer for the Kamloops Forest Region, for giving me the opportunity to initiate this research and for his continual faith in my ability. I am grateful to consultants and staff of the Ministry of Forests who provided assistance, advise and encouragement during the project. In particular, I thank Bob Stathers for installing the microenvironment station and Dennis Lloyd for his keen interest.

Multitudes of people helped with the field and lab work, many of whom are unnamed but not forgotten. Robyn Simard was a driving force behind the establishment of the experiment during the hot summer of 1987. Robyn never faltered, even when the misery factor was maxing-out, and always made me think about what we were doing. Jean Mather and Andrea Gleichoff also provided valuable field assistance during 1987 and 1988, respectively. June Simard, my mother, was always keen to help and was the only school teacher in Kamloops who helped with herbicide application and pre-dawns before class. Peter Simard, my father, relived his youth at Mable Lake when he cleared slash between treatment plots using his chain saw. Carol Glassman provided much needed advise and assistance in the soils laboratory.

The day-to-day trials and tribulations of this endeavor were shared with my friend and confidant, Don Sachs. Don helped in many aspects, from planting trees to computer consulting to providing love.

DEDICATION

*I dedicate this thesis to June Simard,
my mother, who inspired me to develop
my intellect through higher education.*

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**Competition Among Lodgepole Pine Seedlings and Plant Species
in a Sitka Alder-Dominated Shrub Community in the
Southern Interior of British Columbia**

INTRODUCTION

Successful conifer regeneration in British Columbia (B.C.) requires an understanding of the causal biotic and abiotic factors behind poor seedling performance. Although rehabilitation of the backlog of unsuccessfully regenerated lands appears to require reduction of competing vegetation, little is known about the interactions between planted seedlings, competing vegetation and the physical environment. In order to justify the use of expensive competition release treatments, foresters must develop an understanding of the interspecific competitive effects of vegetation on conifer seedlings.

Lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) is an important commercial tree species in the Kamloops Forest Region (K.F.R.) of the southern interior of B.C. Even-aged stands of seral lodgepole pine cover extensive areas in the Montane Spruce (MS) zone (Mitchell and Green 1981). Approximately 10,000 hectares of lodgepole pine sites are harvested annually in the K.F.R., of which 20 to 50% are expected to require vegetation management (Ivanco, 1985¹). The problem is expected to increase annually as lodgepole pine constitutes an increasingly larger proportion of the allowable annual cut.

The MS zone occurs in the Very Dry and Dry Climatic Regions of southern B.C. (Mitchell and Green 1981). It occupies an elevation belt between the upper Engelmann Spruce - Subalpine Fir (ESSF) zone and the lower Interior Douglas Fir (IDF) zone (approximately 1200 to 1700 m elevation). The climate of the MS zone is characterized by long cold winters and moderately short, warm summers. There is a significant growing season moisture deficit. Of all the zones located in the Very Dry and Dry Climatic Regions, the MS zone has the greatest potential for forest productivity (Mitchell and Green 1981).

¹ B. Ivanco, Planning Forester, Kamloops Forest Region, pers. comm.

The dominant understory species in lodgepole pine stands in the MS zone is sitka alder (*Alnus sinuata* (Regel) Rybd.). Shrubs commonly associated with sitka alder include black huckleberry (*Vaccinium membranaceum*), grouseberry (*Vaccinium scoparium*) and thimbleberry (*Rubus parviflorus*). Associated herbs include pinegrass (*Calamagrostis rubescens*) and fireweed (*Epilobium angustifolium*).

A well developed sitka alder-dominated shrub community usually is left intact following the harvest of lodgepole pine stands. Although sitka alder is moderately shade tolerant (Krajina et al. 1982), it thrives in full sunlight and rapidly increases in cover soon after harvest (Haeussler and Coates 1985). It rapidly colonizes exposed mineral soil by seed and sprouts from root crowns and stems damaged after manual cutting or mechanical site preparation. Sitka alder is most abundant on mesic and subhygric sites in the MS zone (Angove and Bancroft 1983), for which Mitchell and Green (1981) have recommended brush management following harvesting. Conard (1984) recognized sitka alder as a potential competitor to forest crop trees in B.C.

Sitka alder efficiently fixes nitrogen at rates ranging from 20 to 62 kg/ha/yr (Crocker and Major 1955, Ugolini 1968, Mitchell 1968, Dalton and Naylor 1975, Binkley 1982a and 1982b). Sitka alder may benefit crop trees by increasing the nitrogen capital of forest soils (Binkley 1982a and 1982b, Harrington and Deal 1982) but the community also may suppress conifers by competing for moisture, light or nutrients. Although there are no studies which specifically examine competitive interactions between sitka alder and lodgepole pine, there is considerable evidence that vegetation communities have a negative effect on the growth and survival of lodgepole pine (Beurmeyer 1984, Corns and Pluth 1984, Cannell et al. 1984, McDonald et al. 1983, Clark and McLean 1979 and 1975, Lotan and Perry 1977, McMinn 1974).

Competing vegetation can negatively affect pine performance by modifying environmental conditions (e.g. temperature) and aggravating resource (e.g. water, light and nutrient) limitations. The consequence of competition is determined by the physiological response of pine individuals to the resources and conditions of their

microenvironment (Radosevich and Osteryoung 1987). To understand the mechanisms underlying competitive interactions between lodgepole pine and the sitka alder-dominated shrub community, it is therefore necessary to identify limiting environmental conditions and resources and plant responses to them. In sub-boreal forests of the interior of B.C., the performance of lodgepole pine seedlings has been affected by soil temperature and light (Coates 1987), moisture and nutrient availability (Vyse and Navratil 1985).

The intent of this study was to investigate competitive interactions between lodgepole pine and plant species in a sitka alder-dominated shrub community. Two approaches were taken. The first approach investigated the response of two year-old planted seedlings to manipulated densities and proximities of sitka alder and associated plants. The abundance of sitka alder and understory plants were systematically varied, and the survival and growth responses of the seedlings were evaluated. In addition, the availability of environmental resources and changes in environmental conditions over the range of competition levels were monitored in order to develop an understanding of the competition processes that were occurring.

Hence, the objectives of the first approach were:

1. To determine the effects of the abundance of sitka alder and associated shrubs and herbs on the performance (survival, growth and plant moisture stress) of lodgepole pine seedlings.
2. To determine the effects of the abundance of sitka alder and associated shrubs and herbs on levels of:
 - (i) environmental resources (soil moisture, available light, total and mineralizable nitrogen), and
 - (ii) environmental conditions (soil and air temperature).
3. To develop relationships between the performance of lodgepole pine seedlings and levels of environmental resources and conditions.

The second approach was a retrospective study of interactions among naturally regenerated lodgepole pine saplings and plant species in an undisturbed sitka alder-dominated shrub community. Neighborhood

techniques were used to develop a number of interspecific competition indices. The indices were used as independent variables in regression models to explain the variation in size of the eight year-old pine saplings. In addition, the relationships between light availability and interspecific competition were examined. Hence, the objectives of the second approach were:

1. To determine the effects of the abundance of sitka alder and associated plants on the size of lodgepole pine saplings.
2. To determine the effects of the abundance of sitka alder and associated plants on light availability.
3. To examine the relationship between the size of lodgepole pine saplings and light availability.

Effects of Abundance of Sitka Alder and Herbs on Lodgepole Pine Seedling Performance and Microenvironment

CHAPTER 1

INTRODUCTION

Lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) is an important commercial tree species in the Montane Spruce (MS) zone in the southern interior of British Columbia (B.C.). The MS is a middle elevation zone (1200 to 1700 m) characterized by long cold winters, moderately short warm summers, and a significant growing season moisture deficit (Mitchell and Green 1981). Approximately 10,000 hectare of lodgepole pine forests are harvested annually in the Kamloops Forest Region, of which 20 to 50% are expected to require vegetation management (Ivanco, 1985²).

Sitka alder (*Alnus sinuata* (Regel) Rybd.) is an abundant understory species in lodgepole pine forests. It increases in abundance following harvesting and burning by capturing the increased growing space, sprouting from damaged stems, and seeding in exposed mineral soil. Sitka alder has been shown to benefit conifer growth through nitrogen fixation (Binkley 1982a and 1982b, Harrington and Deal 1984) but may also compete for light, moisture or nutrients. Other shrub and herb species associated with sitka alder also may negatively interfere with lodgepole pine seedling survival and growth. Shrub alder complexes have been identified as potential vegetation management problems in B.C. (Conard 1984).

Survival and growth of planted lodgepole pine seedlings are affected by both the microclimate and competition with associated vegetation. Soil temperature and light, moisture and nutrient availability affected the performance of lodgepole pine in sub-boreal forests in the interior of B.C. (Vyse and Navratil 1985, Coates 1987).

² B. Ivanco, Planning Forester, Kamloops Forest Region, pers. comm.

Although there are no studies which specifically examine competitive interactions with sitka alder, there is considerable evidence that vegetation communities have a negative effect on the growth and survival of lodgepole pine (Corns and Pluth 1984, Cannell and Rothery 1984, McDonald et al. 1983, Clark and McLean 1979 and 1975, Lotan and Perry 1977).

The objective of this study was to examine the effects of the sitka alder shrub community on the performance of lodgepole pine seedlings and the levels of environmental resources and conditions.

METHODS

Study Site

The study site is located in the Thompson Plateau Dry Montane Spruce (MSb1) biogeoclimatic subzone in the southern interior of B.C. (Mitchell and Green 1981). It is located 13 km northwest of Monte Lake, which is about 45 km southeast of Kamloops, B.C. (Figure 1.1). The elevation is 1400 m. The site occupies a middle slope position and is of north aspect, uniform slope (25%) and uniform topography.

The original maturing seral lodgepole pine stand was harvested using grapple skidders during the summer of 1977. The site was mechanically site prepared the same year. Today the site is dominated by a dense stand of sitka alder and is satisfactorily restocked with naturally regenerated 8 year-old lodgepole pine.

The vegetation type is *Pinus contorta* var. *latifolia* - *Alnus sinuata* - *Pleurozium schreberi*. The site association is classified as zonal (MSb1/1.1) (Lloyd unpubl.). The dominant landform is morainal blanket and the lithology is grano-diorite. The soil classification is Brunisolic Gray Luvisol (Canadian Soil Survey Committee 1978). Soils are well drained with no root-restricting layers within 60 cm. Most roots, however, are within 40 cm depth. Soil texture varies with horizon: silty loam in the Ae and Bm horizons and clay loam in the Bt horizon. Coarse fragment content increases with depth: 5% by volume in the Ae (0-2 cm), 10% in the Bm (2-12 cm) and 40% in the Bt (12-60+ cm). The humus layers are 4 to 9 cm thick. The humus form is Orthihemimor, which is prevalent in dry boreal climates (Klinka et al. 1981). It is characterized by abundant fungal hyphae in the compact Fq horizon. There is little faunal activity in the loose litter horizon.

The climate of the site is characterized by relatively long, cold winters and moderately short, warm summers. There is a significant growing season moisture deficit. Mitchell (1983) estimates the mean annual precipitation as 730 mm, mean snowfall 450 cm, mean annual

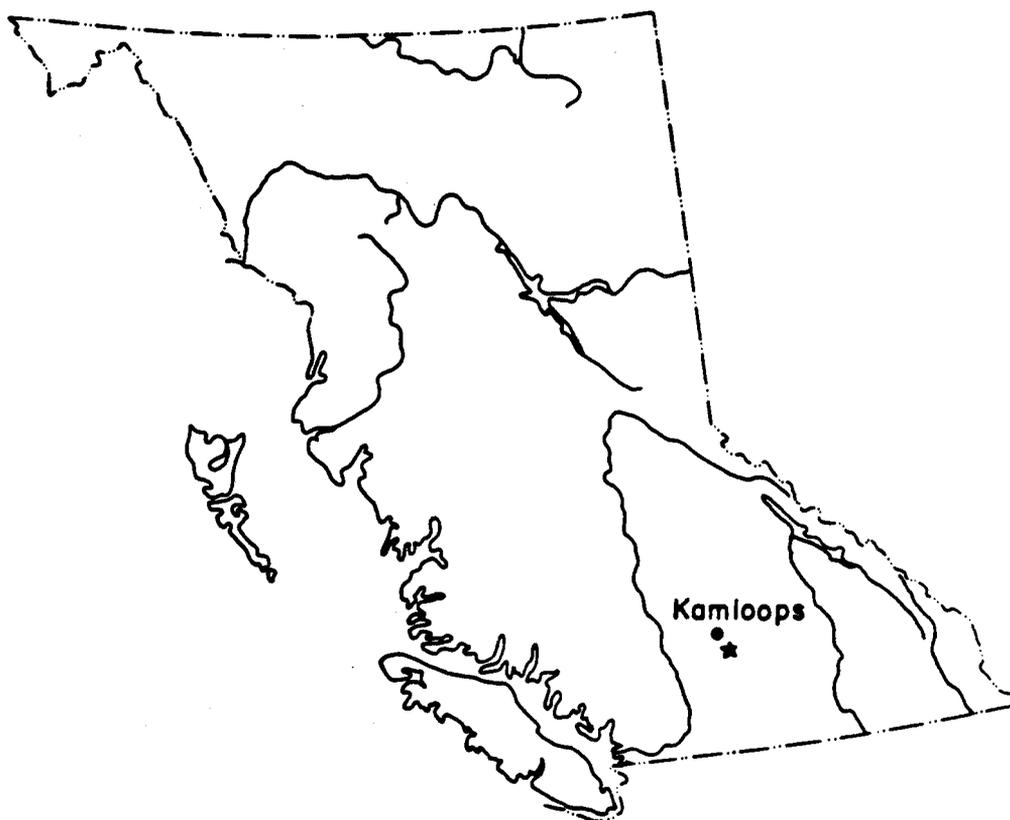


Figure 1.1. The study site, indicated by the star, is located approximately 40 km southeast of Kamloops, British Columbia.

temperature 3⁰C, and frost free period 70 days.

Experimental design

The experimental design was a randomized complete block with three replicates. Seven treatments were randomly assigned to 17.5 m x 17.5 m square plots within each block.

Blocking was done in the following manner. A total of twenty-one treatment plots were located in the upper portion of the clearcut, where sitka alder density was high and relatively uniform. Each treatment plot was surveyed for density and height of individual sitka alder clumps, and percent cover of the understory shrubs and herbs. An importance index was calculated for each treatment plot. The index was a summation of the values for the three biological characteristics measured. An analysis of variance was used to test for significant differences in importance indices among treatment plots, and indices were compared among plots using Waller and Duncan Bayes LSD procedure (Duncan 1975). Based on differences among importance indices, most treatment plots were separated into one of three blocks. Where blocks were incomplete, treatment plots with similar importance indices were added until blocks were comprised of seven treatment plots each. The seven treatment plots in each of the three blocks were contiguous with each other. Block 1 generally occupied the lower slope position, block 2 the middle and block 3 the upper.

Treatments

Seven treatments were applied which covered wide ranges in density of sitka alder (0 to 2514 clumps/ha) and percent cover of herbs (0 to 100%) ("herbs" refers to both herbs and low-growing shrubs). Alder densities were established by first manually cutting all clumps at the root collar and second by controlling the amount of regrowth by selective application of 2,4-D (2,4-dichlorophenoxy acetic acid) amine. The alder treatments were characterized by the density

of sitka alder allowed to sprout. The herb treatments were established by applying glyphosate (isopropylamine salt) to herbs in a specified area of the treatment plots using backpack sprayers. The herb treatments were characterized by the percent ground cover of herbs and low-growing shrubs remaining.

The seven treatments applied are described in Table 1.1 and shown in Figure 1.2. Five treatments (1-5) represented a gradient in alder density and three treatments (5-7) represented a gradient in herb abundance. An even-aged plantation of lodgepole pine seedlings was established among the treatments on July 4, 1987. A total of 1,239 lodgepole pine plugs (PSB 211) were planted. Each treatment plot was planted with 49 seedlings, arranged in a seven by seven grid at a square spacing of 2.5 m. Ten spare seedlings, which were used for destructive sampling, were planted between the rows.

Seedling measurements

Survival and growth

Survival and condition (good, moderate, poor or moribund) were assessed for all planted seedlings in each treatment plot. Assessments were performed at the end of the first (1987) growing season and twice (spring and fall) during the 1988 growing season. Seedling size was measured at the time of planting (spring 1987), at the end of the first growing season (fall 1987), and at the end of the second growing season (fall 1988). All seedlings were planted the spring of 1987 so size measurements in the fall of 1987 and 1988 were measures of one year and two year *growth*, respectively. Consequently seedling size often will be referred to as *growth*.

Only the inner 25 seedlings in each treatment plot were measured, leaving the outer row of seedlings as a buffer. Growth measurements were total height, stem diameter, crown diameter and height to base of live crown. Using these parameters annual diameter increment, annual height increment, D2H (diameter squared x height), height:diameter

Table 1.1 Treatments applied to create gradients in sitka alder density and herbaceous cover.

NUMBER	NAME	DESCRIPTION
1	100% alder:100% herbs	100% of the alder was allowed to regrow (2514 clumps/ha) and the herb layer was left intact.
2	75% alder:100% herbs	75% of the alder allowed was to regrow (1886 clumps/ha) and the herb layer was left intact.
3	50% alder:100% herbs	50% of the alder was allowed to regrow (1258 clumps/ha) and the herb layer was left intact.
4	25% alder:100% herbs	25% of the alder was allowed to regrow (630 clumps/ha) and the herb layer was left intact.
5	0% alder:50% herbs	none of the alder was allowed to regrow and 50% of the herb layer was killed.
6	0% alder:100% herbs	none of the alder was allowed to regrow and the herb layer was left intact.
7	0% alder:0% herbs	none of the alder was allowed to regrow and all of the herb layer was killed.

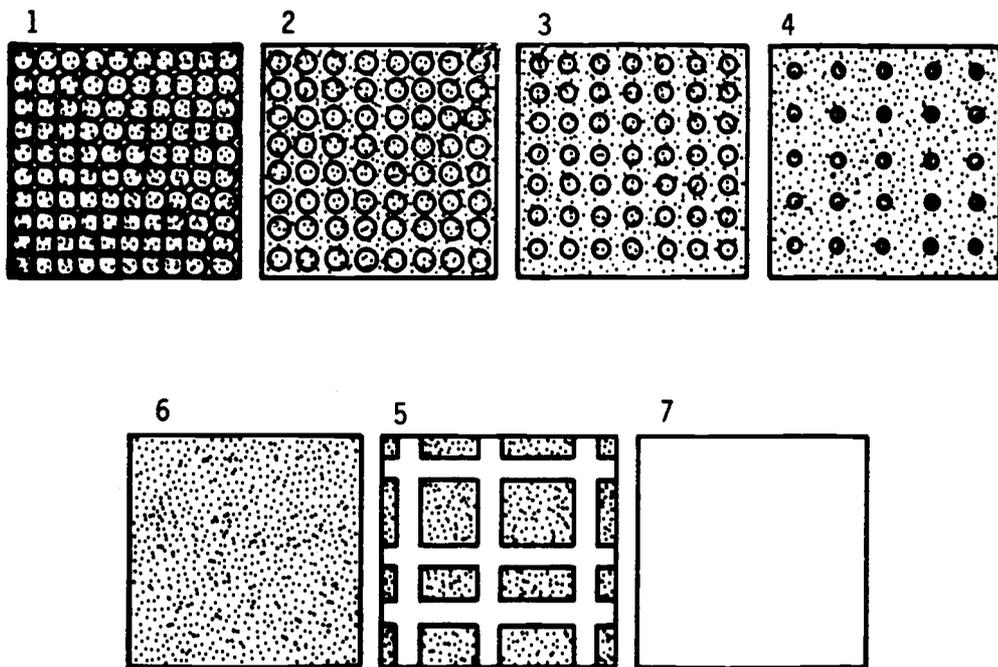


Figure 1.2 Seven treatments were applied which represented varied densities of alder (expressed as the % of the maximum density of 2514 clumps/ha) and percent ground cover of herbs remaining. The treatments were: 1=100% alder:100% herbs, 2=75% alder:100% herbs, 3=50% alder:100% herbs, 4=25% alder:100% herbs, 6=0% alder:100% herbs, 5=0% alder:50% herbs and 7=0% alder:0% herbs.

ratio, crown area and crown volume were calculated. Damage cause and the condition of the tree, leader and stem were assessed concurrently with the growth measurements.

Xylem water potential

Predawn and midday xylem water potentials were estimated on current year lateral branches of spare seedlings in the field using a Scholander pressure chamber (Scholander et al. 1965, Waring and Cleary 1969). A minimum of 2 seedlings per treatment were sampled in treatments 1 (100% alder, 100% herbs), 6 (0% alder, 100% herbs) and 7 (0% alder, 0% herbs). Six measurements were taken at roughly 4 week intervals during the 1988 growing season.

Environment measurements

Environmental conditions were continuously monitored using a Campbell Scientific CR10 data logger, which was installed at a central location between treatments 1 (100% alder, 100% herbs), 5 (0% alder, 50% herbs) and 7 (0% alder, 0% herbs) in block 2. Relative humidity, air temperature and solar radiation were monitored at 1.5 m height at the central location. Precipitation amount and frequency were recorded using a tipping rain gauge attached to the data logger.

Soil and air temperature

Soil and air temperature were continuously monitored at one location in each of treatments 1, 5 and 7 in block 2. Thermocouples attached to thermistors were located 5 and 30 cm below, and 15 cm above the mineral soil surface. The thermocouples used to measure air temperature were shaded with aluminum shields.

Soil moisture

During the 1987 growing season, percent soil moisture was estimated in treatments 1 (100% alder, 100% herbs), 6 (0% alder, 100% herbs) and 7 (0% alder, 0% herbs) using gravimetric sampling. Percent soil moisture was estimated four times during 1987. Samples were collected at three depths (0-10 cm, 10-20 cm and 20+ cm) and sealed in metal gravimetric tins. Samples were weighed, oven dried for 24 hrs at 105°C, then weighed again. Percent soil moisture by weight was calculated by difference.

During the 1988 growing season, soil moisture was measured both gravimetrically and using a Troxler 3300 Series neutron probe. Volumetric water content (and soil water potential) was estimated gravimetrically in Treatments 1, 6 and 7 at 0-10 cm depth on April 24, May 23, July 18 and August 29. Additional samples at 25-30 cm depth were taken on August 29.

Soil water potential was estimated using a neutron probe in Treatments 1, 6 and 7 during the 1988 growing season. Measurements were taken five times at roughly four week intervals. Five access tubes were located in each treatment across the three blocks (total of 45 tubes). Where possible tubes were installed to a depth of 75 cm, however the presence of rocks resulted in considerable variation in tube depths. Count ratios were recorded at depths of 30, 45, 60 and 75 cm, depending on the depth of the access tube. Count ratios were calibrated to volumetric water content using gravimetric sampling (Appendix). Calibration was done on two tubes at two sampling dates, July 25 and October 1, 1988. Relationships between volumetric water content and soil water potential were developed for each depth using pressure-plate analysis (Appendix).

Available light

Photosynthetically active radiation (PAR) available to seedlings was measured using a Licor line sensor. PAR was measured at (a)

seedling terminal bud and (b) 1 m heights for a subset of 15 to 20 seedlings in each of treatments 1, 3, 6 and 7. Only healthy, undamaged seedlings were sampled. Two perpendicular measurements were made at each of the two heights and averaged. The proportion of PAR at 1 m height that reached the terminal bud was calculated by dividing the (a) by (b). Measurements were taken between 12:00 and 14:30 hr. on August 22, 1988. On this day the sky was clear and plant leaves were fully expanded.

Soil nitrogen capital

A baseline analysis of mineral soil total and mineralizable nitrogen was done for each treatment during the fall of 1987. A second analysis will be done in 1992 to examine the effects of varying densities of sitka alder on soil nitrogen capital.

Samples were collected from the top 15 cm of mineral soil on September 21 and 22, 1987. Fifteen subsamples, weighing approximately 20 grams each, were collected from each treatment plot using a standard oakfield core. The subsamples were composited into three samples and stored in plastic bags. The cooled samples were transported to the Forest Sciences Laboratory at Oregon State University. Soil extractions were completed by the end of October and total and mineralizable (NH_4 and NO_3) nitrogen were analyzed on a Technicon Autoanalyzer at the end of January, 1988.

The samples were cleaned of large stones and organic debris. Percent soil moisture content was determined for 10 grams of each sample. Total nitrogen was estimated using the technique described by Bremner and Mulvaney (1982). Total N was estimated on 0.5 grams of the dried 2mm fraction by colorimetry on semi-micro Kjeldahl digests. The sample size was 63 (21 experimental units x 3 samples/unit).

Mineralizable soil nitrogen was estimated using the aerobic incubation technique described by Jenkinson (1968). Mineralizable nitrogen as ammonium-nitrogen ($\text{NH}_4\text{-N}$) and nitrate-nitrogen ($\text{NO}_3\text{-N}$) were determined on field moist samples. Three replications, weighing

10 ± 0.05 grams, were taken from each sample. All replications (total of 189 samples) were analyzed for NH₄-N and only one (total of 63 samples) was analyzed for NO₃-N. Samples were initially extracted in 50 ml 1M KCl and placed in a shaker for 1 hour (hereafter referred to as initial extractions). Additional samples were incubated at 40% moisture content for 21 days at 25°C. The samples were then extracted in 50 ml 1M KCl and shaken for 1 hour (hereafter referred to as mineralized extractions). The supernatant of both the initial and mineralized samples were collected in autoanalyzer vials and analyzed for NH₄-N and NO₃-N on the autoanalyzer. Mineralizable NH₄-N and NO₃-N were calculated as the difference between the mineralized and initial extractions.

Analytical approach

Analysis of variance was used to test for differences between treatment means of pine performance and environment variables. The pine performance variables tested were survival, size (diameter, height, D2H and height:diameter ratio) and xylem water potential. The environment variables tested were soil water potential, available light, and total and mineralizable soil nitrogen. Treatment means were compared using the Waller and Duncan Bayes LSD procedure (Duncan 1975). Means were considered different at the 0.10 significance level. Due to the slow growth of conifers in B.C., differences in size among treatments after only two growing seasons are not easily detectable. Early identification of differences was facilitated by using the 0.10 significance level, which was considered adequate by the researcher in view of the experimental environment. Researchers conducting similar competition experiments have found that differences in conifer size among treatments became progressively larger and more significant year after year (Wagner 1988³).

The mean size (height, diameter, D2H and height:diameter ratio)

³ B. Wagner, Oregon State University, pers. comm.

of lodgepole pine seedlings in different treatment combinations were compared using planned contrasts. The planned contrasts were:

1. Is 100% alder regrowth different from any reduction in alder regrowth?
Treatment 1 vs Treatments 2,3,4,5,6,7
2. Is no alder regrowth different from partial alder regrowth?
Treatment 5,6,7 vs. Treatments 1,2,3,4
3. Is complete herb removal different from no or partial herb removal?
Treatment 7 vs. Treatments 5,6
4. Is 100% alder regrowth and no herb removal different from 0% alder regrowth and complete herb removal?
Treatment 1 vs. Treatment 7
5. Is 100% alder regrowth different from 0% alder regrowth?
Treatment 1 vs. Treatment 6
6. Is no herb removal different from complete herb removal?
Treatment 6 vs. Treatment 7

Response models of the seedling size variables (diameter, height, D2H and height:diameter ratio) were fit to the levels of competition represented in the treatments. Regression equations were developed which described the relationship between the dependent variables representing mean seedling growth and the independent variables: (a) density of alder (100%, 75%, 50%, 25% and 0% of the maximum density of 2514 clumps/ha) and (b) cover of herbs (100%, 50% and 0%). Using seedling diameter as an example of the dependent variable, the general form of two linear models fit were:

$$(a) \text{ diameter} = b_0 + b_1 (\text{alder density})$$

$$(b) \text{ diameter} = b_0 + b_1 (\text{herb cover})$$

The general form of two quadratic models fit were:

$$(a) \text{ diameter} = b_0 + b_1 (\text{alder density}) + b_2 (\text{alder density})^2$$

$$(b) \text{ diameter} = b_0 + b_1 (\text{herb cover}) + b_2 (\text{herb cover})^2$$

RESULTS

Lodgepole pine performance

Survival and condition

Overall seedling survival was 92% by the end of the first growing season (fall 1987) and 88% of the seedlings were in good to moderate condition. There were no significant differences in survival among treatments. However, the lowest survival (84%) generally occurred in treatments 5 and 7, where all of the alder and half or all of the herb cover were killed (Table 1.2). By the fall of 1987, 79% of the seedlings in treatments 5 and 7, and 91% of the seedlings in the remaining treatments were in good to moderate condition.

The main causes of seedling damage in 1987 (Table 1.3) were drought (10%) and browsing (12%) by hares (*Lepus* sp.). In treatments 5 and 7, 15% of the seedlings were affected by drought and 13% were browsed. In addition, aphids may have served as pathogen vectors resulting in very early and severe mortality in treatment 7, block 3, where survival was only 64% by the fall of 1987. In the remaining treatments, only 8% of the seedlings were affected by drought and 11% were browsed.

Overall survival decreased to 87% by the spring and 86% by the fall of 1988. Ninety-six percent of the living seedlings were in good to moderate condition by the end of the second growing season. There were no significant differences in survival among treatments. However, survival in treatments 5 and 7 was generally lower (77%) than in the remaining treatments (90%) by fall of 1988 (Table 1.2). Survival in treatment 7, block 3 plummeted to 53%. Considerable *Armillaria mellea* fruiting bodies were found in this treatment plot, which may have contributed to seedling mortality in 1988.

By the fall of 1988, browsing of seedlings by hares increased to 21% (Table 1.3). The majority of browse damage occurred in the spring immediately after snow melt, when the only green vegetation on the

Table 1.2 Survival and vigour in the fall of 1987, spring of 1988 and fall of 1988 according to treatment. Treatments are referred to as TRT and are described in Table 1.1. Survival among treatments was not different at the 0.10 significance level. ANOVAs were not performed on the vigour data.

	TRT 1 100A:100H*	TRT 2 75A:100H	TRT 3 50A:100H	TRT 4 25A:100H	TRT 5 0A:50H	TRT 6 0A:100H	TRT 7 0A:0H
PERCENT SURVIVAL							
fall 1987	93.2	96.1	93.8	96.6	86.4	92.1	89.8
spring 1988	90.4	92.7	89.3	91.0	81.9	87.6	79.0
fall 1988	90.4	92.1	89.3	90.4	77.4	85.9	76.7
VIGOUR							
fall 1987							
good	65.5	61.8	63.3	70.2	52.3	71.8	63.4
moderate	29.7	37.6	31.3	27.5	41.8	25.2	29.0
poor	4.0	0.6	4.8	1.8	5.2	1.8	7.6
moribund	0.6	0.0	0.6	0.6	0.7	1.2	0.0
spring 1988							
good	74.4	71.3	73.4	70.8	67.6	69.7	64.0
moderate	16.9	20.1	12.7	16.1	22.8	16.1	18.0
poor	8.8	7.9	15.2	13.0	6.2	11.6	13.7
moribund	0.0	0.6	0.6	0.0	3.4	0.3	4.3
fall 1988							
good	90.6	88.3	86.1	84.4	85.4	82.2	78.5
moderate	5.0	8.6	11.4	13.8	12.4	8.6	15.6
poor	4.4	2.5	1.9	1.9	1.5	5.3	3.7
moribund	0.0	0.6	0.6	0.0	0.7	3.9	2.2

* 100A:100H symbolizes the treatment with 100% of the maximum Alder density and 100% of the maximum Herb cover. The remaining symbols refer to the abundance of alder and herbs relative to the maximum.

Table 1.3 Damage causes in the fall of 1987 and 1988 according to treatment. Treatments are referred to as TRT and are described in Table 1.1. Treatment means were not different at the 0.10 significance level.

	TRT 1 100A:100H*	TRT 2 75A:100H	TRT 3 50A:100H	TRT 4 25A:100H	TRT 5 0A:50H	TRT 6 0A:100H	TRT 7 0A:0H
Fall, 1987							
rodents	7.0	8.0	8.0	14.7	12.0	13.3	13.3
climate	8.0	12.0	6.6	10.7	21.3	5.3	9.3
insects	1.3	0.0	0.0	0.0	0.0	0.0	0.0
livestock	0.0	1.3	1.3	0.0	0.0	0.0	0.0
unknown	0.0	1.3	1.3	1.3	0.0	0.0	0.0
Fall, 1988							
rodents	17.1	32.4	22.9	28.6	14.6	21.9	16.8
climate	5.7	1.9	1.9	2.9	3.9	3.8	5.1
insects	1.0	0.0	0.0	0.0	1.0	0.0	0.0
pathogens	0.0	0.0	0.0	0.0	0.0	0.0	2.2
unknown	1.0	2.9	0.0	0.0	0.0	0.0	0.7

* 100A:100H symbolizes the treatment with 100% of the maximum Alder density and 100% of the maximum Herb cover. The remaining symbols refer to the abundance of alder and herbs relative to the maximum.

site was seedlings. The hares cleanly clipped the leader, usually immediately above the lower lateral branches. Although a few of the browsed seedlings died, the majority formed new buds and grew during the 1988 season. The mean diameter and height of damaged seedlings, however, were 18% and 30% smaller than undamaged seedlings. The severity of browse damage did not vary by significantly treatment. Rather, browse damage was most severe in those experimental units located in close proximity to tall alder cover. Seedlings did not appear to be affected by frost events in 1987 or 1988.

Growth

There were no significant differences in mean diameter, height, D2H and height:diameter ratios among treatments immediately after planting in the spring of 1987 (Table 1.4). Mean values were 2.6 mm, 11.2 cm, 0.8 cm³ and 45.7 respectively.

Mean diameter, height, D2H and height:diameter ratio increased to 3.5 mm, 17.7 cm, 2.4 cm³ and 52.6 respectively by the end of the first growing season. First year mean stem diameter and height increment were 0.9 mm and 6.4 cm respectively. Comparisons of size variables resulted in no significant differences among treatments (Table 1.4). However, planned contrasts (Table 1.5) were more sensitive in detecting performance differences among treatments than was the Waller and Duncan Bayes LSD procedure. At the end of the first growing season diameter increment was 64% greater in Treatment 7 (0% alder, 0% herbs) where all of the herbs (or understory) were removed, than in Treatment 6 (0% alder, 100% herbs) where none of the herbs had been removed ($p=0.020$). Diameter increment was insensitive to whether none (Treatment 6: 0% alder, 100% herbs) or some of the herbs were removed (Treatment 5: 0% alder, 50% herbs) ($p=0.040$). In contrast to the herb treatments, the alder regrowth treatments had no significant effects on seedling performance during the first growing season. The minimal effect of alder density on seedling performance was not surprising since mean alder height regrowth after manual cutting in early July

Table 1.4 Mean height, height increment, diameter, diameter increment, D2H, and height:diameter ratio according to treatment in the spring of 1987, fall of 1987 and fall of 1988. Treatments are referred to as TRT and are described in Table 1.1.

	TRT 1 100A:100H ¹	TRT 2 75A:100H	TRT 3 50A:100H	TRT 4 25A:100H	TRT 5 0A:50H	TRT 6 0A:100H	TRT 7 0A:0H	ANOVA RESULTS	
								p-value	standard error ²
HEIGHT (cm)									
spring 1987	10.9	13.2	10.6	10.3	11.3	10.7	11.6	0.2618	0.30
fall 1987	17.2	19.8	17.1	17.4	17.3	17.2	17.5	0.6350	0.42
fall 1988	24.5bc3	28.0a	24.8bc	26.0ab	22.7c	23.1c	23.2	0.0033*	0.28
ANNUAL HEIGHT INCREMENT (cm)									
fall 1987	6.2	6.5	6.5	7.1	5.9	6.3	6.0	0.8902	0.24
fall 1988	6.2	7.4	5.8	7.2	4.5	5.5	5.1	0.1335	0.28
DIAMETER (mm)									
spring 1987	2.7	2.4	2.6	2.3	2.7	2.8	2.6	0.2717	0.01
fall 1987	3.6	3.5	3.4	3.3	3.4	3.4	3.7	0.7636	0.01
fall 1988	5.6b	6.1ab	5.7b	5.9b	5.9b	5.9b	7.0a	0.0588*	0.01
ANNUAL DIAMETER INCREMENT (mm)									
fall 1987	1.0	1.1	0.8	1.0	0.7	0.7	1.1	0.1784	0.01
fall 1988	2.1	2.7	2.2	2.5	2.6	2.5	3.1	0.5785	0.01
D2H (cm)									
spring 1987	0.8	0.8	0.8	0.6	0.8	0.9	0.8	0.5021	0.04
fall 1987	3.0	2.5	2.1	2.0	2.1	2.2	3.0	0.6755	0.20
fall 1988	8.4	11.8	9.2	10.1	9.3	9.1	13.5	0.1241	0.47
HEIGHT:DIAMETER RATIO									
spring 1987	42.1	56.1	42.8	47.9	43.9	39.8	47.2	0.1276	1.41
fall 1987	51.0	57.8	51.8	54.4	51.6	49.9	51.6	0.8798	1.64
fall 1988	47.3a	47.9a	44.2abc	45.1ab	40.1bcd	39.6cd	35.0d	0.0017*	0.65

* significant at the 0.10 level.

- 100A:100H symbolizes the treatment with 100% of the maximum Alder density and 100% of the maximum Herb cover. The remaining symbols refer to the abundance of alder and herbs relative to the maximum.
- standard error of the overall mean.
- means with different letters within rows are different at the 0.10 significance level.

Table 1.5 Means and p-values of planned contrasts. Treatments are referred to as TRT and are described in Table 1.1.

CONTRAST	HEIGHT (cm)	HEIGHT INCREMENT	DIAMETER (mm)	DIAMETER INCREMENT	D2H (cm)	HEIGHT:DIAMETER RATIO
Contrast 1						
TRT 1 vs 2 3 4 5 6	Maximum alder growth and no herb removal vs reduced competition					
1987 means	17.2 vs 17.7	6.2 vs 5.9	3.6 vs 3.5	1.0 vs 0.9	3.0 vs 2.3	51.0 vs 52.9
p-value	0.6714	0.7948	0.4263	0.6469	0.2401	0.0703
1988 means	24.5 vs 24.6	6.2 vs 5.9	5.6 vs 6.1	2.1 vs 2.6	8.4 vs 10.5	47.3 vs 42.0
p-value	0.8876	0.7216	0.0911*	0.2223	0.1400	0.0151*
Contrast 2						
TRT 5 6 7 vs 1 2 3 4	No alder growth vs some alder growth					
1987 means	17.3 vs 17.9	6.1 vs 6.6	3.5 vs 3.5	0.8 vs 1.0	2.4 vs 2.4	51.0 vs 53.8
p-value	0.5993	0.7275	0.7514	0.0951*	0.7447	0.4454
1988 means	23.0 vs 25.9	5.0 vs 6.7	6.3 vs 5.8	2.7 vs 2.4	10.6 vs 9.9	38.2 vs 46.1
p-value	0.0005*	0.0188*	0.0102*	0.1320	0.1538	0.0001*
Contrast 3						
TRT 7 vs 5 6	Total herb removal vs no or partial herb removal (no alder growth)					
1987 means	17.5 vs 17.3	6.0 vs 6.1	3.7 vs 3.4	3.1 vs 2.6	3.0 vs 2.2	51.6 vs 50.8
p-value	0.8301	0.9211	0.3582	0.0217*	0.2241	0.8863
1988 means	23.2 vs 22.9	5.1 vs 5.0	7.0 vs 5.9	3.1 vs 2.6	13.5 vs 9.2	35.0 vs 39.9
p-value	0.7404	0.9082	0.0090*	0.2405	0.0152*	0.0421*
Contrast 4						
TRT 1 vs 7	Maximum alder growth and no herb removal vs no competition					
1987 means	17.2 vs 17.5	6.2 vs 6.0	3.6 vs 3.7	1.0 vs 1.1	3.0 vs 3.0	51.0 vs 51.6
p-value	0.8361	0.8557	0.8652	0.4125	0.9678	0.9318
1988 means	24.5 vs 23.2	6.2 vs 5.1	5.6 vs 7.0	2.1 vs 3.1	8.4 vs 13.5	47.3 vs 35.0
p-value	0.2407	0.3153	0.0030*	0.0724*	0.0128*	0.0003*
Contrast 5						
TRT 1 vs 6	Maximum alder growth and vs no alder regrowth (no herb removal)					
1987 means	17.2 vs 17.2	6.2 vs 6.3	3.6 vs 3.4	1.0 vs 0.7	3.0 vs 2.2	51.0 vs 49.9
p-value	0.9939	0.9078	0.6936	0.1685	0.2957	0.8611
1988 means	24.5 vs 23.1	6.2 vs 5.5	5.6 vs 5.9	2.1 vs 2.5	8.4 vs 9.1	47.3 vs 39.6
p-value	0.2174	0.5016	0.3302	0.4167	0.6870	0.0084*
Contrast 6						
TRT 6 vs 7	No herb removal vs complete herb removal (no alder growth)					
1987 means	17.2 vs 17.5	6.3 vs 6.0	3.4 vs 3.7	0.7 vs 1.1	2.2 vs 3.0	49.9 vs 51.6
p-value	0.8420	0.7663	0.5746	0.0392*	0.3134	0.7947
1988 means	23.1 vs 23.2	5.5 vs 5.1	5.9 vs 7.0	2.5 vs 3.1	9.1 vs 13.5	39.6 vs 35.0
p-value	0.9473	0.7287	0.0193*	0.2810	0.0275*	0.0859*

* significant at the 0.10 level.

was only 19 cm (Table 3.1).

By the end of the second growing season (fall, 1988), seedlings had grown substantially and reached a lower height:diameter ratio than after the first growing season (fall, 1987). Mean diameter, height and D2H were to 6.0 mm, 24.6 cm, 10.2 cm³ respectively and height:diameter ratio was 42.8. Further, treatment effects were clearly significant (Table 1.4). Mean diameter was largest (7.0 mm) in Treatment 7, where all competing vegetation had been removed, and smallest (5.6 mm) in Treatment 1, where 100% alder and 100% herbs were growing ($p=0.0588$). Seedlings were significantly more sturdy in Treatment 7 than 1 ($p=0.0017$), with a mean height:diameter ratio of 35.0 compared to 47.3. These results indicate that an environment free of competing alder and associated shrubs and herbs had a beneficial effect on two year diameter growth and seedling allometry.

Planned contrasts again were more sensitive than multiple comparisons at detecting differences in mean diameter, D2H and height:diameter ratio among varying densities of alder and percent cover of herbs after the second growing season (Table 1.5). Seedlings growing in alder-free environments (Treatments 5,6,7) were significantly larger in diameter ($p=0.0102$) and had smaller height:diameter ratios ($p=0.0001$) than those growing in association with alder (Treatments 1,2,3,4). Furthermore, mean diameter ($p=0.0911$) and height:diameter ratio ($p=0.0151$) were significantly improved when alder density was decreased by any amount from the maximum (Table 1.5). Mean diameter increased and height:diameter ratio decreased with decreased alder densities (Table 1.4). This observation is supported by response models that tested size against decreasing densities of alder (Treatments 1,2,3,4,5) (Table 1.6). The models for D2H ($p=0.0217$), height ($p=0.0440$) and height:diameter ratio ($p=0.0090$) were significant with r^2 values of 0.47, 0.41 and 0.42 respectively (Figure 1.3).

In addition to complete removal of alder, reductions in herb cover resulted in further improvements in mean diameter. Consistent with seedling response after the first growing season, mean diameter

Table 1.6 Response models for pine size after two growing seasons.

MODEL	p-value	r ²
SIZE VS SITKA ALDER RELATIVE CLUMP DENSITY		
D2H = 39.8851 + 0.1655 (density) - 0.0009 (density) ²	0.0217	0.47
HEIGHT = 22.1419 + 0.1478 (density) - 0.0012 (density) ²	0.0440	0.41
HEIGHT: DIAMETER RATIO = 41.3308 + 0.0704 (density)	0.0090	0.42
SIZE VS HERB PERCENT GROUND COVER		
DIAMETER = 0.6965 - 0.0030 (cover) + 2.0253E-5 (cover) ²	0.0539	0.62
D2H = 13.5196 - 0.1245 (cover) + 0.0008 (cover) ²	0.0634	0.60
HEIGHT: DIAMETER RATIO = 35.0322 + 0.1561 (cover) -0.0001 (cover) ²	0.1196	0.51

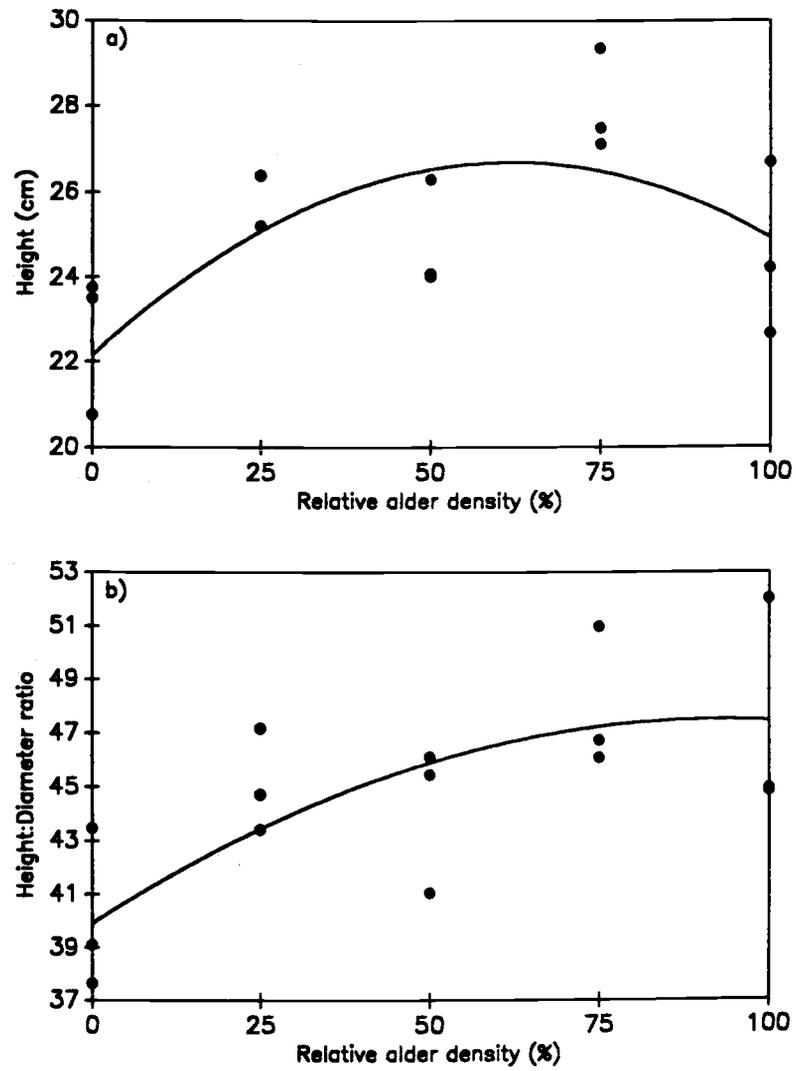


Figure 1.3 Response of lodgepole pine seedling (a) height and (b) height: diameter ratio to alder density.

($p=0.0152$) and D2H ($p=0.0152$) were significantly greater where all herbs had been removed (Treatment 7) than where the herb layer was left intact (Treatment 6) or only partially removed (Treatment 5) ($p=0.0090$) (Table 1.5). Height:diameter ratio also improved with reductions in herb cover ($p=0.0421$). These observations are supported by response models that regressed growth response against decreasing percent cover of herbs (Table 1.6). The models for mean diameter ($p=0.0539$) and D2H ($p=0.0634$) had r^2 values of 0.62 and 0.60, respectively (Figure 1.4)

Mean seedling height was highly variable among treatments by the end of the second growing season (Table 1.4). Seedlings in Treatments 2 (75% alder, 100% herbs) and 4 (25% alder, 100% herbs) were significantly taller than those in the remaining treatments ($p=0.0033$). Seedlings growing in alder-free environments (Treatments 5,6,7) were significantly shorter (23.1 cm) than those growing in association with varying densities of alder (Treatments 1,2,3,4) (25.8 cm) ($p=0.0005$) (Table 1.5). The response model that regressed height against increasing densities of alder was significant ($p=0.0440$) and had an r^2 value of 0.41 (Table 1.6 and Figure 1.3).

These results indicate that height growth was improved by the presence of alder. However, diameter growth was concurrently depressed, resulting in spindly seedlings with a significantly greater height:diameter ratio (46.13) than of those seedlings growing in alder free environments (38.23) ($p=0.0001$). After two growing seasons sprouting alder had gained sufficient height and breadth to have a measurable effect on seedling size (see Table 3.1 for alder size).

Xylem water potential

Seedlings were under significantly more moisture stress in Treatment 1 (100% alder, 100% herbs) than in Treatments 7 (0% alder, 0% herbs) or 6 (0% alder, 100% herbs) ($p=0.0585$) at midday on June 27, 1988 (Figure 1.5). Xylem moisture potentials were -1.05 MPa in Treatment 1 and -0.61 and -0.41 MPa in Treatments 7 and 6

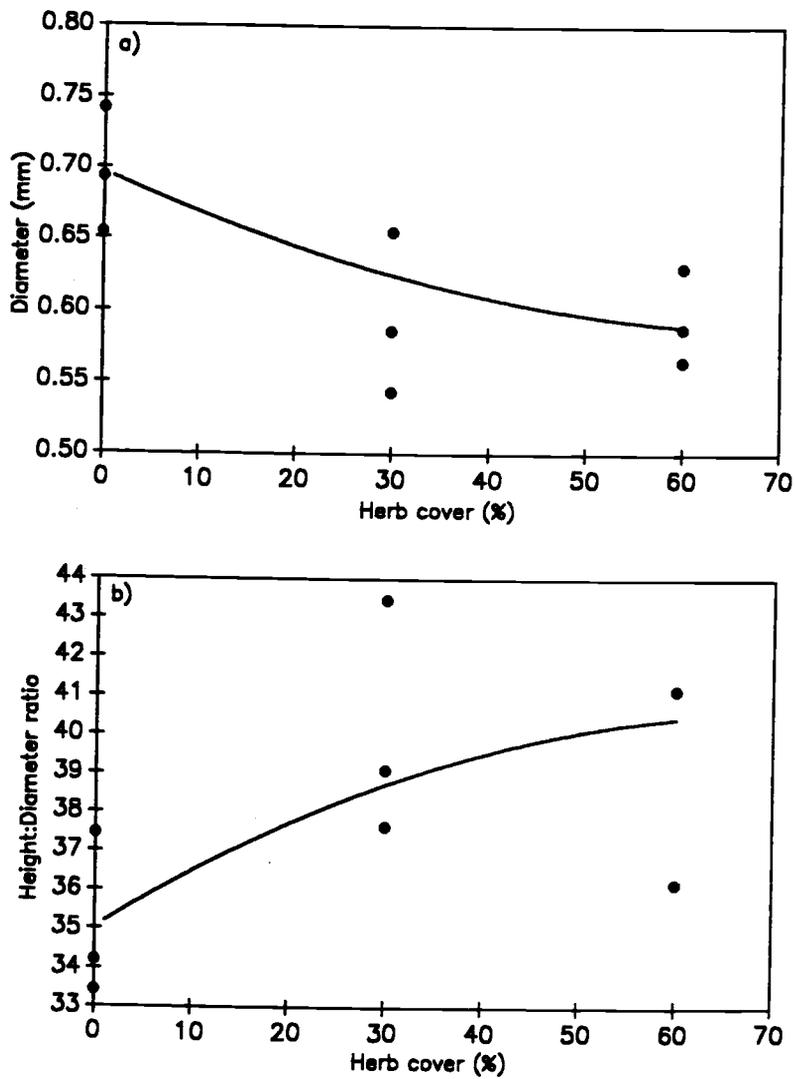


Figure 1.4 Response of lodgepole pine (a) diameter and (b) height:diameter ratio to herb cover.

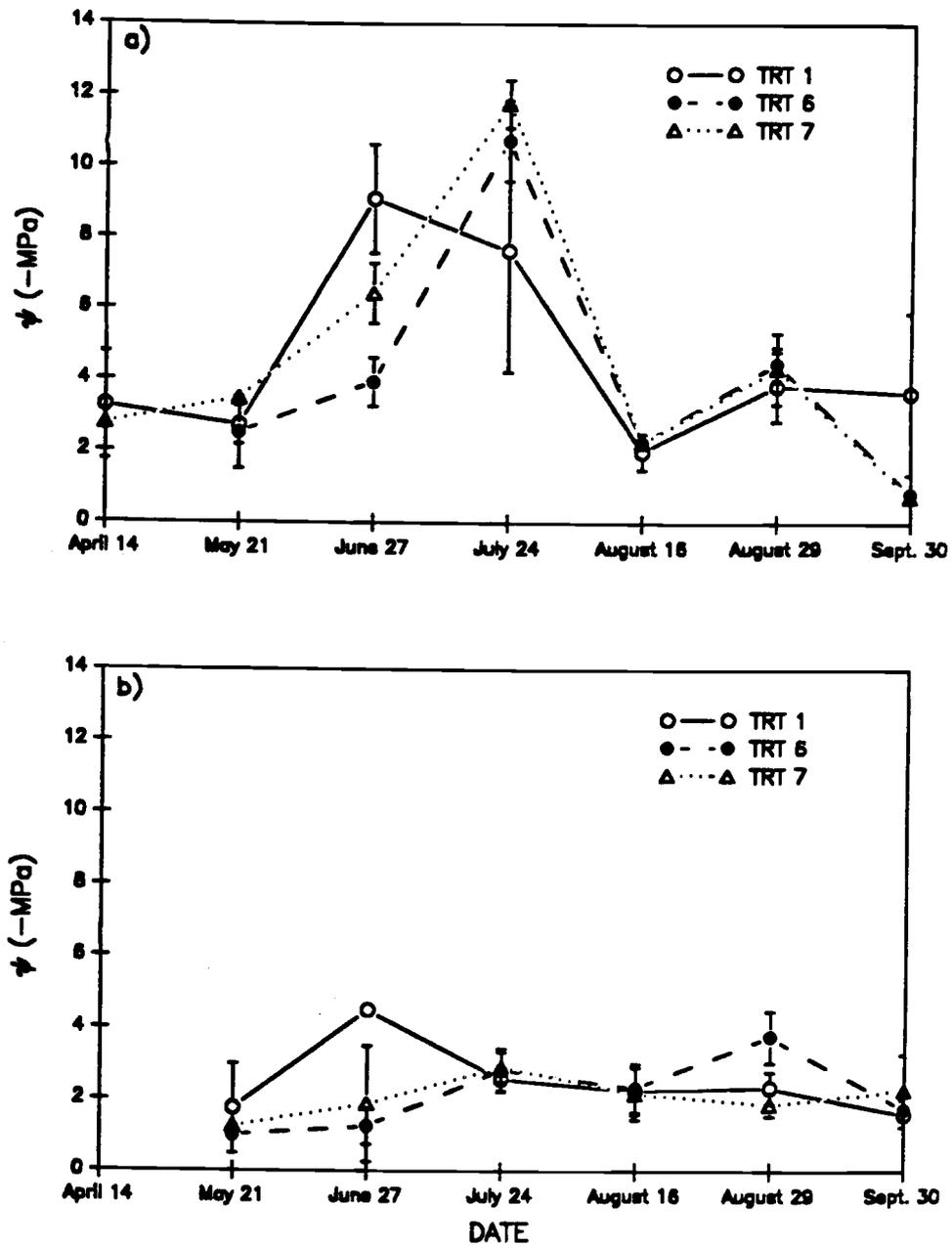


Figure 1.5 Xylem moisture potential of lodgepole pine seedlings measured at (a) mid-day (12:00 to 14:00 hours) and (b) pre-dawn (one hour prior to sunrise). Error bars represent ± 1 standard error.

respectively. Neither midday nor predawn measurements were significantly different among treatments through the remainder of the summer. Midday and predawn xylem moisture potentials were lowest on July 24, averaging -0.87 and -0.30 MPa respectively. Seedlings were under the most stress in mid-summer due to reduced amount and frequency of precipitation. Midday and predawn xylem moisture potentials were highest on September 30, averaging -0.10 and -0.12 MPa respectively. Fall rains had sufficiently rewetted the solum to improve moisture availability to seedlings.

Environmental effects

Climate

The site was free of snow from mid-April to early November in 1988. Between April 25 and September 7, air temperature at 1.5 m ranged from -3 to 33°C and no frost events were recorded after May 20 (Figure 1.6). However, at 15 cm above the ground surface 20 frost events were recorded between May 20 and September 7 (Figure 1.8). Frost occurred throughout the growing season. Accumulated degree days above 5°C at 15 cm averaged 875 (s.e = 24) among treatments (Figure 1.11).

With the exception of a one week drought between June 14 and 21 and a three week drought between July 13 and August 1, precipitation was evenly distributed throughout the snow-free period in 1988 (Figure 1.6). There was 600 mm of precipitation between April 18 and September 7, which was considerably higher than the long term average for the MSb subzone (200 mm).⁴ Average relative humidity ranged between 15 and 95%; it was considerably lower during the droughts (25 to 60%) than during the remainder of the growing season (40 to 80%) (Figure 1.7). Total daily solar irradiance at 1.5 m height was measured between July 13 and September 1 (Figure 1.7). Maximum values

⁴ Normalized average (1940-1970) for six sites in the MSb subzone, Environment Canada and British Columbia Ministry of Environment.

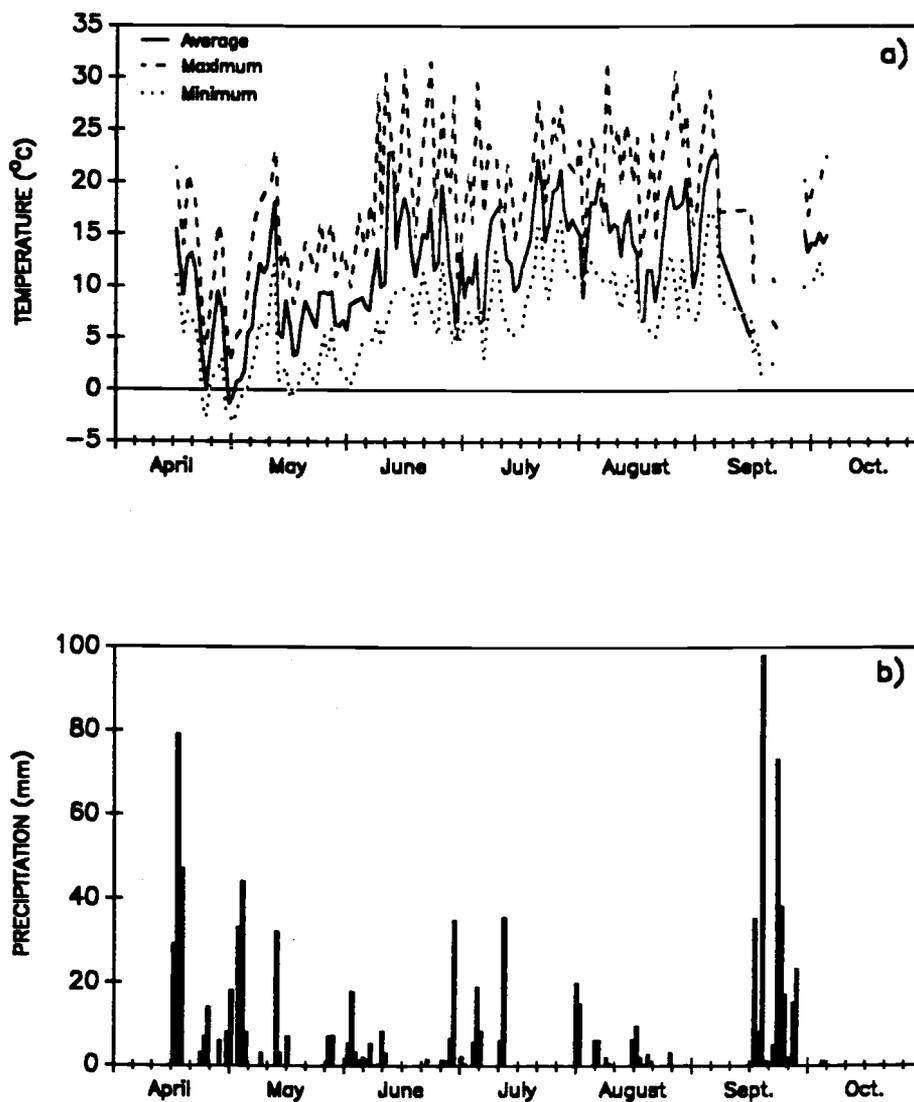


Figure 1.6 (a) Average, maximum and minimum air temperatures at 1.5 m height from April to October, 1988. (b) Precipitation amount and frequency from April to October, 1988.

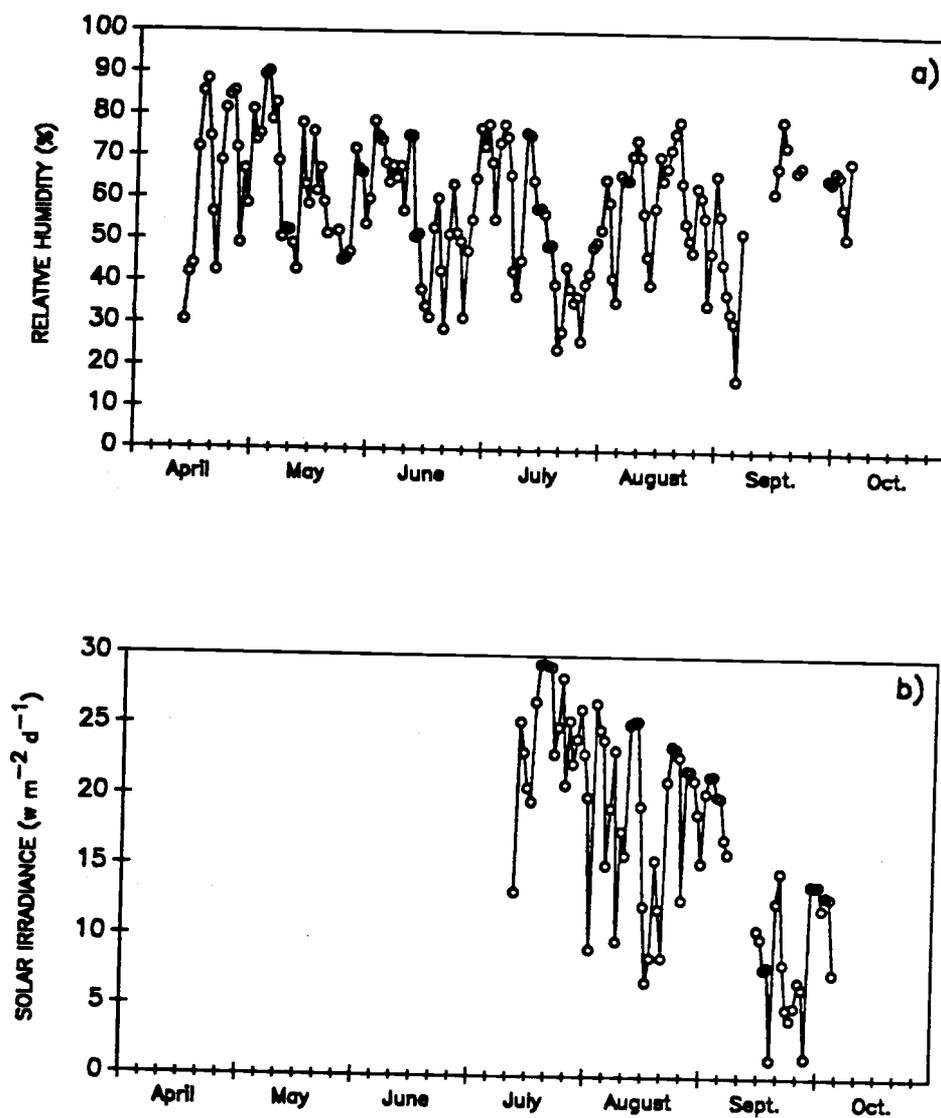


Figure 1.7 (a) Average relative humidity at 1.5 m height from April to October, 1988. (b) Total solar irradiance at 1.5 m height from July to October, 1988.

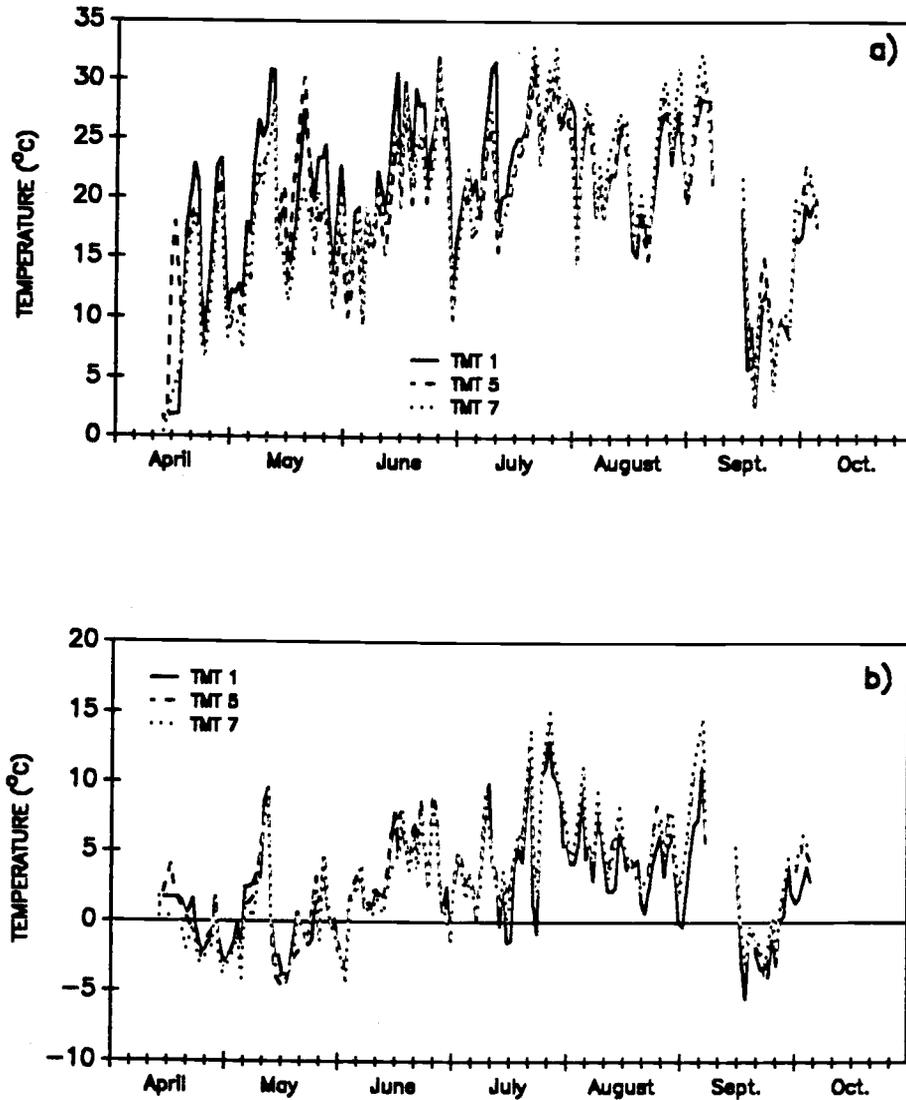


Figure 1.8 Comparison of (a) maximum and (b) minimum daily air temperatures at 15 cm height among Treatments 1 (maximum vegetative cover), 5 (all sitka alder and 50% of the herb cover removed) and 7 (all vegetation removed).

occurred in mid to late July ($1566 \mu\text{E}/\text{s}/\text{m}^2$), after which daily solar irradiance steadily declined. Solar irradiance was $400 \mu\text{E}/\text{s}/\text{m}^2$ on October 5.

Air temperature

Air temperature at 15 cm height ranged from -7 to 33°C from April 18 to October 5, 1988. Maximum air temperature at 15 cm height was greatest in Treatment 1 (100% alder, 100% herbs) until mid-July, when vegetative development was completed (Figure 1.8). Prior to July, maximum air temperatures surpassed 31°C in Treatment 1 and rarely reached 25°C in Treatments 5 (0% alder, 50% herbs) and 7 (0% alder, 0% herbs). The alder and herbs in Treatment 1 appeared to act as thermal traps. By early July, however, differences among treatments were minor; air temperatures reached maximums of 32°C in Treatment 1, 31°C in Treatment 7 and 30°C in Treatment 5. Beyond mid-July, trends in air temperature among treatments reversed. Air temperature maxima in Treatment 7 (approaching 34°C) increasingly surpassed those in Treatment 1 (31°C) and Treatment 5 (30°C). Complete removal of both shrubs and herbs appeared necessary to increase air temperature maxima after seasonal vegetative development was complete at the study site in 1988.

Minimum air temperatures at 15 cm height ranged from -6 to 9°C before mid-July, surpassing 5°C for only 10 days in mid-June. Prior to mid-July, minimum air temperatures did not differ (within 1°C) among treatments 1, 5 and 7 (Figure 1.8). After mid July however, minimum air temperatures considerably increased and were consistently lower in Treatment 1 than in Treatments 7 or 5. Frost events frequently occurred in Treatment 1 while Treatments 5 and 7 remained frost free.

Accumulated growing degree days above 5°C are compared among Treatments 1, 5 and 7 in Figure 1.9. As can be predicted by temperature patterns discussed above, accumulated degree days were higher in Treatment 1 than 5 or 7 until August. By the end of the

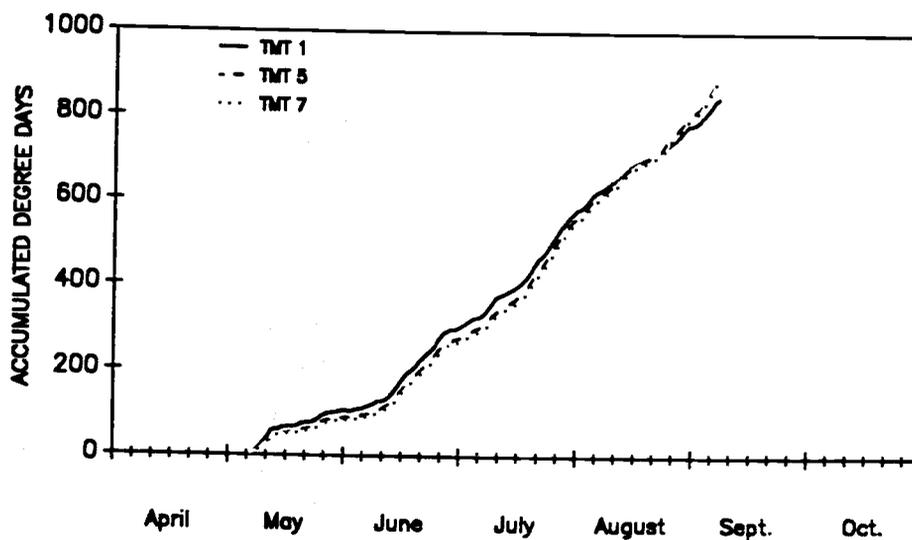


Figure 1.9. Comparison of accumulated growing degree days above 5°C at 15 cm height among treatments 1 (maximum vegetative cover), 5 (all sitka alder and 50% of the herb cover removed) and 7 (all vegetation removed).

growing season, however, accumulated degree days were lower in Treatment 1 (847 DD) than in Treatments 5 (890 DD) or 7 (888 DD).

Soil temperature

Daily soil temperature ranged from 3 to 28°C at 5 cm depth and 3 to 23°C at 30 cm depth between April 18 and October 5 (Figures 1.10 and 1.11). Variation in soil temperature was much greater at 5 cm than at 30 cm depth. Soil temperatures increased considerably during the dry period in mid-June, and remained warm through the remainder of the growing season.

Complete vegetation removal increased mean soil temperature by 2 to 5°C at 5 cm depth and up to 2°C at 30 cm depth between mid-June and mid-August. Maximum soil temperatures approached 28°C at 5 cm and 23°C at 30 cm in Treatment 7 and only 26 and 20°C respectively in Treatment 1 (Figures 1.10 and 1.11).

Accumulated degree days above 5°C during the growing season was consistently highest in the complete removal treatment at both 5 (1693 DD) and 30 cm (1476 DD) depths (Figure 1.12). Partial herb removal (Treatment 5) and complete regrowth (Treatment 1) treatments accumulated similar degree days (1583 and 1600 DD respectively) at 5 cm depth. Partial herb removal (1458 DD), however, was superior to complete regrowth (1368 DD) at 30 cm depth.

Based on the 1988 data, complete vegetation removal was necessary to improve soil and air temperature profiles. Soil and air temperatures generally were not improved by partial vegetation removal.

Soil moisture

In 1987, percent soil moisture at 0-20 cm depth ranged from 10% in August to 53% in September. Weather was unseasonably hot and dry prior to planting on July 4, 1987. However, relatively high rainfall the week following planting increased soil moisture content from 25%

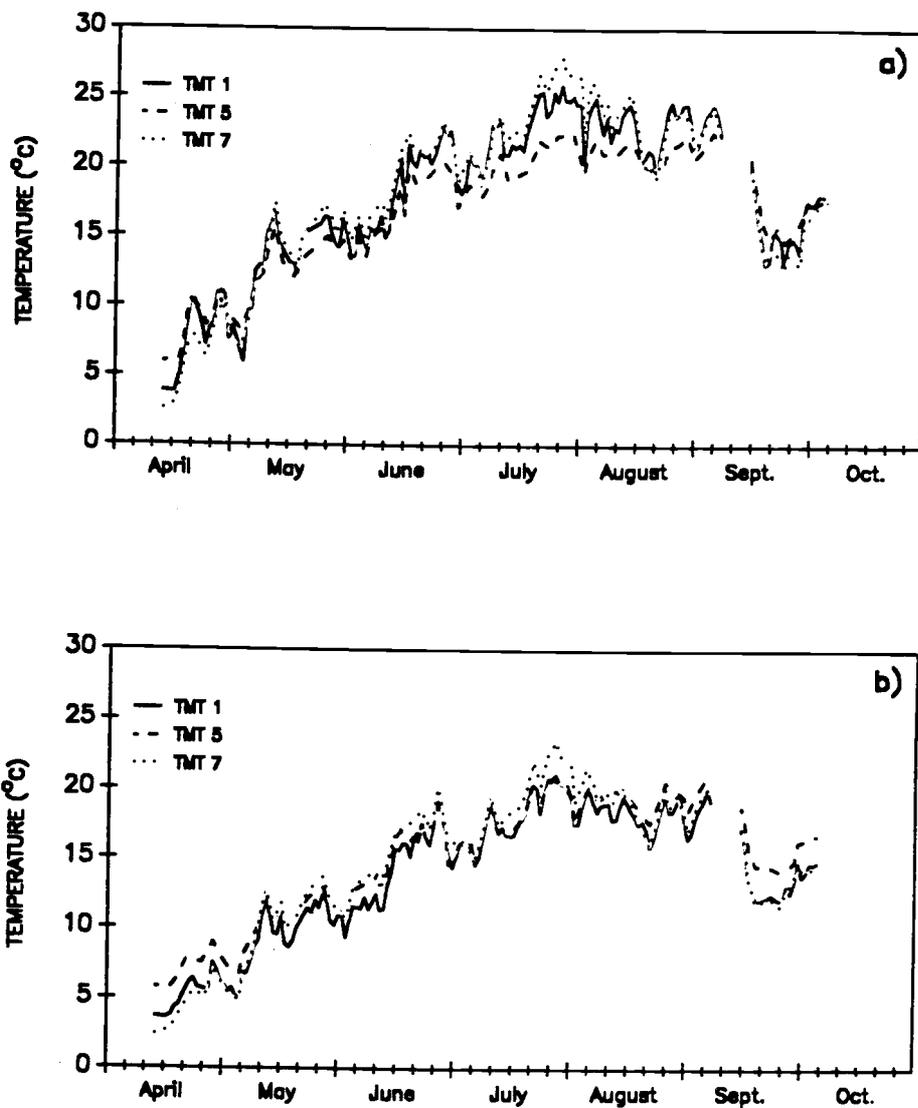


Figure 1.10 Comparison of (a) maximum and (b) minimum daily soil temperatures at 5 cm depth among treatments 1 (maximum vegetative cover), 5 (all sitka alder and 50% of the herb cover removed) and 7 (all vegetation removed).

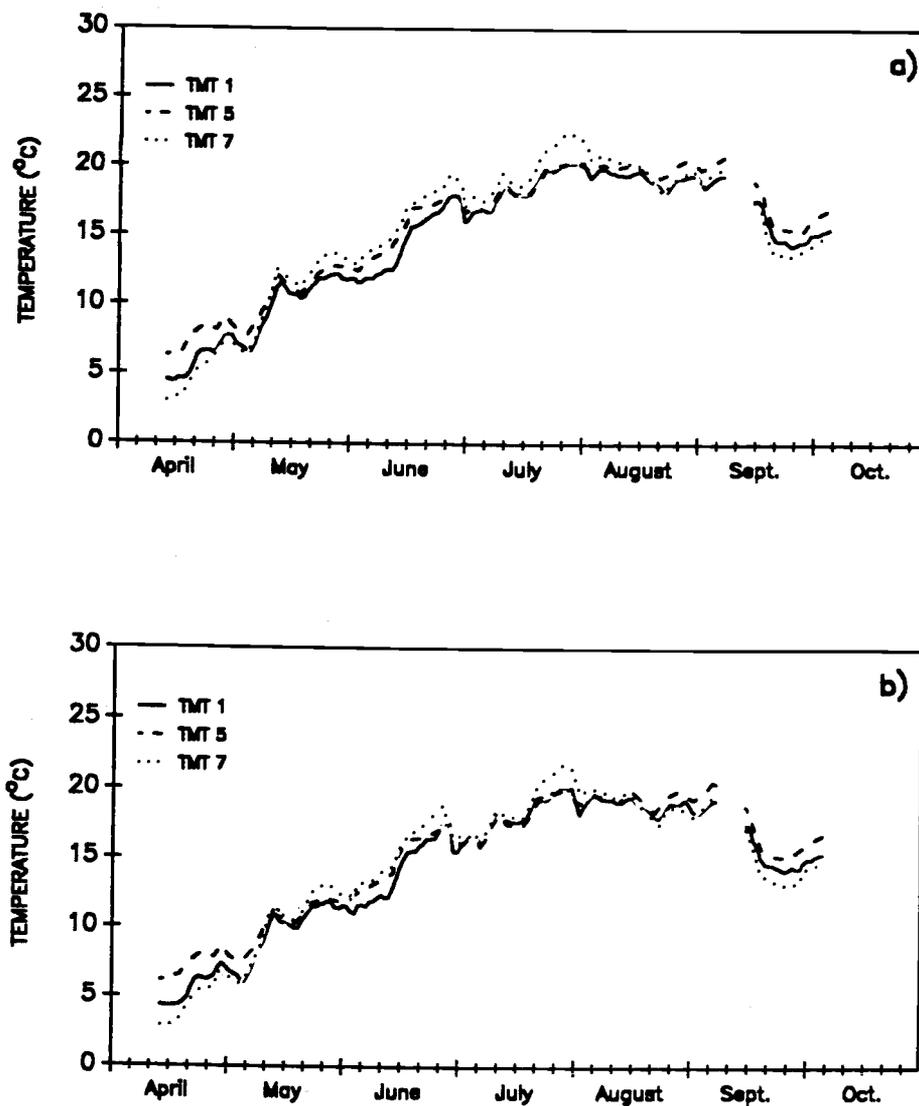


Figure 1.11 Comparison of (a) maximum and (b) minimum daily soil temperatures at 30 cm depth among treatments 1 (maximum vegetative cover), 5 (all sitka alder and 50% of the herb cover removed) and 7 (all vegetation removed).

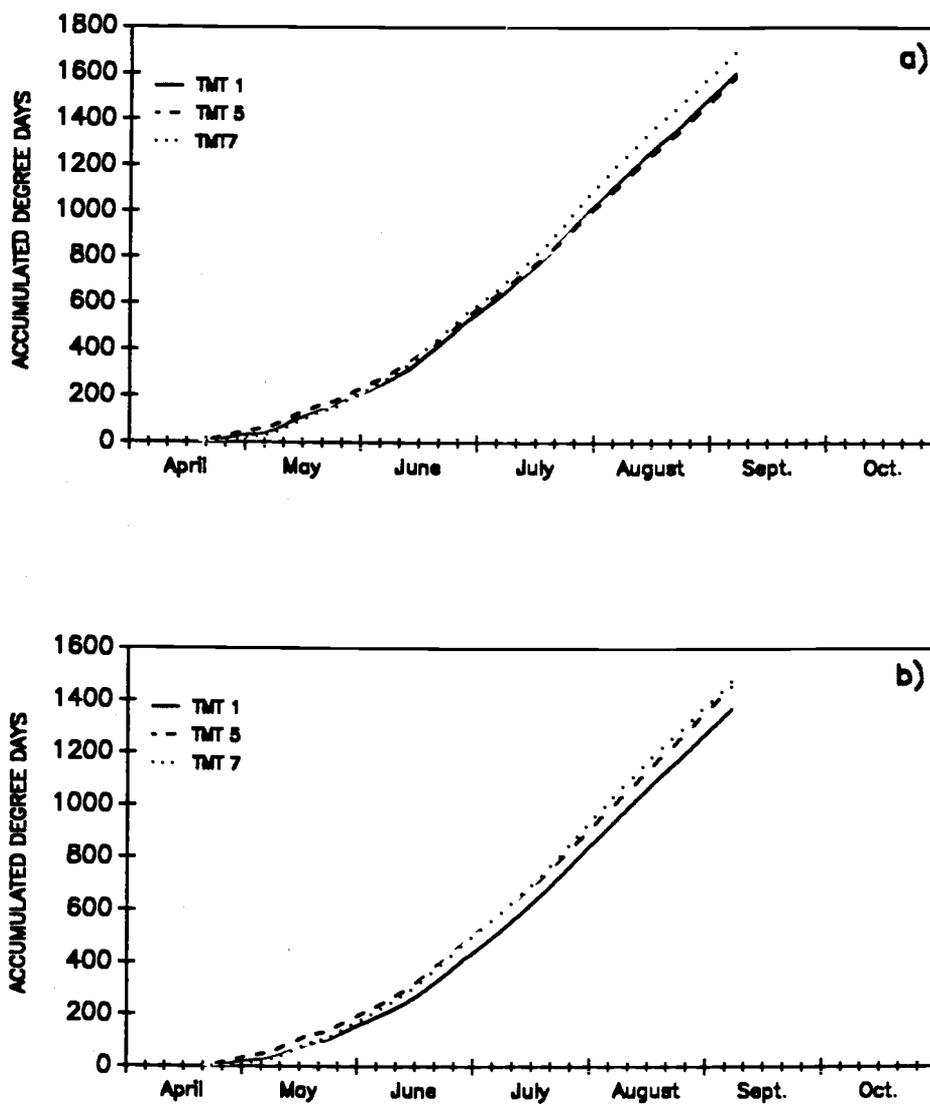


Figure 1.12 Comparison of accumulated growing degree days above 5°C at (a) 5 cm and (b) 30 cm depths among treatments 1 (maximum vegetative cover), 5 (all sitka alder and 50% of the herb cover removed) and 7 (all vegetation removed).

on July 7 to 38% on July 20. There was more soil moisture where all the alder were sprouting and the herb layer was left intact than where all vegetation was removed.

In 1988, soil profiles remained wetted throughout the growing season. Soil water potential never fell below -0.06 MPa at all depths and in all treatments sampled (Table 1.7). Mean soil water potential at 30 and 45 cm depths reached minimums (-0.036 and -0.030 MPa) on July 26 and maximums on September 30 (-0.024 and -0.015 MPa). Mean soil water potential generally increased with depth; however, it was consistently lower at 60 cm throughout the growing season.

Soil water potential at 10 cm depth, from the gravimetric samples, was significantly lower in treatment 1 (-0.07 MPa) where alder and herbs were growing than in treatment 6 (-0.02 MPa) where only herbs were growing. The difference, however, had a minimal effect on seedling moisture stress. Differences in soil water potential among treatments were not significant at 10 or 25 cm depths on the other dates when soils were gravimetrically sampled.

There were no significant differences in soil water potential among treatments at all depths sampled with the neutron probe except on September 30, 1988 (Table 1.7). Soil water potential was significantly lower in treatment 1 (-0.032 MPa) than treatment 7 (-0.018 MPa) at 30 cm depth ($p=0.0701$). Although moisture depletion 30 cm below the soil surface was greater where alder and herbs were growing than where they were removed, the effects on seedling moisture stress were minimal.

Available light

Photosynthetically active radiation (PAR) averaged 1500 ± 35 $\mu\text{E/s/m}^2$ above the vegetation canopy on August 22, 1988. PAR ($p=0.0073$) and the percent of full sunlight ($p=0.0101$) intercepted by seedlings in Treatment 7 (0% alder, 0% herbs) were significantly greater than in treatments where varying amounts of shrubs and herbs were growing (Figure 1.13). Mean PAR intercepted by seedlings was

Table 1.7 Soil water potential (-MPa) according to treatment through the 1988 growing season. Treatments are referred to as TRT and are described in Table 1.1.

	TRT 1 100A:100H ¹	TRT 6 0A:100H	TRT 7 0A:0H	ANOVA RESULTS	
				p-value	standard error ²
<u>April 24</u>					
10 cm	0.03	0.01	0.01	.	.
25 cm	0.00	0.00	0.00	.	0.00
<u>May 23</u>					
10 cm	0.02	0.01	0.04	0.3219	0.01
30 cm	0.04	0.02	0.03	0.1626	0.00
45 cm	0.02	0.01	0.02	0.2077	0.00
60 cm	0.04	0.04	0.05	.	0.00
75 cm	0.01	0.03	0.04	.	.
<u>June 27</u>					
30 cm	0.04	0.04	0.03	0.8244	0.00
45 cm	0.03	0.02	0.03	0.3060	0.00
60 cm	0.04	0.03	0.05	.	0.00
75 cm	0.01	0.02	0.03	.	.
<u>July 18</u>					
10 cm	0.01	0.01	0.01	0.8817	0.00
<u>July 26</u>					
30 cm	0.04	0.04	0.03	0.1888	0.00
45 cm	0.04	0.03	0.03	0.4315	0.00
60 cm	0.05	0.04	0.05	.	0.00
75 cm	0.01	0.02	0.03	.	.
<u>August 29</u>					
10 cm	0.07a ³	0.02b	0.03ab	0.0738*	0.01
25 cm	0.00	0.00	0.01	0.4339	0.01
<u>September 13</u>					
30 cm	0.03	0.05	0.03	0.1648	0.00
45 cm	0.04	0.03	0.02	0.3026	0.00
60 cm	0.06	0.04	0.05	.	0.00
75 cm	0.00	0.01	0.02	.	.
<u>September 30</u>					
30 cm	0.032a	0.020ab	0.018b	0.0701	0.00
45 cm	0.02	0.01	0.02	0.2086	0.00
60 cm	0.03	0.03	0.04	.	0.00
75 cm	0.00	0.01	0.02	.	.

* significant at the 0.10 level.

.

1. 100A:100H symbolizes the treatment with 100% of the maximum Alder density and 100% of the maximum Herb cover. The remaining symbols refer to the abundance of alder and herbs relative to the maximum.

2. standard error of the overall mean.

3. means with different letters within rows are different at the 0.10 significance level.

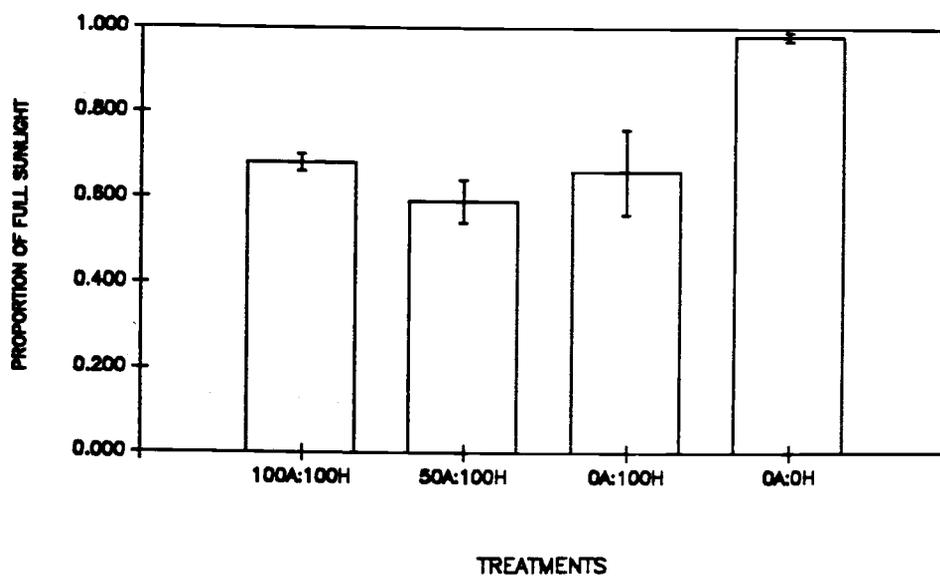


Figure 1.13 Comparison of the mean proportion of full sunlight available to seedlings among treatments 1 (100% alder and 100% herbs growing), 3 (50% alder and 100% herbs growing), 6 (no alder and 100% herbs growing) and 7 (no alder or herbs growing).

1508 $\mu\text{E/s/m}^2$ in treatment 7 and 950 $\mu\text{E/s/m}^2$ in treatments 1, 3 and 6. The mean percent of full sunlight intercepted was 98.3% in treatment 7 and 63.8% in treatments 1, 3 and 6.

There were no significant differences in intercepted PAR and percent of full sunlight among treatments 1 (100% alder, 100% herbs), 3 (50% alder, 100% herbs) and 6 (0% alder and 100% herbs). The lowest recorded PAR was 52 $\mu\text{E/s/m}^2$ in treatment 3 and the highest was 1543 $\mu\text{E/s/m}^2$ in treatment 6. Complete herb removal appears necessary to significantly increase PAR availability. This observation is not surprising since herbaceous vegetation was generally overtopping the two year old seedlings.

Soil nitrogen capital

Mean total nitrogen (N), ammonium nitrogen ($\text{NH}_4\text{-N}$) and nitrate nitrogen ($\text{NO}_3\text{-N}$) were 1,588 (s.e. 33) kg/ha, 23 (s.e. 1) kg/ha and 5 (s.e. 1) kg/ha respectively. Total N varied among blocks ($p=0.0021$) (Table 1.8) and treatments ($p=0.0882$) (Table 1.9). The trend in total N among blocks paralleled forest floor thickness and fine root abundance (personal observation). Blocks 1 and 2 featured a thicker forest floor and/or more herbaceous roots in the surface horizons compared with Block 3. The thicker forest floor would incorporate greater amounts of organic material in the mineral soil, resulting in greater total N in Blocks 1 and 2. Variation in total N among treatments could not reflect vegetation reduction treatments since they were initiated only two months prior to measurement.

Differences in mineralizable $\text{NH}_4\text{-N}$ were significant among blocks ($p=0.0001$) but not treatments. Block 1 had 34 kg/ha, block 2 had 24 kg/ha and block 3 had 11 kg/ha $\text{NH}_4\text{-N}$. Differences in mineralizable $\text{NO}_3\text{-N}$ were significant among treatments ($p=0.03$) but not blocks ($p<0.10$). There was significantly greater $\text{NO}_3\text{-N}$ in treatments 5 (0% alder, 50% herbs) and 7 (0% alder, 0% herbs) than in the other treatments.

Table 1.8 Total nitrogen and mineralizable ammonium-nitrogen (NH₄-N) and nitrate-nitrogen (NO₃-N) (kg/ha) according to block.

	BLOCK 1	BLOCK 2	BLOCK 3	ANOVA RESULTS	
				p-value	standard error ¹
Total nitrogen	1579b ²	1745a	1425c	0.0021*	28.21
NH ₄ -N	34a	24b	11c	0.0001*	1.28
NO ₃ -N	6	6	3	0.1134	0.52

1. standard error of the overall mean.

2. means with different letters within rows are different at the 0.10 significance level.

Table 1.9 Total nitrogen and mineralizable ammonium-nitrogen (NH₄-N) and nitrate-nitrogen (NO₃-N) (kg/ha) according to treatment. Treatments are referred to as TRT and are described in Table 1.1.

	TRT 1 100A:100H ¹	TRT 2 75A:100H	TRT 3 50A:100H	TRT 4 25A:100H	TRT 5 0A:50H	TRT 6 0A:100H	TRT 7 0A:0H	ANOVA
								RESULTS p-value
Total nitrogen	1586ab ²	1531b	1640ab	1506b	1470b	1533b	1817a	0.0882*
NH ₄ -N	32	19	24	22	18	24	23	0.2049
NO ₃ -N	4b	4b	4b	3b	10a	4b	6ab	0.0271*

* significant at the 0.10 level.

1. 100A:100H symbolizes the treatment with 100% of the maximum Alder density and 100% of the maximum herb cover. The remaining symbols refer to the abundance of alder and herbs relative to the maximum.

2. means with different letters within rows are different at the 0.10 significance level.

DISCUSSION

Lodgepole pine performance

Survival

Survival averaged 86% over all treatments two years after planting. Excellent survival rates are not uncommon for lodgepole pine plantations in British Columbia (Vyse and Navratil 1985, Thompson 1984). Seedling survival, however, was not affected by varying abundances of alder and associated shrubs and herbs. Pine survival has been reported in other studies to be insensitive to varying shrub canopy volumes (Lanini and Radosevich 1986, Coates 1987) and varying grass densities (Clark and McLean 1975). In contrast, however, Lotan and Perry (1977) found that survival of lodgepole pine improved when competing vegetation was removed and soil moisture subsequently increased.

Survival in this study was most affected by drought and rodent damage. Mortality due to drought occurred throughout the treatments, and, although not significant, was greatest where all vegetation was removed. Most of the mortality occurred in 1987, the year of treatment initiation and planting. Percent soil moisture in 1987 was least where all vegetation was removed and greatest where alder and herbs were most abundant. Surface evaporation and root mortality may have contributed to low soil moisture retention in the complete removal treatment. Hence, seedling mortality in the complete removal treatment may have been the result of low moisture availability and/or a high radiation load. Early mortality of lodgepole pine seedlings where moisture stress is a factor has been attributed to slow initial root elongation (Brix 1979). Brix (1979) reports that once lodgepole pine is established, however, survival and growth are favored by a sensitive stomatal control of water loss.

Browsing by hares (*Lepus* sp.) was most severe the spring of 1988, before shrub and herb species had sprouted. The greatest damage and

mortality occurred in those experimental units located near high alder cover. The hares damaged 21% of the seedlings by clipping leaders and/or lateral shoots. The mean diameter and height of damaged seedlings were 18% and 30% smaller than undamaged seedlings. Sullivan (1985) reports similar snowshoe hare damage to lodgepole pine plantations in many areas of central B.C. Semi-girdling damage by snowshoe hares clearly suppresses diameter and height growth of juvenile lodgepole pine near Prince George, B.C. (Sullivan and Sullivan 1986).

Growth

Seedling growth was significantly affected by varying abundances of alder and associated shrubs and herbs after two growing seasons. Mean diameter of seedlings growing free of competing vegetation was 25% greater than that of seedlings growing among maximum alder and herb densities. Studies of other conifers consistently show positive diameter responses to shrub canopy removal (Wagner and Radosevich 1987, Coates 1987, Lanini and Radosevich 1986, Cole and Newton 1986, Lotan and Perry 1976). Although mean lodgepole pine diameter increased with decreased alder densities, the most significant improvement in growth resulted from the additional removal of herb and low shrub cover. Clark and McLean (1978) and Cole and Newton (1986) have demonstrated the adverse effects of increasing grass densities on diameter growth of lodgepole pine and dry site Douglas-fir, respectively.

Lodgepole pine height response to varying alder and herb abundances was the reverse of diameter response. Seedlings growing in association with varied densities of alder were 12% taller than those growing in alder-free environments. In those treatments where alder was removed, herb and pinegrass cover increased. Grass competition has been shown to depress height growth of lodgepole pine (Clark and McLean 1979). In contrast to the results of this study, however, shrub competition has been shown to depress height growth in

conifers (McMinn 1974, Perry and Lotan 1977, Howard and Newton 1984, Brand 1986, Lanini and Radosevich 1986).

Seedling morphology was markedly affected by alder density. As alder densities increased, seedling height increased and stem diameter decreased. Depressions in diameter growth concurrent with improvements in height growth as alder densities increased resulted in greater height:diameter ratios (i.e. spindlier seedlings). Increased height growth and height:diameter ratios of seedlings growing among high densities of shrubs has been observed by others (Zedaker et al. 1987, Cole and Newton 1986). Compared with low densities, competition at high densities also can result in less foliage per seedling and consequently lower photosynthetic capacity (Lanner 1985). Changes in seedling morphology in response to competition can be explained by patterns in resource, particularly carbon, allocation. Lanner (1985) proposes that the hierarchy of resource sinks when plants are under stress is probably: developing cones > elongating shoots > active cambium > roots > storage. When sinks are in competition with each other and under high competitive stress from overtopping alder, not only are elongating shoots a higher priority, they also are closer to the sources of photosynthate (i.e. needles). Furthermore, seedlings growing under high competitive stress have small crowns and, therefore, need less stem tissue (i.e. diameter) for support. Increased height growth under increased alder competition is advantageous to seedlings because more foliage is exposed to sunlight. Greater resource allocation to height relative to diameter growth has been observed in conifers as a response to low light intensities (Zedaker et al. 1987, Waring and Schlesinger 1985, Ekwebelam and Reid 1984).

Pine height growth clearly is not a good indicator of the negative effects of interference from neighboring vegetation. Many studies demonstrate that stem diameter growth is consistently more responsive to intra- and interspecific competition than is height growth (Lanner 1985, Lanini and Radosevich 1986, Wagner and Radosevich 1987, Zedaker et al. 1987, Coates 1987). Lodgepole pine exhibits

determinant shoot growth, i.e. the annual shoot growth is fixed by the number of primordia formed in the previous year. Height growth occurs early in the growing season and the developing shoot draws largely on stored carbohydrates. Consequently annual shoot growth is closely related to the competitive environment of the previous year.

Competitive environments in this study were not well established in 1987, thus precluding any distinct differentiation in second year height growth. Diameter growth, on the other hand, is active through the entire growing season and hence depends on current photosynthate after stored carbohydrates have been depleted. Second year diameter growth was therefore closely related to the competitive environment in 1988 (Roberts and Wareing 1975, Lanner 1985, Zedaker et al. 1987).

Xylem water potential

Predawn and midday xylem water potential (PWP and MWP respectively) were high (-0.13 and -0.29 MPa) in April and May, when soil water potential was high (-0.03 MPa at 10 cm) due to snow melt. PWP and MWP decreased through the summer to minimums of -0.30 and -0.87 MPa respectively, which corresponded with a lower soil water potential (-0.04 MPa at 10 cm). Fall rains resulted in an increase in soil water potential to -0.02 MPa and corresponding increases in PWP and MWP to -0.12 and -0.10 MPa respectively. Water potentials in this study were within the range of those reported for lodgepole pine planted in the field (Baldwin and Barney 1976).

Xylem water potentials varied little according to abundance of alder and herbs. Midday water potential was significantly lower on June 27, 1988, however, under maximum alder and herb densities (-1.05 MPa) than when alder was removed (-0.61 MPa). Rates of photosynthesis in lodgepole pine are reported to decline dramatically when xylem water potential falls below -0.66 MPa, and reach zero (upon stomata closure) at potentials between -1.5 MPa and -2.24 MPa (Running 1980, Brix 1979, Dykstra 1974, Lopushinsky 1969). Consequently, pines that were subject to higher moisture stress under the alder and herb canopy

on June 27 likely exhibited reduced growth due to a reduction in photosynthetic rates. Significantly lower moisture stresses have been induced in other *Pinus* spp. upon the removal of competing vegetation (Lanini and Radosevich 1986, Carter et al. 1984). Carter et al. (1984) found that removal of herbs and grasses in addition to shrubs significantly lowered moisture stress. In this study, however, there was no difference in water stress between seedlings growing with and without herb competition.

Predawn and further midday measurements were not significantly different among treatments through the summer. Predawn water potential represents the maximum water stress recovery seedlings attain during the day. Recovery of seedlings ranged from -0.02 to -0.03 MPa, which is well above the minimum predawn water potential of -1.3 MPa at which lodgepole pine seedlings close their stomata (Running 1980).

Environmental effects

Competing vegetation acts directly on the environment in which seedlings grow, by modifying conditions (soil and air temperature) and the availability of resources (water, light and nutrients). Stomatal activity, and hence photosynthesis, of lodgepole pine seedlings respond directly to soil moisture, air temperature, and radiation (Running 1980, Dykstra 1974). Increasing abundances of alder and associated shrubs and herbs had a negative effect on diameter growth of lodgepole pine seedlings through a mediated effect on their microenvironment.

Depletion of soil moisture by competing vegetation has been the nemesis of conifer seedling growth rates in the Pacific Northwest (Radosevich and Lanini 1986, Walstad and Kuch 1987). In this study, however, soil moisture was not depleted by competing vegetation. Soil water potential, averaged over 10, 30 and 40 cm depths, reached a minimum of only -0.04 MPa in mid-summer. Furthermore, lodgepole pine has a greater ability to reduce transpiration rates under high

moisture stress than other western conifers (Baer 1976, Bassman 1985). The stomata close at higher shoot water potentials than other conifers, which suggests more sensitive stomatal control (Lopushinsky 1969). Transpiration rates start to decline when soil water potentials reach -0.1 to -0.2 MPa. Transpiration rates are half of the maximum at -0.5 MPa and stomatal closure occurs between -1.5 and -1.7 MPa (Baer 1976, Lopushinsky and Klock 1974). Clearly soil moisture availability in this study was adequate for photosynthesis throughout the growing season. Soil water stress can not explain the disparities in seedling water potential and growth responses among the alder and herb reduction treatments. Soil water stress has been significantly correlated with lodgepole pine water potential in Colorado (Baldwin and Barney 1976) but not British Columbia (Coates 1987, Vyse, 1987⁵).

Day and night air temperatures profoundly affect the growth and water potential of lodgepole pine (Larcher 1983, Baldwin and Barney 1976, Cochran 1972). Maximum rates of photosynthesis in conifers are attained at air temperatures between 10 and 25°C (Larcher 1983) and needle temperatures of 20°C (Dykstra 1974). Photosynthesis in conifers is limited, however, above 35 to 42°C (Larcher 1983). Air temperature at 15 cm height (roughly corresponding to the middle of seedling crowns) never exceeded 35°C in 1987 or 1988. Rather, maximum air temperatures were nearly optimal for photosynthesis, generally ranging between 20 and 30°C through the growing season. The highest average daily air temperatures prior to July occurred under the alder and herb canopy, and from July to September where all vegetation was removed.

Photosynthesis in lodgepole pine is sensitive to low temperatures. The inability of lodgepole pine to photosynthesize at cold temperatures is at least partially due to the effects of low temperature on stomatal function (Bassman 1985). Below 14°C stomatal resistance becomes increasingly limiting to photosynthesis (Dykstra

⁵ A. Vyse, Res. Silviculturist, Kamloops Forest Region, pers. comm.

1974). Below 0°C xylem water freezes and stomata close. When a warm day is preceded by an overnight frost or cold temperatures, leaf conductance is depressed even after air temperatures have recovered (Running 1980). Running (1980) found that leaf conductance was less than half the expected values after -3 to -4°C nights at a day-time air temperature of 4°C. Overnight frosts were frequent throughout the growing season under the alder and herb canopy. In contrast, night-time air temperatures at 15 cm height consistently stayed above zero where all alder and all or half of the herb cover were removed. The sub-zero night-time air temperatures under the alder and herb canopy may have limited pine leaf conductance and contributed to depressed diameter growth as compared to where all vegetation was removed.

Soil temperatures between 2 and 5°C limit root growth in conifers (Larcher 1983). Minimum daily soil temperatures at 5 and 30 cm depth never fell below 9°C in all treatments throughout the growing season. Maximum soil temperatures occurred where all vegetation had been removed, reaching 28°C at 5 cm and 23°C at 30 cm depth in late July.

Soil temperature affects transpiration in seedlings through its effect on water uptake. Seedlings can extract water from warm soils more readily than from cold soils. Douglas-fir transpiration rates, for example, declined linearly with decreasing soil temperature, and, at 1°C, declined to 19% of the rate at 20°C (Lopushinsky and Kaufmann 1984). Soil temperatures at 5 and 30 cm depths were colder under the alder and herb canopy than where the canopy was removed. The colder soil temperatures may have depressed soil water uptake. This is supported by the fact that xylem water potential in June was significantly lower under the vegetative canopy than where the canopy was removed.

The absorption of radiation by chloroplast drives photosynthesis in seedlings. Dykstra (1974) found that the light compensation point for two year old lodgepole pine seedlings was 6-10 W/m² (approximately 28-46 μE/s/m²) and the light saturation point (i.e. maximum net photosynthesis) was 380 W/m² (approximately 1748 μE/s/m²). The maximum rate of photosynthesis was approximately 10 mg/dm²/h. Barring

other limiting environmental factors, leaf conductance increased nearly linearly with available light from the light compensation to saturation point (Kaufmann 1982, Dykstra 1974, Larcher 1983). Radiation available to pine seedlings did not significantly differ among varying levels of alder reduction unless complete alder and herb removal occurred. Where all competing vegetation was removed, seedlings intercepted an average of $1508 \mu\text{E}/\text{s}/\text{m}^2$. The accurate conversion of photon units ($\mu\text{E}/\text{s}/\text{m}^2$) to radiometric units (W/m^2) is difficult; however, Biggs and Hansen (1979) estimated a conversion factor of 4.6 assuming an equal spectral irradiance over the 400-700 nm range. Using this conversion rate and data from Dykstra (1974), the potential rate of photosynthesis where all competing vegetation was removed, barring other resource limitations, was near the maximum for lodgepole pine. Intercepted radiation was reduced to an average of 64% of full sunlight, or $950 \mu\text{E}/\text{m}^2/\text{s}$, under alder and herb canopies. The potential rate of photosynthesis hence declined to about $8 \text{ mg}/\text{dm}^2/\text{h}$, or roughly 80% of the maximum rate. The 20% decline in photosynthesis rate as PAR declined from 1508 to $950 \mu\text{E}/\text{s}/\text{m}^2$ roughly agrees with the decline in stomatal conductance estimated by Kaufmann (1982). Seedlings receiving the greatest amount of radiation (i.e. in the complete vegetation removal treatment) had significantly larger stem diameters than those receiving lower levels (i.e. varying abundances of alder and herbs). Increases in pine seedling growth with increases in levels of radiation have been found under field (Lanini and Radosevich 1986) and nursery (Ekwebelam and Reid 1984) conditions.

Total and mineralizable mineral soil nitrogen were measured in the fall of 1987 following treatment initiation. Nitrogen nutrition is a critical environmental factor for growth limitation in conifers, and is of particular importance to lodgepole pine since it often grows under conditions of nitrogen stress (Cochran 1985, Ingestad and Kahr 1985). The efficient use of nitrogen and high root growth rate of lodgepole pine contribute to its rapid early development, especially on poor sites (Ingestad and Kahr 1985). The high nitrogen

productivity of lodgepole pine is reflected in its rapid increase in growth in response to nitrogen additions (Weetman et al. 1985, Ingestad and Kahr 1985, Ekwebelam and Reid 1984, Coutts and Philipson 1977, Cochran 1972). Total nitrogen in the top 15 cm of mineral soil averaged 1,583 (s.e. 33) kg/ha. Similar amounts (1,649 kg/ha) of mineral soil total N (15 cm) were found in a 60 year old mixed stand of Douglas-fir and red alder on a poor site at Wind River, Wa. (Sachs, unpubl. data⁶). At Wind River, total N between 15 and 40 cm depth was only 47% of the amount in the top 15 cm of mineral soil. Assuming a similar attenuation with depth on our site and based on bulk densities of 0.70 g/cm³ from 0 to 15 cm and 1.27 g/cm³ from 15 to 40 cm, the total N between 0-40 cm depth (rooting depth) was approximately 3,850 kg/ha. Fahey et al. (1984) found 3,150 to 8,600 kg/ha mineral soil total nitrogen (rooting depth) in lodgepole pine forests in southeastern Wyoming. Ranges of 1753 to 7100 kg/ha (rooting depth) have been reported for other conifers (Kabzems and Klinka 1987, Carlyle 1986). Kabzems and Klinka (1987) differentiated soil nutrient regimes based on mineral soil total N for Douglas-fir ecosystems on southern Vancouver Island; poor to very rich nutrient regimes ranged from 2328 to 7121 kg/ha (0-50 cm). Based on their total N characterizations, our study site would be classified as medium to rich. The relatively high nitrogen capital on the site may be the result of nitrogen fixation by sitka alder.

The majority of total N is unavailable for plant growth. The dominant form of inorganic nitrogen available for plant growth is mineralizable (ammonium and nitrate) nitrogen. Typically available forms represent less than 2% of total N (Carlyle 1986). Ammonium nitrogen and nitrate nitrogen in the top 15 cm of mineral soil on the study site averaged 23 (s.e. 1) kg/ha and 5 (s.e. 1) kg/ha, respectively. They represented only 1.7% of the amount of total nitrogen to that depth. Although total N is high, the majority is immobilized in organic matter. Mineralization is likely slow due to

⁶ D. Sachs, Oregon State University.

cold soil temperatures.

There was 127% more nitrate nitrogen where all or part of the herbaceous cover was killed than where it was left intact. Mortality of herbs likely increased the rate of mineralization by increasing soil temperature and by decreasing competition between heterotrophs and mycorrhizae (Carlyle 1986). The temporary increase in nitrate nitrogen where all or part of the herbaceous cover was removed corresponded with a 10% increase in stem diameter over treatments where the herb layer was left intact.

In summary, the results from this study suggest that several environmental factors may be important to the enhancement of lodgepole pine growth when competing vegetation is removed. Although soil water potential did not increase with vegetation removal, uptake of water by seedlings was improved. The improved uptake may have been a result of increased soil temperatures and improved resource use. The significant increase in diameter growth with complete removal of alder and herbs may have been the result of greater soil water uptake, fewer frost events, increased light availability and increased nitrate-nitrogen.

Neighborhood Competition Among Lodgepole Pine Seedlings and Plant Species in a Sitka Alder-Dominated Shrub Community

CHAPTER 2

INTRODUCTION

Sitka alder (*Alnus sinuata* (Regel) Rybd.) rapidly dominates many lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) sites following clearcutting in the southern interior of British Columbia (B.C.). The effects of neighboring sitka alder and associated species on the growth of planted lodgepole pine seedlings has not been quantified. Quantitatively assessing these effects is difficult due to wide variation in the biotic and abiotic microenvironment conditions of conifer plantations (see Chapter 1).

The presence and behavior of neighbors has a negative effect on the growth, survival and reproductive output of target plants (Mack and Harper 1977, Liddle et al. 1982, Weiner 1982, Silander and Pacala 1985, Matlack and Harper 1986, Goldberg 1987, Goldberg and Fleetwood 1987, Miller and Werner 1987). In particular, vegetation communities have a negative effect on the survival and growth of lodgepole pine (McMinn 1974, Lotan and Perry 1977, Clark and McLean 1975 and 1979, Corns and Pluth 1984, Beurmeyer 1984). Competition occurs when plant population densities are high enough that individuals modify the environmental conditions and supply of resources to each other (Harper 1977, Mack and Harper 1977). Frequently, experiments used to study interspecific competition focus on pairs of plant species, interacting at a constant total density and spatial arrangement (e.g. replacement series, after deWit, 1960). The usefulness of such experiments to natural communities is limited, however, because plants experience heterogeneous densities, spatial relationships and composition of local neighborhoods (Weiner 1982, Goldberg and Werner 1983). In addition, since individual plants interact primarily with nearby neighbors, the proximity of individuals affects the mean performance

of a species (Pacala 1986).

Neighborhood experiments are designed to examine the response of a target individual to local, rather than mean, plant density and proximity. Using this approach, the performance of a target individual is described as a function of the species, number, size, distance or aggregation of its neighbors (Mack and Harper 1977, Liddle et al. 1982, Weiner 1982 and 1984, Goldberg and Werner 1983). The main use of neighborhood experiments is to determine the amount of variation in the performance of target individuals that is explained by the amount or proximity of neighbors. In neighborhood experiments examining herbaceous plants, up to 91% of the variation in plant performance has been explained by interspecific competition (Goldberg and Fleetwood 1987).

Many theoretical models have been developed to describe self-thinning and plant size distributions in even-aged monocultures of conifers. For example, competitive interactions in *Pinus* sp. stands have accounted for up to 52% of the variation in conifer response (Weiner 1984, Cannell et al. 1984). Planted conifer seedlings, however, are faced with diffuse, interspecific competition and few studies have examined individual responses of conifers to the presence of neighbors in a natural community. Conifer response to interspecific competition has been quantified in established stands, and up to 44% of the variation in growth has been explained by competitive effects (Corns and Pluth 1984, Brand 1986a, Chan and Walstad 1987, Wagner and Radosevich 1987). The retrospective approach, however, is confounded by changing competitive relations over the life of the target tree and by underlying environmental causes which may affect both the tree and its competitors directly (Goldberg and Werner 1983, Weiner 1984, Wagner and Radosevich 1987). Experimentally creating a competition (or density) gradient and planting the target seedlings into the gradient overcome the shortcomings of the retrospective approach (Antonovics and Levin 1980, Goldberg and Werner 1983, Wagner and Radosevich 1987).

The objectives of this study were to examine, using neighborhood

techniques, the effects of sitka alder and other dominant species in the community on:

- (1) the growth of lodgepole pine individuals, and
- (2) the availability of light and soil water.

Interspecific competition indices were developed based on a tree-centered approach (Wagner 1982, Howard and Newton 1984, Wagner and Radosevich 1987). Preliminary models predicting individual pine performance from interspecific competition indices were constructed in a compartment fashion (Weiner 1982). The different indices in the models were evaluated to indirectly suggest the mechanisms of competition. Mechanisms of competition also were examined directly by measuring resource (light and soil water) availability across the competition gradient.

METHODS

The study site was located in the Montane Spruce (MS) zone of the southern interior of B.C. The clearcut in which it was located was logged and mechanically site prepared in 1977 and left to regenerate naturally. Ten years after harvest the site was dominated by a dense stand of 3 m tall sitka alder. The dominant understory species were black huckleberry (*Vaccinium membranaceum*), grouseberry (*Vaccinium scoparium*), thimbleberry (*Rubus parviflorus*), pinegrass (*Calamagrostis rubescens*) and fireweed (*Epilobium angustifolium*). For a complete description of the study site refer to the methods in Chapter 1.

Seven treatments were applied in a randomized complete block design to create gradients in alder and herb density and spatial arrangement (see Table 1.1 for a complete description of the treatments). The treatments were replicated three times on the same site. Alder density treatments were established by first manually cutting all stems at the root collar and second by controlling the number of alder clumps allowed to sprout by selective application of 2,4-D amine. Herb cover reduction treatments were established by applying glyphosate to herbs in specified areas in the treatment plots (Figure 1.2).

Lodgepole pine seedlings were planted into the treatments on July 4, 1987. Each treatment plot was planted with 49 seedlings arranged in a seven by seven grid. Pine neighborhoods were defined by 10 m² circular plots ($r=1.78$ m) centered on the seedling stems. The choice of plot size was based on the size of two year-old sitka alder and the diversity of neighboring plant species. The size is within the recommended range (5 to 20 m²) for forest vegetation management trials in British Columbia (Herring and Pollack 1985). Near the end of the second growing season (August 1988), neighborhood measurements were made on the 25 inner seedlings in each treatment plot, leaving the outer row of seedlings as a buffer. At the time of measurement, vegetative development and pine height growth was complete. Due to mortality during 1987 and 1988, only 449 of the original 525 seedlings

planted were included in the study.

Within each neighborhood plot, the performance of pine seedlings was quantified as a function of the species, amount, aggregation and distance to neighbors. The neighborhoods were described by (a) visual estimates of percent cover of neighboring plants (extensive approach), and (b) detailed measurements of above-ground alder size (intensive approach) (after Wagner and Radosevich 1987). The percent cover of (1) all shrubs, (2) all herbs and (3) each of the dominant species listed above were estimated using the quadrant method of Herring and Pollack (1985). Using the intensive approach each alder in the neighborhood plot was measured separately. The height, crown diameter, azimuth, and distance from the target pine to the closest crown edge of each neighboring alder were measured (Figure 2.1).

Seedling performance in each neighborhood plot was quantified as stem diameter, height, annual height increment (1987 to 1988), annual diameter increment, D2H (diameter squared x height) and height:diameter ratio.

The physical environment was partially described for a subset of neighborhood plots. Microtopographic conditions (slope and aspect) of all plots were recorded. Photosynthetically active radiation (PAR) and percent of full sunlight available to seedlings were measured in a subset of 163 plots from Treatments 1, 3, 6 and 7. A Licor line sensor (Sunfleck Ceptometer) was used to take two perpendicular measurements: (1) above the canopy (approximately 1 m) and (2) at seedling height. Measurements were taken between 12:00 and 14:30 hours on August 22, 1988. Soil water potential at 30 and 45 cm depths was estimated through the growing season at five locations in each of Treatments 1, 6 and 7 using a Troxler 3300 Series neutron probe. The neighborhood of each aluminum access tube was defined using the same methods for defining seedling neighborhoods.

Competition indices were calculated using the extensive and intensive neighborhood measures. The indices reflected the amount of interference a target seedling experienced from neighboring vegetation. Each extensive index corresponded to the percent cover of

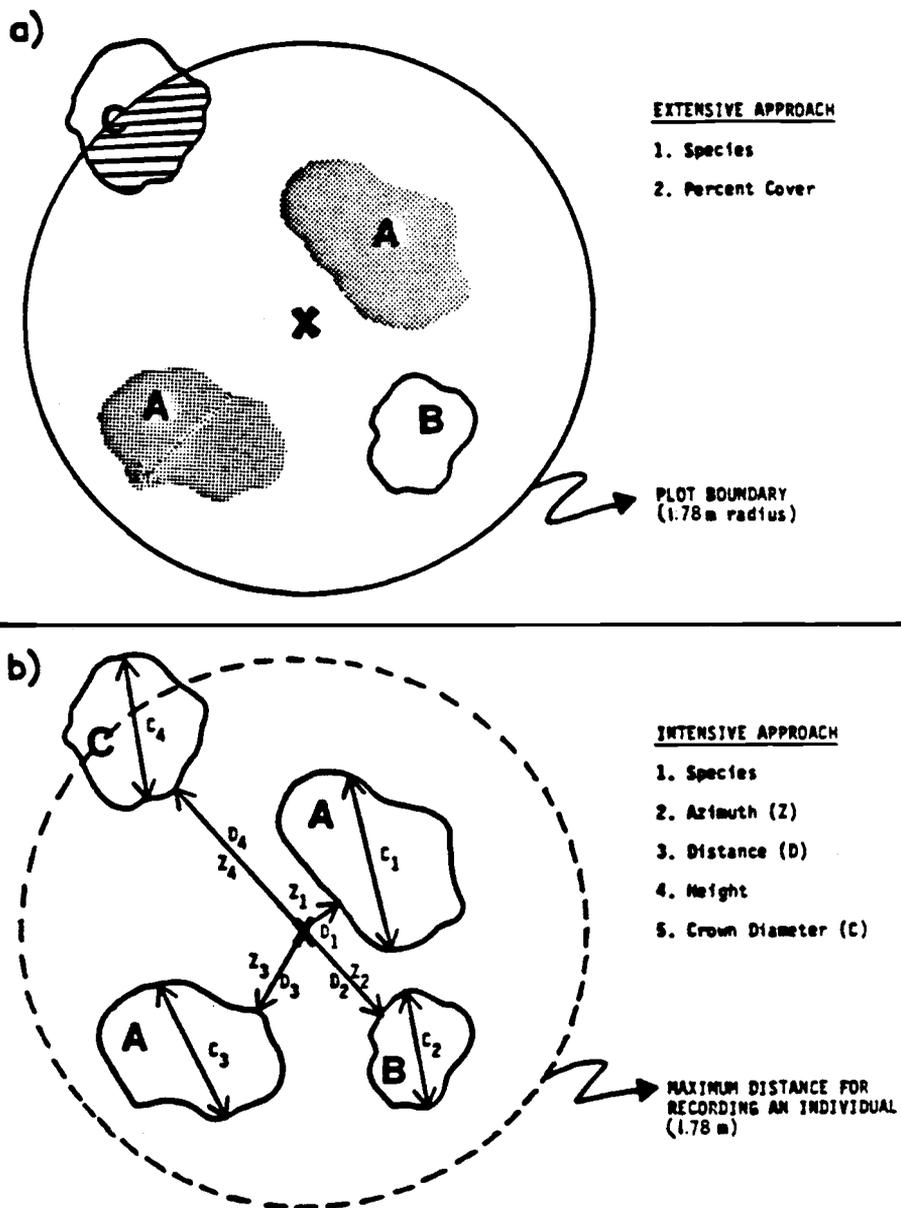


Figure 2.1 Vegetation parameters measured using the (a) extensive and (b) intensive approaches to quantifying interspecific competition. In (a) the shade code for species A is dotted, species B is plain and species C is cross-hatched.

a dominant species in the neighborhood. The extensive indices are presented in Table 2.1. The intensive indices were summations of vegetation parameters from all alder individuals in the plot into a single value. The vegetation parameters and intensive indices are described in Table 2.2. Intensive indices were made distance dependent by dividing crown area or height by distance or the square of distance. Azimuth values were used to calculate angular dispersion, which assigns a value of zero when all competing alders are clumped at one azimuth from the seedling and a value of one when the alders are evenly distributed around the seedling (Zar 1974).

Multiple regression models were developed to predict pine performance (dependent variables) from competition indices (independent variables) for the most responsive performance variables. Logarithmic and reciprocal transformations of the dependent variables were examined. Additional models were constructed to determine how available light and soil moisture were affected by surrounding vegetation. The "best" models were determined by the combination of indices that had the highest adjusted r^2 values and included the fewest number of independent variables.

Table 2.1 Extensive competition indices that were evaluated in the study.

SYMBOL	DESCRIPTION
CI2	percent cover of all shrubs
CI3	percent cover of all herbs
CI4	percent cover of <u>Alnus viridis</u> ssp. <u>sinuata</u>
CI5	percent cover of <u>Vaccinium membranaceum</u>
CI6	percent cover of <u>Vaccinium scoparium</u>
CI7	percent cover of <u>Salix</u> sp.
CI8	percent cover of <u>Calamagrostis rubescens</u>
CI9	percent cover of <u>Rubus parviflorus</u>
CI10	percent cover of <u>Epilobium angustifolium</u>

Table 2.2 Intensive competition indices that were evaluated in the study.

HT = height (cm) of sitka alder individuals within the plot,
 D = distance (cm) from target lodgepole pine stem to the nearest
 crown edge of sitka alder individuals within the plot,
 $CA = 3.1416 * (\text{crown diameter of sitka alder individuals} / 2)^2$,
 z_i = Azimuth from the target tree to the center of alder
 individual i, and
 n = number of individual alders around the target tree.

SYMBOL	DESCRIPTION
<u>INDICES USING 1 VEGETATION PARAMETER</u>	
CAS	sum of CA
HEIGHTS	sum of HT
DISTS	sum of D
IDS	sum of inverse of D ID = 1/D
ID2S	sum of inverse of the square of D ID2 = 1/D ²
ANGDIS	angular dispersion = $\sqrt{\frac{1 - (\cos(z_i))^2 + (\sin(z_i))^2}{n}}$
<u>INDICES USING 2 VEGETATION PARAMETERS</u>	
ADHS	ANGDIS * (sum of HT)
CHS	sum of CA*HT
CDS	sum of CA/D
HDS	sum of HT/D
CD2S	sum of CA/D ²
HD2S	sum of HT/D ²
ADDS	ANGDIS * (sum of D)
ADD2S	ANGDIS * (sum of D ²)
<u>INDICES USING 3 VEGETATION PARAMETERS</u>	
CHDS	sum of (CA * HT)/D
CHD2S	sum of (CA * HT)/D ²
ADCHS	ANGDIS * sum of (CA * HT)
ADHD2S	ANGDIS * sum of (HT/D ²)
<u>INDICES USING 4 VEGETATION PARAMETERS</u>	
ADCHDS	ANGDIS * (sum of (CA * HT)/D)
ADCHD2S	ANGDIS * (sum of (CA * HT)/D ²)

RESULTS

Of the performance variables examined in regression models, individual competition indices explained the most variation in pine diameter and height:diameter ratio. No more than 10% of the variation in diameter and height:diameter ratio was explained by any single extensive or intensive index. Neither reciprocal nor logarithmic transformations of the performance variables improved the r^2 value of any of the models.

When competition indices were regressed against pine performance variables, extensive indices explained more variation than did intensive indices (Table 2.3). Percent cover of all shrubs (CI2) and sitka alder (CI4) explained the most variation in height:diameter ratio, each with r^2 values of 0.10 (Figure 2.2). Percent cover of all herbs (CI3) and fireweed (CI10) predicted 8% and 6% of the variation in height:diameter ratio, respectively. Percent cover of all herbs (CI3) was the most predictive index for stem diameter ($r^2=0.07$), followed by percent cover of all shrubs ($r^2=0.03$), alder ($r^2=0.03$) and pinegrass ($r^2=0.03$) (Figure 2.3). The stepwise regression procedure selected two variable multiple regression models from the extensive indices for height:diameter ratio and diameter (Table 2.4). Percent cover of all shrubs (CI2) and all herbs (CI3) explained 16% of the variation in height:diameter ratio and only 9% of the variation in diameter.

The most predictive intensive indices were DISTS, ANGDIS, and HEIGHTS; they explained 8%, 7% and 7% of the variation in height:diameter ratio, respectively, and only 2% of the variation in diameter (Table 2.3 and Figure 2.4). The model selected by stepwise multiple regression, which related height:diameter ratio to intensive indices, had an r^2 value of only 0.09 (Table 2.4). The model included the distance (DISTS) and aggregation (ANGDIS) of alder with respect to the seedlings.

The size of seedlings at the time of planting is an important determinant of future performance. Initial size was correlated with

Table 2.3 Linear models of competition indices, initial size and browse damage for diameter, height, height: diameter ratio and D2H.

INDEPENDENT VARIABLE	DIAMETER		HEIGHT		HT:DIAM		D2H	
	r ²	p-value						
EXTENSIVE INDICES								
Percent cover of all shrubs (CI2)	0.03	0.0005	0.03	0.0015	0.10	0.0001	0.01	0.0540
Percent cover of all herbs (CI3)	0.07	0.0001	0.00	0.5341	0.08	0.0001	0.03	0.0004
Percent cover of alder (CI4)	0.03	0.0008	0.02	0.0036	0.10	0.0001	0.01	0.0527
Percent cover of pinegrass (CI8)	0.03	0.0006	0.00	0.7131	0.04	0.0001	0.02	0.0122
Percent cover of fireweed (CI10)	0.03	0.0019	0.00	0.2146	0.06	0.0001	0.01	0.0239
INTENSIVE INDICES								
Distance from pine to alder crown edge (DISTS)	0.02	0.0052	0.02	0.0052	0.08	0.0001	0.01	0.0885
Height of alder (HEIGHTS)	0.02	0.0230	0.02	0.0115	0.07	0.0001	0.00	0.0818
Angular dispersion of alder around pine (ANGDIS)	0.02	0.0061	0.02	0.0087	0.07	0.0001	0.00	0.1206
INITIAL HEIGHT	0.03	0.0001	0.14	0.0001	0.06	0.0001	0.07	0.0001
BROWSE DAMAGE	0.09	0.0001	0.22	0.0001	0.09	0.0001	0.10	0.0001
VIGOUR	0.09	0.0001	0.22	0.0001	0.04	0.0001	0.11	0.0001

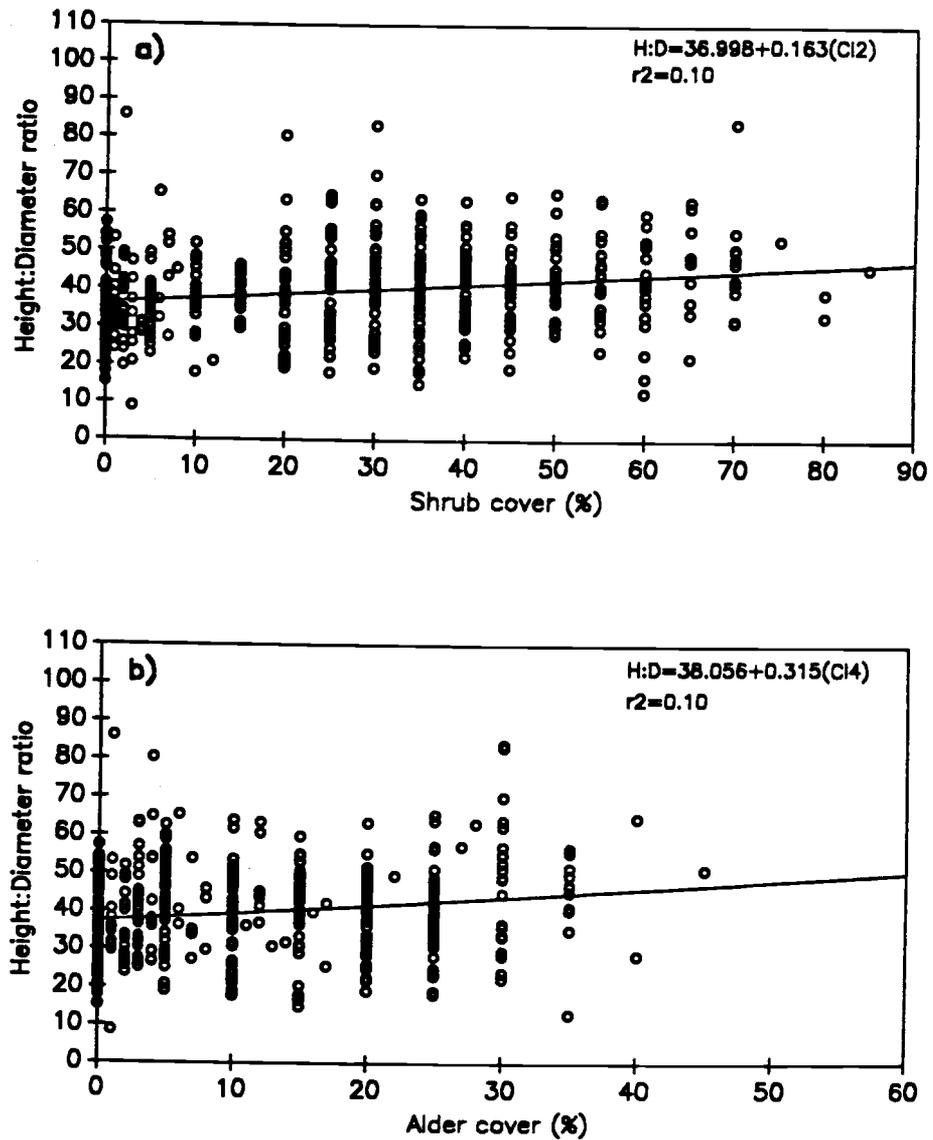


Figure 2.2 Relationship between lodgepole pine height:diameter ratio and the extensive competition indices (a) total shrub cover (CI2) and (b) sitka alder cover (CI4).

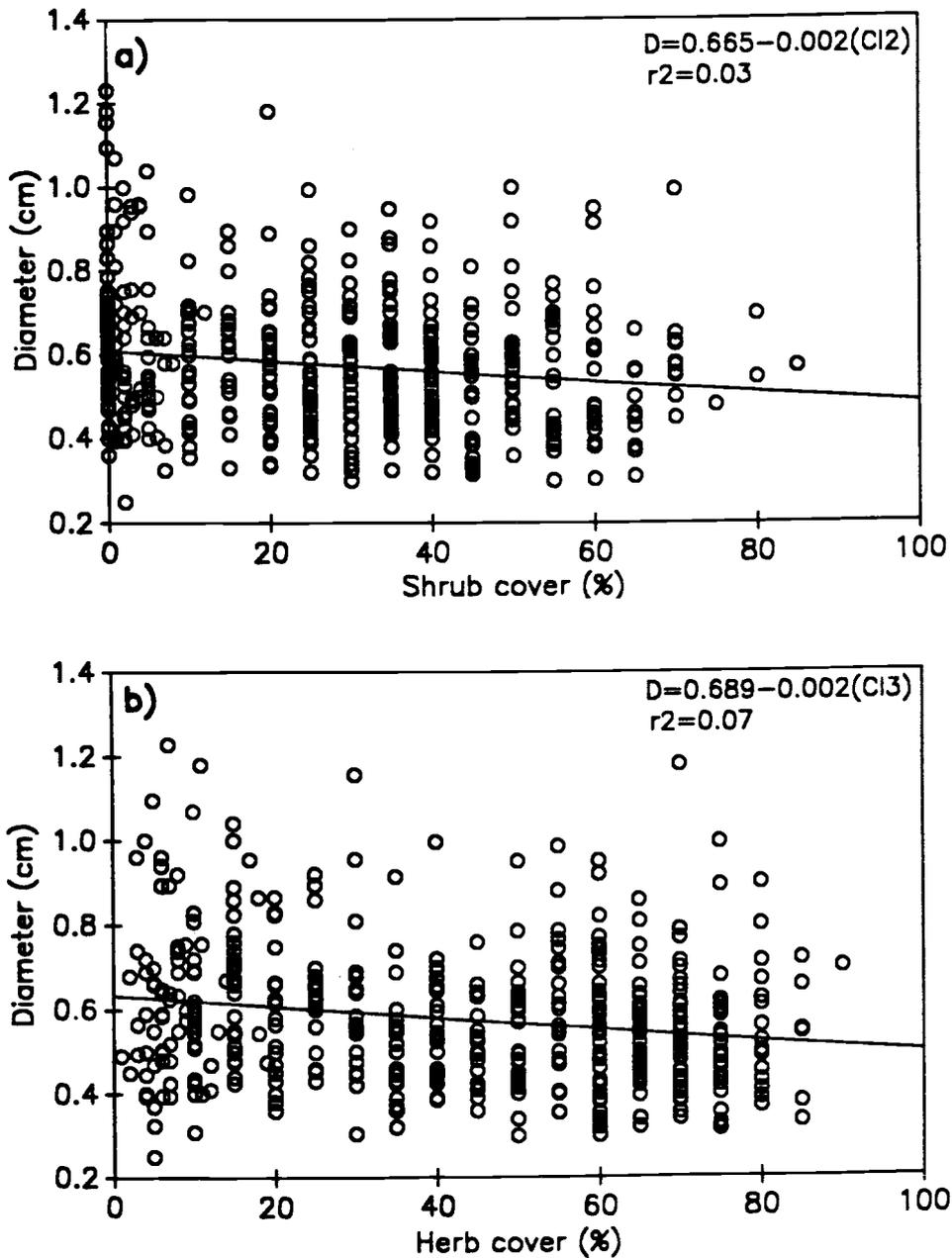


Figure 2.3 Relationship between lodgepole pine diameter and the extensive competition indices (a) total shrub cover (CI2) and (b) total herb cover (CI3).

Table 2.4 Regression coefficients, r^2 values and p-values for "best" models predicting diameter, height, height:diameter ratio and D2H from extensive and intensive competition indices. All variables in the models are significant at the 0.15 level. Partial r^2 values are given in brackets.

COMPETITION INDEX	DEPENDENT VARIABLES			
	DIAMETER	HEIGHT	HT:DIAM RATIO	D2H
EXTENSIVE INDICES				
Intercept	0.71128	23.16088	33.44049	13.07282
Percent cover of all shrubs (CI2)	-0.00118 (0.02)	0.04861	0.14075 (0.11)	****
Percent cover of all herbs (CI3)	-0.00151 (0.07)	****	0.09598 (0.05)	-0.05924
model r^2	0.09	0.03	0.16	0.04
p-value	0.0001	0.0015	0.0001	0.0006
INTENSIVE INDICES				
Intercept	0.63848	23.68331	38.55557	11.09617
Distance from pine to alder crown edge (DISTS)	-0.00014	0.00437	0.01040 (0.08)	****
Inverse of distance from pine to alder crown edge (IDS)	****	****	****	-16.95510
Angular dispersion of alder around pine (ANGDIS)	****	****	4.03884 (0.01)	****
model r^2	0.03	0.02	0.09	0.01
p-value	0.0026	0.0052	0.0001	0.0435

**** variable did not meet the 0.15 significance level for entry into the model.

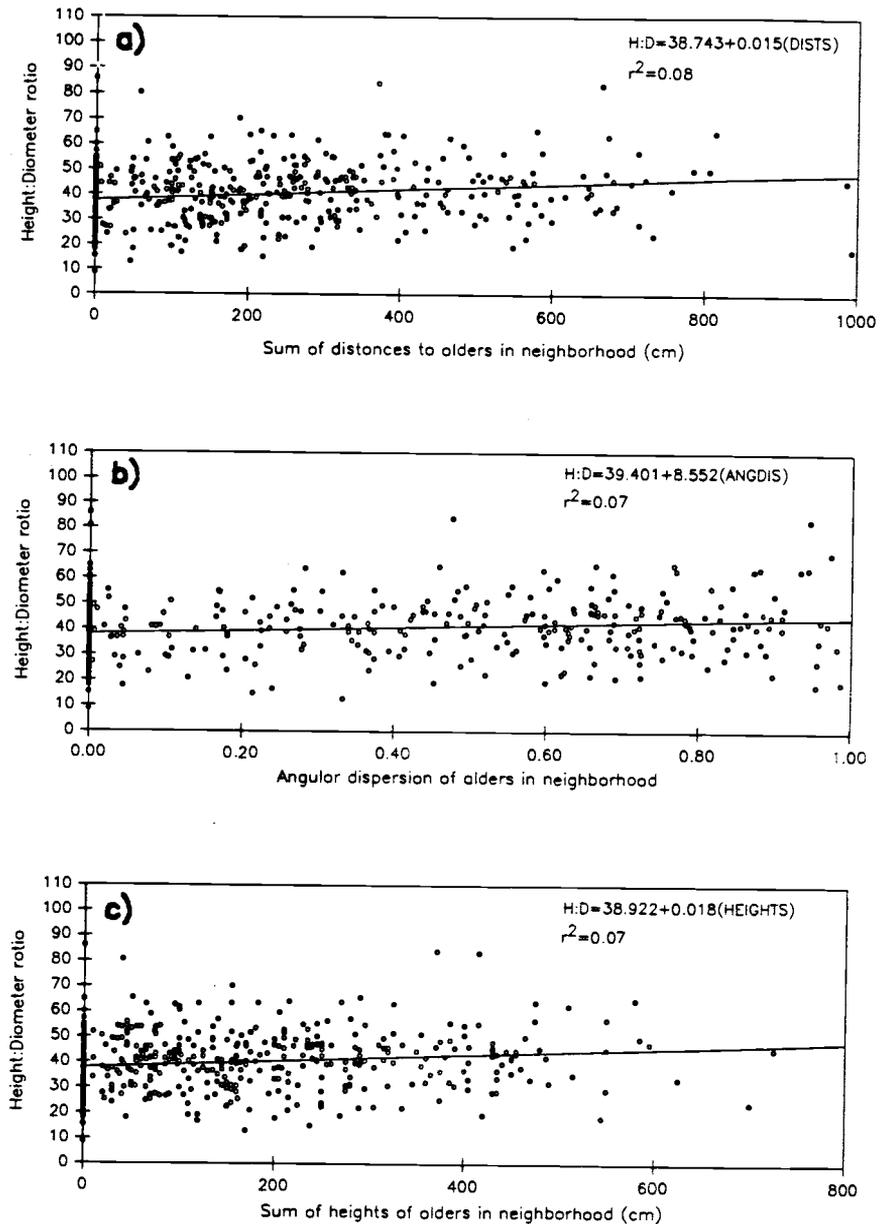


Figure 2.4 Relationship between lodgepole pine height:diameter ratio and the intensive competition indices (a) sum of distances to alders (DISTS), (b) angular dispersion of alders (ANGDIS) and (c) sum of alder heights (HEIGHTS).

performance at the end of the second growing season. Height was the most responsive initial size parameter and was positively correlated with all second year size variables. Initial height explained 14%, 3%, 7% and 6% of the variation in second year height, diameter, D2H and height:diameter ratio, respectively (Table 2.3) (Figure 2.5). Vigour explained 22%, 10%, and 11% and 4% of the variation in second year height, diameter, D2H and height:diameter ratio.

Browsing damage to seedling leaders and laterals by hares (*Lepus* sp.) was extensive on the study site. Twenty-one percent of the seedlings were damaged; however, browsing severity did not vary with treatment (Chapter 1). A two point scale was developed, where damage was assigned a value of one and no damage a value of zero. When damaged seedlings were included in the data set, browsing damage had the greatest effect on height, accounting for 22% of the variation (Table 2.3). In contrast, only 9%, 10% and 9% of the variation in diameter, D2H and height:diameter ratio, respectively, was explained by the browse damage indicator. Seedling height was reduced by 30% and diameter by 18% relative to undamaged trees.

The multiple regression models selected by the stepwise procedure that explained the most variation in seedling height, stem diameter, D2H and height:diameter ratio included the independent variables: competition indices, initial size, vigour, and browse damage (Table 2.5). The model for height had the highest r^2 value (0.43) and included browse damage, initial height, vigour and percent cover of all shrubs as the independent variables. Note, however, that the competition index accounted for less than 1% of the total variation in the model.

The effects of slope and aspect on pine performance were negligible. Less than 1% of the variation in performance was explained by slope and aspect. In contrast, the percent of full sunlight available to seedlings had a significant ($p < 0.05$) effect on performance. Available light accounted for 17%, 22%, 16% and 4% of the variation in diameter, annual diameter increment, D2H and height:diameter, respectively (Figure 2.6).

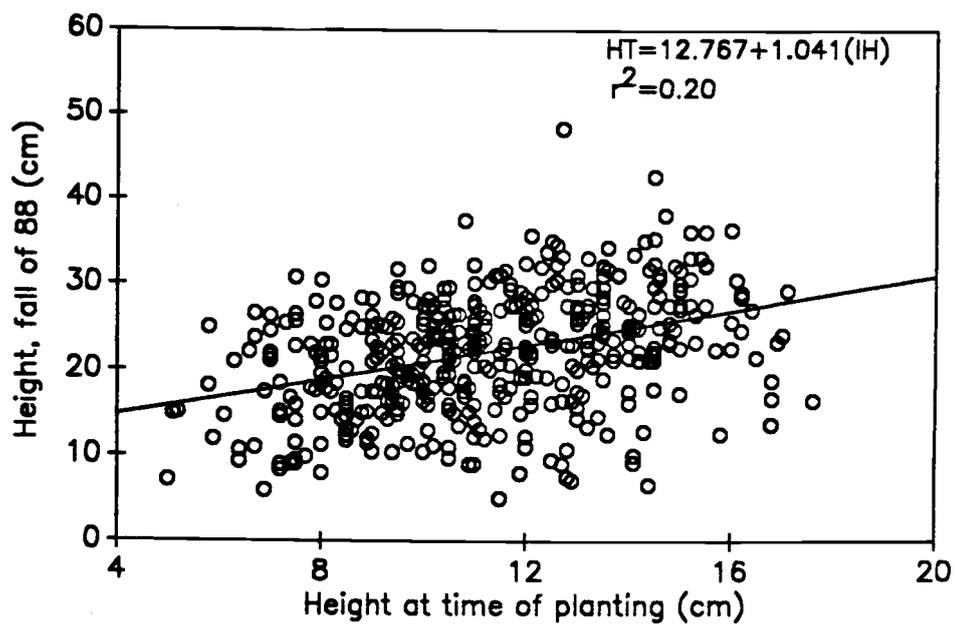


Figure 2.5 Relationship between height of lodgepole pine seedlings two seasons after planting and height at the time of planting.

Table 2.5 Regression coefficients, r^2 values and p-values for "best" models predicting diameter, height, height:diameter ratio and D2H from the independent variables, browse damage, initial height, vigour and competition indices. All variables in the models are significant at the 0.15 level. Partial r^2 values in are given in brackets.

DEPENDENT VARIABLE	DEPENDENT VARIABLES			
	DIAMETER	HEIGHT	HT:DIAM RATIO	D2H
Intercept	0.22029	-0.56854	24.953	-7.59537
Initial height	0.01102 (0.03)	0.93665 (0.13)	0.98927 (0.09)	0.67515 (0.06)
Browse damage	-0.07584 (0.05)	-6.17634 (0.22)	-7.85210 (0.05)	-4.02778 (0.10)
Vigour	0.08336 (0.09)	3.43347 (0.07)	****	2.91155 (0.04)
Percent cover of all shrubs (CI2)	-0.00095 (0.02)	0.02571 (0.01)	0.09358 (0.04)	****
Percent cover of all herbs (CI3)	-0.00101 (0.03)	****	0.06913 (0.02)	-0.03410 (0.01)
model r^2	0.22	0.43	0.20	0.21
p-value	0.0001	0.0015	0.0001	0.0001

**** variable did not meet the 0.15 significance level for entry into the model.

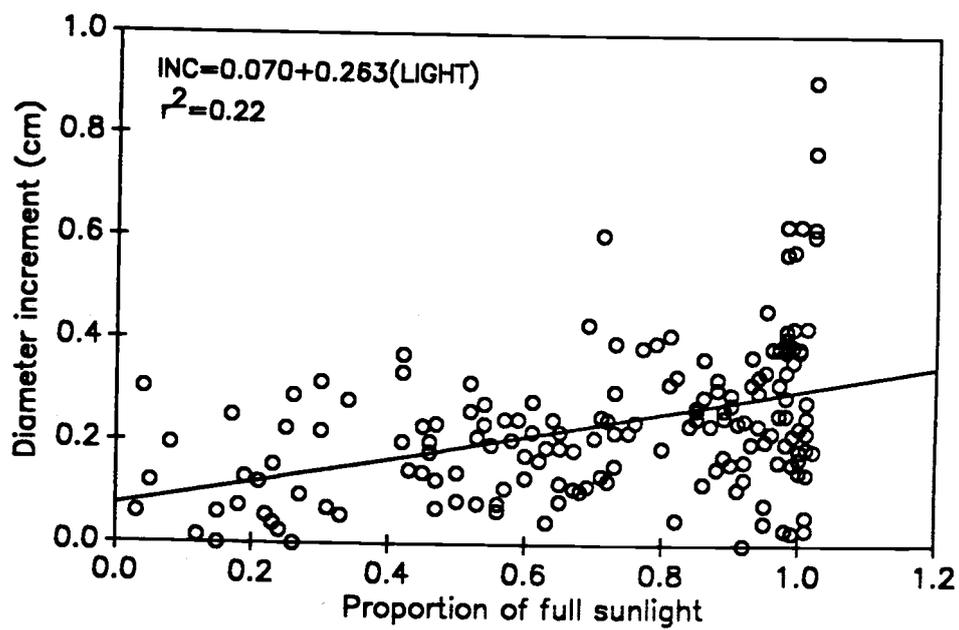


Figure 2.6 Relationship between annual diameter increment and proportion of full sunlight available to lodgepole pine seedlings.

Percent of full sunlight available to seedlings was regressed against extensive and intensive competition indices to determine how light availability was affected by surrounding vegetation. The extensive indices which accounted for the most variation in light were percent cover of all shrubs (CI2, $r^2=0.18$) and percent cover of all herbs (CI3, $r^2=0.18$) (Figure 2.7). Percent covers of individual species were of less predictive value; thimbleberry, pinegrass, sitka alder and fireweed explained 16%, 10%, 7% and 5% of the variation in available light, respectively. The stepwise regression procedure selected a model ($r^2=0.30$) for available light using extensive indices as independent variables; it included percent cover of all shrubs (CI2) and all herbs (CI3). However, since the two independent variables are highly correlated, the equation is of questionable value. Intensive indices accounted for less variation in available light than did extensive indices. Available light was most affected by height (HEIGHTS, $r^2=0.12$), crown area (CAS, $r^2=0.07$), and distance to the nearest crown edge (DISTS, $r^2=0.07$) of alder clumps (Figure 2.8). The "best" predictive model using intensive indices that was generated by the stepwise regression procedure included HEIGHTS and DISTS (Table 2.6). The model was of low predictive value, with an r^2 of only 0.15.

Soil water potential at 30 and 45 cm depths were regressed against extensive indices to determine how moisture availability was affected by individual species through the growing season. The herbs, pinegrass and fireweed, consistently had a negative effect on moisture availability. In contrast, the shrubs, alder, thimbleberry and black huckleberry, consistently had a positive effect. Ironically, vegetation was less predictive of soil water potential at 30 cm than 45 cm (Table 2.7). At 30 cm, percent cover of all shrubs (CI2) accounted for 9% of the variation in moisture availability in July and the dominant herbs, thimbleberry and pinegrass, accounted for 21% in September. Percent cover of sitka alder (CI4) had the most significant effect on soil moisture availability at 45 cm depth throughout the growing season, explaining up to 20% of the variation

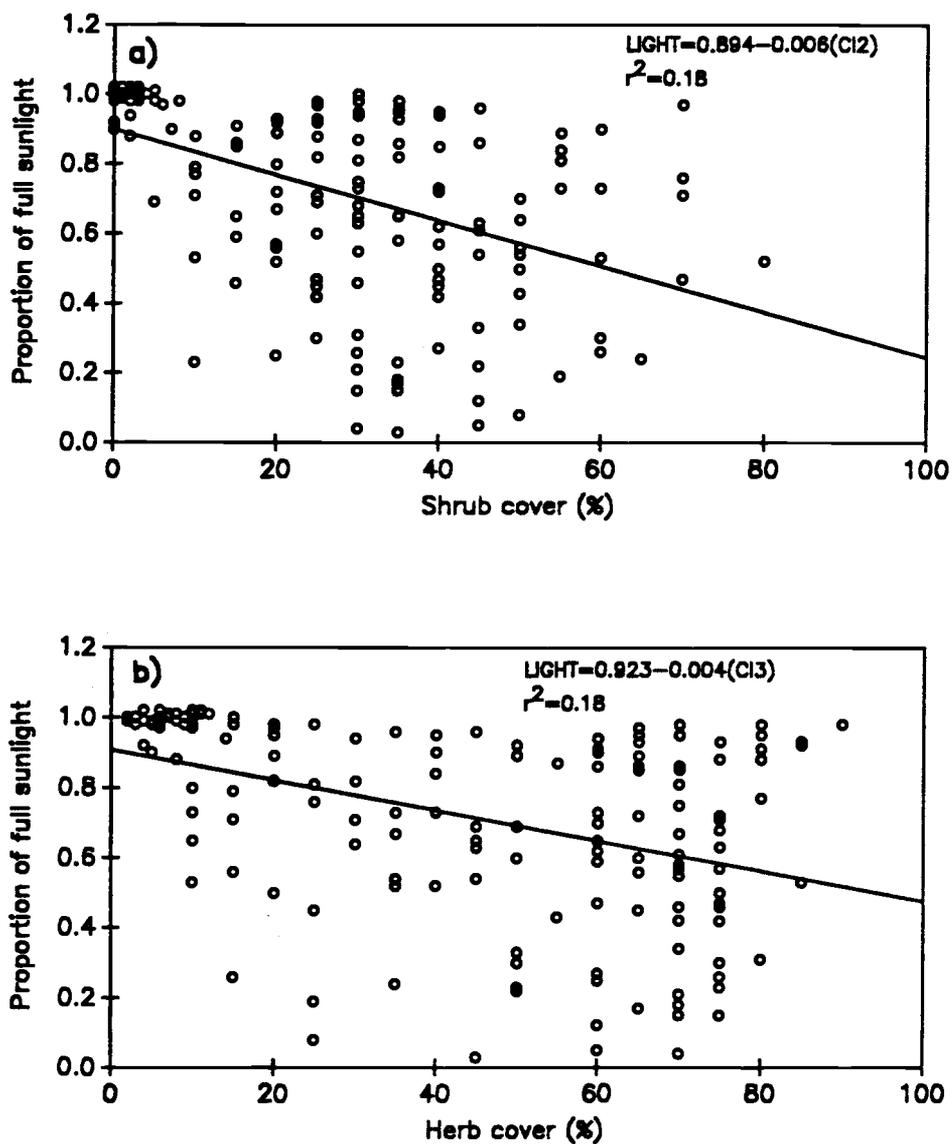


Figure 2.7 Relationship between proportion of full sunlight available to lodgepole pine seedlings and the extensive competition indices (a) total shrub cover (CI2) and (b) total herb cover (CI3).

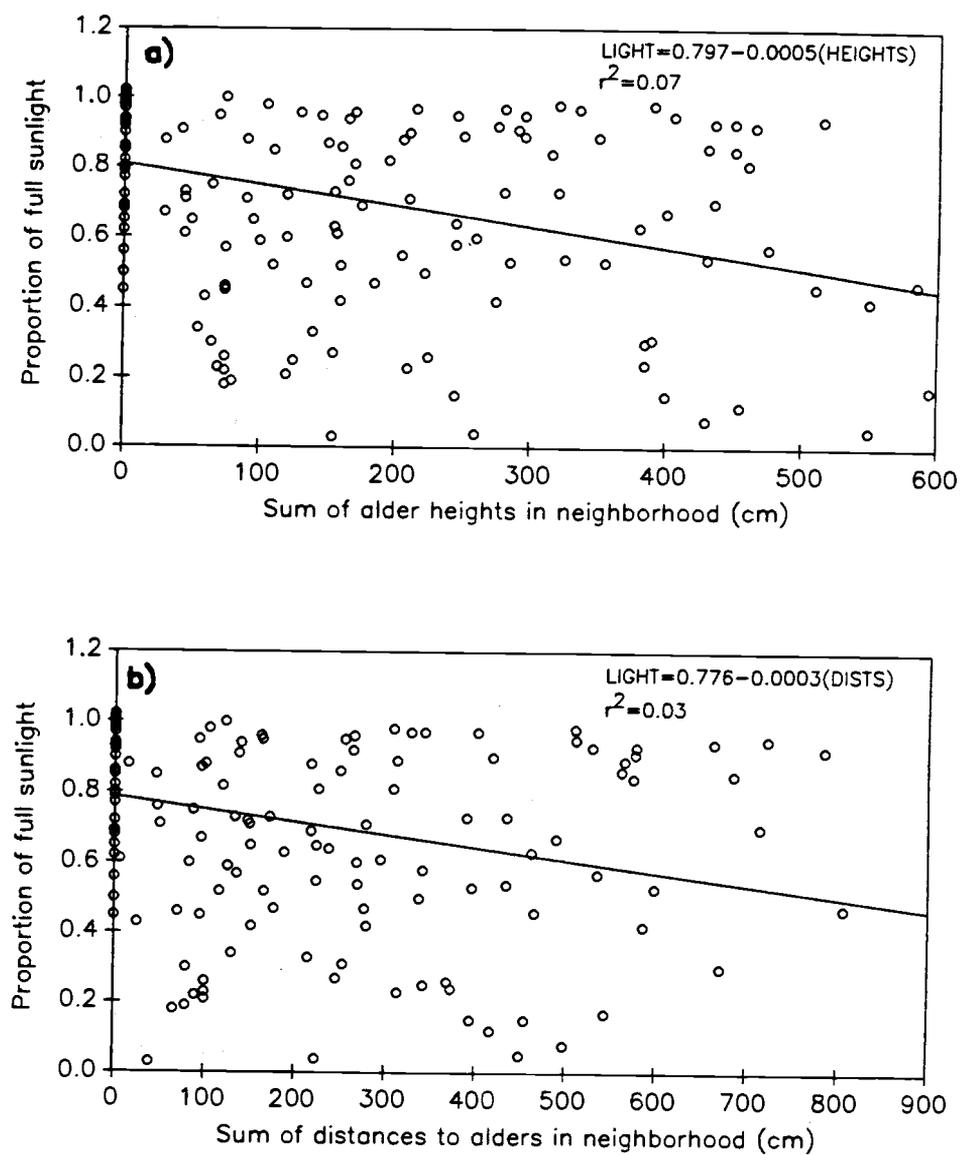


Figure 2.8 Relationship between proportion of full sunlight available to seedlings and the intensive competition indices (a) sum of alder heights (HEIGHTS) and (b) sum of distances to alders (DISTS).

Table 2.6 Regression coefficients, r^2 values and p-values for "best" models predicting percent of full sunlight available to seedlings from extensive and intensive competition indices. All variables in the models are significant at the 0.15 level.

PERCENT OF FULL SUNLIGHT AVAILABLE TO SEEDLINGS			
COMPETITION INDEX	COEFFICIENT	PARTIAL r^2	P-VALUE
EXTENSIVE INDICES			
Intercept	1.02103		0.0001
Percent cover of all shrubs (CI2)	-0.01006	0.21	0.0001
Percent cover of all herbs (CI3)	-0.00145	0.09	0.0001
model r^2		0.30	
model p-value		0.0001	
INTENSIVE INDICES			
Intercept	0.08048		0.0001
Height of alder (HEIGHTS)	-0.00121	0.12	0.0001
Distance from pine to alder crown edge (DISTS)	0.00052	0.03	0.0424
model r^2		0.15	
model p-value			0.0001

Table 2.7 Regression coefficients, r^2 values and p-values for "best" models predicting soil water potential at 30 and 45 cm depths from June to September from extensive and intensive competition indices. All variables in the models are significant at the 0.15 level.

SOIL DEPTH	MONTH		
	JUNE	JULY	SEPTEMBER
<u>30 cm</u>			
Intercept	****	0.02928	0.02757
Percent cover of all shrubs (CI2)	****	0.00036 (0.09)*	****
Percent cover of thimbleberry (CI9)	****	****	0.00087 (0.15)
Percent cover of pinegrass (CI8)	****	****	-0.00021 (0.06)
Percent cover of huckleberry (CI5)	****	****	0.00078 (0.04)
model r^2		0.09	0.25
model p-value		0.0545	0.0091
<u>45 cm</u>			
Intercept	0.02433	0.02696	0.02449
Percent cover of alder (CI4)	0.00092 (0.12)	0.00089 (0.18)	0.00095 (0.22)
Percent cover of pinegrass (CI8)	-0.00024 (0.10)	****	****
Percent cover of fireweed (CI10)	****	-0.00074 (0.04)	-0.00087 (0.06)
model r^2	0.20	0.22	0.28
model p-value	0.0060	0.0066	0.0013

* partial r^2 value

**** variable did not meet the 0.15 significance level for entry into the model.

in soil water potential. The stepwise regression procedure selected models which accounted for up to 28% of the variation in soil water potential at 45 cm depth. The significant variables in the models were percent cover of alder (CI4), pinegrass (CI8) and fireweed (CI10).

DISCUSSION

The results of this study are consistent with other neighborhood studies of competition among plants, i.e. increasing the amount of neighbors had a negative effect on the diameter of pine seedlings. Up to 16% of the variation in pine performance was explained by interference from neighboring shrubs and herbs after two growing seasons. Although the coefficient of determination was low, other researchers examining the performance of newly planted seedlings in conifer plantations using the neighborhood approach have found similar results (Brand 1986a, Coates, 1987, Wagner, 1988⁷). Coates (1987) found that interference indices accounted for no more than 11% of the variation in diameter growth of lodgepole pine seedlings growing in a two-year old plantation in the central interior of B.C.

Stem diameter and height:diameter ratio were the most responsive performance variables to measures of interference (i.e. competition indices). The relative insensitivity of height growth compared to diameter growth under competitive stress has been commonly observed in young plantations when seedlings become spindly as a result of altered light conditions under overtopping vegetation (Lanner 1985, Wagner and Radosevich 1987).

Extensive indices, which were merely visual estimates of percent cover of the dominant species and growth forms (shrubs and herbs), explained more variation in pine performance than did the more detailed intensive indices. Surprisingly, percent cover of sitka alder explained more than 10% of the variation in pine height:diameter ratio, while its more objective analog, the sum of crown areas of all alder individuals in the plot, explained less than 6%. Estimates of percent cover also have proven to be of the greatest predictive value for seedling growth in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Wagner and Radosevich 1987), Engelmann spruce (*Picea engelmannii* Parry) and lodgepole pine (Coates 1987) plantations. The

⁷ B. Wagner, Oregon State University, pers. comm.

most predictive multiple regression equation selected from cover estimates (extensive indices) accounted for 16% of the variation in height:diameter ratio, while the most predictive equation using intensive indices accounted for only 9%. The extensive indices included cover estimates of *all* neighboring species, while the intensive indices included distance and aggregation measures of *only* sitka alder. Clearly other species in addition to alder had a significantly negative effect on pine growth.

Neighborhood experiments usually are used to determine the effect of, or the amount of variation explained by, neighboring species on the performance of target individuals (Mack and Harper 1977, Liddle et al. 1982, Weiner 1982). Goldberg and Werner (1983) suggest, in addition, that the per unit competitive effect of a neighbor species on a target species can be described by the slope of the regression of performance of target seedlings on the amount of neighbors. The cover of sitka alder (CI2) explained more variation in pine performance than any of the other dominant species. Furthermore, the regression coefficient of CI2 was largest when compared with other extensive indices, which suggests that sitka alder had the greatest competitive effect on the performance of pine.

Sitka alder also was the largest neighboring species in the community. Larger plants are likely to have a greater competitive effect simply because they can take up more resources (Harper 1977). Goldberg and Werner (1983) suggest that there is some degree of equivalence of per unit competitive effects among different species since they all require the same resources (light, water, nutrients and CO₂) and that per unit competitive effects often are overshadowed by size differences between individual neighbors. Neighborhood studies of annual plants in natural communities support this hypothesis (Goldberg 1987, Miller and Werner 1987, Goldberg and Fleetwood 1987). In this study, however, there is evidence that shrubs (sitka alder being the dominant species) confer a greater per unit competitive effect than herbs on lodgepole pine seedlings. The shrub cover index explained more variation in pine performance and had a larger

regression coefficient than the herb cover index in the "best" multiple regression equation predicting pine height:diameter ratio.

Different measures of competition can suggest mechanisms of competition (Weiner 1982, Goldberg and Werner 1983, Brand 1986b). The intensive indices tested in regression models could help explain the processes by which sitka alder competes with lodgepole pine seedlings. Angular dispersion of alder clumps, for example, may affect light availability to seedlings (Mack and Harper 1977, Weiner 1984). Increasing the distance from target pine to neighboring alder decreases the negative effects of competition on pine performance. Weiner (1982 and 1984) suggests that the decreasing effect of a neighbor with the square of its distance infers competition for two dimensional space, such as the soil based resources water and nutrients. In contrast, the decreasing effect of a neighbor with simply the distance from the target infers competition for light. Intensive indices that explained the most variation in height:diameter ratio were distance (DISTS, $r^2=0.08$), height (HEIGHTS, $r^2=0.07$), angular dispersion (ANGDIS, $r^2=0.07$) and crown area (CAS, $r^2=0.06$). Regressions using distance dependent indices, however, resulted in a poorer fit of the data. The single parameter indices, DISTS and ANGDIS were significant variables in the "best" regression model explaining variation in height:diameter ratio, suggesting competition for light. However, they did not explain much variation ($r^2=0.09$).

The concept of thresholds is fundamental to vegetation management (Radosevich and Holt 1984). The economic threshold is the weed density at which potential conifer yield loss equals the cost of treatment (Cussans et al. 1986). In the case of timber crops, financial returns must be optimized over several decades. While estimation of the economic threshold for the lodgepole pine - sitka alder community is beyond the scope of this study, preliminary estimations of competition thresholds are feasible. The competition threshold is the weed density, or amount of neighbors, at which competition begins and seedling growth is limited (Cussans et al. 1986). At very low densities there is little loss in yield. Further

increases in weed density cause sharp decreases in yield until a threshold point is reached where growth is independent of density (Goldberg and Werner 1983, Radosevich and Holt 1984). The relationship between seedling yield and competition index was best described by linear regression models. After two years of growth, there was little evidence of a threshold effect. However, seedlings with the largest stem diameters occurred at shrub and herb covers of less than 10% each (Figure 2.3). A competition threshold may become evident after a few years when seedling growth responses to the neighborhood competition are better defined.

The height of seedlings at the time of planting was an important factor in two year seedling performance. Results from the regression analyses indicate that differences in initial height among seedlings increased with time. Variation in conifer response to competitive stress has been strongly influenced by initial size and vigour in other studies of lodgepole pine (Cannell et al. 1984, Smith and Scott 1984) and Douglas-fir (Howard and Newton 1984, Brand 1986, Wagner and Radosevich 1987). Browsing damage over 1987 and 1988 also strongly affected seedling performance after two growing seasons. Over 22% of the variation in seedling performance was explained by the browse indicator in the final model predicting height growth. In a retrospective study of interspecific competition in 4-to-9-year-old Douglas-fir plantations, Wagner and Radosevich (1987) found that animal damage had the greatest effect on height, reducing growth by up to 54%. Consistent with the results of Wagner and Radosevich (1987), the effect of animal browsing on pine seedling height was far greater than the effect of interspecific competition.

Interspecific competition affects tree performance through changes in the availability of resources, most importantly light, moisture and nutrients (Radosevich and Holt 1984). Consequently pine seedling performance was compared with microtopographic conditions, solar radiation availability and soil water relations in an attempt to identify mechanisms of competition on the site.

Due to their effect on incoming radiation, slope and aspect have

previously been related to conifer growth (Stage 1976). Little variation in pine seedling performance was explained by microtopographic conditions, however, presumably due to the uniformity of slope and aspect.

Reductions in solar radiation availability, due to interference by overtopping vegetation, has been shown to result in conifer growth loss and changes in the allometric relationship of height to diameter (Howard and Newton 1984, Pearson et al. 1984, Brand 1986b, Chan and Walstad 1987). Brix (1970) found under controlled conditions that height growth of Douglas-fir and western hemlock was maintained preferentially over basal area growth as light intensity decreased. Brand (1986b) found that 55% of the variation in the relationship of height to basal area for Douglas-fir was explained by competition indices. He indicated that brush competition caused changes in height to basal area allometry by reducing light intensity. Chan and Walstad (1987) used fisheye photography to measure the percentage of sky visible under overtopping vegetation and found that it explained between 43% and 64% of the variation in diameter of Douglas-fir. In this study, shrub and herb cover together accounted for 30% of the variation in light availability at seedling height. However, only 16% of the variation in height:diameter ratio was explained by the shrub and herb cover indices and *only* 4% of the variation was explained by light intensity. In contrast, 22% of the variation in diameter increment was explained by light availability (Figure 2.6). Clearly overtopping shrubs and herbs reduced light availability to seedlings. Reduced light availability partially accounted for reductions in seedling growth, however other factors also strongly affected how seedlings performed.

Competition induced reductions in lodgepole pine diameter growth have previously been related to soil water relations (Smith and Scott 1984). Only 9% of the variation in soil water potential at 30 cm (roughly the seedling rooting depth) during the most active growing period, however, was accounted for by competition indices. The dominant herbs, pinegrass and fireweed, had a negative effect on

moisture availability. Pinegrass is commonly under high moisture stress during the growing season (Nicholson 1989), suggesting poor stomatal control and relatively high water use. In contrast, sitka alder had a positive effect on moisture availability at 30 and 45 cm, explaining up to 20% of the variation in soil water potential. By excluding herbs, alder may have served as a positive surrogate to the negative influence of herbs on soil water potential.

This study has shown that early growth of planted lodgepole pine seedlings was negatively affected by interspecific competition. The potential growth of a seedling was partially a function of its initial size, vigour, browsing damage, and competition level. A considerable amount of variation in seedling size, however, remained unexplained. Furthermore, variation among seedlings increased as competitive interference decreased. The increase in variation has been observed in other neighborhood studies (Wagner and Radosevich 1987, Goldberg 1987, Coates 1988). At high shrub and herb densities, competition had an important influence on seedling size. At low densities, however, other factors such as abiotic conditions became relatively more important (Goldberg 1987). The effects of competition levels on light and soil water availability were investigated to begin to develop an understanding of competitive processes. Light, and to a lesser degree soil water, available to seedlings were reduced by competing vegetation. In addition to the factors investigated in this study, quantification of the heterogeneity in genetic expression, nutrient availability, and pathogen and insect pressures may be necessary to improve the predictive value of the models developed.

Response of Shrubs and Herbs to Sitka Alder Density Reduction Treatments

CHAPTER 3

INTRODUCTION

Sitka alder (*Alnus sinuata* (Regel) Rybd.) dominates many unsuccessfully regenerated (backlog) clearcuts in the southern interior of British Columbia. It often increases in cover following the harvest of lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) sites in the Montane Spruce (MS) zone. Approximately 10,000 hectares of lodgepole pine forests are harvested annually in the Kamloops Forest Region, of which 20 to 50% are expected to require vegetation management (Ivanco, 1985⁸).

Sitka alder is a deciduous multi-stemmed shrub that reaches heights of 3 m on the MS site. It has been shown to improve site productivity through nitrogen fixation (Binkley 1986 and 1982a and 1982b, Harrington and Deal 1982, Dalton and Naylor 1975, Mitchell 1968, Ugolini 1968, Crocker and Major 1955) but also may compete with other species for light, water and nutrients. It grows in the understory of lodgepole pine forests but thrives in full sunlight upon removal of the canopy. Sitka alder sprouts from cut stumps, however there are no studies which describe its sprouting behavior (Haeussler and Coates 1985).

Understory species commonly associated with sitka alder on mesic sites in backlog clearcuts in the MS zone include black huckleberry (*Vaccinium membranaceum*), grouseberry (*Vaccinium scoparium*), thimbleberry (*Rubus parviflorus*), pinegrass (*Calamagrostis rubescens*) and fireweed (*Epilobium angustifolium*). Naturally regenerating lodgepole pine assumes an understory position if the alder canopy is very dense, or is codominant to dominant if the alder canopy is sparse

⁸ B. Ivanco, Planning Forester, Kamloops Forest Region, pers. comm.

to moderately dense.

The *Vaccinium* spp. belong to the Ericaceae family. They grow slowly, tolerate a wide range of moisture and nutrient regimes, and are commonly found on well drained, acidic soils. Black huckleberry grows to 50 cm and grouseberry 25 cm on the MS site. Black huckleberry is more vigorous in the open or partial shade and hence is favored by overstory removal (Haeussler and Coates 1985).

Thimbleberry is a member of the Rosaceae family. It is a deciduous shrub, favors moist or north facing sites, and grows to 70 cm on the MS site. Thimbleberry increases rapidly in cover following overstory removal and dominates over other species due to its rhizomatous root system and dense, multi-layered canopy.

Pinegrass is a member of the Poaceae family. It is a shallow rooted, tufted grass which forms a continuous, dense mat by means of rhizomes. It grows to 50 cm on the MS site. Pinegrass tolerates a wide range of moisture and nutrient regimes but tends to be associated with soils that experience a growing season moisture deficit. It increases in cover following overstory removal at elevations above 1200 m (McLean 1970).

Fireweed is a member of the Onograceae family. It is an herbaceous perennial which forms rhizome-like roots. It reaches heights of over 1 m on the MS site. Fireweed is light demanding and aggressively colonizes mineral soil exposed after logging by seed and vegetative reproduction. It will not, however, invade sites already occupied by other vegetation (Haeussler and Coates 1985).

In order to successfully regenerate backlog lodgepole pine sites, it is necessary to understand the autecology of sitka alder and its associated species. The objectives of this study were to measure the sprouting response of sitka alder to manual cutting and to determine the changes in abundance of other shrubs and herbs under varying densities of sprouting sitka alder.

METHODS

The study site was located in the Montane Spruce (MS) zone of the southern interior of B.C. The clearcut in which it was located was logged and mechanically site prepared in 1977 and left to regenerate naturally. Ten years after harvest the site was dominated by a dense stand of 3 m tall sitka alder. The density of alder averaged 3000 clumps per hectare. The dominant understory species were black huckleberry, grouseberry, thimbleberry, pinegrass and fireweed. For a complete description of the study site refer to methods in Chapter 1.

Seven treatments were applied in a randomized complete block design to create gradients in alder and understory density and spatial arrangement. See Table 1.1 for a complete description of the treatments. Alder density treatments were established by first manually cutting all stems at the root collar and second by controlling the number of clumps allowed to resprout by applying 2,4-D amine to selected clumps. Manual cutting and slash removal was done in late June of 1987. The understory cover reduction treatments were established by applying ground foliar glyphosate to a specified area of the treatment plots. Herbicide application was done in mid-July in both 1987 and 1988.

Vegetation response was measured in 10 m² (r=1.78 m) plots centered on 25 planted lodgepole pine seedlings. Measurements were made in late August of 1987 and 1988. In each tree-centered plot, the crown height and diameter of individual sitka alder clumps were measured. The percent ground cover of sitka alder, black huckleberry, grouseberry, thimbleberry, pinegrass and fireweed were visually estimated using the quadrant method of Herring and Pollack (1985). Changes percent cover and height and diameter of alder from 1987 to 1988 were calculated by difference.

Analysis of variance was used to test for block and treatment effects on vegetation cover. Where differences were significant ($p < 0.10$), means were compared using the Waller and Duncan Bayes LSD procedure (Duncan 1975).

RESULTS AND DISCUSSION

The height and diameter growth responses of sitka alder to manual cutting in treatments 1-4 are given in Table 3.1. Alders treated with 2,4-D, and hence all alders in treatments 5-7, were not included in the analysis. The cover changes of sitka alder, black huckleberry, grouseberry, thimbleberry, pinegrass and fireweed in response to the alder density and herb and shrub cover reduction treatments (treatments 1-7) are given in Tables 3.2 and 3.3.

Sitka alder

Sprouting of sitka alder following manual cutting was moderately vigorous. The mean percent ground cover of alder was 3% in 1987 and expanded to 11% in 1988. Alder clumps grew to an average of 19 cm in height (maximum 79 cm) and 38 cm in diameter (maximum 120 cm) two months following treatment in 1987. During the 1988 growing season, alder more than tripled the height growth and doubled the diameter growth of 1987. Mean alder height in August was 70 cm (maximum 125 cm) and mean diameter was 73 cm (maximum 170 cm). The tallest stems reached 42% of the pre-treatment height. The mean height and diameter increments between 1987 and 1988 were 58 and 42 cm respectively. In contrast, red alder (*Alnus rubra* Bong.) on Vancouver Island reached 2 m one growing season following cutting and by the end of the second growing season was equal to or greater than its pre-treatment height (Haeussler and Coates 1985).

Mean pine height after two growing seasons was only 25 cm (Table 1.3). Although pines were roughly equivalent in height to alder after the first growing season, they were clearly overtopped after the second. Even at maximum alder densities, however, crown closure was far from complete. With the exception of grouseberry, all shrub and herb species also overtopped pine in both 1987 and 1988.

Variation in the density of sprouting alder had an effect on alder growth. In 1987, alder crown height and diameter growth

Table 3.1 Mean response of sitka alder to manual cutting. Treatments are symbolized as TRT and are described in Table 1.1. Treatment means were not compared using ANOVAs.

	TRT 1 100%A:100%H ¹	TRT 2 75%A:100%H	TRT 3 50%A:100%H	TRT 4 25%A:100%H
August, 1987				
height (cm)	18.1 (0.9) ²	27.6 (3.2)	12.9 (0.8)	16.3 (1.5)
diameter (cm)	32.2 (1.4)	38.7 (2.4)	30.8 (3.0)	32.2 (3.8)
August, 1988				
height (cm)	73.2 (4.1)	80.0 (3.4)	67.5 (2.7)	64.8 (3.9)
diameter (cm)	68.9 (4.2)	78.6 (3.3)	73.7 (3.9)	59.5 (3.3)
Increment ³				
height (cm)	53.0 (3.9)	51.4 (3.7)	54.8 (3.5)	58.3 (4.2)
diameter (cm)	34.9 (2.5)	37.5 (3.7)	46.0 (3.0)	34.8 (3.7)

1. 100A:100H symbolizes the treatment with 100% of the maximum Alder density and 100% of the maximum Herb cover. The remaining symbols refer to the abundance of alder and herbs relative to the maximum.
2. Values in brackets are standard errors.
3. Mean increment does not equal mean size in 1988 minus mean size in 1987 because some alders included in the 1987 data set had died before the 1988 measurements and some alders in the 1988 data set had sprouted in 1988. Regardless of the death and recruitment of alders between 1987 and 1988, overall treatment densities were the same from year to year.

Table 3.2 Percent cover of shrubs and herbs according to block in the alder density and understory reduction treatments. P-values for ANOVAs comparing block means are given. The standard error value is for the overall mean.

	BLOCKS			ANOVA RESULTS	
	BLOCK 1	BLOCK 2	BLOCK 3	p-value ¹	standard error ²
August, 1987					
total shrubs	15.5ab ³	13.1b	21.0a	0.0558	1.20
total herbs	46.0a	42.0a	8.6b	0.0002	2.78
sitka alder	2.2a	2.8a	2.8a	0.2562	0.17
huckleberry	5.5b	4.6b	10.5a	0.0163	0.76
grouseberry	0.9b	0.5b	2.2a	0.0136	0.21
thimbleberry	5.1ab	6.8a	2.3b	0.0194	0.55
pinegrass	39.7a	33.3a	4.4b	0.0006	2.86
fireweed	1.6a	2.5a	1.5a	0.0910	0.18
August, 1988					
total shrubs	25.3b	24.8b	33.7a	0.0214	1.24
total herbs	54.8a	53.0a	25.5b	0.0001	1.73
sitka alder	10.3a	11.3a	12.4a	0.6084	0.45
huckleberry	6.8b	4.6b	11.8a	0.0155	0.86
grouseberry	0.9b	0.5b	2.3a	0.0222	0.23
thimbleberry	16.2a	15.3a	8.9b	0.0260	1.02
pinegrass	35.9a	35.2a	7.0b	0.0008	2.57
fireweed	8.5b	12.9a	9.1ab	0.0520	0.72
Increment					
total shrubs	10.1a	11.7a	13.8a	0.1975	0.59
total herbs	8.7a	10.7a	17.2a	0.1276	1.40
sitka alder	8.7a	8.9a	9.6a	0.8384	0.38
huckleberry	1.3a	0.0a	1.0a	0.3282	0.37
grouseberry	0.0a	0.0a	0.0a	0.9649	0.08
thimbleberry	11.0a	8.8ab	6.5b	0.0512	0.67
pinegrass	-3.3b	1.4a	2.1a	0.0285	0.78
fireweed	6.8b	7.3ab	10.3b	0.0438	0.54

1. p-values for ANOVAs comparing block means.
2. standard error value is for the overall mean.
3. means with different letters within rows are different at the 0.10 significance level.

Table 3.3 Percent cover of shrubs and herbs according to treatment following alder density and understory reduction treatments. Treatments are symbolized as TRT and are described in Table 1.1.

	TREATMENTS						
	TRT 1 100%A:100%H ¹	TRT 2 75%A:100%H	TRT 3 50%A:100%H	TRT 4 25%A:100%H	TRT 5 0%A:50%H	TRT 6 0%A:100%H	TRT 7 0%A:0%H
August, 1987							
total shrubs	18.4a ²	24.9a	23.3a	23.6a	5.9b	17.9a	1.7b
total herbs	45.8a	41.6a	42.4a	25.6a	22.5ab	46.0a	1.3b
sitka alder	5.3a	4.8a	4.2a	2.6b	0.1c	0.8c	0.0c
huckleberry	6.0bc	11.8ab	8.6ab	14.5a	0.9c	6.0bc	0.1c
grouseberry	0.8b	1.6ab	2.8a	1.9ab	1.1ab	0.1b	0.1b
thimbleberry	4.4ab	6.5a	8.3a	3.3ab	4.4ab	6.2a	0.0b
pinegrass	41.0a	32.2a	32.6a	19.7ab	15.9ab	38.8a	0.2b
fireweed	1.9ab	2.9a	2.1ab	2.1ab	1.9ab	1.8ab	0.6b
August, 1988							
total shrubs	40.1a	41.6a	40.5a	39.2a	6.7c	26.1b	1.4c
total herbs	55.0a	55.8a	57.5a	41.5b	40.8b	52.7ab	7.6c
sitka alder	22.2a	19.8ab	17.1b	12.7c	2.9d	3.7d	0.5d
huckleberry	8.1b	12.4ab	9.4b	17.8a	0.5c	5.9bc	0.1c
grouseberry	1.2abc	1.4abc	3.1a	2.3ab	0.4bc	0.2bc	0.1c
thimbleberry	14.4b	23.3a	23.4a	10.7b	7.1bc	14.5b	0.7c
pinegrass	42.0a	33.6ab	35.0ab	21.5abc	13.6bc	35.3ab	1.2c
fireweed	8.4ab	14.7a	9.5ab	12.0a	11.5a	10.3ab	4.7b
Increment							
total shrubs	22.2a	16.5b	17.0b	14.7b	0.7d	8.0c	0.2d
total herbs	9.7a	13.7a	14.1a	16.7a	16.5a	6.8a	6.3a
sitka alder	17.1a	15.1ab	12.9b	9.9c	2.8d	2.9d	0.6d
huckleberry	2.2a	0.3a	0.1a	2.9a	-0.3a	-0.2a	-0.1a
grouseberry	0.4a	-0.2ab	0.0ab	0.1ab	-0.5b	0.1ab	0.0ab
thimbleberry	10.1c	17.1a	15.0ab	7.6c	2.2d	8.5c	0.7d
pinegrass	1.4a	0.4a	1.6a	2.6a	-2.9a	-3.6a	1.1a
fireweed	6.5ab	11.2a	6.9ab	10.0a	9.6a	8.5ab	4.1b

1. 100A:100H symbolizes the treatment with 100% of the maximum Alder density and 100% of the maximum Herb cover. The remaining symbols refer to the abundance of alder and herbs relative to the maximum.
2. means with different letters within rows are different at the 0.10 significance level.

increased with increasing alder density in both 1987 ($p=0.0001$) and 1988 up to 1886 clumps/ha (treatment 2), after which growth was suppressed (Figure 3.1). Although total height and diameter in 1988 also peaked at 1886 clumps/ha, increments in height and diameter generally declined as alder density decreased (Figure 3.1). As expected, percent cover of alder increased with alder density in both 1987 and 1988 ($p=0.0001$). Annual increments in percent cover from 1987 to 1988 paralleled alder density; they were least at the lowest alder density and greatest at the highest alder density.

Total shrub and herb cover

Removal of the alder overstory had a positive effect on understory development. Total shrub cover increased by 65% during the 1988 growing season, from an average of 17% two months after treatment in 1987 to 28% in August of 1988. Total herb cover increased by 38%, from an average of 32% in 1987 to 44% in 1988. In addition to sprouting alder, thimbleberry and fireweed accounted for most of the increase in understory abundance. Thimbleberry was more aggressive of the two species, shading other plants. Fireweed grew taller and more robust, and seeded in mineral soil exposed during planting.

Total shrub and herb cover varied considerably among blocks. Blocks 1 and 2 were characterized by moderate shrub and high herb cover, while block 3 was characterized by higher shrub and considerably lower herb cover. In addition to sitka alder, the dominant species in blocks 1 and 2 were pinegrass, thimbleberry and fireweed while in block 3 they were black huckleberry and fireweed. Although shrub cover did not vary significantly among blocks (14%) in 1987, by 1988 there was greater shrub cover in block 3 (34%) than in blocks 1 and 2 (25%) ($p=0.0214$). In contrast, herb cover was considerably higher in blocks 1 and 2 (44%) than block 3 (9%) ($p=0.0002$) in 1987. The trend remained the same in 1988, although cover values were elevated (54% in blocks 1 and 2 vs 25% in block 3) ($p=0.0214$).

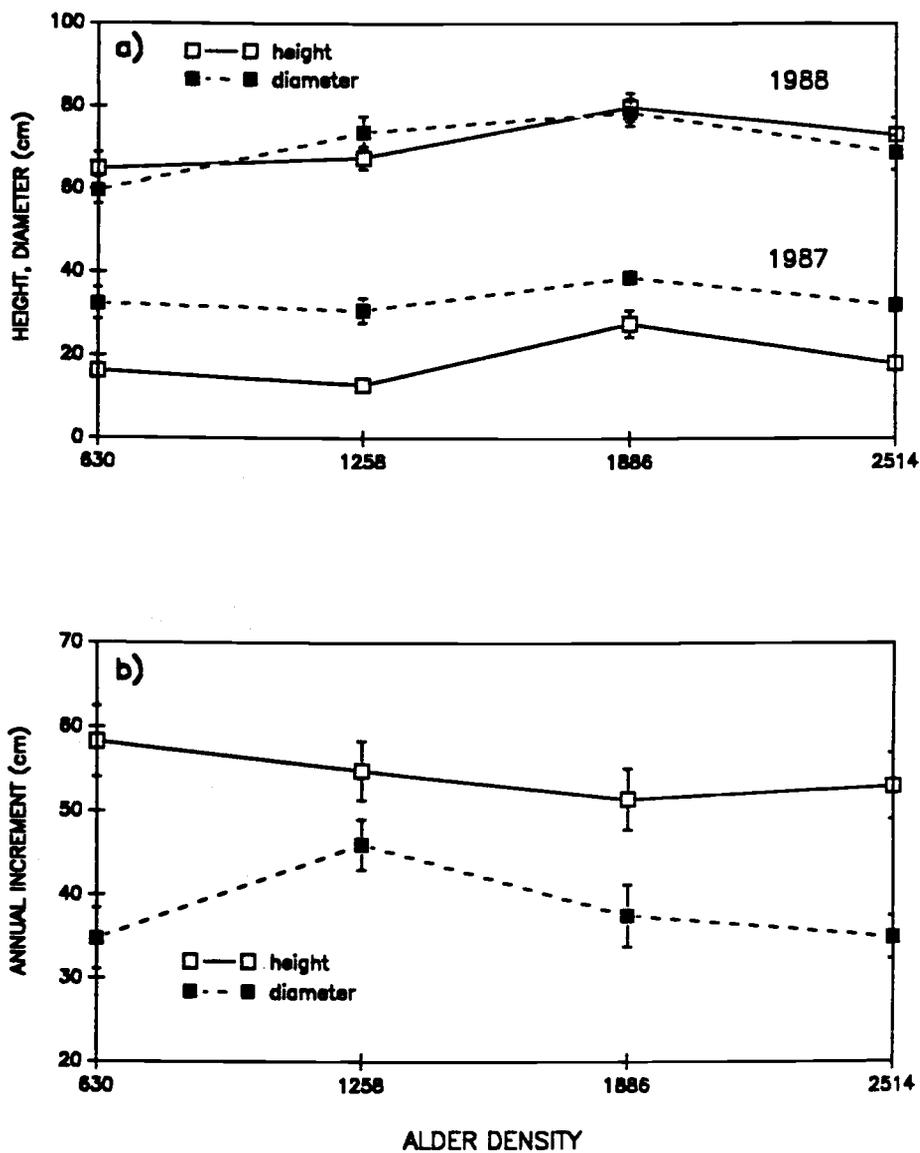


Figure 3.1 (a) Comparisons of height and diameter of alder clumps between 1987 and 1988. (b) Alder height and diameter increment from 1987 to 1988 in response to increasing alder density.

There were no significant trends in shrub or herb cover among the alder density reduction treatments in 1987 or 1988. Shrub ($p=0.0001$) and herb ($p=0.0080$) cover, however, were severely reduced where all alder was removed and the understory was partially or totally removed using glyphosate. While increments in shrub cover from 1987 to 1988 were significantly greater at maximum alder density (22%) than at reduced densities (16%) ($p=0.0001$), increments in herb cover did not vary among treatments.

Thimbleberry

Thimbleberry averaged 5% cover the year of treatment and increased to 13% in 1988. There was significantly more thimbleberry in block 2 (7%) than block 3 (2%) in 1987 ($p=0.0194$). By the fall of 1988, both blocks 1 and 2 (16%) had greater cover of thimbleberry than block 3 (9%) ($p=0.0260$). Changes in percent cover were significant among blocks, with the greatest increase in block 1 (11%) and the least in block 3 (6%) ($p=0.0512$).

Variation in the density of sprouting alder had a significant effect on the development of thimbleberry. Percent cover of thimbleberry was significantly greater (23%) at intermediate densities of alder (1886 and 1258 clumps/ha) than at high (14%) or low (12%) densities in 1988 ($p=0.0006$). Percent cover in 1987 ($p=0.0383$) and increments in percent cover from 1987 to 1988 ($p=0.0002$) followed the same trend. The lowest cover of thimbleberry occurred in treatments 5 (7%) and 7 (1%), where glyphosate was applied to the shrub and herb layer. Thimbleberry was defoliated by glyphosate application, however rosettes of leaves sprouted from rhizomes the same year.

Fireweed

Fireweed cover averaged 2% in 1987 and increased to 11% in 1988. Cover did not vary significantly among blocks or treatments in 1987 or 1988, however it maximized (15%) at the intermediate alder density of

1886 clumps/ha. Broadcast glyphosate application reduced fireweed cover by 75% in 1987 and 55% in 1988. New shoots were dwarfed and deformed.

Pinegrass

Pinegrass responded little to alder density reduction treatments. Pinegrass averaged 26% cover in both 1987 and 1988. There was significantly more pinegrass in blocks 1 (40%) and 2 (33%) than block 3 (4%) in 1987 ($p=0.0006$). The same trend occurred in 1988 ($p=0.0008$), however cover values decreased by 3% in block 1 and increased by 2% in blocks 2 and 3 ($p=0.0285$).

Pinegrass cover varied little among treatments in 1987 and 1988, however it tended to increase with alder density. The increase may have been in response to improve nutrient status. Pinegrass growth has been shown to improve with increased levels of nitrogen, sulfur and phosphorus (Freyman and van Ryswyk 1969). Although increments in pinegrass cover from 1987 to 1988 were not significantly different among treatments, they were greatest (16%) at intermediate alder densities (1886 and 1258 clumps/ha) than at high (10%) or low (8%) densities. Pinegrass cover was severely reduced by glyphosate application in treatment 7 in 1987 (0.2%) ($p=0.0250$) and 1988 (1.2%) ($p=0.0123$).

Black huckleberry and grouseberry

Black huckleberry and grouseberry responded little to alder density reduction treatments. Black huckleberry averaged 7% ground cover the year of treatment and increased to only 8% one growing season later. Grouseberry averaged 1% ground cover in both years. There was significantly more black huckleberry ($p=0.0163$) and grouseberry ($p=0.0136$) in block 3 (11% and 2%) than in blocks 1 or 2 (5% and 1%) in 1987. The same trend occurred in 1988. Increments in cover from 1987 to 1988 did not differ significantly among blocks.

In 1988, percent cover of black huckleberry and grouseberry generally increased with decreasing alder density, possibly due to greater light availability. However, the increased abundance of tall herbs where all alder were removed had a negative effect on the abundance of both species. Shade has been shown to have a negative effect on black huckleberry vigour (Minore et al. 1979). Both species also were significantly reduced in cover after glyphosate application in treatments 5 and 7.

In summary, variation in the density of sprouting alder had a significant effect on most species. While the Ericaceae species responded little to alder density reduction treatments, cover of alder, thimbleberry, fireweed and pinegrass was greatest in the intermediate density range of 1258 to 1886 clumps/ha. It appears that within that alder density range, threshold levels of environmental resources and conditions were reached which resulted in improved growth response. Growth suppression at the highest density, however, may have resulted from competition for moisture and light.

Neighborhood Competition Along a Vegetation Gradient in a 10-Year Old Lodgepole Pine-Sitka Alder Community

CHAPTER 4

INTRODUCTION

Sitka alder (*Alnus sinuata* (Regel) Rybd.) rapidly dominates many lodgepole pine (*Pinus contorta* ssp. *latifolia* Dougl.) sites following clearcutting in the Montane Spruce (MS) zone of the southern interior of British Columbia (B.C.). The competitive effects of sitka alder and associated species on the growth of natural lodgepole pine regeneration, however, has not been quantified. Quantitatively assessing these effects is difficult due to the wide variation in species, growth forms, ages and proximity of neighboring plants in the natural community. Furthermore, the relative importance of environmental factors on species interactions vary as the microtopography and plant community composition change.

Within a plant community, competitive interactions among species change along vegetation and environmental gradients. The B.C. Forest Service classifies ecosystems based on the biogeoclimatic system, which incorporates climate, vegetation and soil information. The ecosystem unit is the fundamental unit for resource management recommendations. To help achieve the objectives of integrated resource management, competitive interactions between conifers and other species must be examined, and subsequent management recommendations made, within the framework of the Biogeoclimatic Ecosystem Classification (BEC) system.

The lack of quantification and objectivity in defining classes of ecosystems has been a major criticism of BEC (Kabzems and Klinka 1987). Quantification of neighborhood interactions within objectively defined ecosystem types is vital to the understanding of competitive processes along vegetation and environmental gradients. However, the complexity and dynamic nature of early seral forest communities often

preclude detailed and accurate measurement of *both* the vegetation and the environment. Vegetation patterns within a community can be objectively defined using multivariate, or ordination, techniques (Gauch 1982). Within vegetation types, which roughly correspond with BEC types, competitive interactions among individual crop trees and neighboring vegetation can be quantified using the neighborhood approach. Based on the pattern and neighborhood analyses, hypotheses about the underlying causal environmental factors to competitive interactions also can be generated (Gauch 1982).

The neighborhood approach examines the performance of a target individual as a function of the species, number, size or aggregation of its neighbors (Mack and Harper 1977, Liddle et al. 1982, Weiner 1982 and 1984, Goldberg and Werner 1983). The main use of neighborhood analyses is to determine the amount of variation in the performance of target individuals that is explained by the amount or proximity of neighbors. In retrospective studies of young established conifer stands, up to 52% of the variation in conifer growth has been accounted for by competitive effects (Weiner 1984, Corns and Pluth 1984, Brand 1986a, Chan and Walstad 1987, Wagner and Radosevich 1987, Coates 1987).

There are limitations to a retrospective approach to studying competition which can only be overcome by experimentally creating competition levels (Goldberg and Werner 1983, Wagner and Radosevich 1987). A natural gradient of neighboring species also may have an underlying environmental cause which affects the target species directly. An advantage to retrospective studies, however, is that preliminary models can be developed in a short period of time. The models can provide reasonable hypotheses of competitive effects that can later be tested under more controlled experimental conditions.

The overall objectives of this study were to characterize vegetation types within a ten year old clearcut dominated by a lodgepole pine - sitka alder community, and to quantify competitive interactions within the types using neighborhood techniques. The specific objectives of the study were:

1. to define vegetation types using multivariate analysis,
2. to quantify interspecific competition within each vegetation type using neighborhood techniques, and
3. to identify environmental factors and vegetation patterns that may be important to competitive interactions within each vegetation type.

METHODS

The study site was located in a clearcut in the MS zone of the southern interior of B.C. The original lodgepole pine stand was harvested and mechanically site prepared in 1977. Ten years after harvest the site was dominated by a dense stand of 3 m tall sitka alder and stocked with naturally regenerated lodgepole pine. The dominant understory species were black huckleberry (*Vaccinium membranaceum*), grouseberry (*Vaccinium scoparium*), thimbleberry (*Rubus parviflorus*), pinegrass (*Calamagrostis rubescens*) and fireweed (*Epilobium angustifolium*). For a complete description of the study site refer to the methods in Chapter 1.

Vegetation neighborhoods of 101 eight-year old target lodgepole pine were sampled in August 1988. The neighborhoods were defined by 10 m² circular plots centered on the target pine. Sample neighborhood plots were chosen to represent a wide range in competitive conditions, from low (0%) to high (100%) sitka alder cover. Once a neighborhood of the desired competitive level was located, three to five occupant target pines and their neighborhood plots were sampled. Only healthy, undamaged lodgepole pines were sampled. At the time of measurement, alder leaf expansion and pine height growth were completed for that season. Within each neighborhood, the performance of the target pine was quantified as a function of the species, amount, aggregation and distance to neighbors. The neighborhoods were described using both an extensive and a more detailed intensive approach (after Wagner and Radosevich 1987). Using the extensive approach, the density of lodgepole pine and the percent cover of (1) all shrubs, (2) all herbs and (3) each of the dominant species were estimated using the quadrant method of Herring and Pollack (1985). Using the intensive approach each alder in the neighborhood plot was measured separately. The height, crown diameter, azimuth, and distance from the target pine to the closest crown edge of each neighboring alder were measured (Figure 2.1).

Target pine performance was quantified as stem diameter, total

height, relative height growth rate $((\text{height (yr } x) - \text{height (yr } x-1))/\text{height (yr } x-1))$, D2H (diameter squared x height) and height:diameter ratio.

The physical environment was partially described for each neighborhood plot. Microtopographic conditions (slope and aspect) were recorded. Available photosynthetically active radiation (PAR) was measured for each target pine using a Licor line sensor (Sunfleck Ceptometer). Four measurements (facing north, south, east and west) were taken on each sapling. The height of measurement was either at the terminal bud, for pines shorter than 1m, or at 1 m, for pines taller than 1m. Measurements were taken between 12:00 and 14:30 hours on August 23, 1988.

Competition indices were calculated using extensive and intensive neighborhood measures. The indices reflected the amount of interference a target tree experienced from neighboring vegetation. Extensive indices were equivalent to the density of pine and percent cover of the dominant competing species in the plot. The extensive indices are presented in Table 4.1. The intensive indices were summations of vegetation parameters from all alder individuals in the plot into a single value (e.g. sum of heights). The intensive indices developed are presented in Table 2.2.

Multiple regression models were developed to predict pine performance (dependent variable) from competition indices and PAR availability (independent variables) for the most responsive performance variables. Logarithmic, reciprocal and square-root transformations of the dependent variables were examined. All possible regressions of pine performance variables and competition indices were evaluated. Additional models were constructed to determine how PAR availability (dependent variable) was affected by surrounding vegetation (independent variables were competition indices). Logarithmic, reciprocal and square-root transformations of PAR were examined. The "best" models were determined by the combination of indices that had the highest r^2 values and included the fewest number of independent variables.

Table 4.1 Extensive competition indices that were evaluated in the study.

SYMBOL	DESCRIPTION
CI1	percent cover of all shrubs
CI2	percent cover of all herbs
CI3	percent cover of <u>Alnus viridis</u> ssp. <u>sinuata</u>
CI4	percent cover of <u>Vaccinium membranaceum</u>
CI5	total number of <u>Pinus contorta</u> var. <u>latifolia</u>
CI6	number of <u>Pinus contorta</u> var. <u>latifolia</u> less than 1 meter tall
CI7	number of <u>Pinus contorta</u> var. <u>latifolia</u> greater than 1 meter tall
CI8	percent cover of <u>Calamagrostis rubescens</u>
CI9	percent cover of <u>Rubus parviflorus</u>
CI10	percent cover of <u>Epilobium angustifolium</u>

Community types (i.e. unique combinations of species) were identified using ordination. First, multivariate relationships between plots were examined using Detrended Correspondence Analysis (DCA) (Hill 1979). A two-way data matrix with species as columns and plots as rows was tabulated. Plots were placed in rank order according to species abundance by their first-axis ordination scores. Second, community types were identified by examining the distribution of species abundance profiles along the plot gradient. Trends in height of sitka alder and lodgepole pine along the gradient were examined. Multiple linear regression models predicting pine performance from competition indices were developed for the subsample of individuals in each community type. Models were compared among community types and with models developed using the full data set.

RESULTS AND DISCUSSION

Multivariate analysis

Detrended correspondence analysis (DCA) of individual species abundance yielded a vegetation gradient among plots along which community composition varied continuously (Figure 4.1). The DCA indicated two extremes in community composition along the gradient. At the one extreme (low end of the gradient), the dominant species were lodgepole pine and pinegrass, a perennial bunchgrass (type I). At the other extreme (high end of the gradient), the dominant species were sitka alder, thimbleberry and black huckleberry (type II). Sitka alder is a 4 m tall, multi-branched, nitrogen fixing shrub exhibiting indeterminate height growth. Thimbleberry and black huckleberry are low, rapidly growing shrubs characterized by determinate height growth. Fireweed, a rhizomatous-like herb, was ubiquitous. Two community types were differentiated based on the abundance distributions of the dominant species (Figure 4.1). The point on the vegetation gradient (90) which separates type I from II is where the dominance from pinegrass to sitka alder cover changes. This point also coincides with a rapid decrease in lodgepole pine and rapid increase in thimbleberry and black huckleberry cover as one moves up the gradient.

Simple linear correlations (Pearson product-moment correlations) between species and growth forms are compared in Table 4.2. Nine out of fifteen of the inter-species correlations were significant ($p < 0.05$). There was a relatively strong negative correlation between the two growth forms: shrub and herb ($r = -0.53$). As the abundance of shrubs increased around a tree, the abundance of herbs decreased. Herbaceous vegetation appeared to be competitively excluded by shrubs. Similarly, as the abundance of sitka alder increased around a tree, the abundance of neighboring pines decreased ($r = -0.48$). Sitka alder appeared to have played a role in the competitive exclusion of lodgepole pine.

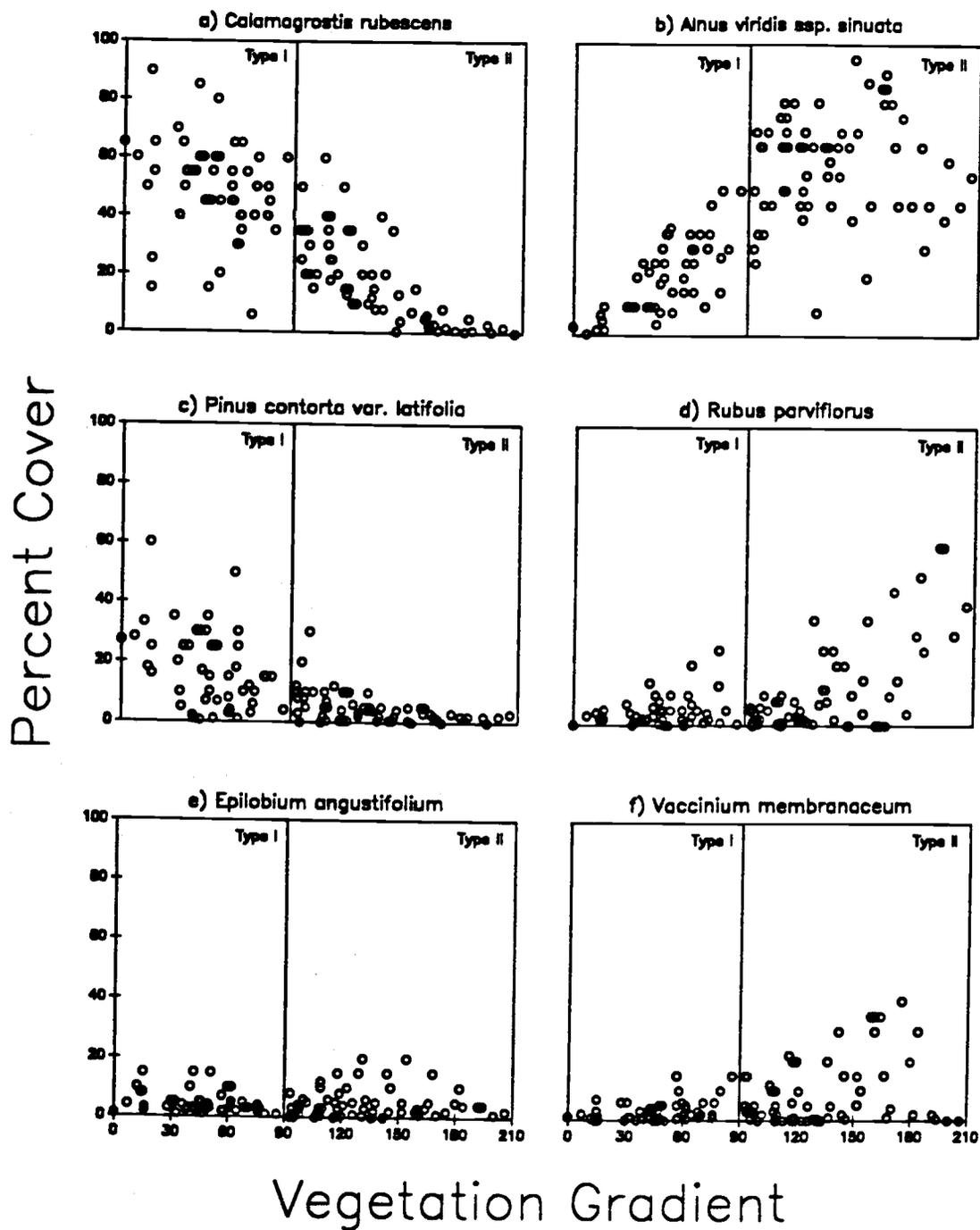


Figure 4.1 Species abundance profiles along the plot gradient produced by detrended correspondence analysis: (a) pinegrass, (b) sitka alder, (c) lodgepole pine, (d) thimbleberry, (e) fireweed, and (f) black huckleberry.

Table 4.2 Correlation matrix of extensive competition indices and light availability. The upper number of each entry is Pearson's product-moment correlation coefficient (r) and the lower number is the p -value.

	EXTENSIVE COMPETITION INDEX							
	CI1	CI2	CI3	CI4	CI5	CI8	CI9	CI10
PAR ($\mu\text{E/s/m}^2$)	-0.43 0.0001	0.40 0.0001	-0.55 0.0001	0.00 0.9692	0.19 0.0535	0.52 0.0001	-0.15 0.1450	-0.23 0.0217
Percent cover of fireweed (CI10)	-0.03 0.7483	0.00 0.9685	-0.10 0.3160	-0.26 0.0046	0.17 0.0677	-0.23 0.0130	0.14 0.1476	
Percent cover of thimbleberry (CI9)	-0.02 0.8015	0.33 0.0004	0.03 0.7793	-0.07 0.4586	-0.18 0.0615	-0.34 0.0002		
Percent cover of pinegrass (CI8)	-0.48 0.0001	0.72 0.0001	-0.53 0.0001	-0.26 0.0051	0.27 0.0041			
Total number of pine (CI5)	-0.04 0.6748	0.18 0.0499	-0.48 0.0001	-0.24 0.0121				
Percent cover of huckleberry (CI4)	0.46 0.0001	-0.37 0.0001	0.40 0.0001					
Percent cover of sitka alder (CI3)	0.84 0.0001	-0.57 0.0001						
Percent cover of all herbs (CI2)	-0.53 0.0001							

Trends in sitka alder and lodgepole pine height along the vegetation gradient are contrasted in Figure 4.2. Sitka alder height increased along the gradient ($r^2=0.15$, $p=0.0001$) while lodgepole pine height ($r^2=0.29$, $p=0.0001$) decreased. Sitka alder was generally of equivalent height to lodgepole pine in community type I, but was overtopping in type II (Figure 4.3). Relative height growth rate (RHGR) of lodgepole pine did not differ much between types from 1982 to 1987 (Figure 4.3). However, the initial height superiority and slight RHGR advantage from 1984 to 1987 of individuals in type I, allowed an increasing height advantage over those in type II. By 1988, the mean height of pines in type I was 56% greater than in type II (Figure 4.4). Trends in lodgepole pine diameter paralleled those of height; diameter decreased as alder competition increased along the vegetation gradient ($r^2=0.32$, $p=0.0001$) (Figure 4.2). By 1988, the mean diameter of pines in type I was 77% greater than in type II (Figure 4.4).

Light available to pines was remarkably greater in type I than in type II. Pines in type I received on average 81% more photosynthetically active radiation (PAR) than those in type II (Figure 4.5).

The differences in light availability and pine height and diameter between the two community types indicates that competitive effects were more suppressive in type II than I. Apparently the dominant species in type II, alder, thimbleberry and black huckleberry, had a more negative effect on pine performance than did pinegrass in type I.

Neighborhood analysis

Evaluation of the regression models predicting the size of individual eight-year old lodgepole pine individuals from competition indices indicated that stem diameter and, to a lesser degree, height of individual pine trees were the most sensitive size measures. Logarithmic transformations of diameter and height helped correct for

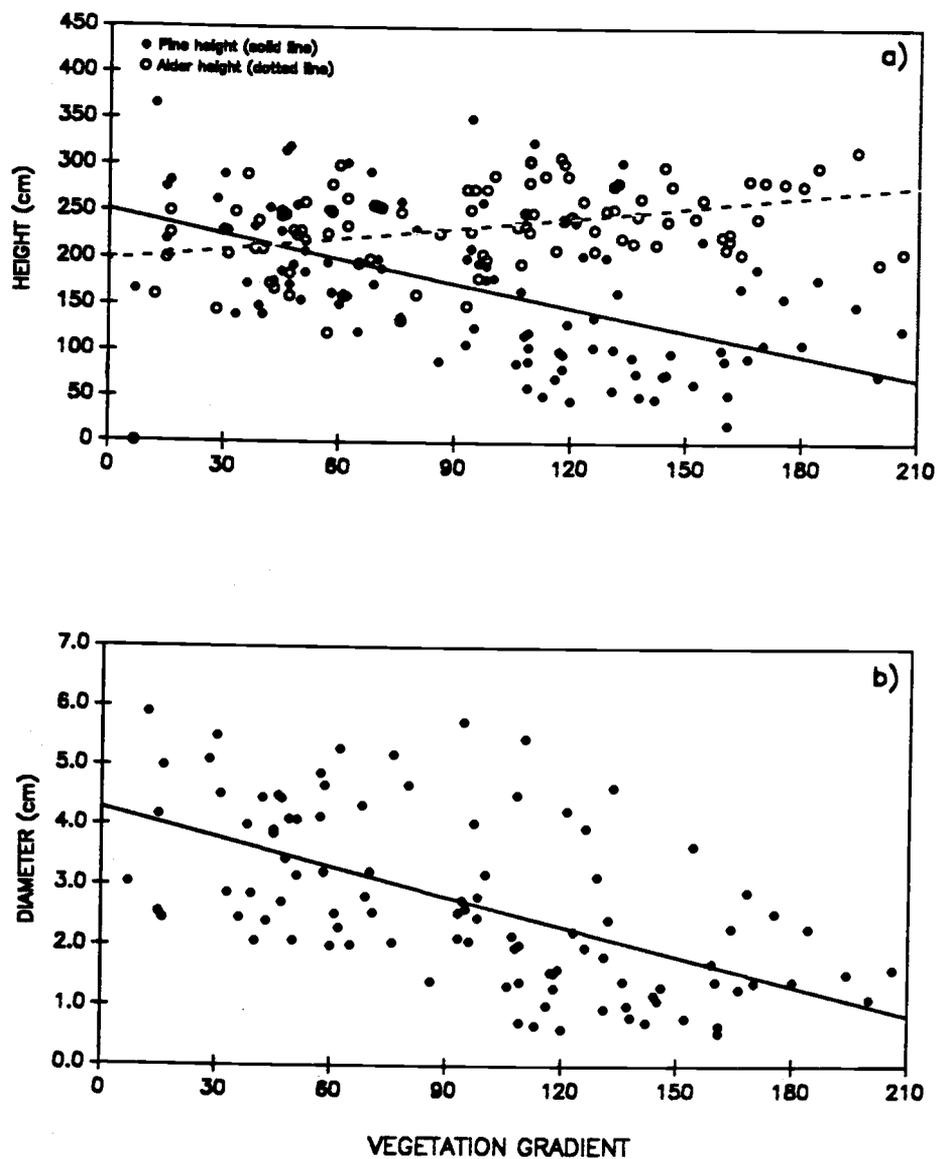


Figure 4.2 Trends in (a) height of sitka alder and lodgepole pine and (b) diameter of lodgepole pine along the plot gradient produced by detrended correspondence analysis.

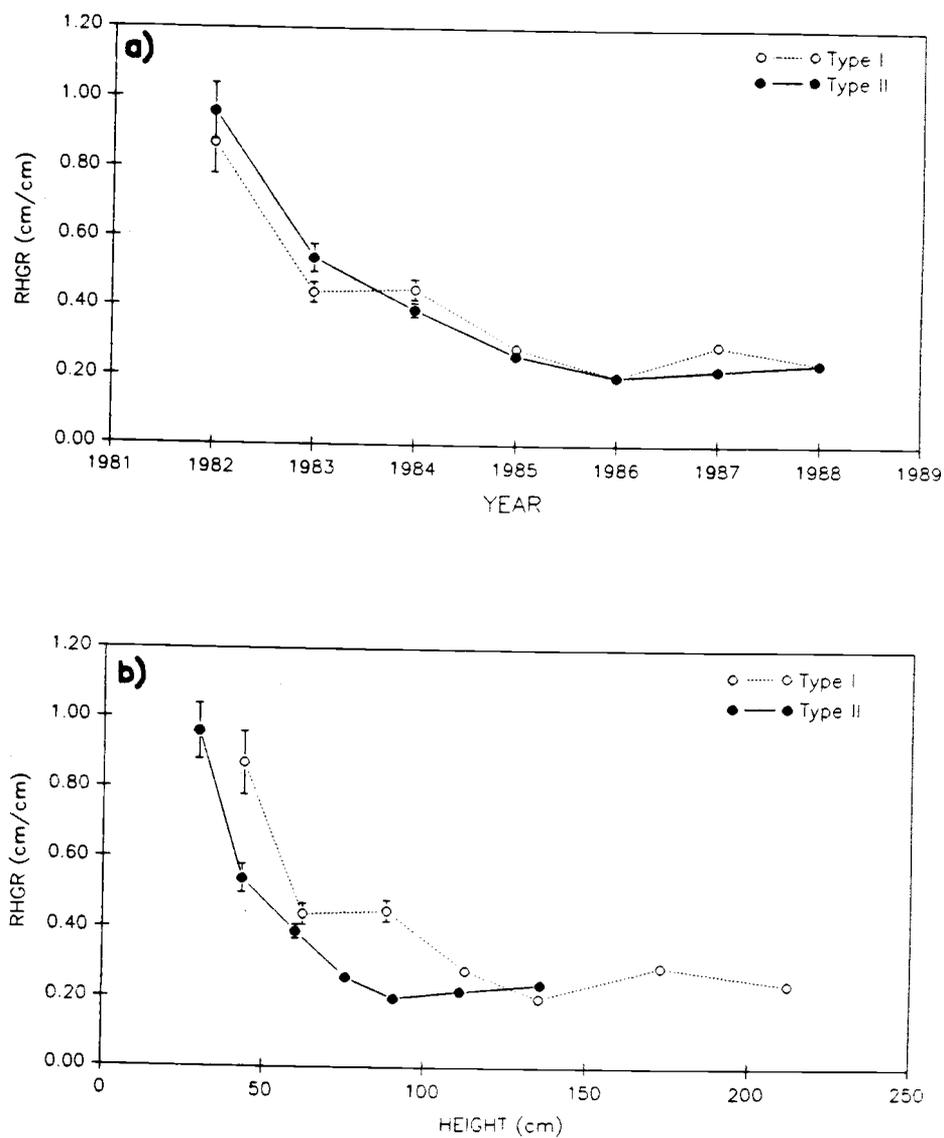


Figure 4.3 Comparisons between community types of (a) relative height growth rate (RHGR) of lodgepole pine from 1982 to 1988 and (b) RHGR with increasing pine heights.

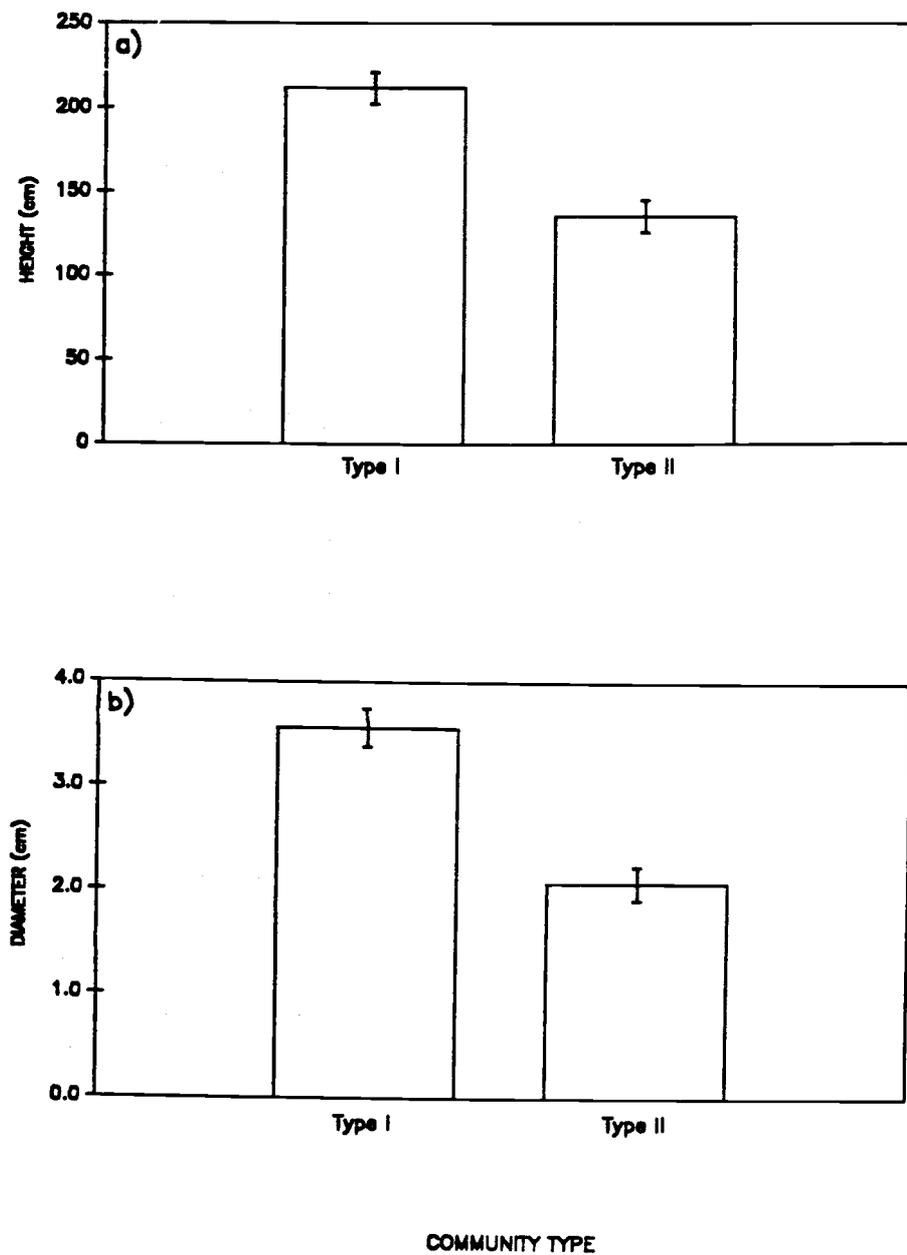


Figure 4.4 Comparison of lodgepole pine (a) height and (b) diameter between community types I and II.

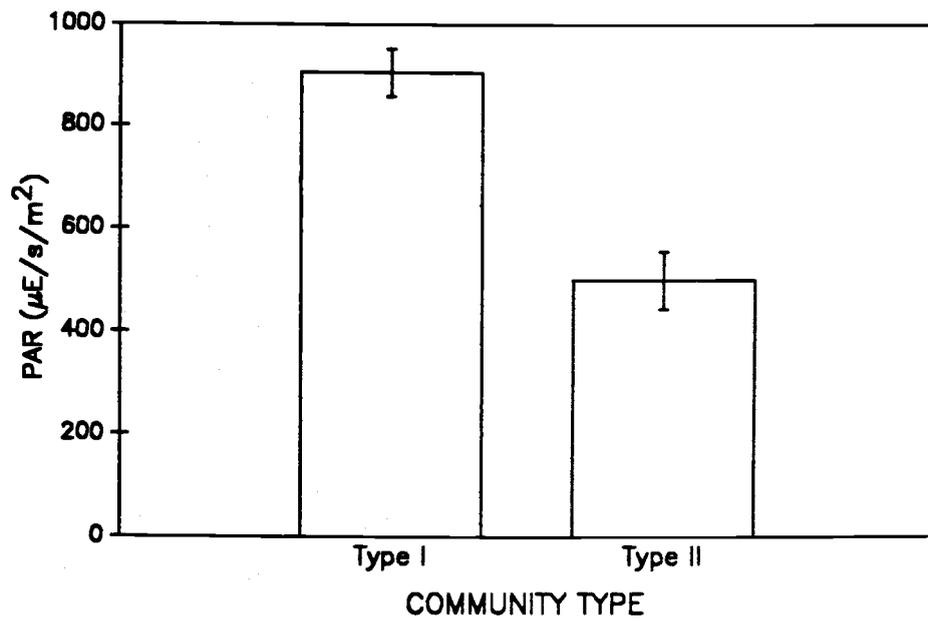


Figure 4.5 Comparison of photosynthetically active radiation available to lodgepole pine between community types I and II.

nonlinearity in the regression models. The relationship between size and competition index was consistent with yield-density theory, where the effect of density on individual plant yield is described by a negative exponential function (Kira et al. 1953, Harper 1977). Stem diameter is a function of a tree's past neighborhood environments, which are different from the present due to the growth, death and recruitment of neighbors. To describe an individual's performance from current neighborhood conditions it should be better to look at recent relative growth rate when neighborhood conditions were not much different from the present (Weiner 1984). However, stem diameter was consistently more responsive than relative height growth rate (RHGR) to measures of competitive interference. Although RHGR was fairly sensitive to competitive interference in 1987, it was insensitive in 1988. Rainfall was higher than the long term average in 1988 (see Chapter 1), which may have nullified competition induced resource limitations to pine growth that year. The insensitivity of height relative to stem diameter response to competitive stress has been commonly observed in young plantations where leaders become spindly under overtopping vegetation (Wagner and Radosevich 1987). Relative diameter growth rate, therefore, may have been a better measure of pine performance than relative height growth rate. Weiner (1984), for example, explained 52% of the variation in annual bole volume increment of *Pinus rigida* from the size and proximity of neighbors.

Regression models for entire vegetation gradient

The regression analyses indicated that increasing the amount of neighbors had a negative effect on pine size. For example, as percent cover of sitka alder (extensive index CI3) increased, pine diameter ($r^2=0.45$) and height ($r^2=0.38$) decreased (Figure 4.6 and Table 4.3). Results from the stepwise regression procedure for selecting the "best" extensive competition indices are presented in Table 4.4. Two variable models, including percent cover of sitka alder (CI3) and

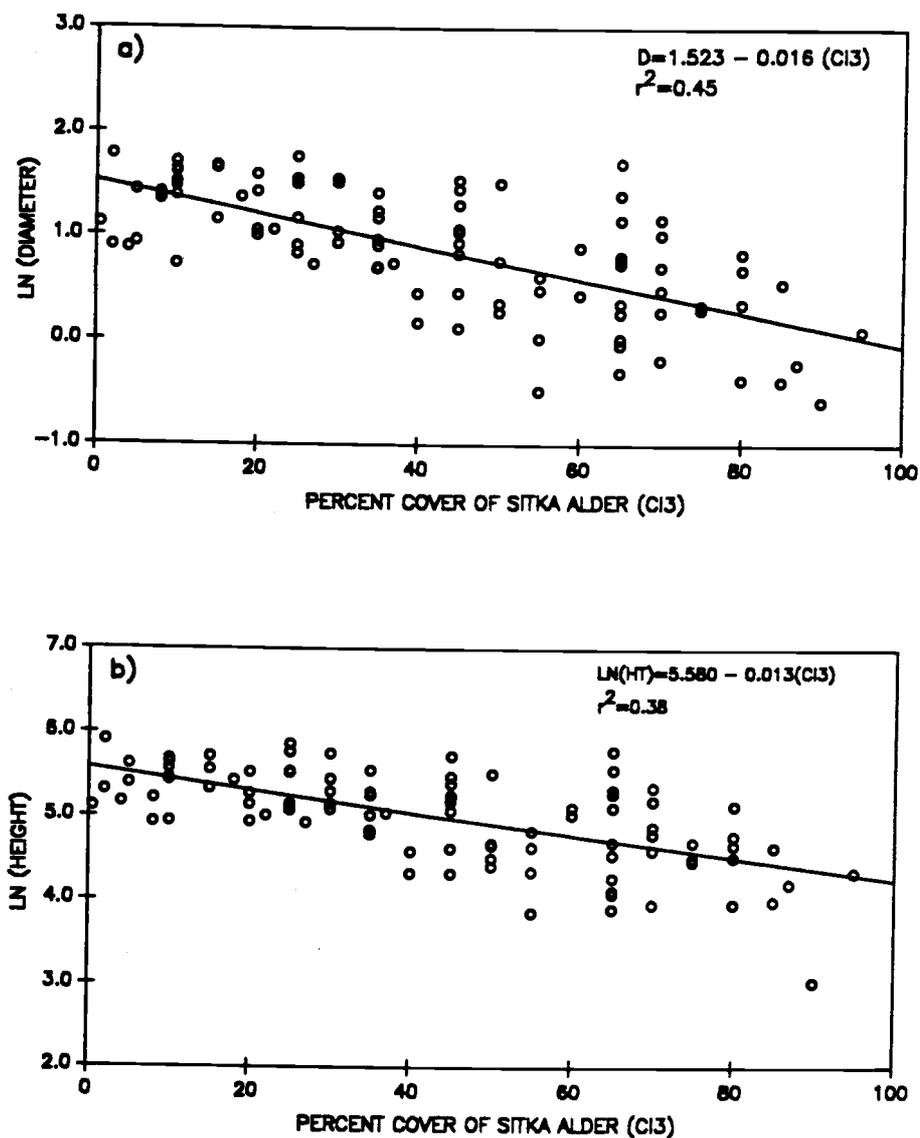


Figure 4.6 Relationships between sitka alder cover (CI3) and lodgepole pine (a) stem diameter and (b) height.

Table 4.3 Linear regression models predicting log transformed diameter and height from extensive and intensive competition indices.

	DIAMETER		HEIGHT	
	r ²	p-value	r ²	p-value
EXTENSIVE INDICES				
Percent cover of all shrubs (CI1)	0.36	0.0001	0.27	0.0001
Percent cover of all herbs (CI2)	0.12	0.0002	0.11	0.0005
Percent cover of sitka alder (CI3)	0.45	0.0001	0.38	0.0001
Total number of pine (CI5)	0.13	0.0001	0.16	0.0001
Percent cover of pinegrass (CI8)	0.16	0.0001	0.11	0.0005
INTENSIVE INDICES				
Height of alder (HEIGHTS)	0.29	0.0001	0.25	0.0001
Crown area of alder (CAS)	0.29	0.0001	0.23	0.0001
Crown area * height of alder (CHS)	0.30	0.0001	0.23	0.0001
Angular dispersion * height of alder (ADHS)	0.24	0.0001	0.20	0.0001
PHOTOSYNTHETICALLY ACTIVE RADIATION	0.28	0.0001	0.20	0.0001

Table 4.4 Regression coefficients, r^2 values and p-values for "best" models predicting log transformed diameter and height from extensive and intensive competition indices. Values in parantheses are partial r^2 values.

INDEPENDENT VARIABLES	DEPENDENT VARIABLES	
	DIAMETER	HEIGHT
EXTENSIVE INDICES		
intercept	1.5223	5.5792
percent cover of sitka alder (CI3)	-0.0145 (0.46)	-0.0121 (0.39)
percent cover of black huckleberry (CI4)	-0.0082 (0.01)	-0.0081 (0.02)
model r^2	0.47	0.41
p-value	0.0001	0.0001
INTENSIVE INDICES		
intercept	1.3475	5.4298
sum of distance to alders (DISTS)	0.0017 (0.11)	0.0013 (0.07)
sum of alder heights (HEIGHTS)	-0.0013 (0.29)	-0.0011 (0.26)
model r^2	0.40	0.33
p-value	0.0001	0.0001

percent cover of black huckleberry (CI4), were selected for diameter ($r^2=0.47$) and height ($r^2=0.41$). The amount of variation accounted for by extensive competition indices was within the range reported in other retrospective studies of interspecific competition in conifer stands (Corns and Pluth 1984, Brand 1986a, Wagner and Radosevich 1987).

Neighborhood experiments usually are used to determine the amount of variation in target individual performance explained by neighboring species (Mack and Harper 1977, Liddle et al. 1982, Weiner 1982). Goldberg and Werner (1983) suggest, in addition, that the competitive effect of a neighbor species on a target species is the slope of the regression of performance of the target individuals on the amount of neighbors. Furthermore, since the slope has a variance associated with it, the competitive effects of several neighbor species can be directly compared statistically and ranked in terms of the magnitude of their effects on the target species. Sitka alder clearly had a more negative effect on pine than any of the other neighboring species. Sitka alder cover (CI3) explained the most variation in pine size (Table 4.4) and a more negative regression coefficient (-0.016) than of the other indices tested (most negative regression coefficient was -0.015 for all shrubs).

The concept of thresholds is fundamental to vegetation management (Radosevich and Holt 1984). The competition threshold is the weed abundance, or amount of neighbors, at which competition begins and conifer growth is limited (Cussans et al. 1986). When weed abundance decreases below the competition threshold, environmental limitations are surpassed and conifer growth rapidly increases. Conifer growth in response to decreasing weed abundance has been described by negative hyperbolic and exponential functions (Weiner 1984, Wagner and Radosevich 1987). Untransformed pine diameter in this study, however, appeared to increase linearly in response to decreasing sitka alder cover (CI3). Although a competition threshold was not obvious, logarithmic transformations of pine performance variables improved linear models predicting performance from alder abundance. This

suggests that there is a tendency toward a negative exponential function and that a competition threshold may exist, but it is obscured by uncontrolled factors such as genetic and microsite variability. Identification of competition thresholds using a retrospective approach to study competitive interactions is difficult due to confounding biotic and abiotic factors, which can only be controlled under experimentally created conditions (Wagner and Radosevich 1987).

Intensive indices explained less variation in pine performance than did extensive indices (Table 4.3). The intensive indices which explained the most variation in pine diameter and height were HEIGHTS (sum of alder heights), CAS (sum of alder crown areas), CHS (sum of (crown area * height) and ADHS (angular dispersion * (sum of alder heights)) (Table 4.3). They explained between 20 and 30% of the variation (Figure 4.7). Different measures of competition can suggest mechanisms of competition (Weiner 1982, Goldberg and Werner 1983, Brand 1986b). Weiner (1984) suggests that one dimensional measures of competition (e.g. height of alder, distance from target pine to alder, angular dispersion of surrounding alders) can indicate competition for light while two dimensional measures (e.g. crown area of alder, square of distance) can indicate competition for two dimensional space (e.g. horizontal and vertical root space). The stepwise regression procedure selected models for pine diameter ($r^2=0.40$) and height ($r^2=0.33$) which included both HEIGHTS and DISTS (Table 4.4), suggesting that light availability has an important effect on pine size.

PAR available to target pines was correlated with extensive and intensive competition indices to determine how light availability was affected by surrounding vegetation. Light availability was negatively correlated with alder cover (CI3) ($r=-0.55$) (Table 4.2). In contrast, it was positively correlated with pinegrass cover (CI8) ($r=0.52$).

A square-root transformation of light helped correct for nonlinearity when developing multiple regression models. The stepwise regression procedure selected a fairly predictive model ($r^2=0.48$) for

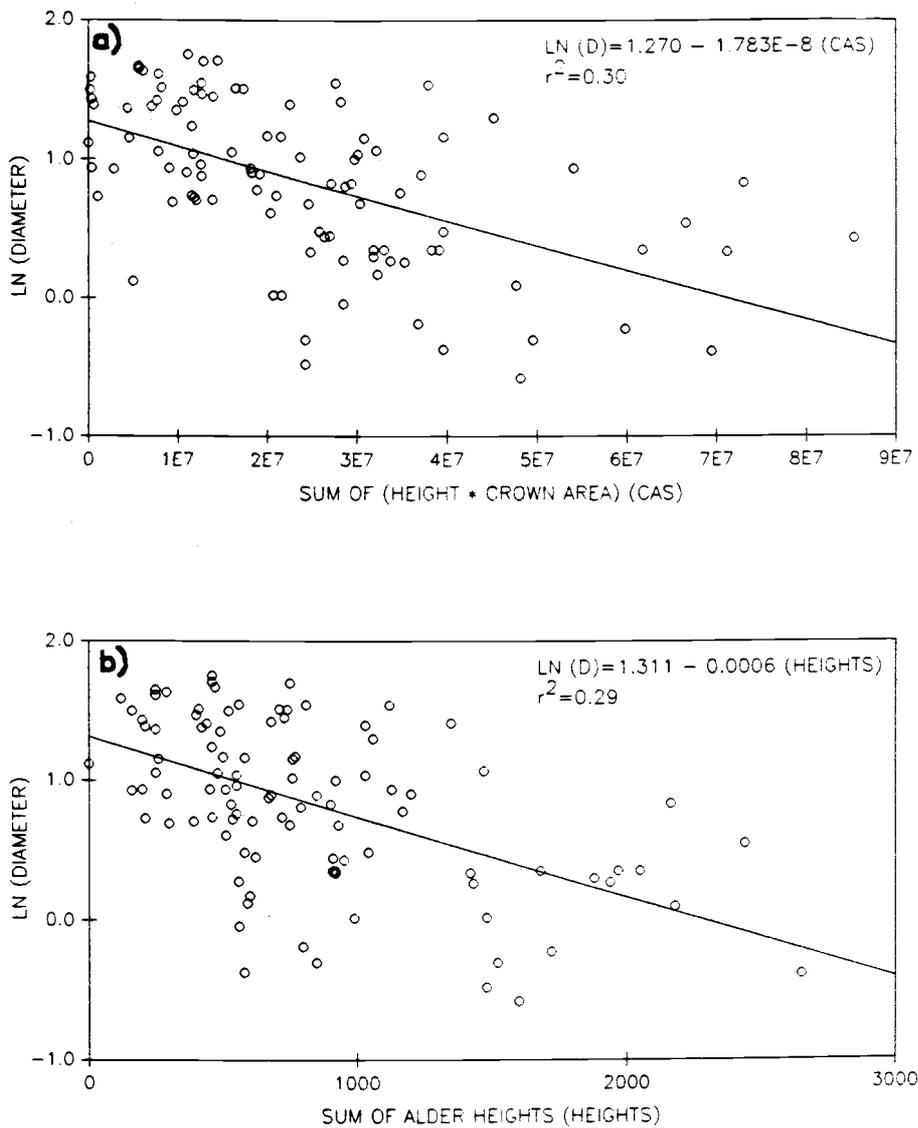


Figure 4.7 Relationships between lodgepole pine diameter and (a) sum of alder (height * crown area) and (b) sum of alder heights in the neighborhood.

available light using the extensive indices, percent cover of alder (CI3), fireweed (CI10), black huckleberry (CI4) and pinegrass (CI8) (Table 4.5). Intensive indices accounted for less variation in available light than did extensive indices, presumably because the former included only measures of sitka alder. Light available to target pines was diminished with decreasing distance to, and increasing height and crown area of, surrounding alders ($r^2=0.40$) (Table 4.5).

Shading by surrounding vegetation had a negative effect on the growth of pines. Available PAR accounted for 27% of the variation in pine diameter and 19% of the variation in pine height (Figure 4.8). The microtopographic conditions in which pine individuals grew also had minor impacts on performance through their effect on light availability. Slope explained the most variation in pine height ($r^2=0.06$) while aspect explained the most variation in diameter ($r^2=0.09$).

Regression models for community types I and II

Splitting the vegetation gradient into two vegetation community types generated a sample size of 43 in type I and 58 in type II. Competition indices generally explained less variation in pine size when the gradient was split into community types than when it was analyzed as a whole. Extensive indices explained the most variation in pine size in type II and intensive indices explained the most in type I.

Percent cover of sitka alder (CI3) was the best single extensive index for predicting pine diameter and height. In community type I, however, only 17% of the variation in diameter and 15% of the variation in height were explained by CI3. In community type II, 22% of the variation in diameter and 16% of the variation in height were explained by CI3. The stepwise regression procedure selected single variable models predicting diameter and height ($r^2=0.17$) from alder cover (CI3) for type I (Table 4.6). Two variable models, which

Table 4.5 Regression coefficients, r^2 values and p-values for "best" models predicting PAR and square-root transformed PAR from extensive and intensive competition indices. Values in parentheses are partial r^2 values.

INDEPENDENT VARIABLES	DEPENDENT VARIABLES	
	PAR	SQRT(PAR)
EXTENSIVE INDICES		
intercept	900.5357	30.6820
percent cover of sitka alder (CI3)	-9.1453 (0.32)	-0.2106 (0.32)
percent cover of fireweed (CI10)	-11.9036 (0.07)	-0.4382 (0.11)
percent cover of black huckleberry (CI4)	10.8854 (0.03)	0.2288 (0.03)
percent cover of pinegrass (CI8)	4.6759 (0.03)	0.0964 (0.03)
model r-square	0.45	0.48
p-value	0.0001	0.0001
INTENSIVE INDICES		
intercept	846.0776	27.9450
sum of alder crown areas (CAS)	-0.0015 (0.12)	-0.00005 (0.13)
sum of distance to alders (DISTS)	1.6683 (0.12)	0.0342 (0.13)
sum of alder heights (HEIGHTS)	-0.7327 (0.07)	-0.0133 (0.05)
model r-square	0.31	0.31
p-value	0.0001	0.0001

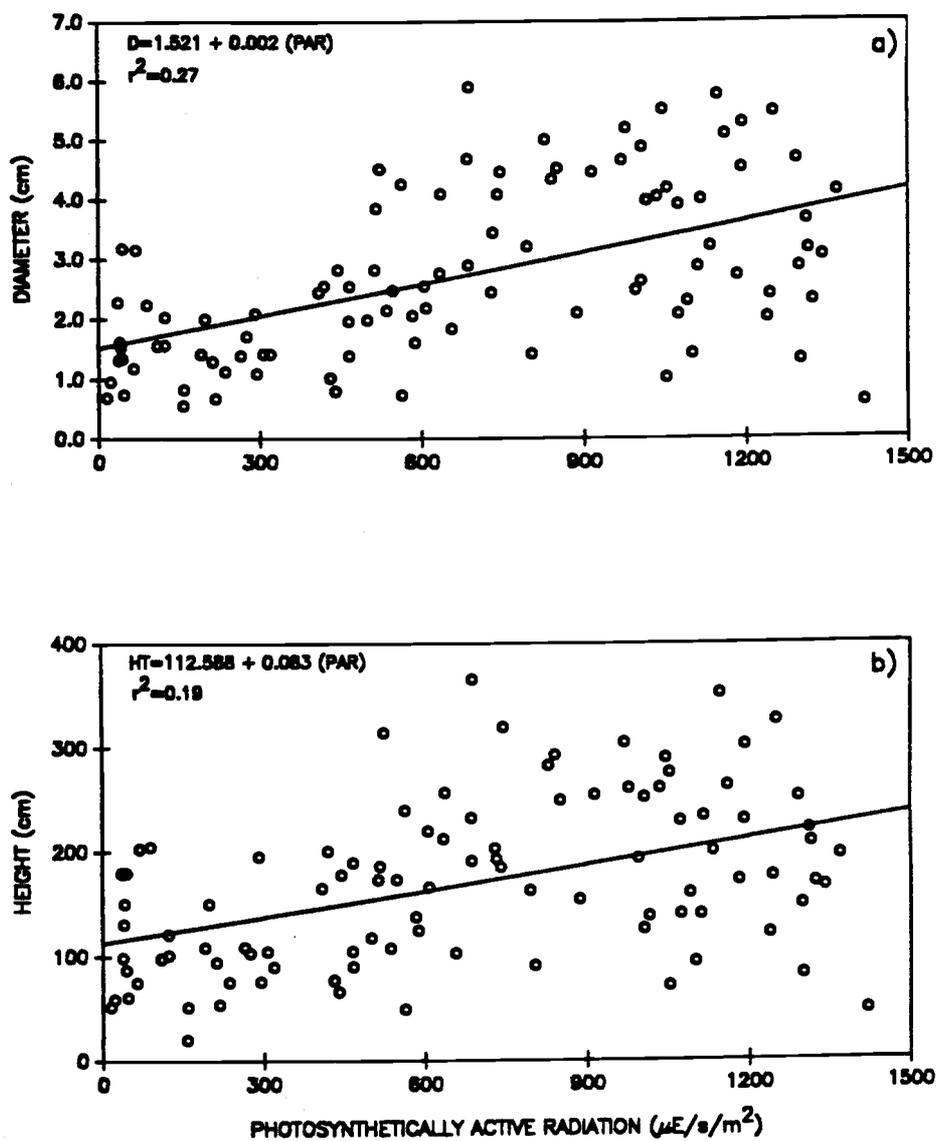


Figure 4.8 Relationship between photosynthetically active radiation available to lodgepole pine and lodgepole pine (a) diameter and (b) height.

Table 4.6 Regression coefficients, r^2 values and p-values for "best" models predicting log transformed diameter and height from extensive and intensive competition indices in community types I and II. Values in parentheses are partial r^2 values.

INDEPENDENT VARIABLES	DEPENDENT VARIABLES			
	COMMUNITY TYPE I		COMMUNITY TYPE II	
	DIAMETER	HEIGHT	DIAMETER	HEIGHT
EXTENSIVE INDICES				
intercept	1.4525	5.5196	1.3994	5.4607
percent cover of sitka alder (CI3)	-0.0116	-0.0099	-0.0163 (0.24)	-0.0139 (0.18)
total number of pine (CI5)	****	****	0.0314 (0.08)	0.0126 (0.08)
model r^2	0.17	0.17	0.32	0.26
p-value	0.0072	0.0071	0.0001	0.0003
INTENSIVE INDICES				
intercept	1.2629	5.3750	1.1035	196.5291
sum of alder crown areas (CAS)	-7.0E-6 (0.10)	-6.0E-6 (0.12)	****	****
sum of alder heights (HEIGHTS)	****	****	-0.0009 (0.14)	-0.1101 (0.10)
sum of distances to alder (DISTS)	0.0013 (0.18)	0.0011 (0.16)	0.0010 (0.05)	0.1377 (0.06)
model r^2	0.28	0.28	0.19	0.16
p-value	0.0015	0.0016	0.0027	0.0086

**** variable did not enter into the model at the 0.15 significance level.

included percent cover of sitka alder (CI3) and density of lodgepole pine (CI5), were selected for diameter ($r^2=0.32$) and height ($r^2=0.26$) for type II (Table 4.6). The results from the regression analyses indicate that sitka alder was the strongest competitor in both community types.

DISTS (sum of distances from the target pine to surrounding alders) was included in all regression models predicting pine performance from intensive indices. Twenty-eight percent of the variation in pine diameter and height were explained by CAS and DISTS in community type I (Table 4.6). In contrast, only 19% of the variation in diameter and 16% in height were accounted for by HEIGHTS and DISTS in type II. The significance of HEIGHTS in type II suggests that pines were competing primarily for light whereas the significance of CAS in type I suggests that pines were competing primarily for two dimensional root space (i.e. soil moisture and nutrients).

PAR available to target pines was regressed against extensive and intensive competition indices to determine how light availability was affected by surrounding vegetation in each community type. Percent cover of alder (CI3) and pinegrass (CI8) explained 25% of the variation in PAR in type I, while alder, pinegrass and huckleberry (CI4) explained 32% in type II (Table 4.7). In community type I, only the height of alders (HEIGHTS) in the neighborhood had a significant effect on light availability ($r^2=0.06$), while in type II the height and distance to alders had significant effects ($r^2=0.29$).

Pine stem diameter was regressed against PAR to compare the magnitude of its effect on performance between community types. Light availability explained 10 times the variation in tree diameter in type II ($r^2=0.20$) than in type I ($r^2=0.02$). Hence, light availability appears to limit pine performance more in type II than I.

In summary, this study has shown that the size of naturally regenerated lodgepole pine saplings was negatively affected by interspecific competition. Furthermore, competition appeared to be more suppressive in community type II than I. Sitka alder, relative

Table 4.7 Regression coefficients, r^2 values and p-values for "best" models predicting PAR from extensive and intensive competition indices in community types I and II. Values in parentheses are partial r^2 values.

INDEPENDENT VARIABLES	PHOTOSYNTHETICALLY ACTIVE RADIATION	
	COMMUNITY TYPE	
	TYPE I	TYPE II
EXTENSIVE INDICES		
intercept	850.4963	757.4418
percent cover of sitka alder (CI3)	-11.7659 (0.15)	-9.2051 (0.08)
percent cover of pinegrass (CI8)	5.9715 (0.10)	9.2244 (0.13)
percent cover of black huckleberry (CI4)	****	10.8854 (0.11)
model r^2	0.25	0.32
p-value	0.0034	0.0001
INTENSIVE INDICES		
intercept	1028.3329	538.7284
sum of distance to alders (DISTS)	****	1.7000 (0.14)
sum of alder heights (HEIGHTS)	-0.2644	-0.6966 (0.15)
model r^2	0.06	0.29
p-value	0.1298	0.0001

**** variable did not enter into the model at the 0.15 significance level.

to the other dominant species in the community, had the greatest competitive effect on pine. Sitka alder, however, was also the largest neighbor and of nearest size symmetry to lodgepole pine. The size difference between sitka alder and the other neighbors likely overshadowed species differences in resource use patterns. Sitka alder clearly had a negative impact on light available to target pines, particularly in community type II. However, the large amount of variation in pine diameter unaccounted for by light availability indicates that other factors also are of importance in driving competitive interactions in the community.

Summary

CHAPTER 5

An understanding of the causal biotic and abiotic factors behind poor conifer regeneration is fundamental to the development of effective silvicultural prescriptions. In British Columbia (B.C.), management of the backlog of unsuccessfully regenerated lodgepole pine sites is afflicted with a lack of understanding of interactions between seedlings, competing vegetation and the physical environment. In this study, the objective was to investigate the relationships between performance (survival and growth) of lodgepole pine, densities of sitka alder and associated plants, and levels of environmental resources and conditions in the Montane Spruce zone.

Survival of lodgepole pine seedlings on the study site was 86% after two growing seasons. Seedling survival was independent of levels of competing vegetation. Rather, herbivory and desiccation following planting were the principal causes of mortality. Although not statistically significant, early seedling mortality (following planting) was actually highest where all alder and all or part of the understory were removed. High seedling moisture stress, and consequently slow initial root elongation, may have been the result of low soil moisture retention. Low soil moisture was likely a result of surface evaporation and root mortality of treated vegetation.

Seedling growth, in contrast, was clearly inhibited by increasing levels of competing vegetation after two growing seasons. Mean diameter of seedlings growing free of competing vegetation was 25% greater than that of seedlings growing under maximum alder and herb densities. Although mean diameter was only 1.4 mm greater in the absence of interference, the early size advantage may favor resource preemption and competitive success of pine seedlings in the community over time. Vegetation removal favored seedling growth by modifying environmental conditions and increasing resource availability. Of greatest importance, soil temperatures increased and the frequency of

frost events decreased between June and August. The improved soil thermal regime had positive effects nitrogen availability and seedling water uptake. In addition, vegetation removal significantly improved light availability to seedlings.

Competition thresholds are fundamental to the management of undesirable forest vegetation. The competition threshold is the weed density, or amount of neighbors, at which competition begins and performance (survival or growth) is limited. When weed densities decrease below the competition threshold, environmental limitations are surpassed and seedling performance rapidly increases. There does not appear to be a competition threshold for lodgepole pine survival. Consistent with lodgepole pine regeneration in B.C., survival was excellent regardless of competition levels. Consequently, relatively little would be gained from the added cost of vegetation control to decrease mortality rates. Similarly, competition thresholds were not clearly defined for lodgepole pine growth. The relationship between growth and increasing levels of competition appeared linear, indicating that any increase in competition would result in a predictable decrease in growth.

This study attempted to quantify pine growth and identify competition thresholds using three experimental approaches. The first two approaches examined the response of planted seedlings to experimentally created levels of competing vegetation. The first was an additive, deterministic approach, whereby different amounts of competing vegetation were removed from an existing population and the mean response of planted pine seedlings was measured. Seedling response was examined as a function of the *mean* density of competing vegetation. Interpretations of results from this type of study are limited in young conifer plantations, however, because there is great heterogeneity of density and proximity, so that most seedlings do not experience the mean effect of any particular competitor. The second approach employed a neighborhood experiment, which overcomes some of the limitations of the first. Using the neighborhood approach, the performance of planted pine seedlings was recorded as a function of

the species, abundance and proximity of neighbors. The focus was on the response of an individual seedling to its unique microenvironment, rather than on the mean response of the population to a mean neighbor density. The third approach also employed neighborhood techniques. However, competitive interactions were retrospectively analyzed within a ten-year old naturally regenerated lodgepole pine-sitka alder community. A major limitation to the retrospective approach is that the effects and responses of neighboring species and target pines may both be the result of the same underlying environmental limitation. An advantage, however, is that hypotheses of competitive effects can be generated in a short period of time.

Results from each of the three approaches indicated that growth or size of lodgepole pine individuals was negatively affected by increasing amounts of interspecific competition. Competition thresholds varied, however, among approaches. Results from the first approach indicated that the mean diameter growth of pine populations increased significantly only when all competing vegetation was removed. In other words the competition threshold occurred at shrub and herb covers of zero percent. In contrast, a clearly defined competition threshold was not identified for pine seedlings using the neighborhood approach. Results indicated, however, that individuals with the largest stem diameters grew among shrub and herb covers of less than 10% each. A competition threshold for growth may become evident in a few years after neighboring interference has had a more measurable effect on seedling growth patterns. Using the neighborhood approach in the undisturbed ten-year old lodgepole pine-sitka alder community, a clearly defined competition threshold also was not identified. Rather, pine size increased linearly as sitka alder densities decreased. Identification of a competition threshold may have been obscured due to lack of experimental control of confounding biotic and abiotic factors.

Each of the three approaches demonstrated similar effects of competing vegetation on the target pine's microenvironment. Results from the seedling population approach clearly demonstrated that

vegetation removal improved mean light availability and air and soil temperatures. There were no significant effects, however, of vegetation on mean soil moisture availability. In contrast, results from the seedling neighborhood experiment demonstrated that *both* light and soil moisture availability increased in response to decreasing vegetation density. Individual seedling growth responded favorably to the increases in resource availability. Similarly, the neighborhood analysis in the ten-year old community implicated light as an important resource driving competition, particularly in community type II where sitka alder clearly overtopped pine saplings. Both neighborhood analyses detected that other factors, in addition to light and soil moisture availability, were of equal importance to seedling performance. Other factors included initial seedling size, vigour, browsing damage and genetic variability.

Regressions of target pine performance on amount of competing vegetation, from the neighborhood studies, indicated that variation among target seedlings increased as the abundance of competing vegetation decreased. While competition was an important constraint on seedling size at high shrub and herb densities, other factors in addition to competition had important influences on individual pine performance at low densities. Goldberg (1987) suggests that competition acts as a boundary constraint on the maximum potential size of individuals rather than as an accurate predictor of actual size. Seedlings that are growing below the boundary are not necessarily unaffected by competition. Heterogeneity in genotype, initial size, herbivory, and the microenvironment, however, underlie the variability of performance within similar neighbor densities.

Results from the three approaches indicated similar trends in pine seedling response to increasing levels of competition and subsequent modifications of the microenvironment. However, management implications differ somewhat among approaches. The seedling population approach implies that *all* competing vegetation must be removed to improve mean growth performance. The seedling neighborhood approach, on the other hand, implies that the greatest individual

growth can be achieved with up to 20% vegetative cover (barring sitka alder). In contrast, neighborhood results from the ten-year old community imply that any reductions in vegetative competition, particularly sitka alder, will result in predictable increases in pine growth. Explicit silvicultural prescriptions clearly are difficult to derive from the conflicting results of this study. Of particular importance, the regression models should not be used as accurate predictors of pine growth, but rather as means for identifying factors which are important to performance. Once the important factors limiting pine growth are identified, prescriptions can be developed which utilize appropriate methods for ameliorating the seedling's environment.

Seedling size at the time of planting and browsing by hares were the most important factors determining seedling size after two growing seasons. Consequently large stock should be planted and, where possible, seedlings should be protected from herbivory. In addition, prescriptions that aim to decrease competing vegetation and improve air and soil temperatures and resource availability, particularly light, should favor pine seedling growth during the first few years following planting. However, due to other overriding factors, not all seedlings in the plantation will respond favorably to vegetative control. To maximize *mean* seedling growth, total vegetative cover should be maintained below 20%, at least during the first two years following planting. Removal of herbs and low growing shrubs, in addition to sitka alder, appears necessary to significantly improve growth.

In the undisturbed lodgepole pine-sitka alder shrub community, pine saplings with the largest stem diameters occurred in neighborhoods that were free of sitka alder. The increase in light availability as overtopping alder decreased had a beneficial effect on pine size. Silviculture prescriptions for rehabilitating older, alder dominated clearcuts should aim to decrease overtopping sitka alder as much as is practically possible, since any decrease in alder cover should result in increases in pine growth. Little effort need be

concentrated on the control of herbs and low-growing shrubs, since those plants appear to have a minor effect, relative to sitka alder, on pine sapling size. Although herbs and low-growing shrubs may compete with pine saplings for limiting resources, they appear to play an important role in the competitive exclusion of the more competitive sitka alder.

Competitive interactions among target pines and neighboring vegetation vary as species composition of community types change. Although the causal factors (e.g. site history, microsite) behind the differences in species composition between community types I and II were unknown, lodgepole pine was clearly more suppressed by alder in type II than I. Pines were generally of equivalent height to alder in type I and soon will be above the alder canopy. Pines were much more suppressed in type II, however, and may never reach a free-growing status. The productivity of type II for pine growth appeared greater than that of type I due to the relative sizes of pine stumps remaining on the site and the vigour of alder growth (personal observation). Consequently, silviculture programs may benefit more by concentrating efforts more on rehabilitation of type II than type I sites.

Studies of competitive interactions between conifers and other vegetation are necessary to determine the relationship between conifer growth and amounts of competing vegetation. Once the general relationship is identified, competition thresholds can be estimated and effective silvicultural prescriptions developed. Identification of thresholds, however, is a difficult and time-consuming process. The process can be improved through refined experimental techniques. Suggestions for improvement were evident from this study. First, reasonable hypotheses about competitive interactions between pine and alder could have been generated through a neighborhood analysis in the natural community *prior* to the initiation of the experiment. Hypothesis formulation would have improved the focus of the variables investigated. Second, confounding of competitive effects by other factors, such as pathogen, insect and herbivore loads, could have been reduced by a more thorough examination of site conditions prior to the

initiation of the experiment. Third, the efficiency of the study could have been increased if fewer treatments (i.e. competition levels) had been applied. Five treatments representing combinations of 100%, 50% and 0% alder and herb abundance (i.e. 100% alder:100% herbs, 50% alder:100% herbs, 0% alder:100% herbs, 0% alder 50% herbs, 0% alder:0% herbs) would have reduced the work load and yielded similar results. Fourth, more precise equipment than the neutron probe may have detected differences in soil water potential among treatments. The Decagon SC-10A Thermocouple Psychrometer, for example, is accurate, relatively easy to use and generally non-destructive. The psychrometer's portability makes it ideal for estimating soil water potential near target individuals in retrospective neighborhood studies.

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APPENDIX

APPENDIX

Table I.1 Regression equations relating (a) count ratio (CR) to volumetric water content (VWC) and (b) VWC to soil water potential (SWP) at various depths.

EQUATION	r ² value	p-value
<u>(a) VWC and CR</u>		
VWC = 68.6775 - 154.5962 (CR) + 132.4336 (CR ²)	0.81	0.0014
<u>(b) SWP and VWC</u>		
10 cm depth (for gravimetric samples):		
log ₁₀ SWP = 0.1172 - 0.0527 (VWC)	0.78	0.0004
30 cm depth:		
log ₁₀ SWP = 1.8338 - 0.1278 (VWC)	0.95	0.0001
45 cm depth:		
log ₁₀ SWP = 2.3597 - 0.1532 (VWC)	0.94	0.0001
60 cm depth:		
log ₁₀ SWP = 0.8076 - 0.0808 (VWC)	0.79	0.0001
75 cm depth:		
log ₁₀ SWP = 0.7423 - 0.0855 (VWC)	0.79	0.0004

Table I.2 Mean count ratios at 30 cm depth from May to September in 1988.

DATE	TRT 1	TRT 6	TRT 7	p-value
May 23	0.67a*	0.78a	0.75a	0.0966
June 27	0.63a	0.70a	0.74a	0.1079
July 26	0.59b	0.58ab	0.76a	0.0530
Sept. 13	0.55b	0.65ab	0.76a	0.0210
Sept. 30	0.71b	0.79b	0.80b	0.0417

* values with different letters within rows are significantly different at the 0.10 level.