AN ABSTRACT OF THE THESIS OF

K. David Coates for the degree of Master of Science in Forest Science presented on December 10, 1987.

Title: Effects of Shrubs and Herbs on Conifer Regeneration and Microclimate in the *Rhododendron-Vaccinium-Menziesia* Community of South-Central British Columbia.

Abstract approved: Signature redacted for privacy.

William H. Emmingham

A field study was established to determine the impact of interfering vegetation on survival and growth of Engelmann spruce (*Picea engelmannii* Parry) and lodgepole pine (*Pinus contorta* var *contorta* Dougl.) at a site in the high elevation Engelmann spruce-Subalpine fir (ESSF) zone, of south-central British Columbia. The study examined (1) the influence of varying amounts of shrubs and herbs on microclimate and planted seedling performance, (2) relationships between various measures of vegetation interference and conifer seedling growth, and (3) the response of six major shrub and herb species to manual cutting and mechanical scarification.

After two growing seasons survival of both conifers was greater than 97%, except in the presence of the highest levels of interfering vegetation, where survival was 82% to 84%. Diameter was the most responsive conifer growth measure to levels of interference. In the absence of interfering vegetation mean diameters of spruce and pine were 21.3% and 27.5% greater, respectively, than mean diameters of seedlings in the undisturbed brush. Height growth generally did not respond to interference levels. Soil water potential was never lower than -0.01 MPa and was the same at all levels of interference throughout the growing season. Midday and predawn spruce xylem water potential also did not vary by vegetation removal treatment. Even though

soil water was ample, moderate water stress was observed, most likely because of restricted uptake caused by cold soil temperatures. Light levels under undisturbed vegetation were low enough to impair photosynthesis. Results suggest that low soil and air temperatures and low light levels may be the most important primary factors inhibiting conifer seedling performance beneath the undisturbed brush community.

The relationship between growth of individual spruce and pine and various measures of vegetation interference was always negative. Measures of percent vegetation cover were consistently the best predictors of seedling growth. A maximum of 25% of the variation in seedling growth was explained by measures of interference. The response of conifer seedlings to interference may be nonlinear, with a decreasing response observed at high amounts of interference. Tentative threshold points where growth can dramatically improve were identified. However, more than two growing seasons are probably required for the shape of the response curve or model to become clear in the slow-growing ESSF environment. Large variance in seedling growth at low levels of interference suggests either that microsite variability or genotype differences constrain seedling performance even in the absence of interference.

Recovery of the four dominant shrubs, white-flowered rhododendron (*Rhododendron albiflorum* Hook.), black huckleberry (*Vaccinium membranaceum* Dougl.), oval-leaved blueberry (*V. ovalifolium* Smith.), and false azalea (*Menziesia ferruginea* Smith.) following manual cutting was slow. After two growing seasons, the height of the tallest stems averaged between 10 cm and 15 cm (or about 10-30% of precut levels), and had not overtopped the conifers. Shrub vigour appeared unaffected by one additional cutting. The two major herb species, Sitka valerian (*Valeriana sitchensis* Bong.) and Indian hellebore (*Veratrum viride* Ait.) had recovered to precut levels by early in the second growing season. Sitka valerian vigour decreased after multiple cutting. Mechanical scarification either severely damaged or completely killed the shrub species. Herb species responded to mechanical scarification as they did to manual cutting.

Effects of Shrubs and Herbs on Conifer Regeneration and Microclimate in the *Rhododendron-Vaccinium-Menziesia* Community of South-Central British Columbia

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INTRODUCTION

Within British Columbia there are extensive areas of forest land, termed "backlog" areas, that have failed to regenerate successfully after harvesting or natural disturbance. In the Kamloops Forest Region, located in south-central B.C., there are approximately 200,000 ha of backlog, of which 70,000 ha occur in the high-elevation Engelmann Spruce-Subalpine Fir (ESSF) zone[1]. The majority of backlog in the ESSF zone results from failed regeneration practices following harvesting. The current harvesting rate in the ESSF zone is approximately 10,000 ha per year and is expected to increase in the future[1]. The commercial importance of this zone, coupled with its low rate of reforestation success, indicates a need for research aimed at developing effective regeneration strategies.

The major commercial conifer species found in the ESSF zone are Engelmann spruce (*Picea engelmannii* Parry), lodgepole pine (*Pinus contorta* var *contorta* Dougl.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Only Engelmann spruce and lodgepole pine are commonly planted in the ESSF zone.

The harsh climate of the ESSF zone may be one of the primary reasons for the failure of regeneration efforts. The ESSF zone is the zone of high elevation forest lying just below timberline between approximately 1300 and 1900 m elevation (Coupé 1983). The climate is a moist, snowy, continental subalpine type with short, cool growing seasons and long cold winters. Clearcuts are generally free of snow between late May or the middle of June and early October.

[1]D. Lloyd, Regional Ecologist, Kamloops Forest Region, personal communication, March 1986.

Most logging in the ESSF zone occurs during the winter months when snow cover protects the understory from damage. As a result, a well-developed brush community often is present immediately following harvesting. The community is dominated by the four Ericaceous shrubs, white-flowered rhododendron (*Rhododendron albiflorum* Hook.), black huckleberry (*Vaccinium membranaceum* Dougl.), oval-leaved huckleberry (*V. ovalifolium* Smith.), and false azalea (*Menziesia ferruginea* Smith.). Sitka valerian (*Valeriana sitchensis* Bong.) and Indian hellebore (*Veratrum viride* Ait.) are the dominant herbs. This vegetation complex is abundant on ESSF clearcut areas, and is thought to be a major impediment to successful forest regeneration (Conard 1984). However, there has been virtually no research on how the dominant species of the community interfere with conifer establishment and growth.

Light availability, soil moisture and temperature, and nutrient supply directly affect seedling survival and early growth of both Engelmann spruce (Dobbs 1972, McMinn 1982, Draper *et al.* 1985, David 1987) and lodgepole pine (Vyse and Navratil 1985). There is considerable evidence that vegetation communities have a deterimental affect on coniferous tree survival and growth through competition for light, water, or nutrients (Wilde *et al.* 1968, Eis and Craigdallie 1983, Carter *et al.* 1984, Howard and Newton 1984, Stewart *et al.* 1984, McMinn 1985, Brand 1986, Elliott and White 1987, Walstad and Kuch 1987). However, most of this research has been carried out in relatively productive environments. In a stressful high elevation environment such as the ESSF zone, where the climate itself imposes severe limitations on tree establishment and growth, interactions between conifer performance and associated vegetation are poorly understood.

Before an effective strategy can be developed for regenerating backlog areas in the ESSF zone, it is essential to understand the limitations to conifer survival and growth. The ecology of the major shrub and herb communities of the ESSF zone must be examined. Specifically, the effect that shrubs and herbs have on resource availability and microclimate and the way they respond to disturbance treatments must be understood. Accordingly, the objectives of this study were;

1. To identify limitations placed on seedling establishment and growth by the ESSF zone climate.

2. To measure changes in microclimate associated with varying amounts of shrubs and herbs.

3. To develop a model of the response of planted conifers to varying proximity and abundance of shrubs and herbs.

4. To measure the response of the dominant shrubs and herbs to disturbance treatments.

Effect of Shrub and Herb Reduction Treatments on Conifer Performance and Microclimate

Chapter 1

INTRODUCTION

The Engelmann Spruce-Subalpine Fir (ESSF) zone is an area of high elevation forest lying between alpine tundra and lower elevation forests over the southern two-thirds of the interior of British Columbia (Coupé 1983). The major commercial conifer species found in the ESSF zone are Engelmann spruce (*Picea engelmannii* Parry), lodgepole pine (*Pinus contorta* var *contorta* Dougl.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Only Engelmann spruce and lodgepole pine are commonly planted in the ESSF zone.

Environmental conditions play an important role in conifer survival and growth at upper elevations (Tranquillini 1979). Trees at high elevations are influenced by the short growing season, low soil and air temperatures, wind and snow damage, desiccation stress, and interference from associated vegetation. The ability of seedlings to become established and grow depends on the interactions among these biotic and abiotic factors and the varying stress they may impose on planted seedlings.

There has been relatively little research on the physical environment of the ESSF in south-central B.C. (David 1987), and no studies that examine how abiotic conditions and interspecific interference interact to influence establishment and growth of conifer seedlings. However, in the sub-boreal forests, generally found at middle elevations below the ESSF zone, silvicultural treatments that increase soil temperature, control competing vegetation, and minimize nutrient losses can improve survival and growth of spruce (Herring and McMinn 1980, McMinn 1982, Eis and Craigdallie 1983, Draper *et al.* 1985).

The objective of this study was to quantify the influence of varying amounts of interspecific interference on microclimate and on conifer establishment and growth in the ESSF zone of south-central B.C.

METHODS

Study Area

A single study site was located within the ESSF zone of south-central British Columbia. The site was at an elevation of 1550 m, approximately 25 km northeast of Clearwater B.C. (Figure 1.1). The study site is within the Shushwap Highlands Moist Central biogeoclimatic subzone (ESSFm1) (Lloyd 1983). The dominant vegetation type is the *Rhododendron albiforium - Gymnocarpium dryopteris - Veratrum viride* site association (ESSFm1/01.2) (Lloyd 1983). The old-growth Engelmann spruce-subalpine fir stand that originally occupied the site was harvested in the winter of 1977-1978. No further disturbance has occurred on the site.

The study site has been repeatedly glaciated (Holland 1964) and the dominant landform is a morainal blanket. The terrain is flat to gently rolling with slopes rarely exceeding 25%. The dominant aspect is north to northwest. Soils are moderately well to well drained, loam to clay loam, Orthic Humo Ferric Podzols (Canadian Soil Survey Committee 1978). Organic horizons are 4-8 cm thick, loose to matted Humihemimors (Klinka *et al.* 1981); decomposition is primarily fungal, with some faunal activity present. Few roots occur below the top 30 cm of the mineral soil.

The site has a continental cold humid climate characterized by long, cold, snowy winters and short, cool, wet summers. Most of the precipitation occurs as snow. Krajina (1965) estimates snowfall to be between 175 and 1016 cm and total annual precipitation of between 41 and 183 cm over the range of the ESSF zone. The closest long term weather station is at Boss Mountain (1532 m), approximately 50 km north west of the study site. There annual precipitation is 118 cm, snowfall 782 cm, growing season precipitation 40 cm, mean annual temperature $1^{o}C$, mean July monthly temperature $12^{o}C$, and there are 672 growing degree days greater than $5^{o}C$ (Atmos. Envir. Serv. 1982ab). The snow-free period typically extends from early June to late

September. Frosts can occur at any time of the year.

Experimental Design and Treatments

A randomized complete block design, with 3 blocks, was used. Within each block, 14 distinct treatments were randomly assigned to 12 m x 12 m square plots. Each treatment was a unique combination of three factors: (1) the amount of shrubs and herbs present (8 levels) (defined as the percentage of surface area in each plot with either shrubs or herbs present), (2) presence or absence of mineral soil exposure, and (3) the species of conifer planted (2 species). Not all combinations of the three factors were included in the design.

All plots had uniform, nearly continuous, shrub and herb cover prior to the treatments being applied. Manual brush cutting with no soil disturbance (NSD) or mechanical scarification with soil disturbance (SD) (a crawler tractor with a brush blade) was used to remove shrubs and herbs. All partial vegetation removal treatments were done by manually cutting randomly located strips in each plot so that the desired amount of shrubs or herbs were present. Each treatment plot was planted with 36 trees at 2 m x 2 m spacing in 6 rows of 6 trees each. All treatments were planted in the first week of July, 1986. Trees were shovel planted by an experienced planting crew. Because organic horizons were thin, only minor screefing was required. All trees were considered healthy and in good condition. Eight treatment plots were planted to Engelmann spruce (stocktype 1+0 PSB 313)[2] (hereafter referred to as spruce) and 6 to lodgepole pine (stocktype 1+0 PSB 211) (hereafter referred to as pine).

A complete summary of the 14 treatment plots follows (the %S and %H abbrevation refers to the area in each plot with either shrubs (S) or herbs (H) present after the treatments were applied):

[2]This stocktype refers to a 1 year old seedling grown in a styrofoam block container (plug). The 313 plug measures 3 cm in diameter by 13 cm in length.

Figure 1.1 Location of the study area (●) within south-central British Columbia.

TRT 1 - Spruce; TRT 2 - Pine: no vegetation removal/no soil disturbance (100%S 100%H NSD). This treatment represents the undisturbed shrub/herb community and provided the highest level of interfering vegetation.

TRT 3 - Spruce; TRT 4 - Pine: half-vegetation removal maintained/no soil disturbance (50%S 50%H NSD). Half the area of each plot was cleared of shrubs and herbs and plants were repeatedly cut as necessary to ensure a 50% reduction in interfering vegetation.

TRT 5 - Spruce; no Pine TRT plot: 25% shrubs and no herbs/no soil disturbance (25%S 0%H NSD). All herbs and 75% of the shrubs were cut and were repeatedly cut to ensure that only 25% of the area in each plot had shrubs.

TRT 6 - Spruce; TRT 7 - Pine: herbs only/no soil disturbance (0%S 100%H NSD). All shrubs were cut or removed and the treatment was kept shrub-free.

TRT 8 - Spruce; no Pine TRT plot: no shrubs and 25% herbs/no soil disturbance (0%S 25%H NSD). 25% of the plot area was allowed to grow in herbs; all shrubs were excluded.

TRT 9 - Spruce; TRT 10 - Pine: 1 cutting of all shrubs and herbs/no soil disturbance (1 Removal NSD). All shrubs and herbs were cut at the start of the experiment and then allowed to regrow.

TRT 11 - Spruce; TRT 12 - Pine: total vegetation removal/soil disturbance (0%S 0%H SD). The plot was mechanically scarified, exposing mineral soil, then all shrubs and herbs were removed as necessary to maintain bare mineral soil.

TRT 13 - Spruce; TRT 14 - Pine: total vegetation removal/no soil disturbance (0%S 0%H NSD). All shrubs and herbs were cut or removed and were repeatedly cut as necessary to exclude all shrubs and herbs.

The treatments had both quantitative and qualitative properties. Quantitative treatments include different levels or amounts of one factor, e.g. shrub and herb reduction levels. Qualitative treatments are different in kind, e.g. a given level of shrubs and herbs created by different disturbance types. For this reason, a number of treatment combinations and analytical techniques were employed to analyse the data.

Conifer Measurements

Conifers were measured at the time of planting (spring 1986), and at the end of the first (fall 1986), and second (fall 1987) growing seasons. Mortality and tree condition was also observed in spring 1987. Survival, tree condition, leader condition, stem condition, and type and cause of damage were recorded on all 36 trees per plot. Only the interior 16 trees on each treatment plot served as growth measurement trees. Total height and stem diameter (at 1 cm) were recorded on each measurement tree. Annual height increment, annual diameter increment, D2H (diameter squared x height), and height:diameter ratio were calculated for each measurement tree.

Environmental Measurements

Environmental conditions were monitored in 4 shrub and herb reduction treatments: (1) in the undisturbed shrub/herb community (TRT 1 or 2: 100%S 100%H NSD), (2) where the shrub/herb community was cut once and then allowed to regrow (TRT 9 or 10: 1 Removal NSD), (3) total vegetation removal with mineral soil exposure (TRT 11 or 12: 0%S 0%H SD), and (4) total vegetation removal without soil disturbance (TRT 13 or 14: 0%S 0%H NSD). Where possible all environmental measurements were taken in plots planted to spruce, but, because of treatment randomization and equipment limitations, plots planted to pine were also monitored.

Soil and air temperature were recorded with a data logger (Campbell Scientific 21x) at one representative location in TRT 1, TRT 9, TRT 11, and TRT 14. Soil temperature was measured at depths of 10 and 20 cm (from the mineral soil surface) with thermistors. This meant that in TRT 1, TRT 9, and TRT 14 the sensors were 4-8 cm deeper below the ground surface than in TRT 12 (where mineral soil was exposed) because of the presence of the organic horizons. Soil temperature was recorded at one minute intervals, and average hourly temperature and daily mean, maximum, and minimum temperatures were calculated. Air temperature was measured at 2 and 20 cm above the ground surface with shaded copper-constantan thermocouples. Air temperature was also recorded every minute, but only daily mean, maximum, and minimum air temperatures were retained. Because of limited channels on the data logger no air temperature readings were taken in the mechanically scarified TRT 11 (0%S 0%H SD). In addition, soil temperature at 50 cm depth and air temperature at 150 cm above the ground surface were recorded. Precipitation amount and frequency were recorded by a tipping bucket rain gauge attached to the data logger.

In all three experimental blocks, soil moisture was monitored by gypsum soil moisture blocks at five randomly selected locations in TRT 1, TRT 9, TRT 11, and TRT 13. Moisture blocks were buried at 10 and 20 cm depths (from the mineral soil surface). Moisture readings were taken with a resistance meter. Soil samples for determination of gravimetric water content were also taken at the same two depths. The samples were stored in sealed metal cans to prevent water loss, weighed before and after oven drying at 105^{o}C for 48 hr, and soil moisture content by weight was determined. All soil moisture data were collected at roughly three week intervals. Additional soil samples were taken for pressure-plate analysis to determine soil water potentials of the gravimetric samples.

Photosynthetic photon flux density (PPFD) and percent of incoming PPFD received at the soil surface was measured in treatments 1, 9, 11, and 13 on August 9, 1987. A Li-Cor 2100 data logger with a point sensor (placed above the shrub/herb canopy) and a 1 m long line light sensor placed under the shrub/herb canopy (that integrates light reaching it over the 1 m surface) was used (Li-Cor, Inc.). Individual measurements were taken at 5 random locations in each of the four treatments between 11:00 and 14:00 hr. The weather was sunny with scattered clouds, resulting in considerable variation among the PPFD measurements above the shrub/herb canopy, but the percent of incoming PPFD received under the shrub/herb canopy remained consistant.

Physiological Measurements

Predawn (2:00-4:00 hr) and midday (13:00-15:00 hr) xylem water potential of spruce seedlings was measured in TRT 1 (100%S 100%H NSD) and TRT 13 (0%S 0%H NSD) in all three blocks using a pressure chamber (PMS Instruments Co.) and techniques described by Ritchie and Hinckley (1975). Lateral branches from 2 sample trees per treatment were cut and measured in the field. Measurements were taken at roughly 3 week intervals during 1987.

Statistical Analysis and Data Evaluation

All data were analysed on personal computers using the Statistical Analysis System (SAS Institute 1985) programs.

Differences in growth between treatments were compared using analysis of variance. Where a significant F-value indicated a difference at the 0.05 probability level, the means were compared and separated by Waller and Duncan's Bayes LSD procedure (Petersen 1985). In addition, the following planned contrasts were tested to compare the effects of different qualitative treatment combinations:

1. Is any amount of shrub and/or herb reduction different from no removal?

   Spruce: TRT 1 vs TRT 3, 5, 6, 8, 9, 11, 13

   Pine: TRT 2 vs TRT 4, 7, 10, 12, 14

2. Is 50% shrub and herb removal as effective as more removal?

   Spruce: TRT 3 vs TRT 5, 6, 8, 9, 11, 13

   Pine: contrast not tested

3. Is complete shrub and herb removal different from partial removal (NSD treatments only)?

   Spruce: TRT 13 vs TRT 3, 5, 6, 8

   Pine: TRT 14 vs TRT 4, 7, 9

4. Given a competition-free environment, do trees perform differently where mechanical scarification disturbs the organic horizons and exposes mineral soil than where the soil is not disturbed?

   Spruce: TRT 11 vs TRT 13

   Pine: TRT 12 vs TRT 14

5. Is no removal different from complete removal (NSD treatments only)?

   Spruce: TRT 1 vs TRT 13

   Pine: TRT 2 vs TRT 14

6. Is a site growing back to herbs only, different from one growing back to herbs and shrubs?

   Spruce: TRT 6 vs TRT 9

   Pine: TRT 7 vs TRT 10

7. Is spruce performance different on a site with 25% shrubs and no herbs than on a site with no shrubs and 25% herbs?

   Spruce: TRT 5 vs TRT 8

   Pine: contrast not tested

RESULTS

Environmental Measurements

General climate

Throughout southern B.C., the 1987 growing season was much drier than the long-term average. However, precipitation at the study site was evenly distributed throughout the snow-free period (Figure 1.2), with 63 mm of rain falling between late May and early October. This was considerably lower than the long-term average for the area (Atmos. Envir. Serv. 1982a).

In 1986 the snow-free period extended from early June to mid-October; in 1987 from late May to mid-October. On May 25, 1987 one of the 3 blocks was still covered with snow, while the remaining blocks had scattered patches of snow. Between late May and early October, 1987 maximum and minimum air temperatures at 150 cm above the ground surface rarely exceeded 25^{o}C and 8^{o}C, respectively and mean soil temperature at 50 cm hovered near 5^{o}C (Figure 1.3). Temperatures in 1986 were similar. Frost could occur at any time during the snow-free period. In 1987, two frosts occurred between June 1 and August 31; and in both cases temperatures were -1^{o} to -2^{o}C (Figure 1.3). The longest frost-free interval during the summer period was 46 days. Frost frequency and intensity were similar in 1986.

Soil temperature

Total vegetation removal without soil disturbance (TRT 14: 0%S 0%H NSD) increased mean soil temperature at a depth of 10 cm by 4^{o}-7^{o}C and also increased diurnal temperature variation compared to where the vegetation was undisturbed (TRT 1: 100%S 100%H NSD) (Figures 1.4 and 1.5ab). In TRT 1 soil temperature at 10 cm never exceeded 10^{o}C and generally ranged between 6^{o} and 8^{o}C throughout the snow-free period (Figure 1.5a). In contrast, temperature in the complete removal TRT 14 (0%S 0%H NSD) reached 15^{o}-17^{o}C

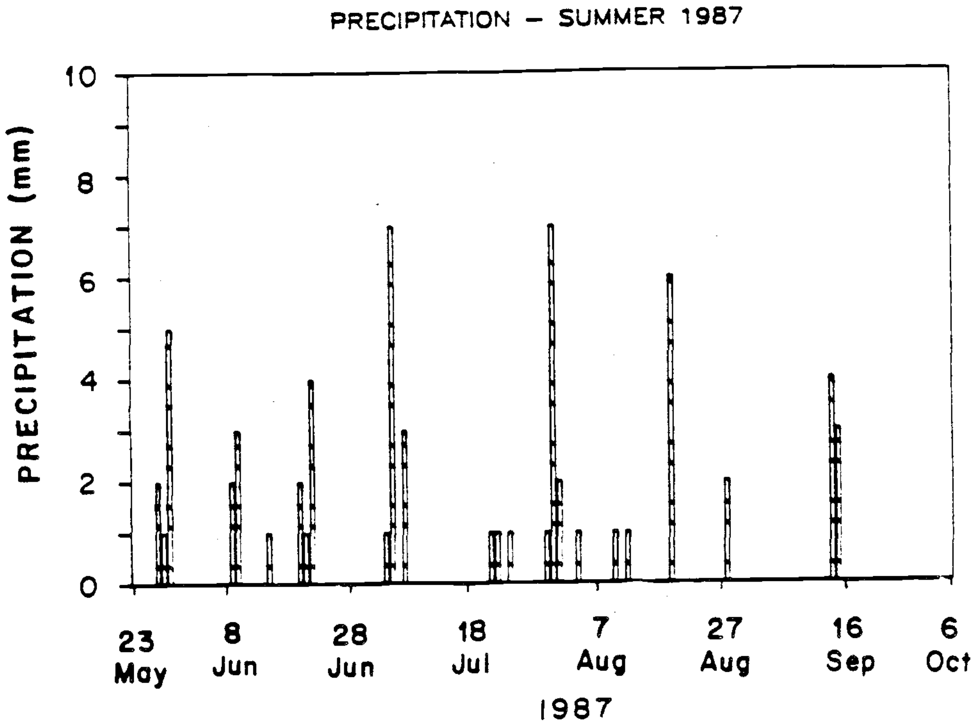


Figure 1.2 Precipitation amount and frequency.

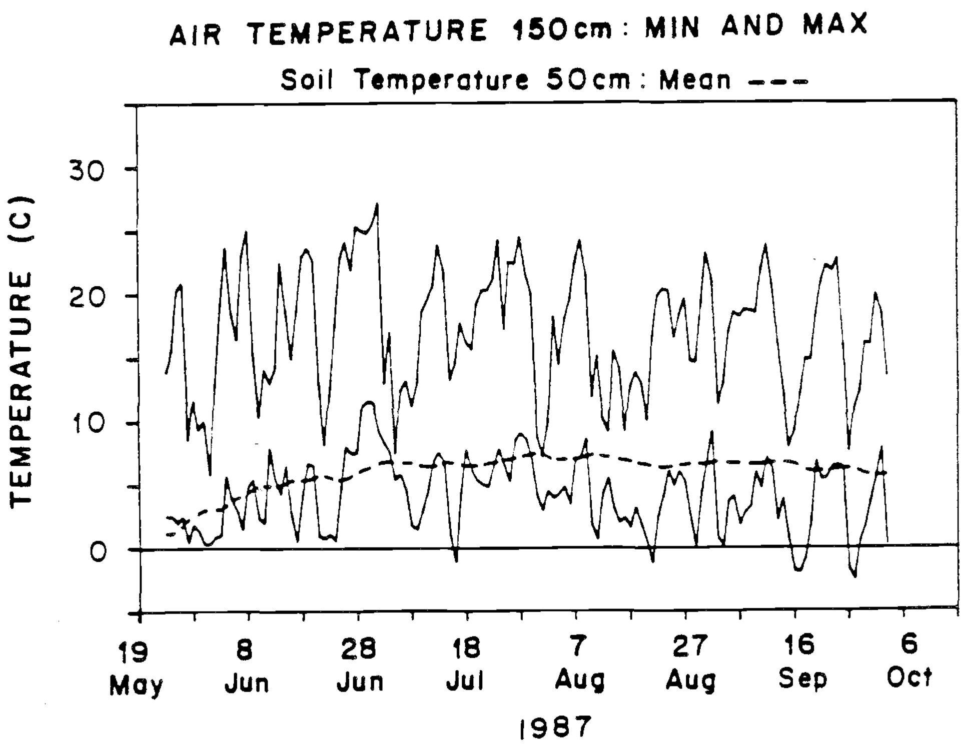


Figure 1.3 Maximum and minimum air temperature at 150 cm above the ground surface, and mean soil temperature at a depth of 50 cm.

(Figure 1.5b). In the one cut TRT 9 (1 removal NSD) where vegetation had been recovering for two growing seasons, soil temperatures varied little from those in the total removal TRT 14 until late in the second growing season when they became 1^{o}-$2^{o}C$ lower (Figures 1.4 and 1.5bc). Exposure of mineral soil in the mechanically scarified TRT 12 (0%S 0%H SD) slightly increased soil temperature at 10 cm over that found in TRT 14 (0%S 0%H NSD) where the organic horizons were not disturbed (Figures 1.4 and 1.5bd). The mechanically scarified plot also had the largest daily fluctuations in soil temperature (Figure 1.5d). Minimum soil temperatures at 10 cm in all four treatments were around $6^{o}C$ throughout the growing season (mid-to-late June to early August). Temperature at 20 cm depth (not shown) followed similar patterns to those at 10 cm on all treatments except that variation was reduced, mean temperatures were 1^{o} to $2^{o}C$ lower, and differences among treatments were less pronounced.

The effect of vegetation removal on soil temperature at 10 cm depth is most apparent in Figure 1.6 which shows cumulative degree-days above $5^{o}C$ in 1987. Cumulative degree-days to early October was 293 in the no removal TRT 1 compared to 638-667 in the three vegetation removal treatments (TRT 9, TRT 12, TRT 14).

Air temperatures

Cumulative degree-days above $5^{o}C$ (20 cm above the ground surface) in 1987 varied little between the no removal TRT 1 (100%S 100%H NSD), the 1 cut TRT 9 (1 Removal NSD), and the total removal TRT 14 (0%S 0%H NSD), although TRT 14 was slightly higher (Figure 1.7).

Maximum air temperature at 2 cm above the ground surface in 1987 was greatest in the total removal TRT 14 where it approached $40^{o}C$, compared to approximately $30^{o}C$ in the one cut TRT 9 where shrubs and herbs were regrowing, and $28^{o}C$ in TRT 1 where the brush community was not disturbed (Figures 1.8 and 1.9). Seasonal temperature maxima can apparently occur at any time in the growing season. In 1987 seasonal high temperatures were well distributed throughout the snow-free season. In 1986, which was a cooler

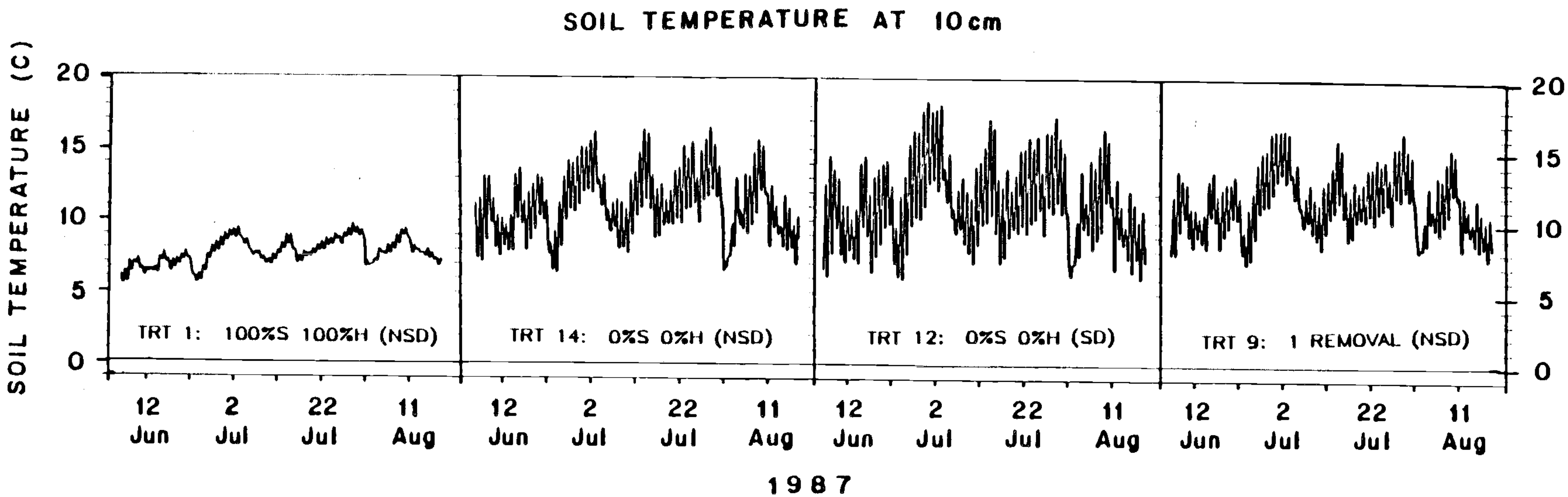


Figure 1.4 Comparision of daily soil temperature variation in four treatments at a depth of 10 cm.

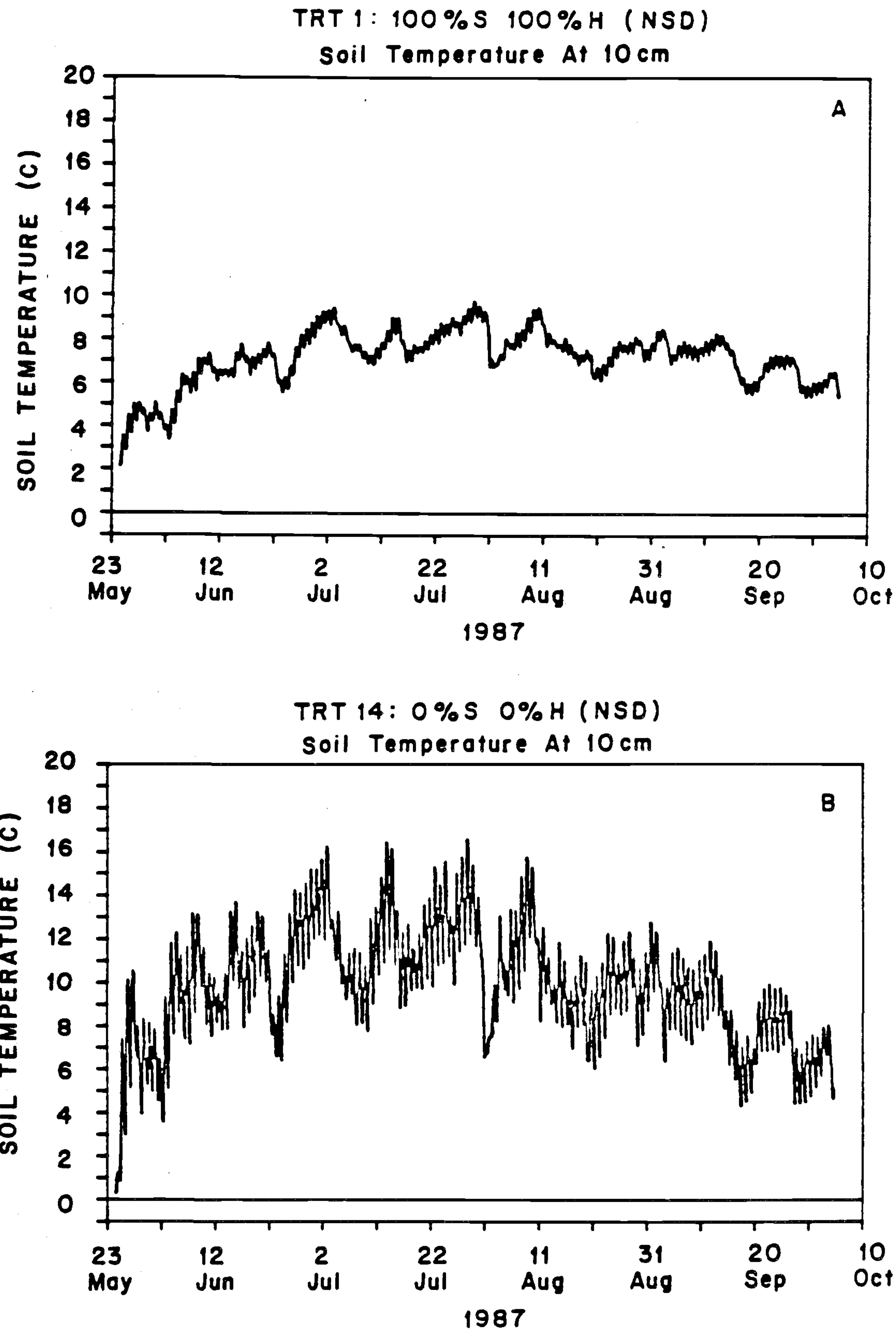
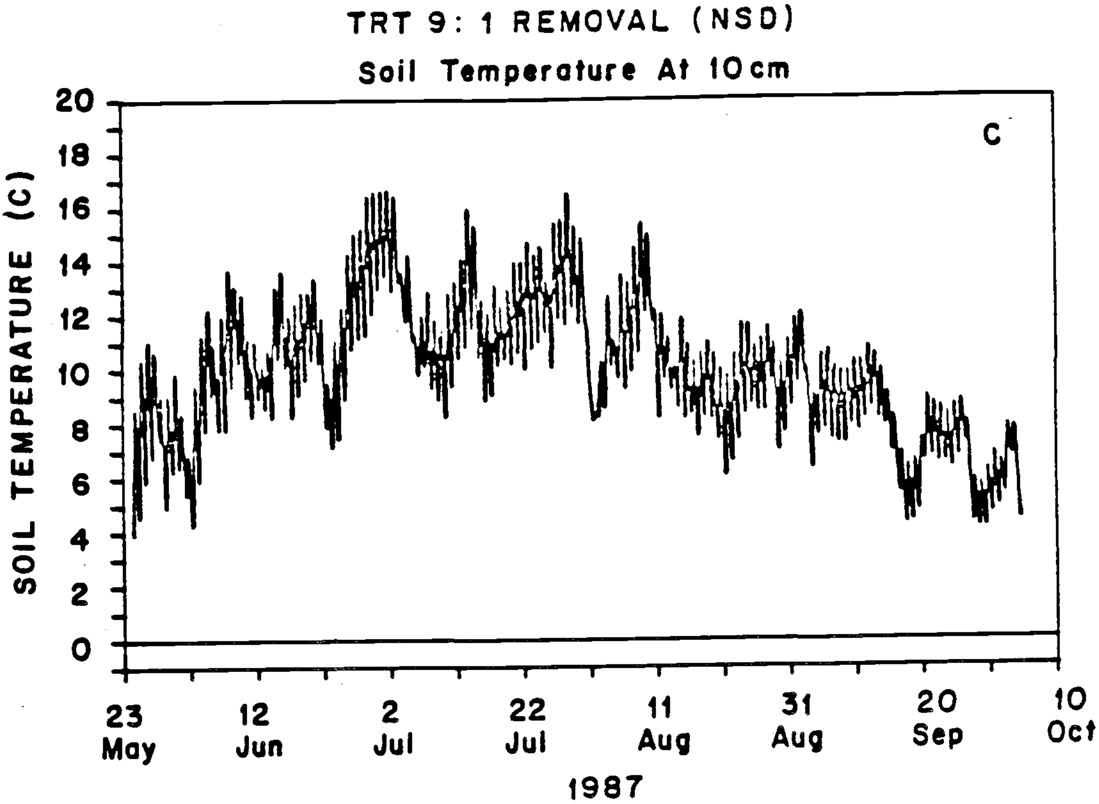
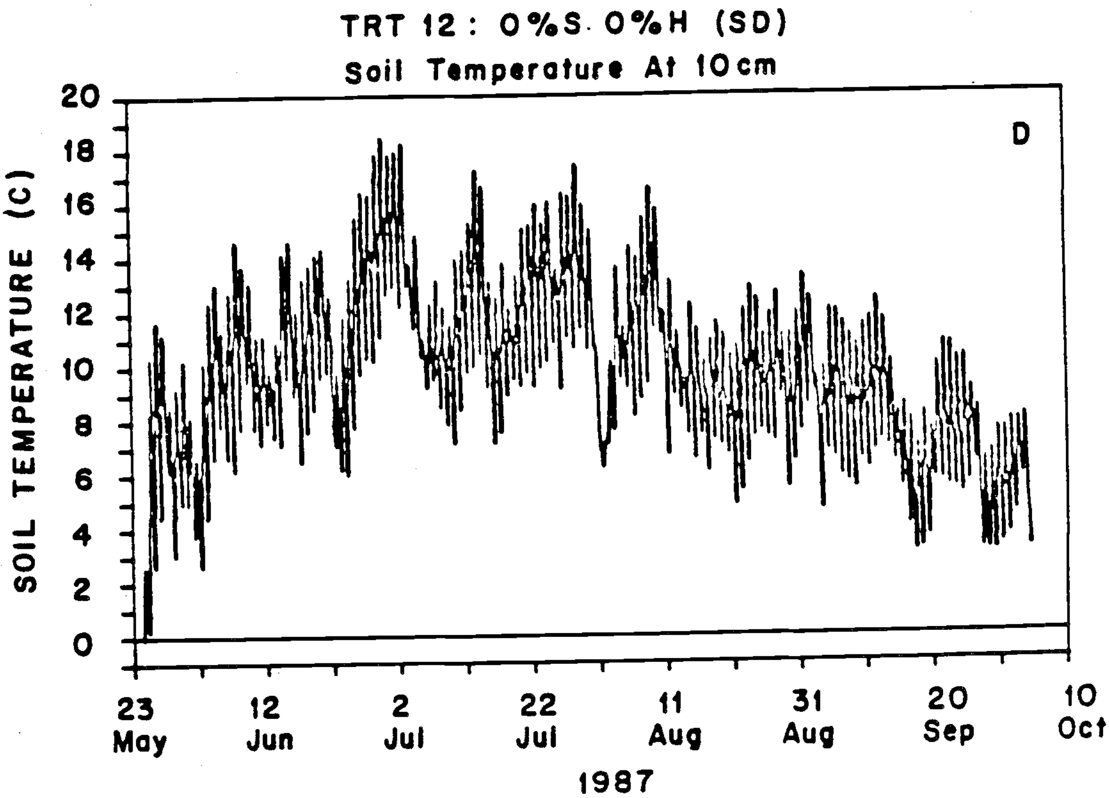


Figure 1.5 Daily soil temperature in TRT 1 (100%S 100%H NSD) (A), TRT 14 (0%S 0%H NSD) (B), TRT 9 (1 Removal NSD) (C), and TRT 12 (0%S 0%H SD) (D) at a depth of 10 cm.





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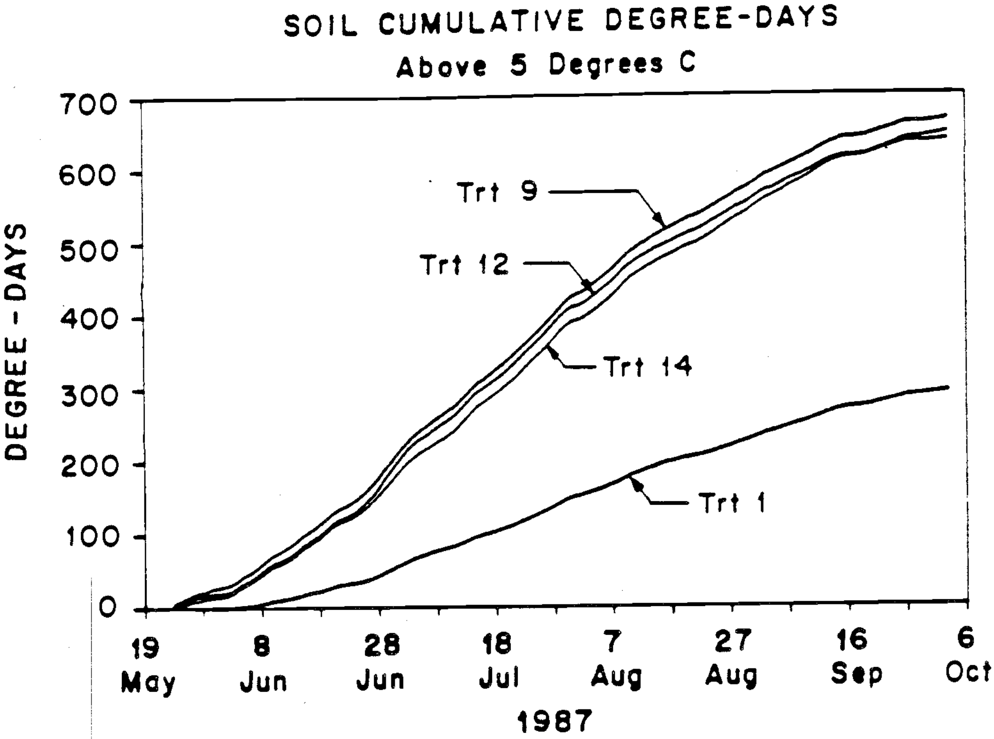

Figure 1.6 Cumulative soil temperature above 5°C in four treatments at a depth of 10 cm.

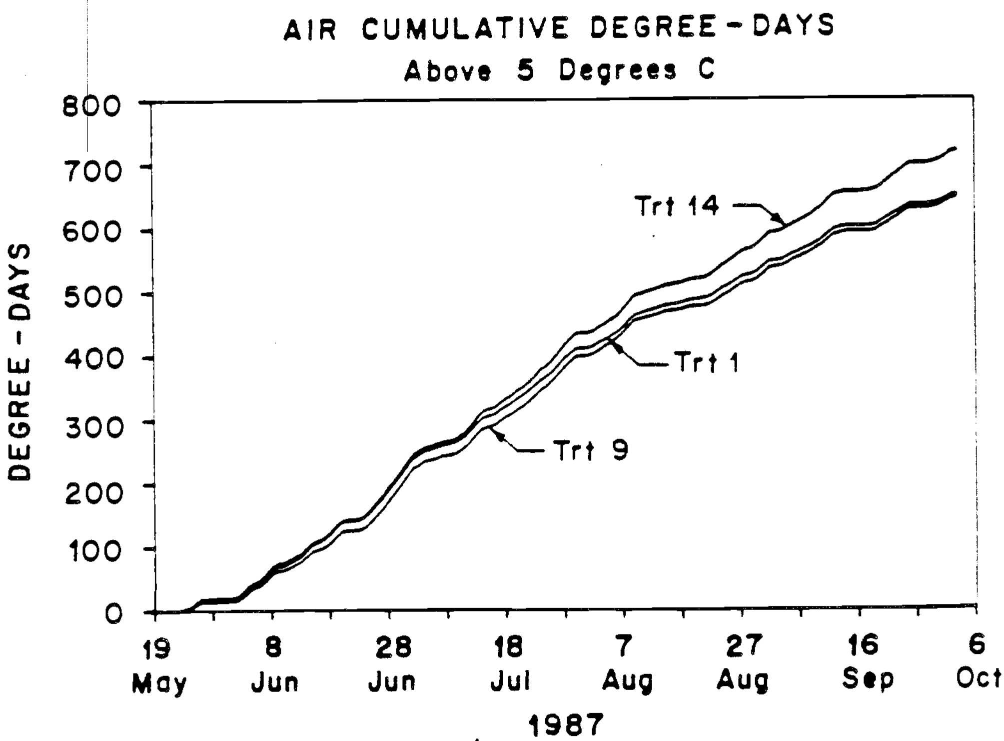

Figure 1.7 Cumulative air temperature above 5°C in three treatments at a height of 20 cm.

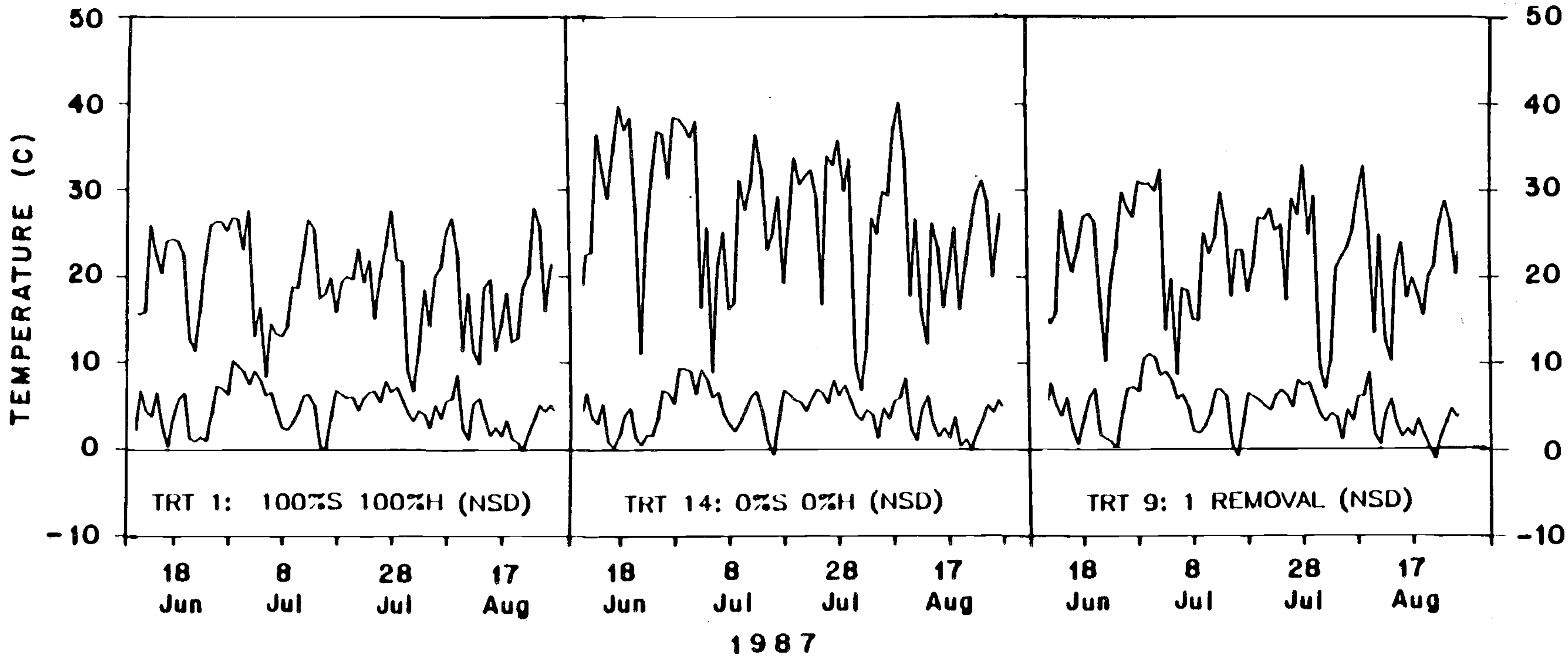

Figure 1.8 Comparision of maximum and minimum air temperatures 2 cm above the ground surface during the growing season in three treatments.

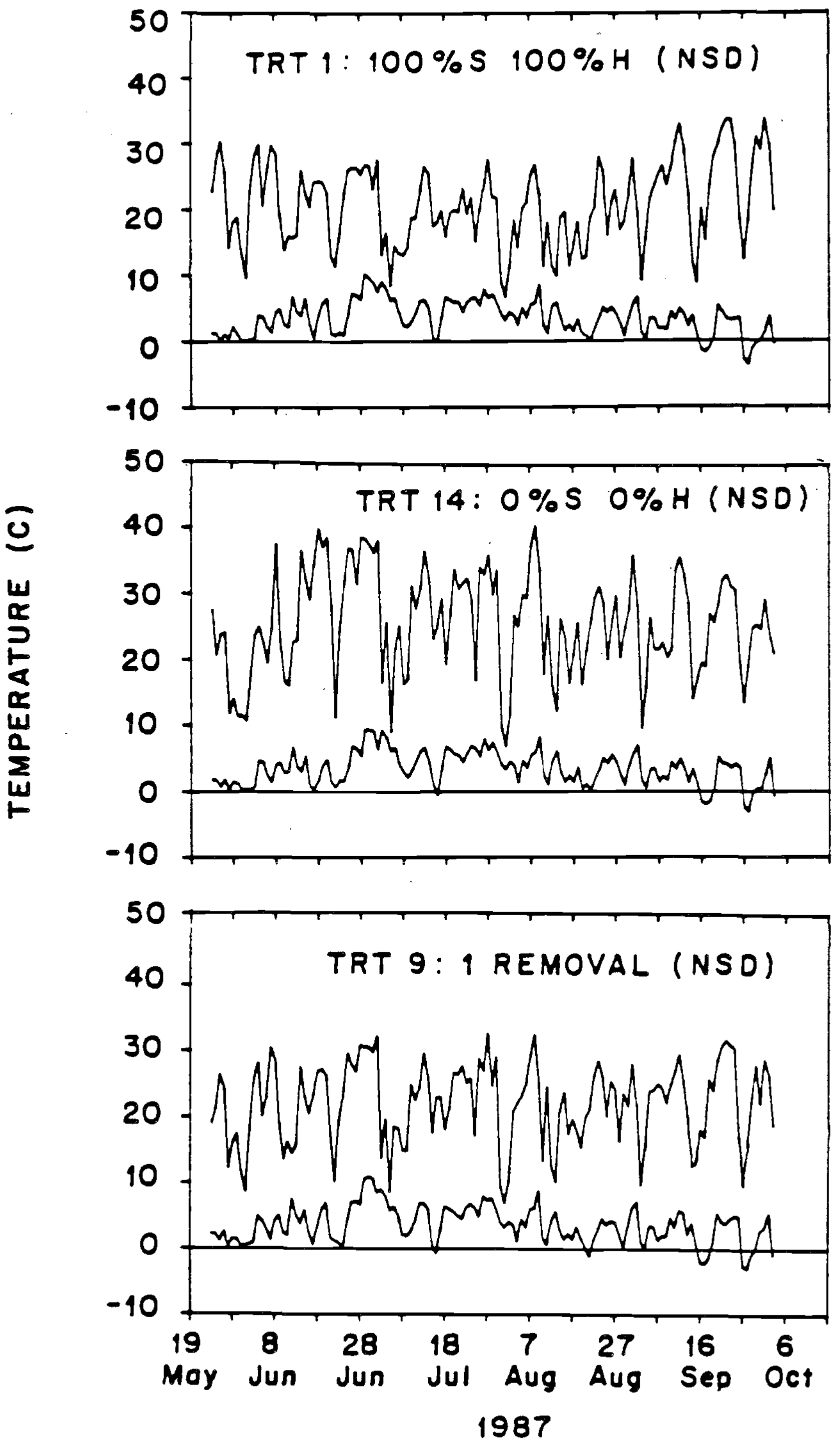

Figure 1.9 Maximum and minimum air temperatures at 2 cm above the ground surface in three treatments.

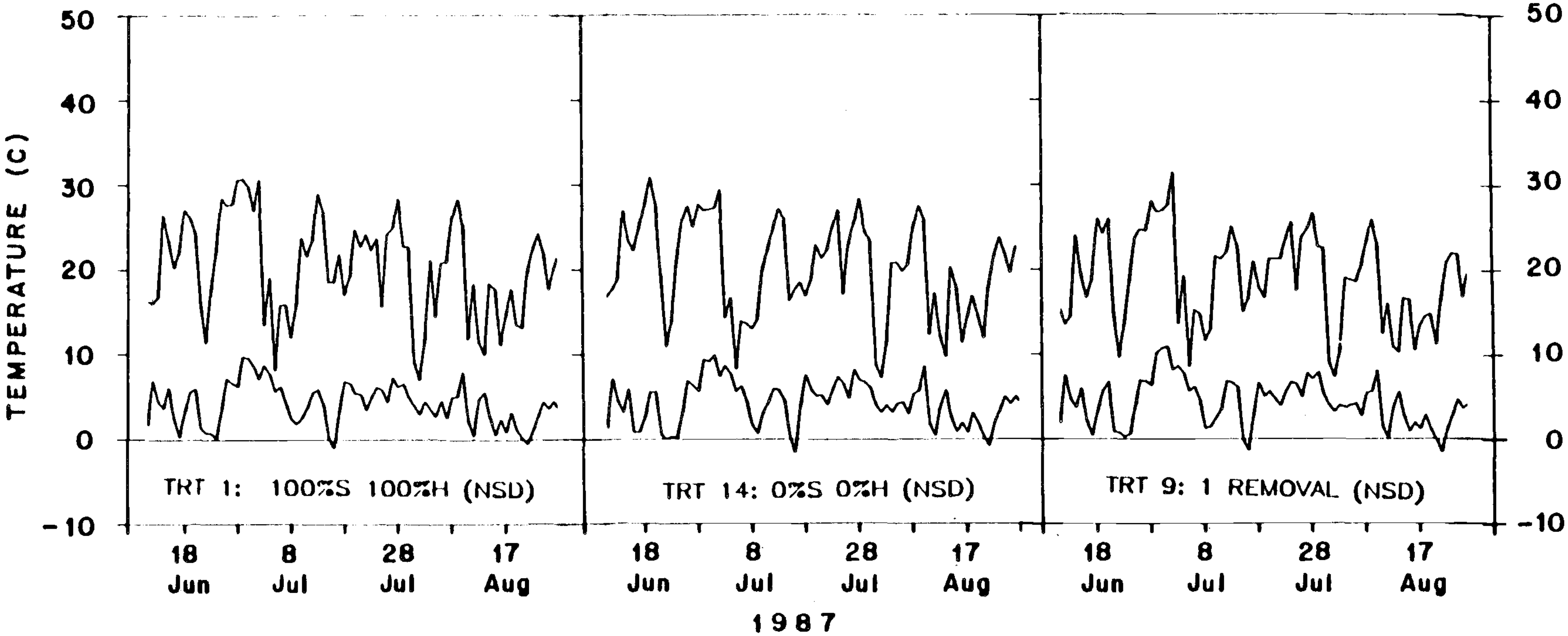

Figure 1.10 Comparision of maximum and minimum air temperatures 20 cm above the ground surface during the growing season in three treatments.

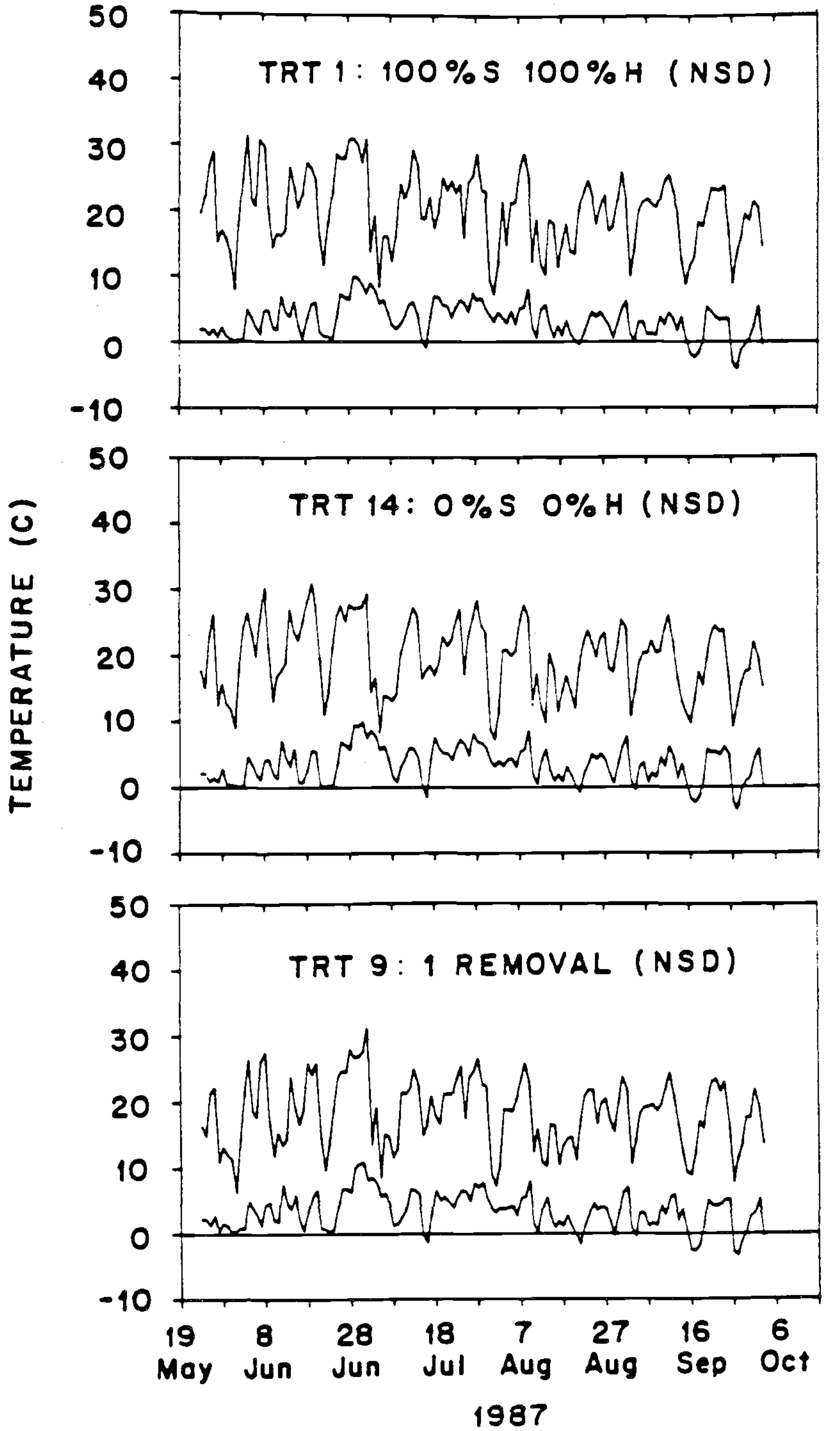

Figure 1.11 Maximum and minimum air temperatures at 20 cm above the ground surface in three treatments.

summer, maximum air temperature never exceeded 35°C in any treatment, and the maximum temperatures were restricted to the month of August (not shown).

In TRT 1, TRT 9, and TRT 14, in 1987, maximum air temperatures at 20 cm above the ground surface rarely exceeded 30°C and generally were between 25 and 28°C (Figure 1.10). In 1986, maximum temperatures were similar to those shown for 1987. In the total removal TRT 14, maximum air temperatures were 5° to 10°C higher at 2 cm than at 20 cm. The total removal TRT 1 and one cut TRT 9 differed very little from one another, and maximum temperatures at the two heights were nearly identical.

Minimum air temperatures varied little among the three treatments and were identical at 2 cm and 20 cm above the ground surface (Figures 1.8-1.11). Minimum temperatures were never below -2°C and were above 10°C on only a few days between June and August in both 1986 and 1987. Maximum duration of freezing temperatures during the growing season was 1-2 nights in both years. Minimum air temperatures averaged between 5° and 7°C throughout the growing season.

Soil moisture

Soils appeared moist to wet throughout the snow-free period in both 1986 and 1987. Soil water potential was never lower than -0.01 MPa (or 42% soil moisture by weight) in any of the 4 treatments during the 1987 growing season, indicating an ample supply of soil water (Figures 1.12).

Percent soil moisture, from the gravimetric samples, did not differ between treatments or depths at 4 of the 5 sampling dates ($p>0.05$). The late August sample differed among treatments ($p=0.035$) and between depths ($p=0.023$). Soil water content in the one cut TRT 9 (1 Removal NSD) averaged 97.5% and was greater than that in the other three treatments (Figure 1.12).

Except for the late August sample there was little evidence to suggest differences between treatments or depths. Figure 1.12 presents moisture conditions in each treatment, averaged for the 2 depths, during the summer period. Saturation occurs at 81.5% moisture by weight. The gypsum soil moisture blocks indicated uniform moisture conditions throughout the snow-free period.

Light conditions

On average, PPFD levels of 995 µE (S.D.±410) were found in open areas or above the shrub and herb canopy. This value represents the amount of photosynthetically active light reaching the planted trees in all total removal treatments. In the no removal TRT 1 (100%S 100%H NSD) where the shrub/herb layer was undisturbed 135 µE (S.D. 89) of active light reached the soil surface, or on average, 13.5% (S.D.±11.9) of full light. The lowest and highest recorded levels in TRT 1 were 4.0% and 46.0% of full light, respectively. In the one cut TRT 9 (1 Removal NSD) where shrubs and herbs were regrowing active light was 514 µE (S.D.±247) or, on average, 61.7% (S.D.±15.4) of full light. The lowest and highest active light levels at the soil surface in TRT 9 were 32.3% and 89.0% of full light.

Physiological Measurements

Xylem water potential

There was no difference in spruce predawn or midday xylem water potential between the undisturbed brush community (TRT 1: 100%S 100%H NSD) and the total removal treatment (TRT 13: 0%S 0%H NSD) during the growing season (Figure 1.13). Predawn xylem water potential was highest in late May, immediately after snow melt, at about -1.0 MPa for both treatments. Predawn xylem water potential ranged between -0.5 MPa and -0.7 MPa in both treatments at sampling dates in July, August, and early September, 1987. Midday xylem water potential was also slightly higher in the spring. In the total removal TRT 1 it averaged -1.8 MPa in May, while the average for both TRT 1 and TRT 13 was between -1.3 MPa and -1.6 MPa during the summer months (Figure 1.13).

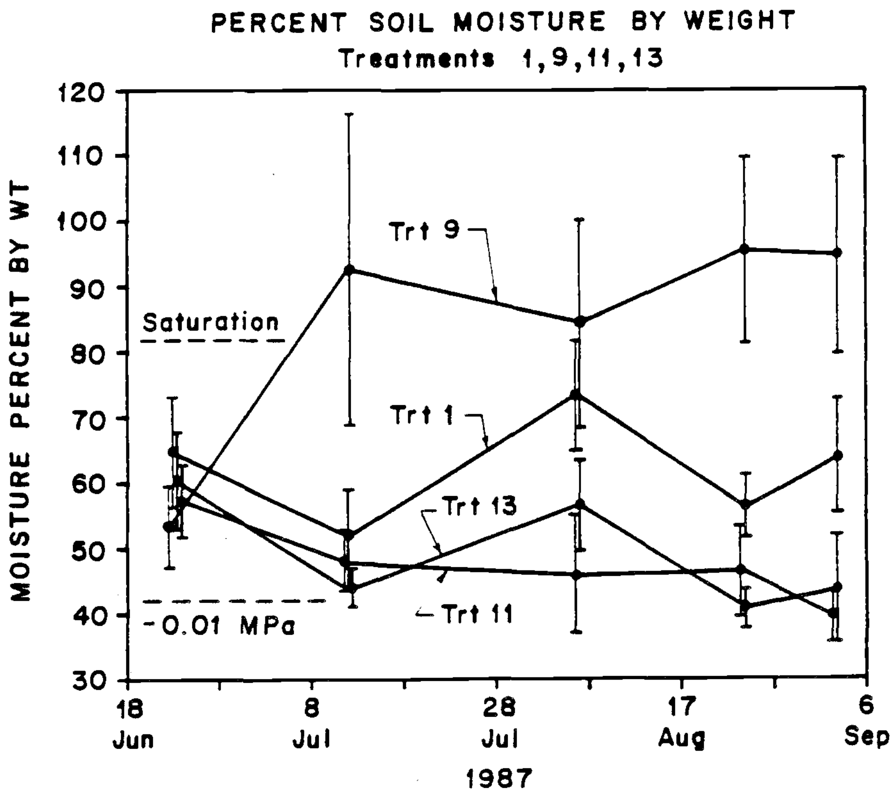

Figure 1.12 Percent soil moisture by weight in four treatments (error bars are 1 S.E.).

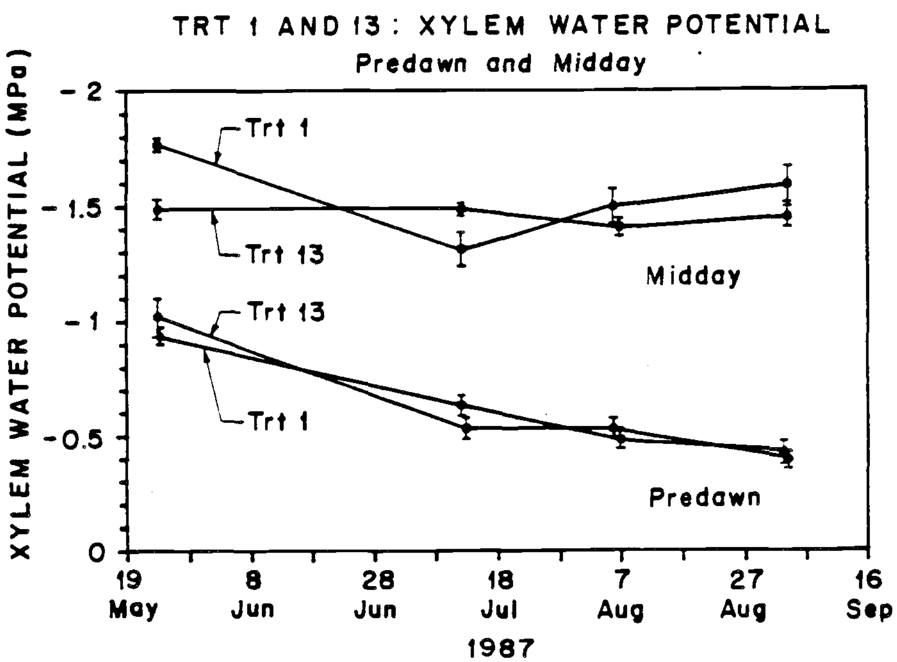

Figure 1.13 Spruce predawn and midday xylem water potential in two treatments (error bars are 1 S.E.).

Conifer Response

In 1987 buds swelled and flushed in the third week of June on most of the spruce and pine seedlings; in 1986 buds flushed a week or two later than in 1987. In both years new buds were set by late July.

Spruce survival and vigour

Spruce survival was greater than 99% in all treatments in the fall of 1986 (Table 1.1). Survival was lowest in the undisturbed brush community (TRT 1 100%S 100%H NSD), decreasing to 89.8% by the spring of 1987 and further decreasing to 81.5% by the fall of 1987. In the other seven treatments, survival remained above 97% after two growing seasons. The vigour of living trees followed the same trend as survival. By the end of the second growing season, only 73.8% of surviving trees in TRT 1 had good to moderate vigour compared to 99.1% in the mechanically scarified TRT 11 (0%S 0%H SD) and 95.4% in the total removal TRT 13 (0%S 0%H NSD) (Table 1.1). The other treatments had between 81 and 92% good to moderate trees. Total shrub and herb removal resulted in the best tree vigour after two growing seasons.

Spruce seedlings in all treatments were damaged by freezing weather in mid August, 1986. Minimum temperatures were -1^{o} to $-2^{o}C$ for 2 nights. Frost damage was not reduced by the presence of adjacent or overtopping vegetation (Table 1.2). In fact, damage was generally lowest in treatments with a complete lack of vegetation. In the fall of 1986, 11.5 percent of all spruce showed evidence of frost damage; this increased to 31.9 percent in the spring of 1987, indicating either that damage symptoms take time to become visible, or that further damage occurred over the winter. Only minor frost damage occurred during the 1987 growing season (Table 1.2), even though frost frequency and intensity were similar to 1986 conditions.

The severity of frost damage (e.g. dead terminal bud or dead leader) also varied by treatment (Table 1.2). In the spring of 1987, 22.7 percent of all trees in the total removal TRT 1 had dead leaders compared to 0.9 percent in the scarified treatment (TRT 11 0%S 0%H SD) and 4.6 percent in the total removal TRT 13. Absence of vegetation decreased the number of trees that showed frost damage and exposure of mineral soil apparently minimized the severity of damage.

In the spring of 1987, 9.6 percent of all spruce had bent leaders or stems. This was caused either by vegetation press or by snow. At the end of the growing season only 0.6 percent of the trees had bent leaders or stems, indicating that spruce with bent leaders or stems can recover.

Pine survival and vigour

Pine survival was the lowest in the no removal TRT 2 (100%S 100%H NSD), followed by half removal TRT 4 (50%S 50%H NSD) (Table 1.3). Overall survival was greater than 99 percent in the fall of 1986. Survival decreased to 93.5 percent in no removal TRT 2 and 92.5 percent in half removal TRT 4 by the spring of 1987, and further declined to 84.2 and 89.8 percent, respectively, by the end of the second growing season. Survival was greater than 97 percent in all other treatments after 2 growing seasons. Unlike spruce, the living tree vigour of pine varied little among treatments (Table 1.3). More than 90 percent of all surviving trees had good to moderate vigour at all assessment dates.

Pine trees were not affected by the frost event that damaged the spruce. In the spring of 1987, 16.4 percent of all pine trees had a bent leader or stem. The highest incidence of bent leaders and stems (24.5%) was in the total removal TRT 14 (0%S 0%H NSD) and the lowest (9%) in the no removal TRT 1 (100%S 100%H NSD). The majority of damage was caused by snow press. In the fall of 1987 only 2.4 percent of the trees had bent leaders or stems. Like spruce, most two year old pine trees quickly recovered from snow damage. Clipping by rodents was most common in treatments with overstory shrub cover. In the spring of 1987, 9.3 percent of pine were clipped in half-removal TRT 4 and 3.7 percent in no removal TRT 2 compared to less than 1 percent in the other treatments.

Table 1.1 Engelmann spruce survival and vigour of living trees after one growing season (fall 1986), after the first winter (spring 1987), and at the and at the end the second growing season (fall 1987) by shrub and herb reduction treatment.

	SHRUB AND HERB REDUCTION TREATMENTS							
	TRT 1 100%S 100%H NSD	TRT 13 0%S 0%H NSD	TRT 11 0%S 0%H SD	TRT 9 1 REMOVAL NSD	TRT 6 0%S 100%H NSD	TRT 3 50%S 50%H NSD	TRT 5 25%S 0%H NSD	TRT 8 0%S 25%H NSD
PERCENT SURVIVAL								
fall 1986	100	100	100	100	99.1	100	100	100
spring 1987	89.8	100	100	100	99.1	98.1	100	98.1
fall 1987	81.5	100	99.1	100	98.1	97.2	98.1	97.2
LIVING TREE VIGOUR								
Fall 1986								
good-moderate	93.6	99.1	100	100	99.1	97.2	99.1	98.2
poor	3.7	0.9	0	0	0.9	2.8	0.9	0.9
moribund	2.8	0	0	0	0	0	0	0.9
Spring 1987								
good-moderate	82.5	97.2	100	94.4	89.7	91.5	88.9	94.3
poor	12.4	2.8	0	4.6	10.3	8.5	11.1	3.8
moribund	5.2	0	0	0.9	0	0	0	1.9
Fall 1987								
good-moderate	73.8	95.4	99.1	87.0	91.5	84.8	81.2	87.6
poor	20.5	4.6	0.9	13.0	8.5	12.4	17.0	9.5
moribund	5.7	0	0	0	0	2.9	1.8	2.9

Table 1.2 Percent of living Engelmann spruce trees damaged after one growing season (fall 1986), after the first winter (spring 1987), and at the and of the second growing season (fall 1987) by shrub and herb reduction treatment.

	SHRUB AND HERB REDUCTION TREATMENTS							
	TRT 1 100%S 100%H NSD	TRT 13 0%S 0%H NSD	TRT 11 0%S 0%H SD	TRT 9 1 REMOVAL NSD	TRT 6 0%S 100%H NSD	TRT 3 50%S 50%H NSD	TRT 5 25%S 0%H NSD	TRT 8 0%S 25%H NSD
FROST DAMAGE (%)								
fall 1986	15.7	9.3	4.6	5.6	10.3	13.9	14.8	17.6
spring 1987	41.7	13.9	19.4	25.9	39.8	42.6	45.6	25.9
fall 1987	0.0	1.9	0.9	1.9	0.9	5.7	3.7	2.9
TIP OF LEADER OR TERMINAL BUD DEAD (%)								
fall 1986	8.3	1.9	0.9	1.9	4.7	7.4	1.9	2.8
spring 1987	26.8	10.2	17.6	18.5	26.2	31.1	37.0	17.9
fall 1987	1.1	2.8	0.9	1.9	0.9	5.7	5.7	2.9
ENTIRE LEADER DEAD (%)								
fall 1986	5.6	1.9	0	0	1.9	0.9	0.9	3.7
spring 1987	22.7	4.6	0.9	5.6	11.2	10.4	8.3	8.5
fall 1987	11.4	0	0	3.7	1.9	1.9	2.8	1.9
LEADER OR STEM BENT (%)								
fall 1986	7.4	0.9	0	2.8	1.9	1.9	3.7	0.9
spring 1987	12.4	11.1	7.4	6.5	6.5	14.2	10.2	8.5
fall 1987	0	0.9	0.9	0	0.9	0	0.9	0

Table 1.3 Lodgepole pine survival and vigour of living trees after one growing season (fall 1986), after the first winter (spring 1987), and at the end the second growing season (fall 1987) by shrub and herb reduction treatment.

	SHRUB AND HERB REDUCTION TREATMENTS					
	TRT 2 100%S 100%H NSD	TRT 14 0%S 0%H NSD	TRT 12 0%S 0%H SD	TRT 10 1 REMOVAL NSD	TRT 7 0%S 100%H NSD	TRT 4 50%S 50%H NSD
PERCENT SURVIVAL						
fall 1986	100	99.1	100	99.1	100	100
spring 1987	93.5	98.2	100	99.1	99.1	92.5
fall 1987	84.2	98.2	97.2	98.2	98.1	89.8
LIVING TREE VIGOUR						
Fall 1986						
good-moderate	98.1	100	100	100	99.1	100
poor	0.9	0	0	0	0	0
moribund	0.9	0	0	0	0.9	0
Spring 1987						
good-moderate	91.1	96.2	99.1	97.2	96.3	92.0
poor	3.0	2.8	0.9	1.9	0.9	5.0
moribund	5.9	0.9	0	0.9	2.8	3.0
Fall 1987						
good-moderate	96.7	96.2	97.1	96.2	93.4	92.8
poor	1.1	1.9	1.9	2.8	3.8	5.2
moribund	2.2	1.9	1.0	0.9	2.8	2.1

Spruce growth

At the time of planting, spruce mean height, diameter, D2H, and height:diameter ratio were 14.0 cm, 3.55 mm, 1.82 cm^3, and 40.0 respectively. Initial diameter, which ranged from 3.35 to 3.75 mm, was significantly different among treatments at planting (p=0.019) (Table 1.4). Mean diameter was the greatest (3.75 mm) in the undisturbed brush community (TRT 1 100%S 100%H NSD), while the mechanically scarified TRT 11 (3.52 mm) (0%S 0%H SD) and total removal TRT 13 (3.58 mm) (0%S 0%H NSD) were near the average. By the end of the second growing season there was strong evidence that shrub and herb amount were affecting diameter growth (p=0.0001). Trees in the no removal TRT 1 were smallest (4.23 mm) while trees in the mechanically scarified TRT 11 were largest (5.27 mm). Trees in the total removal TRT 13 were also large (5.13 mm), indicating that diameter growth of trees planted into the undisturbed brush community was depressed compared to trees in a competition-free environment. This trend is evident in the 1987 diameter increment results (Table 1.4) which show that trees in TRT 11 had twice the increment of trees in TRT 1. D2H followed a similar pattern to diameter (Table 1.4).

Initial height, while not significant at the 0.05 probability level (p=0.065), did vary considerably among treatments at planting (Table 1.4). The total removal TRT 13 was the tallest (16.5 cm) and the mechanically scarified TRT 11 the shortest (12.0 cm) with all other treatments, except TRT 5 (13.1 cm) (25%S 0%H NSD), falling near the mean of 14.0 cm.

Tree height did not respond to the levels of shrubs and herbs to the same degree as diameter. Nonetheless, there is strong evidence that trees in the total removal TRT 13 were taller after both the first year (p=0.008) and the second year (p=0.016) than trees in no removal TRT 1 (Table 1.5), although trees in TRT 13 had an initial, but not statistically significant, height advantage. The effect that total vegetation control can have on height performance is evident when total removal TRT 13 is compared to partial removal treatments. There again total vegetation removal produced the tallest trees after 2 growing seasons (Table 1.5). However, trees in both the no removal TRT 1 and the half removal TRT 3 (50%S 50%H NSD) were no shorter after the first or second seasons than the average of all removal treatments combined.

A response model was used to test whether diameter and height performance of spruce could be predicted by the amount of shrubs and herbs present. The shrub and herb amounts used were TRT 1 (100%S 100%H), TRT 3 (50%S 50%H), TRT 5 (25%S 0%H), and TRT 13 (0%S 0%H). The model for 1987 total height was not significant ($p=0.173$), whereas the models for 1987 diameter increment ($p=0.003$) and total diameter ($p=0.0001$) were highly significant, with R^2 equalling 0.69 and 0.90, respectively.

Although trees growing in the no removal TRT 1 were smaller in size at the end of the second growing season than those in the complete removal TRT 13, their height:diameter ratios were quite similar (50.9 vs 51.8 $p=0.814$), suggesting that although trees are smaller in TRT 1 they are morphologically, just as well balanced as those in TRT 13 (Table 1.5).

Both diameter ($p=0.0001$) and D2H ($p=0.017$) were smaller at the end of the second growing season in TRT 9 (1 Removal NSD) where shrubs and herbs had been removed once and allowed to regrow than in the all herbs TRT 6 (0%S 100%H NSD) (Table 1.5). Diameter was also smaller in TRT 5 (25%S 0%H NSD) than TRT 8 (0%S 25%H NSD) after two growing seasons ($p=0.049$). There were no significant differences between these treatments at planting or after the first growing season.

Within a competition-free environment, exposure of mineral soil neither improved nor depressed spruce growth. Although trees in the total removal TRT 13 (0%S 0%H NSD) where soil was not disturbed were significantly taller than those in mechanically scarified TRT 11 (0%S 0%H SD) (Table 1.5), this is largely explained by the initial height advantage at the time of planting (Table 1.4).

Table 1.4 Engelmann spruce mean height, height increment, diameter, diameter increment, D2H, and height:diameter ratio in different shrub and herb reduction treatments at the time of planting (spring 1986), after one growing season (fall 1986), and at the end of the second growing season (fall 1987).

	SHRUB AND HERB REDUCTION TREATMENTS								ANOVA RESULTS	
	TRT 1 100%S 100%H NSD	TRT 13 0%S 0%H NSD	TRT 11 0%S 0%H SD	TRT 9 1 REMOVAL NSD	TRT 6 0%S 100%H NSD	TRT 3 50%S 50%H NSD	TRT 5 25%S 0%H NSD	TRT 8 0%S 25%H NSD	p-value	STANDARD ERROR
HEIGHT (cm)										
at planting	14.5	16.5	12.0	13.7	13.8	14.2	13.1	14.0	0.065	0.81
fall 1986	22.9	27.1	21.2	22.7	24.0	22.4	21.8	22.9	0.02	0.95
fall 1987	21.5	26.8	21.8	23.1	23.8	21.0	21.5	23.0	0.155	1.38
ANNUAL HEIGHT INCREMENT (cm)										
fall 1986	8.4	10.6	9.3	9.0	10.2	8.3	8.7	8.9	0.019	0.43
fall 1987	1.8	1.3	1.6	2.0	2.0	1.7	1.8	1.9	0.365	0.21
DIAMETER (mm)										
at planting	3.75	3.58	3.52	3.43	3.35	3.65	3.67	3.50	0.019	0.06
fall 1986	3.50	3.96	3.87	3.89	3.89	3.85	3.75	3.85	0.0005	0.05
fall 1987	4.23	5.13	5.27	4.63	5.18	4.76	4.85	5.06	0.0001	0.07
ANNUAL DIAMETER INCREMENT (mm)										
fall 1986	-0.25	0.34	0.35	0.46	0.54	0.20	0.08	0.35	0.003	0.10
fall 1987	0.69	1.18	1.38	0.72	1.29	0.91	1.11	1.18	0.0001	0.07
D2H (cm)										
at planting	2.06	2.14	1.52	1.67	1.62	1.91	1.86	1.81	0.019	0.11
fall 1986	2.95	4.40	3.87	3.64	3.80	3.41	3.20	3.53	0.015	0.22
fall 1987	4.03	7.43	6.35	5.18	6.78	4.98	5.45	6.28	0.001	0.42
HEIGHT:DIAMETER RATIO (cm)										
at planting	39.5	47.1	34.5	40.6	42.1	39.6	35.8	40.4	0.106	2.64
fall 1986	66.7	68.5	54.9	58.4	62.2	58.5	58.7	59.7	0.007	2.12
fall 1987	50.9	51.8	41.5	49.8	45.6	44.2	44.0	44.9	0.13	2.67

Table 1.5 Engelmann spruce planned contrasts.

CONTRAST		TOTAL HEIGHT	DIAMETER	D2H	HEIGHT DIAMETER RATIO
TRT 1 vs 3 5 6 8 9 11 13		No shrub and herb removal vs some removal			
	1986 means	22.9 vs 23.2	3.5 vs 3.87	2.95 vs 3.69	66.7 vs 60.1
	p-value	0.815	0.0001	0.014	0.012
	1987 means	21.5 vs 23.0	4.23 vs 4.98	4.03 vs 6.06	50.9 vs 46.0
	p-value	0.324	0.0001	0.0004	0.106
TRT 3 vs 5 6 8 9 11 13		50% removal vs more removal			
	1986 means	22.4 vs 23.3	3.85 vs 3.87	3.41 vs 3.74	58.5 vs 60.4
	p-value	0.415	0.698	0.332	0.415
	1987 means	21.0 vs 23.3	4.76 vs 5.02	4.98 vs 6.25	44.2 vs 46.3
	p-value	0.141	0.003	0.014	0.478
TRT 13 vs 3 5 6 8		Total shrub and herb removal vs some removal			
	1986 means	27.1 vs 22.8	3.96 vs 3.84	4.4 vs 3.49	68.5 vs 59.8
	p-value	0.0006	0.064	0.002	0.0008
	1987 means	26.8 vs 22.3	5.13 vs 4.96	7.43 vs 5.87	51.8 vs 44.7
	p-value	0.01	0.032	0.003	0.033
TRT 11 vs 13		No competition: soil disturbance vs no soil disturbance			
	1986 means	21.2 vs 27.1	3.87 vs 3.96	3.87 vs 4.4	54.9 vs 68.5
	p-value	0.0007	0.254	0.005	0.0005
	1987 means	21.8 vs 26.8	5.27 vs 5.13	6.35 vs 7.43	41.5 vs 51.8
	p-value	0.024	0.17	0.087	0.016
TRT 1 vs 13		No shrub and herb removal vs total removal			
	1986 means	22.9 vs 27.1	3.5 vs 3.96	2.95 vs 4.4	66.7 vs 68.5
	p-value	0.008	0.0001	0.0004	0.554
	1987 means	21.5 vs 26.8	4.23 vs 5.13	4.03 vs 7.43	50.9 vs 51.8
	p-value	0.016	0.0001	0.0001	0.814
TRT 6 vs 9		Regrowing to herbs vs regrowing to shrubs and herbs			
	1986 means	24.0 vs 22.7	3.89 vs 3.89	3.80 vs 3.64	62.2 vs 58.4
	p-value	0.344	0.981	0.61	0.232
	1987 means	23.8 vs 23.1	5.18 vs 4.63	6.78 vs 5.18	45.6 vs 49.8
	p-value	0.725	0.0001	0.017	0.282
TRT 5 vs 8		25% shrubs and no herbs vs no shrubs and 25% herbs			
	1986 means	21.8 vs 22.9	3.75 vs 3.85	3.2 vs 3.53	58.7 vs 59.7
	p-value	0.43	0.175	0.307	0.75
	1987 means	21.5 vs 23.0	4.85 vs 5.06	5.45 vs 6.28	44.0 vs 44.9
	p-value	0.463	0.049	0.178	0.809

Trees damaged by the late growing season frost or other agents in 1986 lost an average of 23.9 percent of their 1986 height increment gain (based on where 1987 growth started) or 2.2 cm of the 9.2 cm mean height increment. Mean height loss of frost damaged trees was not different among treatments ($p=0.673$). In 1987, height increment of frost damaged trees was 1.67 cm compared to 1.88 cm for undamaged trees. Mean 1987 height increment of both damaged and undamaged trees combined was 1.73 cm, and there was no difference among treatments ($p=0.365$) (Table 1.4).

Pine growth

At the time of planting, mean height, diameter, D2H, and height:diameter ratio of pine were 9.9 cm, 2.60 mm, 0.54 cm^3, and 30.5, respectively, and there were no significant differences among treatments ($p>0.05$) (Table 1.6). At the end of the first growing season, mean height, diameter, D2H, and height:diameter ratio had increased to 13.5 cm, 2.96 mm, 1.21 cm^3, and 45.5, respectively. There were still no differences between individual treatment means at the 0.05 probability level; however the no removal TRT 2 (100%S 100%H NSD) had significantly lower total height ($p=0.04$), diameter ($p=0.018$), and D2H ($p=0.02$) when contrasted with all treatments with partial or total vegetation removal (Table 1.7).

At the end of the second growing season, pine diameter ($p=0.0004$) and D2H ($p=0.003$) are clearly less in the no removal TRT 2 than than total removal TRT 14 (0%S 0%H NSD) (Table 1.7). Diameter increment in TRT 2 was only 33.3% of that in TRT 14 in 1987 (Table 1.6). Once again, there was strong evidence that diameter and D2H were smaller in TRT 2 than in all removal treatments combined ($p=0.0006$). Although trees in the no removal TRT 2 were the shortest (Table 1.6), there were no significant differences in height increment or total height (0.05 probability level) among treatments after the 1987 growing season (Table 1.6) or between TRT 2 and all other treatments combined (Table 1.7). Trees in the mechanically scarified TRT 12 (0%S 0%H SD) had significantly lower height:diameter ratios than all other treatments except the total removal TRT 14.

Within a competition-free environment, the exposure of mineral soil had neither a positive nor a negative impact on pine growth (Table 1.7). Although the pine trees in the herbs only TRT 7 (0%S 100%H NSD) were similar in size to those in TRT 10 (1 Removal NSD) where both shrubs and herbs were regrowing (Table 6), the pine trees in TRT 10, like the spruce trees in TRT 9 (1 Removal NSD), did not appear to be performing as well as those in the herbs only TRT 7.

Table 1.6 Lodgepole pine mean height, height increment, diameter, diameter increment, D2H, and height:diameter ratio in different shrub and herb reduction treatments at the time of planting (spring 1986), after one growing season (fall 1986), and at the end of the second growing season (fall 1987).

	SHRUB AND HERB REDUCTION TREATMENTS						ANOVA RESULTS	
	TRT 2 100%S 100%H NSD	TRT 14 0%S 0%H NSD	TRT 12 0%S 0%H SD	TRT 10 1 REMOVAL NSD	TRT 7 0%S 100%H NSD	TRT 4 50%S 50%H NSD	p-value	STANDARD ERROR
HEIGHT (cm)								
at planting	7.7	8.4	7.0	7.9	8.4	8.2	0.145	0.37
fall 1986	12.3	14.0	12.8	13.6	14.6	13.4	0.132	0.57
fall 1987	13.9	15.9	14.7	15.8	16.7	15.9	0.31	0.84
ANNUAL HEIGHT INCREMENT (cm)								
fall 1986	4.5	5.6	5.8	5.8	6.1	5.2	0.325	0.50
fall 1987	1.9	2.2	2.1	2.1	2.5	2.4	0.96	0.47
DIAMETER (mm)								
at planting	2.60	2.60	2.60	2.60	2.60	2.60	--	--
fall 1986	2.87	2.94	2.96	2.99	3.04	2.98	0.413	0.06
fall 1987	3.31	4.22	4.24	3.70	3.96	3.78	0.003	0.12
ANNUAL DIAMETER INCREMENT (mm)								
fall 1986	0.27	0.34	0.36	0.39	0.43	0.38	0.451	0.05
fall 1987	0.42	1.26	1.28	0.69	0.92	0.82	0.011	0.14
D2H (cm)								
at planting	0.52	0.56	0.47	0.53	0.58	0.56	0.159	0.03
fall 1986	1.02	1.24	1.14	1.26	1.36	1.21	0.10	0.07
fall 1987	1.59	3.10	2.81	2.28	2.75	2.43	0.031	0.46
HEIGHT:DIAMETER RATIO (cm)								
at planting	29.6	32.1	26.9	30.4	32.4	31.6	0.139	1.39
fall 1986	42.9	47.8	43.4	45.9	48.2	45.0	0.324	1.89
fall 1987	42.0	37.6	35.1	42.9	42.3	42.1	0.026	1.57

Table 1.7 Lodgepole pine planned contrasts.

CONTRAST		TOTAL HEIGHT	DIAMETER	D2H	HEIGHT DIAMETER RATIO
TRT 2 vs 4 7 10 12 14		No shrub and herb removal vs some removal			
	1986 means	12.3 vs 13.7	2.87 vs 2.98	1.02 vs 1.24	42.9 vs 46.1
	p-value	0.04	0.018	0.02	0.161
	1987 means	13.9 vs 15.8	3.31 vs 3.98	1.59 vs 2.67	42.0 vs 40.0
	p-value	0.066	0.0006	0.004	0.268
TRT 14 vs 4 7 10		Total shrub and herb removal vs some removal			
	1986 means	14.0 vs 13.9	2.94 vs 3.0	1.24 vs 1.28	47.8 vs 46.4
	p-value	0.567	0.448	0.966	0.325
	1987 means	15.9 vs 16.1	4.22 vs 3.81	3.1 vs 2.49	37.6 vs 42.4
	p-value	0.913	0.059	0.104	0.117
TRT 12 vs 14		No competition: soil disturbance vs no soil disturbance			
	1986 means	12.8 vs 14.0	2.96 vs 2.94	1.14 vs 1.24	43.4 vs 47.8
	p-value	0.159	0.883	0.351	0.131
	1987 means	14.7 vs 15.9	4.24 vs 4.22	2.81 vs 3.1	35.1 vs 37.6
	p-value	0.357	0.899	0.46	0.283
TRT 2 vs 14		No shrub and herb removal vs total removal			
	1986 means	12.3 vs 14.0	2.87 vs 2.94	1.02 vs 1.24	42.9 vs 47.8
	p-value	0.053	0.34	0.062	0.098
	1987 means	13.9 vs 15.9	3.31 vs 4.22	1.59 vs 3.1	42.0 vs 37.6
	p-value	0.126	0.0004	0.003	0.074
TRT 7 vs 10		Regrowing to herbs vs regrowing to shrubs and herbs			
	1986 means	14.6 vs 13.6	3.04 vs 2.99	1.36 vs 1.26	48.2 vs 45.9
	p-value	0.339	0.578	0.363	0.409
	1987 means	16.7 vs 15.8	3.96 vs 3.7	2.75 vs 2.28	42.3 vs 42.9
	p-value	0.517	0.162	0.237	0.817

DISCUSSION

Effect of Shrub and Herb Reduction Treatments on Conifer Survival and Growth

The study results indicate that after two growing seasons the presence of shrubs and herbs has had a negative impact on survival and growth of spruce and pine. The natural densities of shrubs and herbs found on the study area depress conifer survival, but complete removal of associated vegetation is apparently not necessary to attain excellent survival rates after two years. Survival exceeded 97 percent in all but one of the vegetation removal treatments, but averaged 82-84 percent where shrubs and herbs were undisturbed (Tables 1.1 and 1.3). While this survival rate in the undisturbed shrub/herb community is still good, survival may decrease dramatically in the future. Eis and Craigdallie (1983) reported 95, 49, and 6 percent survival of white spruce (*Picea glauca* (Moench) Voss) after 1, 3, and 5 years of growth in undisturbed vegetation in Sub-boreal forests.

Seedling growth, more so than survival, responded to varying levels of shrub and herb interference. In both species, tree diameter was the most responsive growth measure to reductions in interfering vegetation. Mean diameter of seedlings growing without interference was 21.3 and 27.5 percent larger for spruce and pine, respectively, than for seedlings in undisturbed vegetation. Diameter growth of both species decreased incrementally with decreasing levels of interfering vegetation.

Spruce height growth appeared to respond to complete removal of interference but not to partial removal. Hellum (1967) and Sutton (1975) found significant increases in height growth of white spruce after control of interfering vegetation. Vyse (1981) in a survey of 90 interior spruce plantations in central B.C., where interfering vegetation was always present, found no differences in spruce height growth by competing vegetation class.

Although confounding factors could explain the lack of response to levels of interfering vegetation in the plantation survey, these results, along with the controlled experiments and the current study, suggest that spruce height growth will only respond to nearly complete control of interfering vegetation. Pine height was the shortest in the undisturbed brush community, but height was not statistically different among treatments. Early pine height growth may not be a good indicator of interference from associated vegetation. There is very little literature available on the response of pine to different levels of interfering vegetation (Ross and Walstad 1986).

The lack of a strong height growth response to levels of interference in either spruce or pine may be explained by source-sink physiology (Lanner 1985). Lanner considers carbohydrate allocation to the new shoot to be the strongest sink after developing cones (not an issue with planted seedlings). Because height growth occurs early in the season when carbohydrate reserves are high, a leading shoot can draw the necessary carbohydrate even when the tree is under high competition stress. Radial growth, on the other hand, depends more on current photsynthetic output, and so will be influenced more by resource limitations brought about by interfering vegetation. Studies of other conifer species (Zutter *et al.* 1986, Lanini and Radosevich 1986, Wurtz and Zasada 1986, Elliott and White 1987) consistently show that diameter growth is more responsive to varying levels of interference than height growth.

By the end of the second growing season, diameter growth of both species (especially spruce) was depressed where shrubs and herbs were allowed to regrow compared to where only herbs were growing (Tables 1.5 and 1.7). Since herb development in both treatments was similar by early in the second growing season, it appears that the presence of regrowing shrubs in addition to herbs has suppressed conifer diameter growth. Regrowing shrubs had not overtopped conifers (see chapter 3) by the end of the second season, suggesting that below-ground interference may be contributing to seedling growth reductions.

Resource Availability and Microclimate

Survival and growth performance of planted spruce and pine in the ESSF zone was apparently influenced by the harsh ESSF zone climate, interference from associated vegetation, or interactions between the climate and vegetation. At this high elevation site, growth rates of both species in all treatments, including total interference removal, can not be considered high. However, the results show that both growth and survival of the two species is affected by the level of shrub and herb interference, and that the impact is negative. Interfering vegetation can negatively affect conifer seedling performance by competing for resources (water, light, CO_2, nutrients) or by modifying the abiotic environment.

Competition for soil moisture has been identified as one of the major reasons for poor conifer performance in low elevation Pacific Northwest forests where summer drought limits forest productivity (Walstad and Kuch 1987). Moisture stress reduction by removal of competition has also resulted in dramatic growth improvement of white fir (*Abies concolor (*Gord & Glend.) Lindl.) in high-elevation California forests (Conard and Radosevich 1982). However, northern forests or forests near timberline only rarely become dry enough to restrict growth of trees because of their low water deficits (Larson 1980, Tranquillini 1979).

At the high-elevation ESSF study site there was no evidence that competition for water was the reason for poor survival or growth of conifers. The presence of shrubs and herbs did not decrease soil water content during the snow-free period. In fact, the driest soil samples often came from plots with complete vegetation control, presumably because of higher surface evaporation. Soil water potential was never lower than -0.01 MPa (42% water by weight), indicating ample soil moisture throughout the growing season. In some instances, soils were at saturated levels (>81.5% water by weight) in the middle of the growing season (Figure 1.10). Spruce xylem water potential, an estimate of water stress, also did not vary between complete vegetation removal and no removal during either midday or predawn measurements (Figure 1.11). Adequate water supplies were probably maintained because evapotranspirative losses were low during the short, cool growing season, and because supplemental water was supplied to the site through downslope flow of seepage water from melting snow and rainfall at higher elevations.

Air temperature is one of the primary environmental limitations to photosynthesis and carbon gain in conifers (Kramer and Kozlowski 1979). Both low and high air temperatures can restrict photosynthesis (Larcher 1983). The optimum air temperature range for conifer photosynthesis is 10^{o} - 25^{o}C; high temperature begins to limit photosynthesis above 35^{o} - 42^{o}C (Larcher 1983). There is little evidence that high temperature impaired seedling growth at the ESSF study site. The minimum/maximum air temperature data (Figures 1.8 and 1.9) show that daytime temperatures generally were within the optimum range for photosynthesis during the growing season. Maximum air temperatures were approximately 25^{o} - 30^{o}C, except at 2 cm when vegetation was absent, where maximum temperature was 35^{o} - 40^{o}C. Maximum air temperatures within the crown of both spruce and pine (2-30 cm above the ground) only occasionally reached limiting temperatures and never approached levels that would be considered lethal (e.g. >46^{o}C for spruce (Seidel 1986)).

Cool night temperatures may have a larger effect on spruce growth than day-time temperatures. Hellmers *et al.* (1970) showed that low night-time temperatures can dramatically decrease Engelmann spruce diameter and height growth. Under controlled conditions, extreme fluctuations in day/night temperature (e.g. 25^{o}C/3^{o}C or 35^{o}C/7^{o}C) were less favourable to growth than constant temperatures. Optimum growth occured at 19^{o}C day and 23^{o}C night temperatures. In that laboratory study, a 15^{o}C/3^{o}C day/night temperature regime resulted in diameter and height growth that was about 10% and 1%, respectively, of the growth at optimum temperatures. At the ESSF study site, minimum air temperatures at both 2 cm and 20 cm above the ground surface were in the -1^{o} to $10^{o}C$ range throughout the growing season (Figures 1.8 and 1.9). There is no evidence in the literature that the range of night temperatures recorded at the study site should limit pine leaf conductance and dry weight production (Cochran 1972, Kaufmann 1976 and 1982, Running 1976).

Removal of interfering vegetation did not raise minimum air temperature to the extent necessary to significantly improve growth of spruce at the ESSF site. However, damage to spruce caused by a mid-August 1986 frost (pine was not damaged) was considerably less in treatments without interference (7.0%) than under the undisturbed shrub and herb canopy (15.7%) (Table 1.2). The severity of damage was least where mineral soil was exposed, possibly because heat radiating from the surface during the night was greatest on mineral soil and least where shrubs and herbs insulated the ground surface (Cochran 1969, Menzies and Chavasse 1982). Frosts were just as frequent and of the same intensity during the 1987 growing season as in 1986, yet less than 3 percent of all spruce trees were damaged by frost compared to 11.5 percent in 1986. Planted spruce were apparently better acclimated to the environment by the second year. High incidence of frost damage is common in young white spruce plantations (Clements *et al.* 1972, Harding 1986), but growth is rarely impeded the year after damage, nor is there any long-term impact on form (Nienstaedt 1985). In the ESSF study, although frost damaged trees lost, on average, 23.9 percent of their 1986 increment gain, growth of frost damaged trees was not significantly different than that of undamaged trees the year after damage occurred.

Many researchers consider soil temperature to be one of the most important factors limiting regeneration performance in northern forests (Endean 1972, Tranquillini 1979, Soderstrom 1981, McMinn 1982). Low soil temperatures can delay budburst, reduce root or shoot growth, increase water flow resistance into the roots, increase water stress, and decrease photosynthesis rates in conifers (Kaufmann 1975, Tranquillini 1979, Running and Reid 1980, Lopushinsky and Kaufmann 1984, Goldstein *et al.* 1985).

Resistance to water movement increases dramatically in Engelmann spruce at temperatures below 5^{o} - $7^{o}C$ (Kaufmann 1975) and in pine below $6^{o}C$ (Running and Reid 1980). At the ESSF study site, xylem water potential varied little in the presence or absence of other plants over the growing season, suggesting soil temperatures were not sufficiently different between treatments to affect water uptake. However, low soil temperatures may explain why the trees were under moderate water stress. Soil water potentials were never less than -0.01 MPa which should be adequate for maximum transpiration rates in both spruce and pine (Lopushinsky and Klock 1974). Yet, mid-day xylem water potential of spruce during the growing season was generally between -1.4 and -1.6 MPa, recovering to -0.5 to -0.8 MPa at night. Under controlled conditions, photosynthesis in white spruce (Brix 1979) and amabilis fir (*Abies amabilis* (Dougl.) Forbes) (Teskey *et al.* 1984) was unaffected at water potentials less negative than -1.2 and -1.5 MPa, respectively. White spruce stomatal closure occurs at -1.7 to -1.8 MPa (Goldstein 1981, in Goldstein *et al.* 1985). Pine photosynthesis decreases at xylem water potentials below -0.66 MPa (Brix 1979) and complete stomatal closure occurs between -1.46 and -2.00 MPa (Lopushinsky 1969, Fetcher 1976, Running 1980). Although photosynthesis was not directly measured in the current study, the data suggest that both spruce and pine photosynthesis may be restricted by water stress even though water supplies were adequate, and that, most likely, the stress occurred as a result of restricted water uptake because of cold soils. This conclusion is further supported by the fact that the highest xylem water potentials were recorded immediately after snow melt when soils were coldest. Poor water uptake could also be explained by poor seedling root development, which again could be caused by low soil temperatures.

Low soil temperatures may restrict carbon gain in young ESSF seedlings, by inducing water stress, regardless of the presence or absense of other vegetation. However, soil temperature at a depth of 10 cm was increased from an average of 6^{o} to $8^{o}C$ under undisturbed vegetation, to between 10^{o} and $15^{o}C$ in the absense of vegetation, and a further 1^{o} - $2^{o}C$ when mineral soil was exposed. After two growing seasons there was no evidence that the differences in soil temperature affected spruce water uptake, but both spruce and pine seedlings from treatments with the warmest soils did have significantly greater diameter growth than those from colder soils. Seedlings growing in warmer soils should have superior root growth and more easily take up water and nutrients than trees in cooler soils (Kramer 1983), and eventually show superior growth over seedlings in colder soils.

Adequate levels of light are crucial for tree seedling vigour and growth. Light levels in the study were clearly lower at ground level in undisturbed shrub and herb plots than in either the one removal treatment (where vegetation is regrowing) or the total removal treatment. In greenhouse experiments, maximum rates of net photosynthesis for pine are attained at 380 W m^{-2} (multiply by 4 to 5 for $\mu E\ s^{-1}\ m^{-2}$) with a rapid decline in photosynthesis below 200 W m^{-2}; the light compensation point was between 6 and 10 W m^{-2} (Dykstra 1974). Kaufmann (1982) found that conductance of both spruce and pine gradually increased as photosynthetic photon flux density (PPFD) increased. Using data from Kaufmann's (1982) study, I estimate that conductance of spruce and pine in the undisturbed shrub/herb community was approximately 40 percent, respectively, of that found at full light. In one cut treatments, estimated conductance was approximately 75 percent of that found at full light for both species. A 60 percent reduction in conductance for seedlings under an undisturbed shrub and herb canopy should result in a significant decrease in photosynthetic capacity relative to seedlings growing where shrubs and herbs have been totally removed.

Neither soil nor foliar nutrient levels were measured at the ESSF study site. Low nutrient levels, especially nitrogen, are considered a limitation to growth of northern forests (Larsen 1980). Improved nutrient conditions were cited by Sutton (1975) as one reason for increased white spruce growth after removal of competing vegetation. Burdett *et al.* (1984) considered nutrient limitations to be the main factor limiting shoot growth of container spruce stock in British Columbia, but their study did not take into account interference from other vegetation. David (1987), studied nutrient availability in different-aged clearcuts at ESSF sites near the current study site. He found no nitrogen limitations for spruce or subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) for up to 11 years after harvesting (oldest age examined). Nonetheless, improved nutrient conditions should not be excluded as a possible reason for superior growth of both spruce and pine with decreasing levels of shrub and herb interference at the ESSF study site. Certainly organic matter breakdown, nitrogen mineralization, tree root growth, and nutrient and water uptake should be enhanced at the warmer soil temperatures associated with total vegetation control.

Under field conditions it is difficult to determine with certainty which environmental factors are most important in causing growth and survival of spruce and pine to be improved at lower levels of interfering vegetation. Air and soil temperature, light levels, and water and nutrient availability, are all interrelated. Two year results from this study suggest that low soil and air temperatures and low light levels may be the most important primary factors inhibiting conifer seedling performance beneath the undisturbed ESSF shrub/herb community. Light levels beneath the undisturbed vegetation community were low enough to impair photosynthesis, and may have been responsible for the marked reduction in survival and growth at the highest levels of vegetation interference. Removal of interfering vegetation had little effect on air temperatures, but increased soil temperatures above critical thresholds that may limit conifer root development, water uptake, or photosynthesis. Although it was not possible to detect any improvement in water uptake, there was a significant increase in conifer diameter growth on treatments with higher soil temperatures. Increased growth could be explained by more lengthy periods of maximum conductance. In warmer soils, conductance levels may be maintained at higher rates for longer periods than in cold soils, even though midday xylem water potentials were similar. Alternatively, the growth response could be due to a combination of increased root growth and nutrient availability at the higher soil temperatures.

Neighbourhood Study

Chapter 2

INTRODUCTION

Most experimental studies of interspecific interference have focused on the mean performance of plants in relation to density. In such experiments, differences in mean plant performance can obscure important variation in individual plant response (Weiner 1984). Neighbourhood studies focus on the response of an individual plant rather than the mean population response and examine plant performance as a function of the number, proximity, and abundance of the neighbouring species present (Mack and Harper 1977, Goldberg and Werner 1983). Most neighbourhood experiments have studied herbaceous species (Mack and Harper 1977, Waller 1981, Liddle *et al.* 1982, Weiner 1982, Watkinson *et al.* 1983, Matlack and Harper 1986, Firbank and Watkinson 1987, Goldberg 1987). Only a few studies have addressed survival and growth of newly planted conifers on an individual basis (Carter *et al.* 1984, Brand 1986, Wagner and Radosevich 1987). In this paper I analyse the survival and growth performance of planted Engelmann spruce (*Picea engelmannii* Parry) and lodgepole pine (*Pinus contorta* var. *contorta* Dougl.) seedlings with respect to the abundance, proximity, and species of neighbours.

Plants, because they are sedentary, experience the environment only within their immediate fixed surroundings, or neighbourhoods (Antonovics and Levin 1980). The presence of a plant changes the environment of its neighbours (Harper 1977). Neighbouring plants may compete for resources or influence the physical environment of their immediate associates. In newly planted forest clearcuts each tree faces a distinct micro-environment with respect to resource availability and array of neighbours. A comprehensive model that predicts individual tree performance in natural settings must address heterogeneity in the physical environment, the genetic variability among individuals, and the presence of neighbours. In this study, the neighbourhood approach was used to construct a model to predict the effects of neighbour proximity and abundance on performance of individual conifers in a relatively homogenous natural setting. Chapter 1 examined how varying amounts of competiting vegetation affected resource availability and the abiotic environment for planted spruce and pine seedlings.

Interference from neighbours may be one of the most important sources of local variation in conifer performance. Interference from other vegetation has been shown to limit both survival and growth of conifers (McMinn 1985, Brand 1986, Cole and Newton 1986, Elliott and White 1987, Walstad and Kuch 1987). Exclusion of competitors or early release often has resulted in substantial increases in either conifer survival or growth (Wilde *et al.* 1968, MacLean and Morgan 1983, Stewart *et al.* 1984, Walstad and Kuch 1987). Predictive models should be built in compartment fashion as individual variables and their interactions are assessed (Weiner 1982). The intent of this study was to begin model construction with the influence that neighbours have on conifer performance.

METHODS

A single study site was located in a 9 year old clearcut, at an elevation of 1550 m within the Engelmann Spruce - Subalpine fire (ESSF) zone of south-central B.C., approximately 25 km northeast of the town of Clearwater. The dominant plants were the four Ericaceous shrubs white-flowered rhododendron (*Rhododendron albiflorum* Hook.), black huckleberry (*Vaccinium membranaceum* Dougl.), oval-leaved huckleberry (*V. ovalifolium Smith.), and false azalea (Menziesia ferruginea* Smith.). Sitka valerian (*Valeriana sitchensis* Bong.), fireweed (pilobium angustifolium L.), and Indian hellebore (*Veratrum viride* Ait.) were the dominant herbs.

Engelmann spruce (hereafter called spruce) and lodgepole pine (hereafter called pine) were planted into an array of shrub and herb reduction treatments in the spring of 1986. As suggested by Goldberg and Werner (1983), areas with high densities of neighbours were selected and treatment plots were thinned to create an array of neighbour abundance and spatial distribution ranging from complete removal to the highest abundance of neighbours. Treatment plots were arranged in a randomized complete block design, with 3 blocks. For a full description of the study site and the shrub and herb reduction treatments see Chapter 1.

Individual sample trees were randomly selected from a representative subset of trees within each treatment plot. Neighbourhood plots were defined as 1.3 m radius areas centred around each conifer stem. A total of 110 neighbourhood plots were selected for each conifer species. Within each plot, the proximity and abundance of neighbours was recorded by taking extensive and intensive plant measurements using a modified version of the approach described by Wagner and Radosevich (1987) (Figure 2.1). Extensive measurements were percent cover of (1) all plants, (2) all herbs, (3) each shrub species, and (4) each of the 3 most abundant herb species (by the quadrant method of Herring and Pollack 1985). Each plant within the

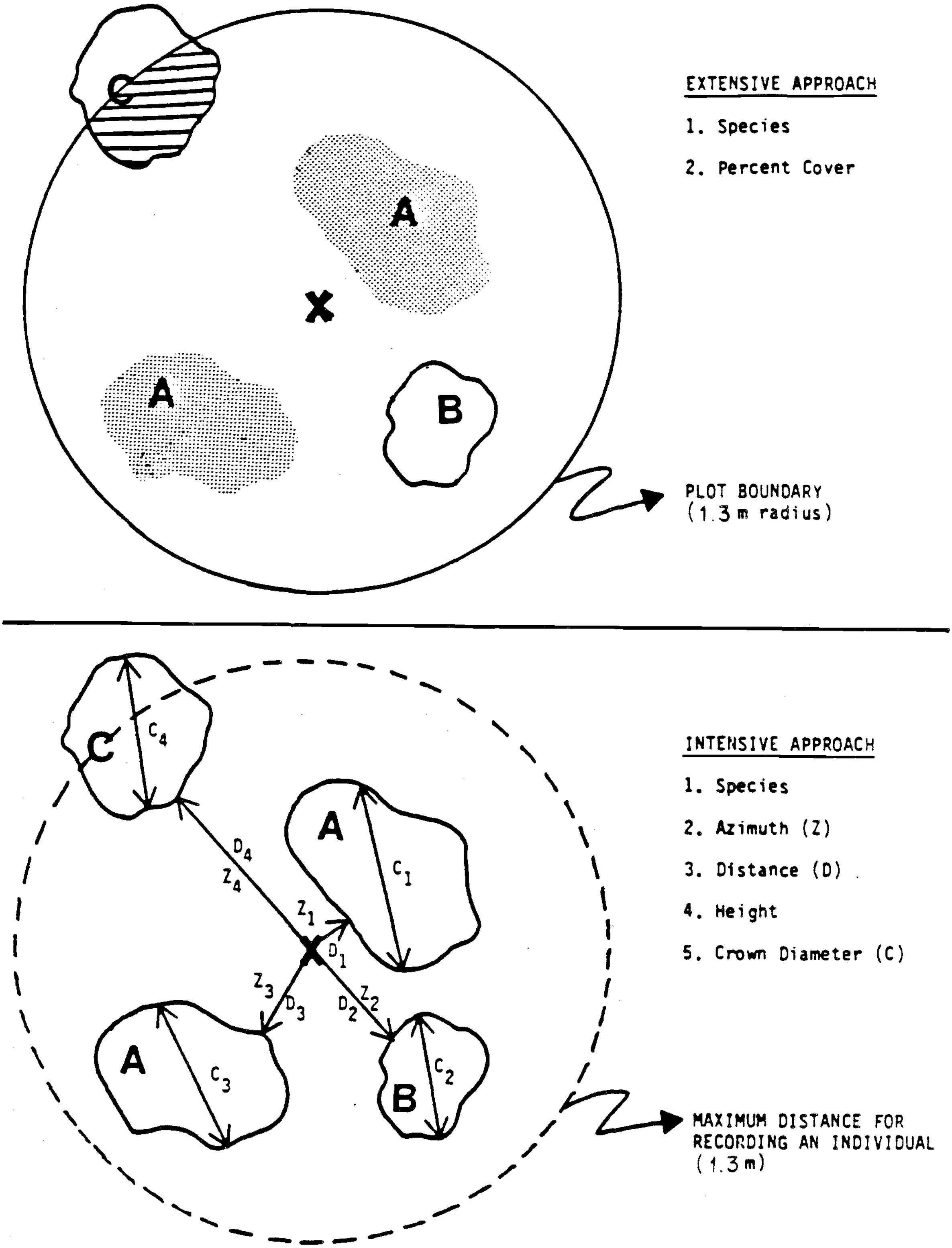

Figure 2.1 Comparision of extensive and intensive measures for quantifying the effect of local measures of interference from neighbours (modified from Wagner and Radosevich 1987).

neighbourhood plot was measured separately for the intensive approach. The azimuth and distance to the nearest crown edge of each neighbour was recorded from plot centre. Total height and crown diameter (based on 2 perpendicular measurements at mid-canopy) of each neighbour also were recorded. All measurements were were taken in the late summer after leaf extension and height growth of all plants was complete.

Conifer measurements taken in each neighbourhood plot included: (1) survival, (2) vigour, (3) diameter at 1 cm, (4) height, and (5) the number of buds, excluding the terminal bud (spruce only), on the current years leader. From these measures annual height and diameter increment, D2H (diameter squared x height), and the height:diameter ratio were calculated.

The following general information also was recorded for each neighbourhood plot: (1) percent slope, (2) aspect, (3) humus depth, and (4) percent mineral soil exposure.

The following variables were calculated to act as indices of the level of neighbourhood interference experienced by each sample tree:

1. percent cover indices (PC=percent cover):

PC1: percent cover of *Rhododendron albiflorium*

PC2: percent cover of *Menziesia ferrugina*

PC3: percent cover of *Vaccinium membranaceum*

PC4: percent cover of *Vaccinium ovalifolium*

PC5: percent cover of *Valeriana sitchensis*

PC6: percent cover of *Epilobium angustifolium*

PC7: percent cover of *Veratrum viride*

PC8: percent cover of all shrubs

PC9: percent cover of all herbs

PC10: percent cover of all plants

2. crown area indices (CA=3.1416(crown diameter/2)):

$\Sigma CA1_i$ to $\Sigma CA7_i$ for all individuals (i) of species 1 through 7 indicated above

CAS=crown area of all shrubs

CAH=crown area of all herbs

CASH=crown area of all shrubs and herbs

3. height indices (HT=height):

$\Sigma\, HT1_i$ to $\Sigma\, HT7_i$

HTS= HT_i all shrubs

HTH= HT_i all herbs

HTSH= HT_i all shrubs and herbs

4. distance indices (D=distance to the centre of the plant):

$\Sigma\, D1_i$ to $\Sigma\, D7_i$

where D=(c/2)-d

d=distance to the nearest crown edge

c=crown diameter

5. inverse distance indices:

$\Sigma\, ID1_i$ to $\Sigma\, ID7_i$ where $ID=1/D^2$

IDS= ID_i for all shrubs

IDH= ID_i for all herbs

IDSH= ID_i for all shrubs and herbs

6. crown area and height indicies:

$\Sigma\, CH1_i$ to $\Sigma\, CH7_i$ where CH=(CA)(HT)

CHS= CH_i for all shrubs

CHH= CH_i for all herbs

CHSH= CH_i for all shrubs and herbs

7. crown area and distance indices:

$\Sigma\, CD1_i$ to $\Sigma\, CD7_i$ where $CD=CA/D^2$

CDS= CD_i for all shrubs

CDH= CD_i for all herbs

CDSH= CD_i for all shrubs and herbs

8. height and distance indices:

   $\Sigma\ HD1_i$ to $\Sigma\ HD7_i$ where $HD=HT/D^2$

   HDS= HD_i for all shrubs

   HDH= HD_i for all herbs

   HDSH= HD_i for all shrubs and herbs

9. crown area, height, and distance indices:

   $\Sigma\ CHD1_i$ to $\Sigma\ CHD7_i$ where $CHD=(CA \times HT)/D^2$

   CHDS= CHD_i for all shrubs

   CHDH= CHD_i for all herbs

   CHDSH= CHD_i for all shrubs and herbs

All data were analysed on personal computers, using the Statistical Analysis System (SAS Institute 1985) programs. Results are based on second growing season data. Linear regression models were calculated for each measure of tree performance (dependent variable) and each interference index (independent variable). The intent was to select the most sensitive conifer growth variables and the most predictive interference indices. The selected growth variable and the set of predictive interference indices were then tested in multiple regression models using the Stepwise procedures in SAS.

RESULTS

Spruce

Spruce diameter and D2H were the most sensitive growth variables when regressed against individual measures of interference. All simple linear regressions on total height, height:diameter ratio, second growing season height and diameter increment, and number of buds on the leader produced a coefficient of determination (r^2) of 0.05 or less.

Regressions using the reciprocal of diameter or D2H resulted in models with a slightly higher r^2 than the untransformed variable (Table 2.1 and Figure 2.2), but did not improve the distribution of residuals. Other transformations of diameter or D2H were of no value in improving either r^2 or the residual distribution.

Extensive measures of interference were equal or better predictors of spruce performance than the intensive measures (Table 2.1). Total percent cover of all plants (PC10) was the best predictive index for diameter and D2H, followed by total shrub cover (PC2), and total cover of rhododendron (PC4) (Table 2.1). Of the many intensive measures of interference only two (CA1 and CDSH) predicted diameter and D2H nearly as well as the percent cover indices (Table 2.1).

The physical descriptors of the neighbourhood plots (percent slope, aspect, humus depth, and percent mineral soil exposure) were of no predictive value for any of the spruce growth variables. No regressions with two or fewer independent variables exceeded an R^2 of 0.05.

The Stepwise regression procedure selected a model for reciprocal diameter including total percent cover (PC10) and percent cover of all shrubs (PC8) from the interference indices listed in Table 2.1. Because these two independent variables are highly correlated, and the model accounted for only slightly more variation (R^2=0.27) than the single variable model with total percent cover (r^2=0.25), the equation is of questionable value. No multiple regression models were selected for the reciprocal of D2H.

In the early spring of 1987, 31.9 percent of all spruce trees were recorded as damaged by either a mid-August 1986 frost, or over-winter frost damage (see Chapter 1). Frost-damaged trees did not have significantly different ($p>0.10$) intercepts or slopes for reciprocal diameter or D2H than undamaged trees.

Pine

Pine diameter, D2H, and height:diameter ratio were the most sensitive growth variables when regressed against individual measures of interference. However, none of the interference indices accounted for more than 11 percent of the variation in pine growth. The greatest variation in diameter was explained by the intensive index CDSH (CA/D^2 - summed for all shrubs and herbs) with r^2 0.10 (Table 2.2 and Figure 2.4). Total percent cover of all shrubs (PC8) and percent cover of rhododendron (PC1), both accounted for 8 percent of diameter variation. Pine D2H was predicted best by either the percent cover of all shrubs (r^2=0.08) or percent cover of all rhododendron (r^2=0.08) (Table 2.2 and Figure 2.5). Total percent cover of all plants accounted for only 4 percent of the variation in diameter and had no predictive value for D2H.

Pine height:diameter ratio, unlike that of spruce, was significantly correlated with percent cover of Sitka valerian (r^2=0.11), the sum of the height of all herbs (r^2=0.10), total percent cover (r^2=0.09), and the intensive index CDSH (r^2=0.04) (Table 2.2 and Figure 2.6).

Transformations of diameter, D2H, and height:diameter ratio did not improve any of the models. None of the physical descriptors of the neighbourhood plots (percent slope, aspect, humus depth, and percent mineral soil exposure) had regressions with two or fewer independent variables exceeding a R^2 of 0.05.

The stepwise regression procedure selected a single multiple variable model for predicting pine diameter. The model included the interference indices CDSH and PC1 (percent cover of rhododendron), but had a R^2 of 0.12, accounting for just 1 percent more variation than the single variable model containing only CDSH.

Table 2.1 Comparision of linear and reciprocal models of several measures of interference for diameter and D2H of individual spruce trees.

MEASURE OF INTERFERENCE	DIAMETER				D2H			
	Linear Model		Reciprocal Model		Linear Model		Reciprocal Model	
	r^2	p-value	r^2	p-value	r^2	p-value	r^2	p-value
Percent cover of all plants (PC10)	0.22	0.0001	0.25	0.0001	0.14	0.0001	0.16	0.0001
Percent cover of all shrubs (PC8)	0.19	0.0001	0.22	0.0001	0.09	0.002	0.14	0.0001
Percent cover of rhododendron (PC1)	0.18	0.0001	0.21	0.0001	0.09	0.002	0.14	0.0001
Crown area of rhododendron (CA1)	0.15	0.001	0.17	0.0001	0.08	0.004	0.12	0.0001
Crown area/D^2; summed for all shrubs and herbs (CDSH)	0.18	0.0001	0.20	0.0001	0.08	0.003	0.11	0.0006

Table 2.2 Linear models of several measures of interference for diameter, D2H, and height:diameter ratio of individual pine trees.

MEASURE OF INTERFERENCE	DIAMETER		D2H		HEIGHT:DIAMETER RATIO	
	r^2	p-value	r^2	p-value	r^2	p-value
Percent cover of all plants (PC10)	0.04	0.043	-	0.149	0.09	0.002
Percent cover of all shrubs (PC8)	0.08	0.005	0.08	0.005	-	0.398
Percent cover of rhododendron (PC1)	0.08	0.004	0.08	0.005	-	0.338
Percent cover of Sitka valeriana (PC5)	-	0.814	-	0.557	0.11	0.0007
Sum of the heights of all herbs (HTH)	-	0.75	-	0.656	0.10	0.001
Crown area/D^2; summed for all shrubs and herbs (CDSH)	0.10	0.001	0.05	0.02	0.04	0.039

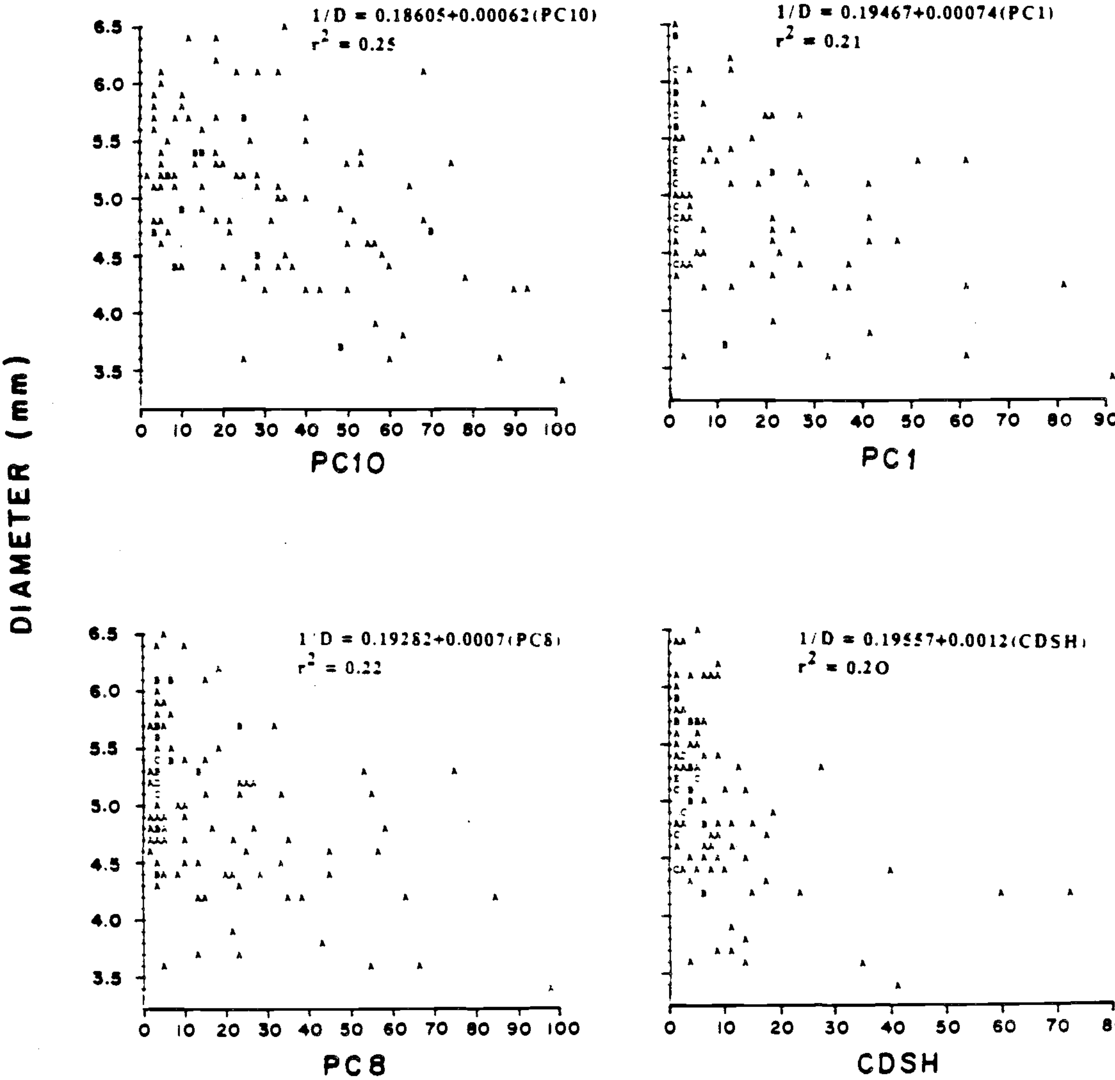

Figure 2.2 Influence of various measures of interference on spruce diameter (PC10=percent cover of all plants, PC1=percent cover of rhododendron, PC8=percent cover of all shrubs, and CDSH=crown area divided by distance summed for all shrubs and herbs).

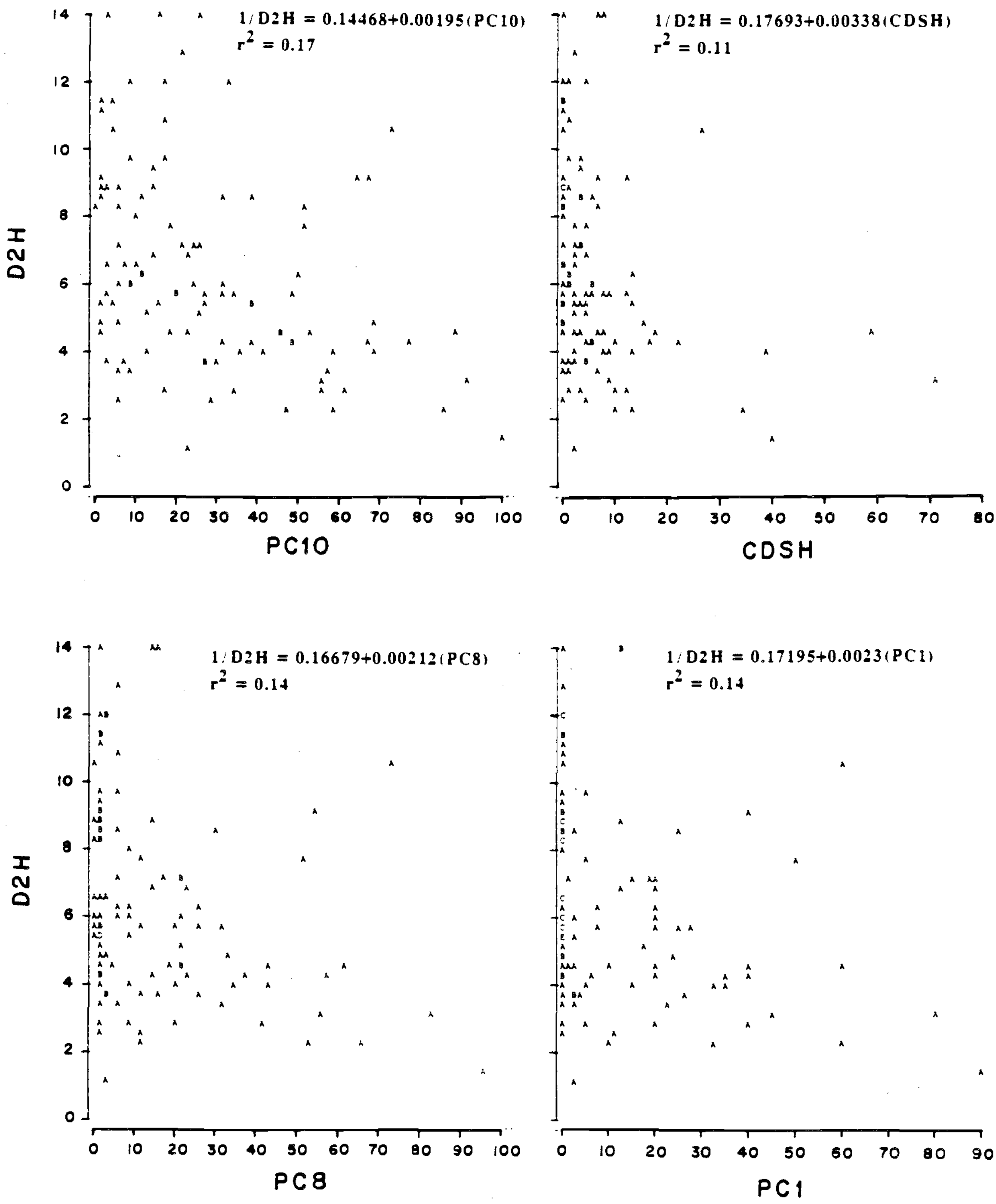

Figure 2.3 Influence of various measures of interference on spruce D2H (PC10=percent cover of all plants, PC1=percent cover of rhododendron, PC8=percent cover of all shrubs, and CDSH=crown area divided by distance summed for all shrubs and herbs).

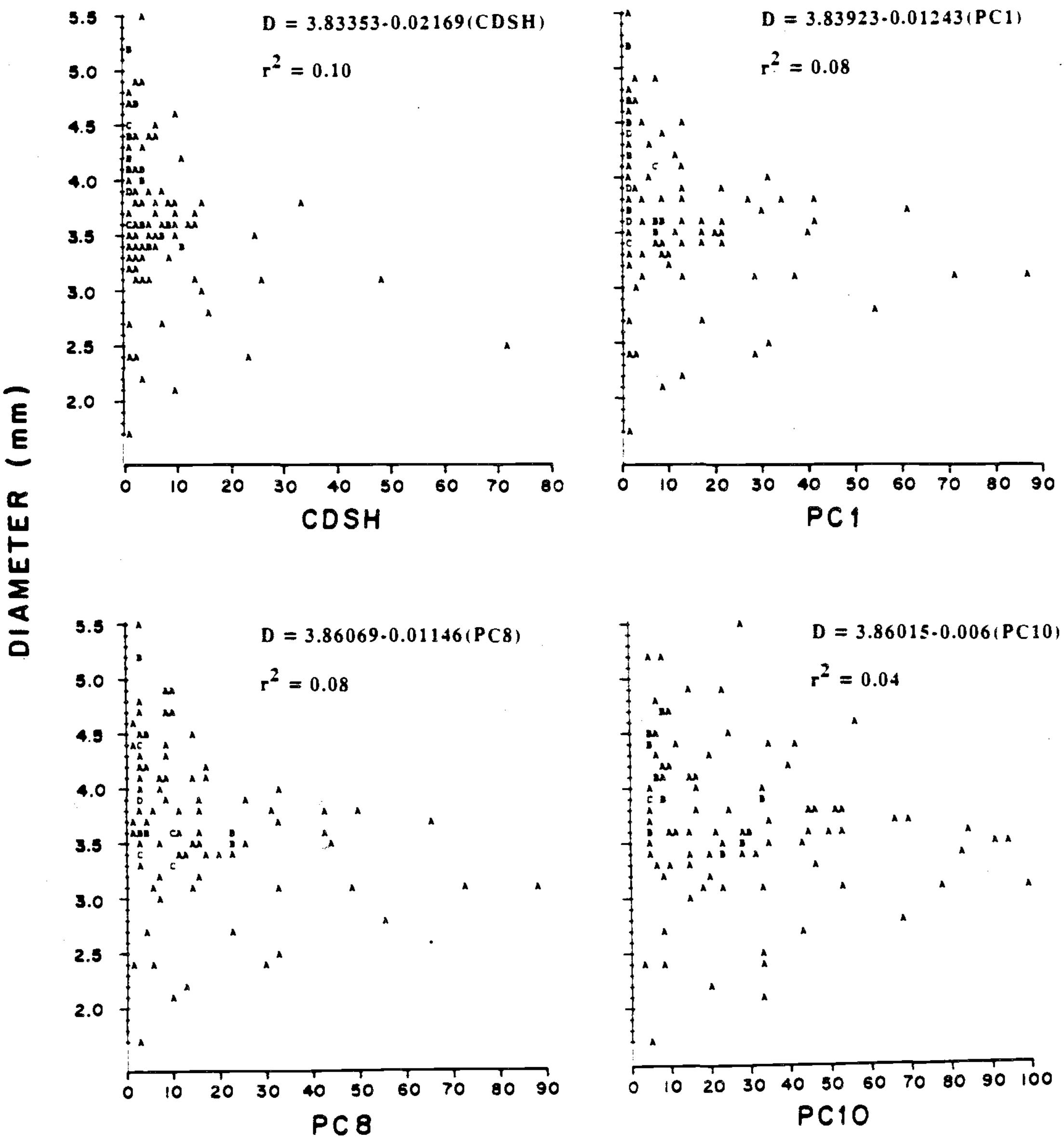

Figure 2.4 Influence of various measures of interference on pine diameter (PC10=percent cover of all plants, PC1=percent cover of rhododendron, PC8=percent cover of all shrubs, and CDSH=crown area divided by distance summed for all shrubs and herbs).

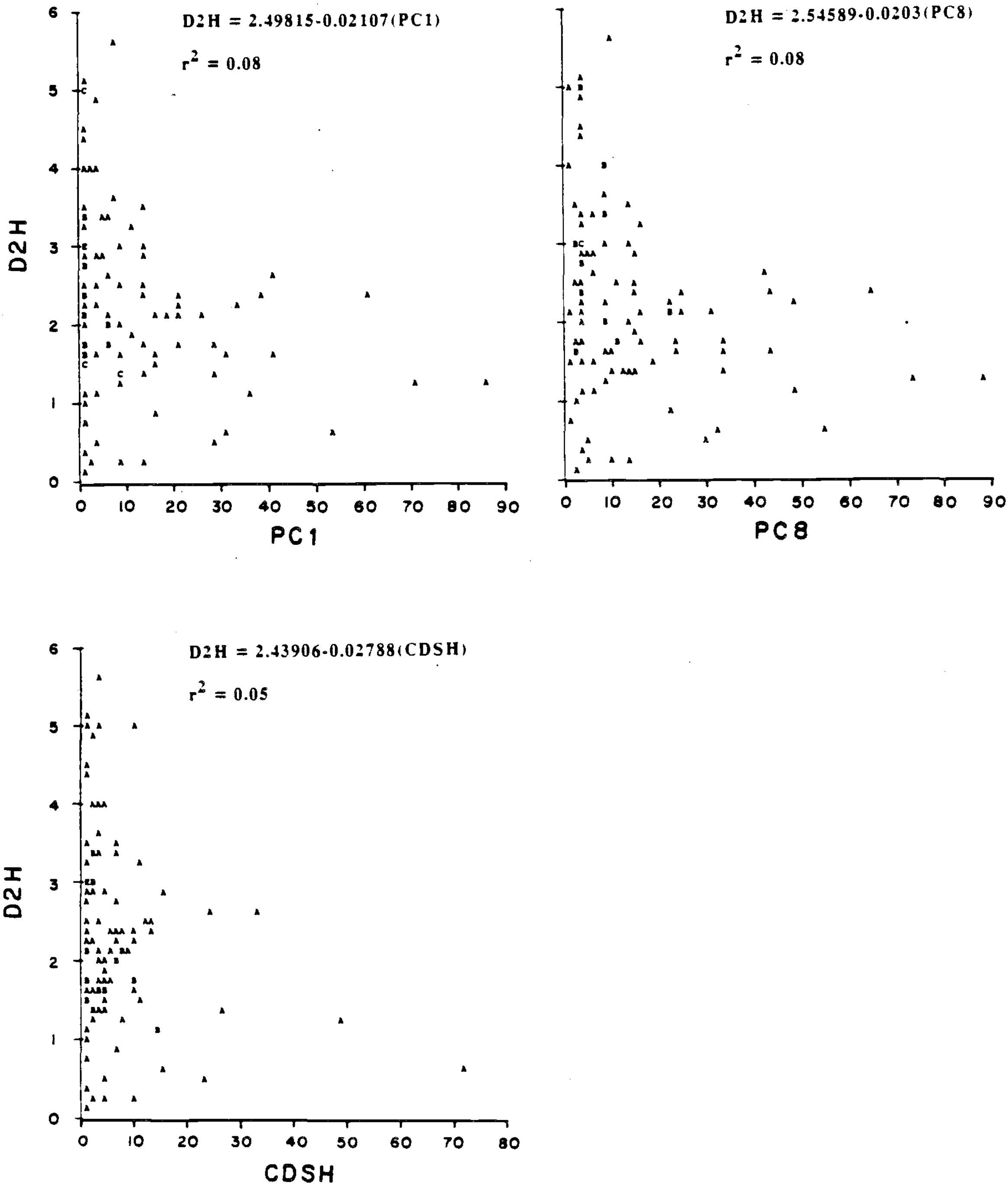

Figure 2.5 Influence of various measures of interference on pine D2H (PC1=percent cover of rhododendron, PC8=percent cover of all shrubs, and CDSH=crown area divided by distance summed for all shrubs and herbs).

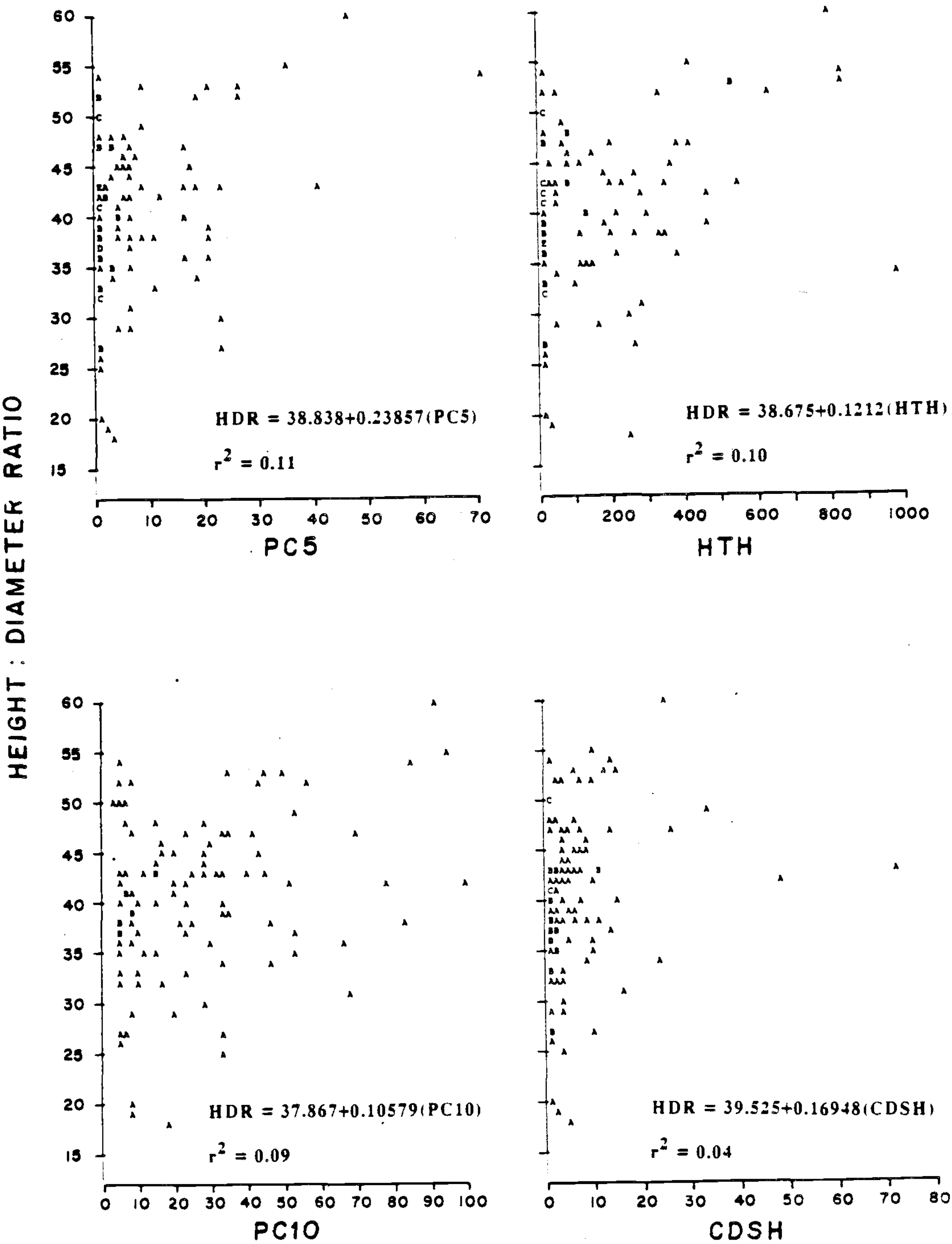

Figure 2.6 Influence of various measures of interference on pine height:diameter ratio (PC10=percent cover of all plants, PC5=percent cover of Sitka valerian, HTH=summed height of all herbs, and CDSH=crown area divided by distance summed for all shrubs and herbs).

DISCUSSION

The results clearly indicate that spruce and pine seedling growth was inhibited by the presence of neighbours. Relationships between individual seedling performance and measures of neighbourhood interference were always negative (Figures 2.2 to 2.6). Conifer seedling diameter, D2H, and height:diameter ratio were the most sensitive growth descriptors to measures of proximity and abundance of neighbours. After two growing seasons up to 25 percent of the variation in seedling growth was attributable to measures of neighbourhood interference (Tables 2.1 and 2.2). The regression models produced in this study have similar coefficients of determination to those published by other researchers studying the relationship between neighbourhood interference and individual plant growth (Waller 1981, Liddle *et al.* 1982, Weiner 1984, Firbank and Watkinson 1987, Goldberg 1987).

Interference indices derived from visual estimates of percent vegetation cover were consistently the best predictors of seedling growth. Of the many intensive measures of interference tested (see methods), few were as predictive as the simple percent cover estimates. The best of these indices usually included crown area, which should produce a similar quantity to percent cover, but is much more time-consuming to measure. Wagner and Radosevich (1987) also found that estimates of percent cover explained the greatest variation in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedling growth. An estimate of percent cover can be viewed as an integrative measure of neighbourhood interference, and because of its ease of measurement, it has practical utility for making vegetation management decisions.

An underlying concept of neighbourhood studies is that closer neighbours have a greater competitive effect than more distant neighbours (Mack and Harper 1977, Weiner 1982 and 1984). In the current study, even though one of the three intensive indices selected was distance-dependent, distance-dependent indicies generally were not as predictive as distance-independent indices. However, since none of the intensive indices explained much of the variation in seedling growth, it is premature to make distinctions between distance-dependent and distance-independent indices or to draw any conclusions about the importance of neighbour distance on conifer growth after two growing seasons.

Yield density theory predicts that individual seedling growth follows a negative exponental function in which growth is highest at low levels of interference, then decreases rapidly as interference increases until a threshold point where increasing amounts of interference have little effect on seedling performance (Goldberg and Werner 1983) (Fig. 2.7). After two growing seasons at the ESSF study site, individual seedling growth was inversely related to the measures of interference and the relationship tended toward a negative exponential function. However, quadratic models were not the most predictive. For spruce, models that predicted the reciprocal of diameter and D2H explained the most variation. For pine, linear models were just as predictive as those involving inverse or quadratic transformations.

In order to prescribe effective vegetation management treatments it is important to know whether growth limiting thresholds exist beyond which increasing interference does not significantly affect conifer growth. If such a threshold exists, then levels of interfering vegetation must be reduced below the critical threshold (point x on Fig. 2.7) to improve seedling growth. Alternatively, if the relationship is linear, then any amount of vegetation control should result in some improvement of seedling growth. In this study, preliminary results suggest a possible threshold effect. Growth of both species began to improve when there was less than 60-70 percent total vegetation cover, and was best when cover was below 20-30 percent. These conclusions are tentative because conifer growth in the harsh ESSF environment is slow (see chapter 1), and the response of the trees to neighbourhood interference is not yet clear.

Liddle *et al.* (1982) and Goldberg (1987) have suggested that competition from neighbouring plants acts primarily as an upper boundary on

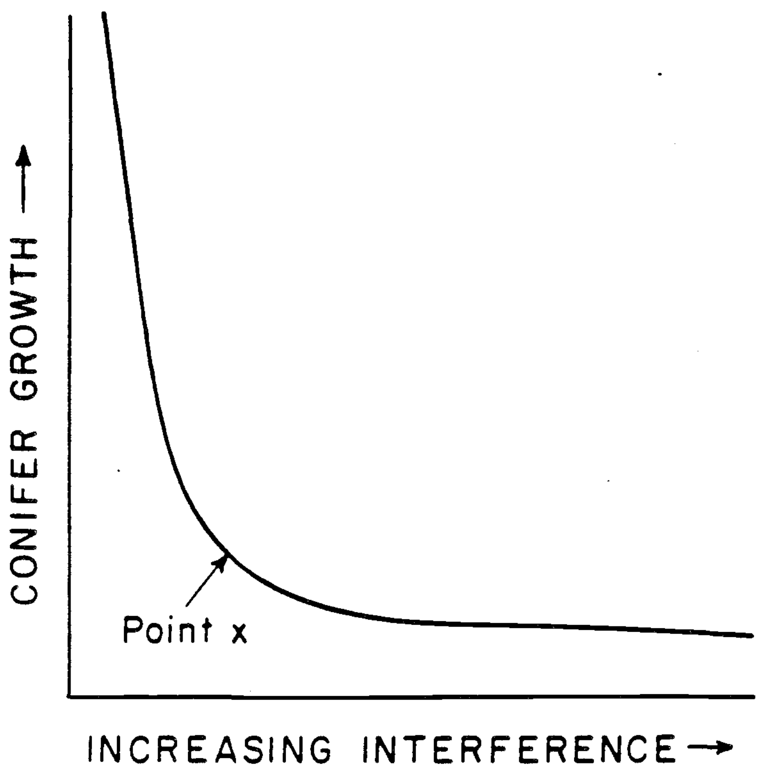

Figure 2.7 A possible relationship between growth performance of individual conifer seedlings and measures of interference.

the size that an individual can attain. Below this boundary, individual size can vary widely, thus competition may not be a good predictor of the actual size of individuals. The results from this study were consistent with the concept of a boundary line constraining maximum size. As the amount of interference increased, maximum size decreased, and the variance in seedling performance decreased (Figures 2.2 to 2.6). The large variation in seedling performance at low levels of neighbourhood interference suggests that factors other than interference can have a strong effect on seedling growth in relatively competition-free environments. At high levels of interference, growth is severely constrained by neighbours, and other factors become relatively less important. Factors that may confound the influence of interfering neighbours by affecting seedling growth include microsite variation, herbivory and other types of seedling damage, and differences in seedling genotype.

Wagner and Radosevich (1987), in a retrospective study of many different cutting units, found that including slope and aspect as independent variables significantly improved the predictive power of their individual tree growth model. In the current study, microsite descriptors of each neighbourhood plot (slope, aspect, humus depth, and mineral soil exposure) were of little value in explaining variation in seedling performance. However, since the study site was fairly uniform, the poor correlation between site predictors and seedling performance may simply reflect the overall uniformity of the site. Few trees were browsed in the experiment (see chapter 1), and browsed trees were excluded from the data set. Growth of frost damaged and undamaged trees was not significantly different. Given the considerable variation in seedling performance at low levels of interfering vegetation, it seems that either genotypic variation or seedling quality are very important, or that more complex site descriptors (for example detailed evaluation of light, temperature, nutrient, and soil moisture variation with microsite) are required to improve the predictive ability of the model.

In summary, the neighbourhood approach has the potential to identify critical thresholds that must be exceeded if control treatments are to be effective, and provides a technique for quantifying the influence of number, proximity, and abundance of neighbours has on conifer seedling performance. After two growing seasons seedling growth potential was clearly constrained at high neighbour percent cover, and tentative thresholds can be identified, but because of the slow seedling growth in the harsh ESSF zone environment the relationships are not yet well developed.

Response of Six ESSF Zone Shrub and Herb Species to Disturbance

Chapter 3

INTRODUCTION

Within British Columbia there are extensive areas of forest land, termed "backlog" areas, that have failed to regenerate successfully after harvesting or natural disturbance. In the Kamloops Forest Region, located in south-central B.C., there are approximately 200,000 ha of backlog, of which 70,000 ha occur in the high-elevation Engelmann Spruce-Subalpine Fir (ESSF) zone. Many of the backlog areas have a well developed shrub/herb community comprised of white-flowered rhododendron (*Rhododendron albiflorum* Hook.), black huckleberry (*Vaccinium membranaceum* Dougl.), oval-leaved blueberry (*V. ovalifolium* Smith.), false azalea (*Menziesia ferruginea* Smith.), Sitka valerian (*Valeriana sitchensis* Bong.), and Indian hellebore (*Veratrum viride* Ait.). This vegetation complex is thought to be a major impediment to successful forest regeneration (Conard 1984).

The four shrub species belong to the Heather family (Ericaceae). Members of this family in British Columbia are typically acid-loving, slow growing, woody plants with simple leaves and perfect (bisexual) flowers. All four species are deciduous. On the ESSF study site, rhododendron forms the dominant shrub layer (80-140 cm in height), with the two huckleberries usually in a codominant position under the taller rhododendron. False azalea has a similar growth form to rhododendron, but occurs infrequently at the study site. Sitka valerian (Valerianaceae) is a fibrous-rooted perennial herb with a stout, branched rhizome that is generally between 30 cm and 80 cm tall on the study site. Indian hellebore (Liliaceae) is a tall perennial with a simple stem and long, coarsely veined clasping leaves; it averages between 40 cm and 90 cm in height at the study site.

Effective vegetation management decisions require a basic understanding of the ecological characteristics of individual competitors and how they respond to silvicultural treatments. Few studies have considered the response of the dominant species found in high-elevation ESSF clearcuts to silvicultural treatments such as manual cutting, mechanical site preperation, broadcast burning, or herbicide application (Coates and Haeussler 1986). The objective of this part of the study was to monitor the response of the six major ESSF species to a single manual cut, repeated cutting, and a single mechanical scarification treatment.

METHODS

For a complete description of the study area refer to the methods section in Chapter 1 of this text. Three disturbance treatments were applied to individuals of each of the six selected shrub and herb species. The treatments were (1) a single cutting at the start of the experiment (early July, 1986), (2) multiple cutting (early July and late August, 1986, and late June and late August 1987 for herbs; only early July 1986 and late-June, 1987 for shrubs), and (3) one mechanical scarification at the start of the experiment. At the time the first treatments were applied, shrub leaves were about three quarters developed and the two herb species had nearly reached maximum leaf extension and were both coming into flower. False azalea plants in the single-cut treatment were not cut for the first time until the third week of July. All other plants were cut in the first week of July. For shrubs, the second cutting involved removal of all new foliage and the many new shoots by hand. Removal of herbs was with a hoe, hence the plants were decapitated at or below the ground surface.

Five sample plants of each species were monitored in each treatment. Each plant was marked by a small wooden stake. The wooden stake served as plot centre for a 50 cm radius plot used to record information on each sample plant. A sample plant within the 50 cm radius plot may thus have been comprised of more than one individual genet. Each sample plant was measured prior to the treatments being applied and remeasured prior to further cutting or at the end of each growing season. The following information was recorded for each plant before the treatments were applied: (1) number of stems (in the 50 cm radius plot), (2) height of the tallest stem, (3) diameter of the largest stem (at 1 cm above the ground surface), and (4) canopy diameter (based on two perpendicular measurements at the base of the crown). Sitka valerian is a basal sprouting herb that grows in thin-to-dense clumps with numerous individual stems. Relatively dense clumps were selected. If a clump had greater than 15 individual stems, the number of stems was recorded as 15. Post-treatment measurements included; (1)-(4) above, and additionally (5) the number of cut stems with new growth (shrubs only), and (6) the number of new basal sprouts (a new stem arising through soil or organic matter from the root collar) or suckers (a new stem arising at some distance from the root collar) (shrubs only). At the end of the first growing season the number of new shoots per individual cut stem with new growth also was counted (2 sample plants, shrubs only). In the one cutting treatment, for shrubs only, the number of original cut stems with new growth and the number of sprouts or suckers was not recorded in the second growing season. The profuse regrowth made it impossible to obtain this data accurately without damaging the sample plants.

After the initial cutting, shrub stumps were about 10 cm tall. Measured mean height of the regrowing stems did not include the 10 cm original stump. Therefore, the actual mean height of the tallest stems from the ground surface is usually 2-6 cm greater than the figures given in Tables 3.1 to 3.3.

Comparision of treatment means was done on personal computers using the Statistical Analysis System (SAS Institute 1985) programs.

RESULTS

After One Growing Season

Single-cut treatment

Height growth of the shrubs in the first season was not vigorous. The tallest new shoots were found on black huckleberry (8 cm) followed by oval-leaved blueberry (6.2 cm), rhododendron (2 cm), and false azalea (1.3 cm) (Table 3.1). Those heights represented 15.7, 17.2, 1.7, and 1.1 percent respectively, of each species' height before cutting. Mean sprout diameter varied between 0.2 and 1.6 mm (Table 3.1). Crown diameter regrowth of rhododendron and false azalea was less than one percent of their precut levels, while the two huckleberries regained about 30 percent of their precut levels (Table 3.1). Sitka valerian averaged 11.2 cm or 32 percent of its original height and regained 84.6 percent of its original crown diameter by the end of the growing season. Indian hellebore was eliminated for the 1986 growing season by a single cutting.

On all four shrub species, the majority of new shoots arose from buds on old stems rather than as basal sprouts or suckers (Table 3.1). The number of original stems with new shoots averaged between 50 and 78 percent after the first growing season, except for false azalea in the single-cut treatment (26%). The average number of new shoots per original cut stem with new growth varied between 3 and 6 (Table 3.4).

Multiple-cutting treatments

Because of limited regrowth none of the four shrub species were cut a second time during the first growing season (1986). Sitka valerian stems cut for the second time on August 28, 1986 did not resprout that year. Accordingly, for both shrubs and herbs the results were similar to those of the one-cut treatment. At the end of the first growing season, oval-leaved blueberry had the tallest average stem height (9.2 cm or 19.1% of original),

Table 3.1 Mean response of shrubs and herbs to a single-cutting.

	Rhodendron	False azalea	Black huckleberry	Oval-leaved huckleberry	Sitka valerian	Indian hellebore
Pre-treatment (July 5, 1987)						
height (cm)	114.4	114.2	51.0	36.0	35.0	36.6
diameter (mm)	17.0	13.6	9.4	7.0	--	--
crown diameter (cm)	115.0	88.0	36.0	32.0	36.4	36.0
total stems	43.0	18.0	10.8	10.2	10.6	6.0
August 28, 1986						
height (cm)	2.0	1.3	8.0	6.2	11.2	0.0
diameter (mm)	0.2	0.3	1.6	1.4	--	--
crown diameter (cm)	0.4	1.3	10.2	10.4	30.8	0.0
original stems with new shoots	27.2	4.6	8.8	6.4	--	--
new sprouts	0.8	0.0	0.0	0.0	12.8	0.0
new suckers	0.0	0.0	0.6	1.6	--	--
June 22, 1987						
height (cm)	9.8	4.2	11.4	8.8	29.8	37.6
diameter (mm)	1.9	0.8	1.6	1.3	--	--
crown diameter (cm)	33.6	4.8	30.2	21.4	44.4	36.2
original stems with new shoots	27.4	7.0	9.8	8.6	--	--
new sprouts	4.4	1.0	0.0	0.0	13.6	6.0
new suckers	0.0	0.0	5.2	1.2	--	--
August 25, 1987						
height (cm)	12.0	14.8	10.0	11.4	38.4	62.0
diameter (mm)	3.3	2.7	2.3	2.0	--	--
crown diameter (cm)	56.4	26.8	34.4	28.2	46.6	43.6
original stems with new shoots (1)	--	--	--	--	--	--
new sprouts (1)	--	--	--	--	13.4	6.0
new suckers (1)	--	--	--	--	--	--

(1) because of the amount of new growth in the second growing season it was not possible to obtain this data for the shrubs without damaging the sample plants.

Table 3.2 Mean response of shrubs and herbs to multiple-cutting.

	Rhodendron	False azalea	Black huckleberry	Oval-leaved huckleberry	Sitka valerian	Indian hellebore
Pre-treatment (July 5, 1987)						
height (cm)	117.2	99.8	62.4	48.2	37.4	48.6
diameter (mm)	16.2	14.2	9.4	7.8	--	--
crown diameter (cm)	121.0	87.0	37.0	52.0	54.0	48.4
total stems	58.8	30.6	14.4	38.6	14.4	6.0
August 28, 1986						
height (cm)	2.6	3.6	5.0	9.2	11.0	0.0
diameter (mm)	1.0	1.4	1.2	1.8	--	--
crown diameter (cm)	4.4	9.2	4.0	11.8	41.0	0.0
original stems with new shoots	37.6	20.2	8.4	26.0	--	--
new sprouts	0.4	0.2	0.0	0.0	14.8	0.0
new suckers	0.0	0.0	0.0	1.6	--	--
June 22, 1987						
height (cm)	6.2	8.2	7.6	11.6	18.6	53.2
diameter (mm)	1.5	1.5	1.3	1.6	--	--
crown diameter (cm)	42.2	22.8	15.4	31.6	71.0	46.4
original stems with new shoots	52.0	19.6	10.8	24.6	--	--
new sprouts	6.0	3.6	0.0	0.0	14.8	5.6
new suckers	0.0	0.0	0.0	1.6	--	--
August 25, 1987						
height (cm)	2.6	3.2	2.4	3.2	7.0	0.0
diameter (mm)	0.8	1.8	0.8	0.9	--	--
crown diameter (cm)	10.4	9.6	4.6	9.0	25.2	0.0
original stems with new shoots	53.6	25.6	8.0	16.6	--	--
new sprouts	1.0	0.8	0.0	0.0	13.2	0.0
new suckers	0.0	0.0	0.0	0.6	--	--

followed by black huckleberry (5 cm or 8% of original), false azalea (3.6 cm or 3.6% of original), and rhododendron (2.6 cm or 2.2% of original) (Table 3.2). Mean shrub diameter varied between 1.0 and 1.3 mm (Table 3.2). Crown diameter regrowth of rhododendron was less than one percent of its precut levels, false azalea and black huckleberry about 10 percent of precut levels, and oval-leaved blueberry was about 20 percent of precut levels (Table 3.2). The tallest stems of Sitka valerian averaged 11.0 cm or 29.4 percent of their original height. Sitka valerian, as in the single-cut treatment, regained 75.9 percent of its original crown diameter before being cut a second time. Indian hellebore was eliminated for the 1986 growing season.

Mechanical scarification

Scarification uprooted and removed most of the shrub species; it removed most the aerial parts and some of the root/rhizome system of the herb species. Shrubs not totally removed by mechanical scarification were extensively damaged and put on little, if any, growth over the summer. Individuals measured at the end of the growing season were therefore restricted to those surviving the treatment. Out of the original five shrub sample plants for each species, only one rhododendron and oval-leaved blueberry, and two false azalea and blach huckleberry survived. The measurements recorded for the shrubs after the first growing season (Table 3.3) are meaningless except as a base for monitoring second year growth. The main result was that when all shrub tops were removed or the entire plant was uprooted, there was no evidence of recovery after one growing season. Surviving plants did produce a few new shoots (Table 3.3).

Sitka valerian responded to mechanical scarification in much the same way as it responded to cutting. At the end of the growing season the average height of the tallest stem was 11.5 cm or 30.1 percent of its original height. Crown diameter was 53.3 percent of its pre-treatment level. Indian hellebore was eliminated for the 1986 growing season by mechanical scarification.

Table 3.3 Mean response of shrubs and herbs to mechanical scarification.

	Rhodendron	False azalea	Black huckleberry	Oval-leaved huckleberry	Sitka valerian	Indian hellebore
Pre-treatment (July 5, 1987)						
height (cm)	110.8	95.6	53.3	55.0	38.2	45.4
diameter (mm)	17.4	12.8	8.6	7.2	--	--
crown diameter (cm)	123.0	77.0	37.0	35.0	77.0	40.4
total stems	41.8	19.4	10.0	11.0	15.0	4.6
August 28, 1986						
height (cm)	21.0	32.0	46.0	52.2	11.5	0.0
diameter (mm)	13.0	8.0	7.0	8.0	--	--
crown diameter (mm)	4.0	3.0	22.5	15.0	41.0	0.0
original stems with new shoots	2.4	0.2	3.0	0.2	--	--
new sprouts	0.0	0.6	0.0	0.0	10.2	0.0
new suckers	0.0	0.0	0.0	2.0	--	--
June 22, 1987						
height (cm)	2.0	3.5	31.0	8.0	41.5	39.5
diameter (mm)	0.5	1.6	5.6	1.8	--	--
crown diameter (cm)	3.0	8.5	29.0	13.0	90.8	30.5
original stems with new shoots	0.8	0.6	0.8	0.6	--	--
new sprouts	0.0	0.0	0.0	0.0	10.0	0.8
new suckers	0.0	0.0	2.6	0.8	--	--
August 25, 1987						
height (cm)	10.0	9.0	24.5	10.2	79.2	50.5
diameter (mm)	2.4	2.1	4.8	2.2	--	--
crown diameter (cm)	20.0	18.3	26.8	35.4	95.8	32.5
original stems with new shoots	4.0	2.0	3.0	4.0	--	--
new sprouts	0.0	0.0	0.0	0.0	12.0	2.0
new suckers	0.0	0.0	1.8	9.0	--	--

Table 3.4 Percent of original stems (before cutting) with new shoots and mean number of new shoots per cut stem having new growth one growing season after cutting.

	Rhododendron	False azalea	Black huckleberry	Oval-leaved huckleberry
Single-cut percent of stems with new growth	63.2	25.5	77.8	50.0
Multiple-cutting percent of stems with new growth	63.9	66.0	58.3	67.4
Mean number of new shoots per stem with new growth	3.4	5.6	3.3	2.9

After Two Growing Seasons

Single-cut Treatment

Shrub height growth was more vigorous in the second year than in the first. By the end of the second growing season of recovery, mean height of the tallest stems of rhododendron, false azalea, black huckleberry, and oval-leaved blueberry were 12.0 cm, 14.8 cm, 10.0 cm, and 11.4 cm, respectively (Table 3.1). Those heights represented 10.5, 13.0, 19.6, and 31.7 percent, respectively of precut heights. Mean stem diameter of each shrub species varied between 2.0 and 3.3 mm (Table 3.1). Mean shrub crown area for rhododendron, false azalea, black huckleberry, and oval-leaved blueberry were 49, 30, 96, and 88 percent of precut levels (Table 3.1). All four shrubs continued to produce a few sprouts or suckers from below the soil, but the majority of new growth was from the new shoots growing out of the old cut stems. By late June, 1987 both Sitka valerian and Indian hellebore had almost completely recovered to their precut sizes (Table 3.1). By the end of the second growing season, both herb species were larger than at the time of initial cutting and had the same or greater numbers of stems. None of the shrubs or herbs were killed by the single-cut treatment, and all sample plants were considered healthy and vigorous at the end of the second growing season.

Multiple-cutting Treatment

At the time the shrubs were cut a second time (June 23, 1987) regrowth was similar to that in the single-cutting treatment (Tables 3.1 and 3.2). The response of all four shrubs to a second cutting was much like their response to the first cutting. With the possible exception of oval-leaved blueberry, the second cutting did not appear to have depressed the regrowth vigour of the shrub species (Table 3.2). Sitka valerian mean height in late June, 1987 (after 2 cuttings) was 50 percent of precut levels; crown diameter was 31 percent greater than precut levels. At the end of the second growing season (after 3 cuttings) mean height and crown diameter were 19 and 24 percent, respectively, of their precut levels. Indian hellbore growth just before recutting was the same as or exceeded that of the precut levels. Following cutting, Indian hellebore did not recover during the growing season.

Mechanical Scarification

Some surviving stems of all four shrub species died or died back over the winter resulting in a reduction in either mean height or mean diameter for all shrubs at the June measurement date when compared to the previous year (Table 3.3). Mean height increased over the growing season for all shrub species except black huckleberry, which experienced further stem mortality. No new sprouts or suckers emerged from below the soil surface on any of the five rhododendron or false azalea sample plants. Two black huckleberry sample plants that showed no recovery in 1986 produced suckers in the second growing season. Plants of both *Vaccinium* species with surviving aerial stems continued to produce new suckers in the second year. Growth of all new suckers was slow. Original stems of all shrubs were of moderate to poor vigour. Sitka valerian recovered to or exceeded pretreatment levels by early in the second growing season (Table 3.3), even though one sample plant was killed by the mechanical scarification treatment. Three of the five Indian hellebore sampling plants appear to have been killed by the scarification treatment, showing no recovery to the end of the second growing season. The remaining two sample plants recovered as well as those in the other treatments.

DISCUSSION

Recovery of all four shrub species from manual cutting was slow. After two growing seasons mean shrub height of the tallest stems was between 10 cm and 15 cm (Table 3.1). By contrast, mean spruce height after two growing seasons varied between 21 cm and 27 cm, and mean pine height varied between 14 cm and 17 cm (Tables 1.4 and 1.6). Clearly, after two growing seasons conifer seedlings were in little risk of being overtopped by regrowing shrubs. However, Sitka valerian, unless repeatedly cut, recovered much of its pretreatment size by the end of the first growing season, and had completely recovered to pretreatment levels early in the second growing season (Table 3.1 and 3.2). This result is not surprising given the growth habit of the species. However repeated cutting (3 times), appeared to reduce the vigour of Sitka valerian compared to the single-cut treatment. The increase in mean height and crown diameter within the single-cut treatment over pretreatment levels reflects the difference in measurement time (beginning of season vs end of season). Indian hellebore, although totally eliminated above-ground in the year of cutting, recovered completely the next year. This monocot species has determinate growth from a basal meristem and does not appear capable of regenerating in midseason from adventitous buds.

Mechanical scarification either severely damages or completely kills the shrub species. Above ground stems not removed by the initial treatment were of low vigour after two growing seasons, and many died. Surviving huckleberries were suckering, but growth was very slow. In contrast, both herb species, unless uprooted, recovered completely from the treatment by early in the second growing season (Table 3.3).

Either manual cutting or mechanical scarification offer good control of all four shrub species. Regrowth is slow, and as long as conifer seedlings are planted promptly after the shrub reduction treatment, the trees are unlikely to be overtopped by shrubs. However, shrubs are not killed by manual treatments. If below-ground interference is important, as suggested by results indicating reduced spruce diameter growth in plots with both shrub and herb regrowing compared to herbs only (see chapter 1), then conifer growth reductions can occur even when they are not overtopped by shrubs. Mechanical scarification causes high mortality rates followed by slow growth of the survivors. Based on lower vigour of Sitka valerian after repeated cutting, a vegetation management treatment such as sheep grazing (used in areas similar to the study site in southern B.C.) sustained over a few years, may offer good control in areas with high densities of Sitka valerian.

Silvicultural Implications

Chapter 4

The purpose of this study was to begin developing an understanding of the underlying causes for poor conifer regeneration performance in the ESSF zone. Assuming good stock that is correctly handled and planted, then it is the microsite conditions faced by individual conifer seedlings that ultimately determine seedling performance. These microsite conditions result from the interaction between the ESSF zone climate and interfering vegetation. In order to prescribe effective silvicultural prescriptions in the ESSF zone, the relationships between interfering vegetation, climate, and seedling performance must be understood.

Effective regeneration treatments are cost effective, result in acceptable rates of survival and growth of crop trees, and minimize infringement on other resource values. For a silvicultural prescription to be effective it must affect the environmental factor or factors that need modification in order to achieve the desired management objective. There is little the silviculturist can do to modify the climate, but any limitations the climate places on seedling performance must be understood. The silviculturist can, however, modify the microclimate to some extent by manipulating non-crop vegetation. Interfering vegetation can modify the physical environment (for example, shading reduces soil temperature) or compete directly for resources (light, water, nutrients) with the planted seedlings. Thus, vegetation management can be directed toward improving physical conditions for seedling growth or remedying resource limitations.

Once the cause of poor seedling performance is identified, the means (or operational tool) by which an appropriate treatment is applied becomes a matter of cost and operational feasability. In this study, after two growing seasons, survival was reduced only in the presence of the highest levels of shrubs and herbs (about 84% vs >97%). It appears that a combination of competition for light and lower soil temperatures was the principal cause of the lower survival and that only partial vegetation control is necessary to achieve the highest levels of survival. There are many ways in which partial (or complete) removal of vegetation can be accomplished to improve light and temperature conditions.

An important concept in forest vegetation management is the concept of ecological thresholds. When the threshold level for a certain environmental resource or condition is surpassed, seedling performance can dramatically improve. There are several considerations in applying the concept of ecological thresholds to silvicultural management. First, it is important to note that threshold points where survival and growth improve will not necessarily be the same. Secondly, it is important to distinguish between those situations where a threshold exists, and those where none exist. Where critical thresholds exist, silvicultural treatments that do not exceed those thresholds will not be effective in achieving the desired results. Equally, surpassing threshold points may yield relatively little gain for the added cost of more complete vegetation control. On the other hand, where thresholds are absent, conifer response to improving conditions may be more-or-less linear; hence any improvement in the environment of the seedling should result in predictable increases in conifer performance.

This study attempted to quantify conifer response and identify critical thresholds if they exist. It appears that a threshold exists for seedling survival and only partial brush reduction is necessary to exceed the threshold. This threshold is probably a response to light levels, but may also involve soil temperature effects. Growth response results are not yet clear after two growing seasons, but will probably become more apparent in the next 2-4 years. The response of spruce to decreasing levels of interference tends toward a negative exponential function suggesting the presence of a threshold, whereas pine response was more linear. Determining the shape of the relationship between conifer growth or survival and the amount of interfering vegetation is important for making silvicultural decisions. Once the relationship is determined, then cost effective treatments can be prescribed that achieve desired survival and growth levels.

Control of interfering vegetation improved mean growth performance at the ESSF zone site. However, the absolute growth improvement was small. Mean diameter of both conifers was only 1 mm greater in the absense of interference. Although this growth increase represented a 25 percent improvement over mean diameter in the undisturbed brush community, it may be of little importance in operational silviculture. In other forest regions, for example the southeastern and western US, where substantial gains in seedling growth have been documented following vegetation control, improvement in moisture conditions has often been cited as the principal reason (numerous examples in Walstad and Koch 1987). In essence, vegetation control in these regions extends the length of the growing season, allowing trees under low levels of moisture stress to continue growing longer than trees which must slow or stop growth due to moisture stress. This type of growth response should not be expected in the ESSF zone for two reasons. First, ample soil water is apparently available throughout the growing season and there was no evidence that water uptake by vegetation induces moisture stress. Second, the growing season in the ESSF zone is very short, and is constrained by temperature factors largely outside the control of the silviculturist. Temperature data from the study show that control of interfering vegetation does not increase the effective duration of the growing season in the ESSF zone. However, it may be possible to substantially improve the quality of the short growing season. Improving the soil thermal regime is one example of how the quality of the growing season can be improved. According to the literature, root growth and water uptake of both spruce and pine can dramatically improve when soil temperatures exceed a threshold of around 5^{o} to $7^{o}C$ (see chapter 1). At the ESSF zone site, soil temperatures were within this range for most of the summer under the undisturbed brush community. Vegetation removal doubled cumulative soil degree-day temperatures above $5^{o}C$ (Figure 1.6).

Both light availability and soil temperature appear to be important factors limiting conifer performance. Beyond the threshold where survival is satisfactory, further reductions in interfering vegtation must be justified on the basis of improved growth performance. It is not clear from this study whether further improvement in light conditions or increased soil temperature lead to the improved growth performance. It is important to determine which factor needs modifying to improve seedling growth, since treatments designed to improve light or soil temperature (once the survival threshold is exceeded) may be quite different. Silvicultural prescriptions that lower interfering vegetation below threshold levels for survival and increase soil temperature throughout the growing season should create favourable conditions for conifers in the ESSF zone.

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