AN ABSTRACT OF THE THESIS OF

Alison Campbell Nicholson for the degree of Master of Science in Forest Science presented on April 14, 1989.

Title: Water Relations, Survival and Growth of Douglas-fir Seedlings at a Pinegrass Dominated Site in the Interior Douglas-fir Zone of South-central British Columbia.

Abstract approved: ____________________

S.R. Radosevich

A field study was conducted to determine the impact of microclimate and vegetation on survival and growth of planted Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) at a pinegrass (*Calamagrostis rubescens* Buckl.) dominated clearcut in the Interior Douglas-fir Zone of south-central British Columbia. The study focussed on (1) the water balance of the site, (2) the response of Douglas-fir and pinegrass to moisture deficits, and (3) the influence of environmental factors and the pinegrass-dominated vegetation on Douglas-fir survival and growth.

Survival and growth, physiological and microclimate measurements were made within the framework of a replacement series and neighbourhood experiment. Evapotranspiration and surface resistance were calculated based on data including air temperature, solar radiation, rainfall and soil water content measures using gravimetric sampling and the neutron moderation method.

After three growing seasons, survival of the Douglas-fir in the absence of pinegrass was 43%. Mortality resulted from a variety of factors including drought, frost, and rodent damage. Poor seedling quality at the time of planting was also suspected to have contributed to mortality. In the presence of the native vegetation Douglas-fir seedling growth was reduced and risk of death increased. Results suggested that: (i) reducing the leaf area index around the seedlings to below 0.5 effectively improved seedling performance and (ii) removing all vegetation immediately adjacent to a seedling was preferable to partial removal.

A comparison of the relative growth rates of the Douglas-fir and pinegrass indicated that rapid growth of pinegrass early in the growing season when moisture is least limiting gave it a competitive advantage. Soil temperatures beneath pinegrass dominated vegetation were cooler and warmed more slowly in the spring than beneath bare soil suggesting that native vegetation may cause restricted root growth of Douglas-fir by influencing soil temperature.

Longterm climate records showed that amount and distribution of precipitation near the study site varies greatly from year-to-year. Unfavourable early spring growing conditions may be expected 80% of the time. Furthermore, soil water content profiles suggested water deficits develop rapidly at the beginning of the growing season.

Predawn twig xylem water potentials suggested that, even in the absence of pinegrass, Douglas-fir were moderately stressed by mid-June in all three growing seasons. At this time, the roots of the Douglas-fir remained in the top 15 cm of soil where moisture deficits were the greatest. In contrast, predawn leaf xylem water potentials of the pinegrass were found to be more responsive to varying weather conditions because pinegrass' roots extend throughout the soil profile.

Although the pattern and timing of soil moisture depletion differed in each of the three growing seasons, measurements of total growing season evapotranspiration were similar. Because minor precipitation events resulted in substantially elevated soil evaporation at times, it was difficult to separate surface evaporation from transpiration using a technique which treated the entire soil profile as one layer. Regardless, it appears that pinegrass transpiration is responsible for removing most of the water from below 10 cm. Pinegrass in fact played a major role in the water balance of the site.

Several implications of study results to silvicultural practices are discussed. These include: (i) the importance of considering longterm climatic data when formulating rehabilitation/regeneration strategies; (ii) the increased importance of planting stock handling on harsh sites; (iii) the appropriate selection of species and stocktype; (iv) planting strategies; and (v) site treatment to reduce competition and ameliorate environmental restraints.

Finally, the author discusses the limitations of the study and devotes a chapter to suggestions for studying vegetation competition with respect to reforestation problems.

Water Relations, Survival and Growth of Douglas-fir Seedlings at a Pinegrass Dominated Site in the Interior Douglas-fir Zone of South-central British Columbia

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of the requirements for the degree of

Master of Science

Completed April 14, 1989

Commencement June, 1990

APPROVED:

Professor of Forest Science in charge of major

Head of Department of Forest Science

Dean of Graduate School

Date thesis is presented April 14, 1989

Typed by Alison Nicholson

ACKNOWLEDGEMENTS

The many experiences this thesis provided me were enthusiastically shared by my husband, Rodger. I am indebted to him for his encouragement, patience and assistance throughout.

Steve Radosevich, my academic supervisor, provided guidance and friendship. Thanks also go to the other members of my committee, Bill Emmingham and Paul Doescher, for their careful reviews and comments.

I greatly enjoyed my brief time at Oregon State University and will miss the friendly, stimulating atmosphere. It was always a pleasure to consult with my friends and fellow graduate students who assisted me in various phases of the study.

Between my trips to Oregon State University I enjoyed the continued support and interest of my colleagues at the British Columbia Ministry of Forests. I am grateful to Ted Baker who provided me with the opportunity to conduct this research. I am indebted to Dave Spittlehouse who provided me with valuable advice and help throughout the project and who was a good friend. Wendy Bergerud's statistical advice was limitless and sincerely appreciated.

Through the numerous long field days Mike Christian provided energetic and conscientious assistance. Many others helped with various aspects of the field work including my parents, Jean and Tony, Tracy Fleming, Evelyn Hamilton, Tim Harrington, Nigel Livingston, Del Meidinger, Paul Nystedt, George Reynolds, Bob Stathers, and Bill Watt. I also thank Warren Mitchell and the Forest Science section of the Cariboo Forest Region for their support.

This project was funded by the Research Branch of the British Columbia Ministry of Forests and the Canada-British Columbia Forest Resource Development Agreement (F.R.D.A. Project 3.1).

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INTRODUCTION

The forest industry in British Columbia currently faces extensive growth losses due to a phenomenon known as not satisfactorily restocked (NSR) forest lands (Pearse *et al.* 1986). In the province's southern interior approximately 75 000 ha of NSR lands lie within the Interior Douglas-fir (IDF) Biogeoclimatic Zone[1]. The IDF Zone occupies middle elevations in the drier parts of the southern Interior Plateau and southern Rocky Mountain Trench. NSR lands are typically clearcut or wildfire sites where natural regeneration or plantations have been unsuccessful (Mather 1986).

Although uneven age (selection) management is now recognized as a preferred silvicultural option for avoiding NSR problems in the IDF, solutions are still required to reforest existing and future NSR lands resulting from unsuccessful silvicultural efforts or natural disturbances. Reforestation is of immediate concern because: (i) Douglas-fir (*Pseudotsuga menziessii* (Mirbel) Franco var.*glauca* (Beissn.) Franco) is a valuable commercial species, (ii) many NSR sites are considered to be of relatively high productivity, and (iii) much of the NSR is close to population centres.

This introduction is intended to provide an overview of a study to investigate factors affecting reforestation of an NSR site in British Columbia's IDF zone. It begins with a description of the problem being addressed and study objectives. Subsequently the reader is provided with a brief description of the approach employed to meet the study objectives. In addition to this introduction, the study has been divided into five chapters each describing a different component of the study or recommendations derived from its' results.

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1 D.Lloyd, Regional Ecologist, Kamloops Forest Region, and O.Steen, Regional Ecologist, Cariboo Forest Region, personal communication, October 1987.

The Problem

In the IDF zone of British Columbia, the cumulative effects of drought, unfavourable temperatures, and competition for moisture with native plants, particularly pinegrass (*Calamagrostis rubescens* Buckl.), are considered to have prevented reforestation on NSR sites. Up to the time of this thesis, however, little attention had been directed at determining the timing and processes of competition between Douglas-fir seedlings and pinegrass. This thesis describes a study that was initiated to increase our knowledge of the environmnetal constraints and competitive relationships that appear to prevent successful regeneration of dry pinegrass dominated sites in the IDF zone of the province.

The specific objectives of the study were to:

(1) quantitatively assess the relationships between temperature, moisture conditions, pinegrass competition and Douglas-fir seedling survival and growth;
(2) determine the physiological responses of Douglas-fir seedlings and pinegrass to moisture stress; and
(3) examine the water balance for an IDF site dominated by pinegrass.

The Approach

To address this problem, I proposed a study to identify and understand the factors most strongly influencing the physiology of tree seedling survival and growth on these sites. This information was considered essential to predict the effects of silvicultural techniques and in determining appropriate ones.

The result of this proposal was a three year project, supported by the Canada-British Columbia Forest Resource Development Agreement (F.R.D.A. Project 3.1). The study focusses primarily on water relations, survival and growth of Douglas-fir seedlings planted on an IDF clearcut dominated by pinegrass near Williams Lake, British Columbia. The site was selected because it was considered typical of IDF problem sites and in fact in the 14 years since the site was logged very little natural regeneration had occurred.

In 1985 over 3000 Douglas-fir seedlings were planted within a two ha fenced enclosure at the site. The seedlings were planted in a randomized block replacement series design which was chosen because, over the longterm, it would provide the framework necessary to quantify the stand growth response of the seedlings to competition with native vegetation. In an additional experiment, 250 Douglas-fir seedlings were planted to test the effect of the amount of native vegetation on individual seedling survival and growth. In this neighbourhood experiment, a randomized design with 11 treatments resulting from manipulations of pinegrass leaf area around individual seedlings was used. In order to relate environmental variables to plant performance, both the water balance of the site and physiological responses of the Douglas-fir and pinegrass to water stress were examined. Microclimate and physiological measurements were made within the framework of the two experiments.

Format of Study Presentation

Study results are presented in five chapters which follow.

Chapter One quantifies survival and growth of Douglas-fir with respect to environmental stresses and controlled levels of neighbouring pinegrass dominated vegetation. In addition, growth rates of the Douglas-fir and pinegrass are compared.

Chapter Two examines water use characteristics of Douglas-fir and pinegrass. Characteristics examined include: (i) seasonal and diurnal courses of xylem water potential, (ii) relationships between transpiration and soil water potential, and (iii) the ability of Douglas-fir to osmotically adjust through the first growing season following outplanting. In addition, values of stomatal conductance are combined with measured hourly average vapor pressure deficit and leaf area to estimate daily water use of the Douglas-fir and pinegrass. Seedling water stress is also examined in relation to seasonal trends in soil water deficit and surface resistance.

Chapter Three presents long-term climatic information and emphasizes temperature and precipitation conditions that can be expected. In addtion, a water balance model for the study site quantifying growing season soil water deficits and rates of water loss with and without a pinegrass dominated ground cover is presented.

Chapter Four discusses Douglas-fir seedling survival and growth in relation to silvicultural regeneration treatments. Factors that may influence survival that are discussed include: time of planting, stock quality, appropriateness of stocktype and species planted, competition and site treatment.

Finally, Chapter Five provides a general strategy for future vegetation management research. This strategy is discussed within the context of the study's shift in emphasis from the influence of competition on tree performance to the influence of environmental factors and modification of site conditions by pinegrass. This shift provided a means of accounting for the poor seedling survival and growth in the study.

Effects of Environment and Competition on Douglas-fir Seedling Survival and Growth

Chapter One

INTRODUCTION

Foresters working in the southern interior of British Columbia face significant regeneration problems on clearcut and wildfire sites in the Interior Douglas-fir (IDF) Biogeclimatic Zone where native grasses have encroached. Failures of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations have been attributed mainly to drought which may be exacerbated by competition from pinegrass (*Calamagrostis rubescens* Buckl.), the dominant understory species through much of the IDF (Clark 1975, Crane *et al.* 1983). Longterm climate records for the IDF Very Dry Montane Subzone (IDFb) also suggest that frosts during the growing season are common (Environment Canada 1982). Thus, planted seedlings must be tolerant to abiotic and biotic stresses to perform well. Recently, the competitive response of the seedlings to surrounding vegetation has been recognized as an increasingly important determinant of plantation success (Radosevich and Osteryoung 1987).

Pinegrass is a slender, perennial rhizomatous grass that is ubiquitous on many sites in the southern interior of British Columbia that are classified as being NSR. It is moderately shade tolerant and responds dramatically to increased light conditions forming a continuous vegetative mat. Two recent studies, Krueger and Bedunah (1988) and Stout and Brooke (1985), examined the characteristics of pinegrass clearcuts versus forested sites and the growth of pinegrass respectively in the IDF near Kamloops, British Columbia. Despite these studies the patterns and processes of competition between pinegrass and Douglas-fir remain unclear.

This lack of clarity is understandable because of the complexity of the patterns and processes of competition and interactions among plants that share the same environments. Indeed plants compete for limited resources, such as water and nutrients. Plants may modify environmental conditions, for example by shading. Plants may also act indirectly to affect the environment, for example by altering predator behaviour. Furthermore, different species of plants may respond to competition or interference in different ways; some plants respond through plastic growth responses and some by an altered risk of death (Harper 1977).

This chapter describes a study to examine factors affecting the growth and survival of Douglas-fir on sites where pinegrass is dominant. The objectives were to:

(1) quantify the survival and growth of planted Douglas-fir seedlings with respect to the microclimate;

(2) quantify the survival and growth of planted Douglas-fir seedlings with respect to controlled levels of pinegrass vegetation; and

(3) compare growth rates of the pinegrass and Douglas-fir during the plantation establishment phase.

METHODS

Site Description

The experimental site is located on the Fraser Plateau (51^{o} 40' 45" N, 121^{o} 57' 30" W) and is characterized by a continental climate; summers are warm and dry and winters cold with relatively little snowfall. Climate data from Williams Lake Airport located approximately 50 km north of the site are summarized in Figure 1.1.

The site is in a 57 ha pinegrass dominated clearcut representative of a mesic site in the Interior Douglas-fir Very Dry Montane Subzone, East Fraser Plateau Variant (IDFb2) (B.C. Ministry Forests 1987). The experimental area (approximately 2 ha) was fenced to prevent grazing by cattle and horses. The elevation is 1150 m, aspect 300^{o} and slope 8%. In addition to pinegrass, other common species on site include *Shepherdia canadensis* (L.) Nutl., *Rosa acicularis* Lindl., *Arctostaphylos uva-ursi* (L.) Spreng., *Aster conspicuus* Lindl., *Festuca ovina* L., *Linnaea borealis* L., and *Poa pratensis* L. The adjacent climax forest, common and widespread in the IDF, is a multi-aged stand of Douglas-fir. Throughout the subzone an extensive fire history has also maintained even-aged lodgepole pine stands as a dominant landscape feature. The soil at the site is a deep (1 m), well drained, silt loam Orthic Gray Luvisol over compact glacial till (Canada Soil Survey Committee 1978). The site was harvested in early 1971 and slash burned in July of the same year. Very little Douglas-fir or lodgepole pine regeneration has occurred since then and the area is considered typical of NSR problem sites in the IDFb.

Weather Measurements

Micrometeorological measurements were made beginning in May 1985 and continuing through 1986 and 1987. Solar irradiance was measured with a horizontally positioned pyranometer (Model Li-200SB, Licor Inc.). Rainfall was collected in a tipping bucket rain-gauge (Sierra-Misco Model 2501) which has a 1 mm resolution. Air temperature and relative humidity

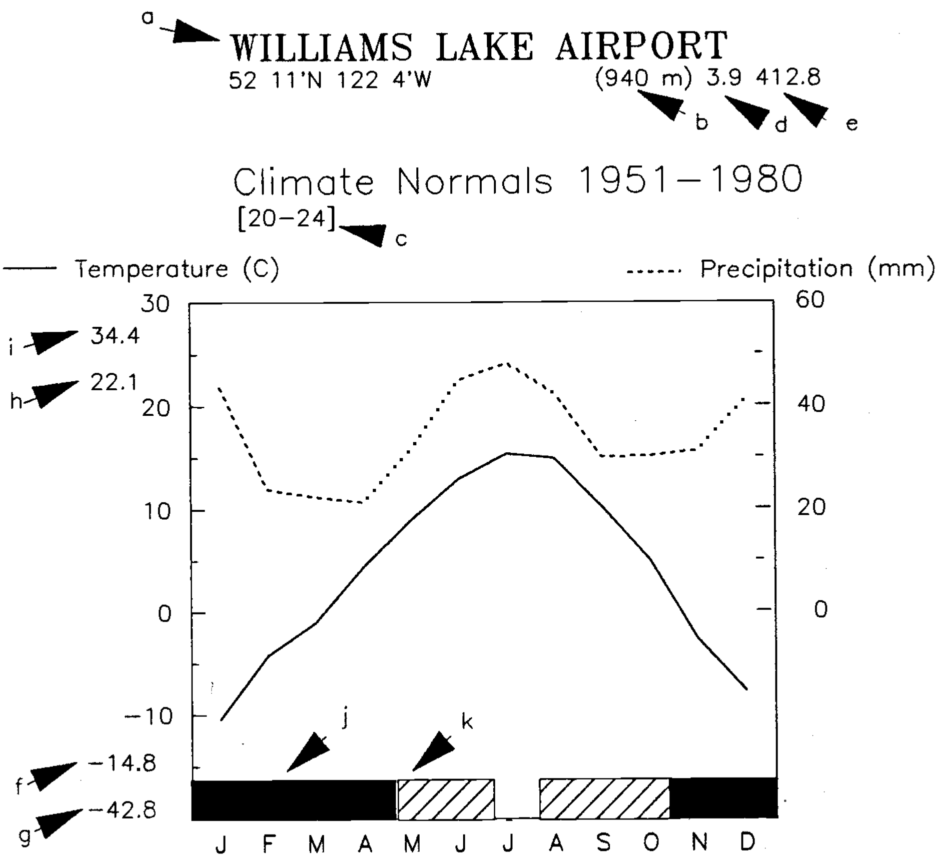

Figure 1.1 Climatic diagram after Walter (1973) summarizing data from nearby Williams Lake Airport (Environment Canada 1980): a=station, b=elevation in m a.s.l., c=duration of observations in years, d=mean annual temperature in °C, e=mean annual precipitation in mm, f=mean daily minimum of coldest month, g=lowest temperature recorded, h=mean daily maximum temperature of warmest month, i=highest temperature recorded, j=months with mean daily minimum below 0 °C (black)=cold season, k=months with absolute minimum below 0 °C (diagonal shading)=late or early frosts occur.

were measured in a Stevenson Screen at 2 m height. In addition, air temperature at seedling height (0.15 m) was measured in 1986 and 1987. Air temperature was measured with a Model UUT-51J1 thermistor (Fenwal Electronics Corp.) and relative humidity was measured with a Model PL 2-200 vaisala sensor (Micromet Systems Inc.) in 1985, and Phys-Chemical Research PCRC-11 sensor (Model 207, Campbell Scientific) in 1986 and 1987. Wind speed was measured at 2.5 m with a Met One 013 anemometer with a starting threshold of 0.5 m/s. Climatic data were recorded as one hour totals or averages throughout the growing season (from May until October) and as daily totals or averages throughout the winter, using a Model 21X data logger (Campbell Scientific).

Experimental Design

Two separate experiments were conducted to examine the relationships among moisture, temperature conditions, levels of native pinegrass dominated vegetation and the performance of Douglas-fir seedlings. A replacement series experiment was employed to provide a method for interpreting the effects of inter- and intra-specific competition on the pinegrass and Douglas-fir over the longterm. In addition, a neighbourhood tree-centred experiment was employed in which amounts of native vegetation around the seedlings were varied to assess the response of individual trees to a wide range of competition levels. The two experiments are explained below.

Replacement series design

A randomized block replacement series design was established in the spring of 1985 to study the occurrence of competition and to approximate critical pinegrass density levels for optimal survival and growth of the tree seedlings (de Wit 1960, Harper 1977). This longterm assessment examines the growth response of the stand as a whole rather than the growth response of individual plants. The experiment is substitutive whereby total relative cover or yield of the stand remains constant while the proportions or ratios of Douglas-fir seedlings to the pinegrass vegetaion are varied.

In mid-May 1985 over 3000 Douglas-fir seedlings (seedlot 3087, stocktype 1+0 PSB 313)[2] , were dibble planted into hand scalped 0.25 m^2 patches. Five competitive regimes were established in each of four blocks. To create the five competition levels, the proportions or ratios of Douglas-fir seedlings to pinegrass were varied while total relative yield and spatial arrangement were held constant. The five proportions of Douglas-fir to pinegrass included 100:0, 90:10, 75:25, 50:50, and 0:100 (Figure1.2). The corresponding number of seedlings per 15 m x 15 m plot were 142, 129, 108, 72, and 0 respectively. In addition, to account for the possible effect of tree density in the results, "monoculture" plots were installed in each block at densities corresponding to each mixture proportion (Jolliffe *et al.* 1984).

The experiment is best illustrated by considering the 50:50 proportion. In the 50:50 treatment plots, the native vegetation was removed from 50% of the total ground area using a chess/checker-board pattern. A 1.56 m^2 patch of native vegetation was chosen to be equivalent to one Douglas-fir seedling. (This corresponds to the operational stocking rate, i.e., 2.5 m x 2.5 m spacing in a 25:75 Douglas-fir pinegrass proportion). To kill the native vegetation growing in the seedling squares, Roundup (active ingrdient isopropylamine salt of glyphosate) was hand sprayed at 2.0 kg a.i. per ha in early July, 1985 and late June, 1987. Seedlings were covered to protect them from the herbicide.

Corresponding "monoculture" plots for the 50:50 treatment were pure stands of: (i) Douglas-fir planted at the same spacing as in the 50:50 plot, and (ii) a chess board plot of native vegetation patches alternating with bare ground. Other predetermined ratios were established accordingly. In order to maintain the original seedling densities in the experiment, approximately 800 Douglas-fir seedlings (seedlot 2439, stocktype 1+0 PSB 313) were planted in mid May of 1986 to replace seedlings that had died.

Thirty thermistors (UUA35J1 Fenwall Unicurve) were installed in the various treatment plots of the replacement series experiment to measure soil temperature. Thermistor depths were 0.005 m, 0.05, 0.15 m, 0.30 m and 0.50 m. Soil temperatures were recorded every two weeks at 1300 hr PST using a handheld meter (Model 44011C Atkins Technical Inc.). In

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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.

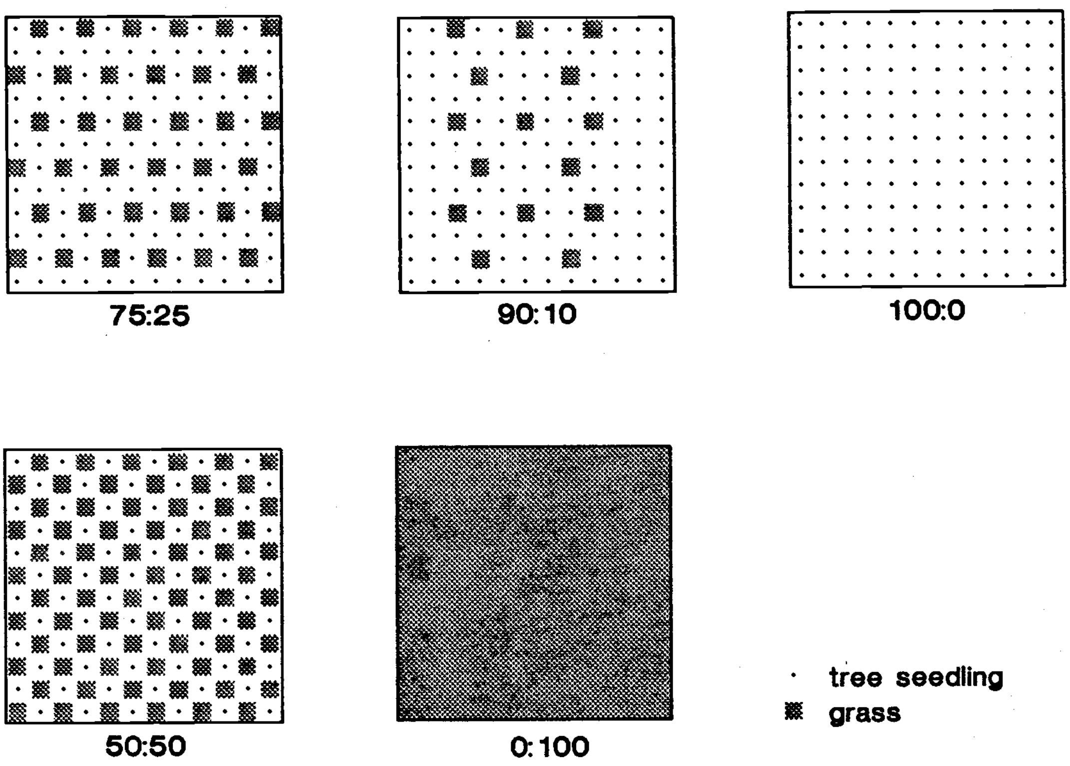

Figure 1.2 Replacement series design treatment proportions Douglas-fir:pinegrass

addition, one depth profile in each 100:0 and 0:100 Douglas-fir:grass treatment plot in Block 3 was continuously monitored using a CR 21X data logger (Campbell Scientific) and UUT51J1 Fenwall Unicurve thermistors. Holes approximately 0.15 m in diameter were excavated to install thermistors. Small access holes for the thermistors were then established in the side of the 0.15 diameter holes at the various depths. The thermistors were inserted and the holes refilled.

To determine the relative competitiveness of the Douglas-fir versus the pinegrass, growth responses of each species in the treatment mixture were compared to the response of each species grown at corresponding densities in monoculture (cf. Jolliffe *et al.* 1984). Conifer measurements included total height, stem diameter (at 1 cm), length of current seasons leader, and maximum canopy diameter and canopy diameter perpendicular to maximum. Tree canopy volumes were calculated on the basis of the equation for a right cone (Wakimoto 1977). Height:diameter ratio and D2H (diameter squared * height) were also calculated. Twenty trees in the interior of each plot were measured on a monthly basis during the 1985 and 1986 growing seasons and at the beginning and end of the 1987 growing season. At the end of each growing season, an additional 20 trees were measured, harvested, oven-dried at 60 ^oC for 24 hours and weighed. Least-squares regression analysis of the relationship of aboveground biomass (W) with the various tree measurements indicated that stem diameter (X) was the best predictive measurement according to the formula:

$$\ln W = -1.024 + 0.431X \; (r^2 = 0.67, p < 0.0001)$$

The condition of every seedling in the replacement series experiment was subjectively assessed each month throughout all three growing seasons. The condition code for live trees was based on the amount of foliage yellowing or browning: good was less than 1% chlorosis; fair showed between 1% and 5% chlorosis; poor showed between 5% and 30% chlorosis; moribund was greater than 30% chlorotic foliage. Mortality also was recorded. In addition, other indicators of seedling vigor, including degree of wilt, frost damage, insect damage, and stem damage by rodents were noted.

In 1985, growth rate and yield of the pinegrass were quantified using monthly percent cover estimates of ten grass patches per treatment. In addition, 30 representative biomass patches were selected outside of the treatment area and the vegetation was clipped to two cm above the ground. Pinegrass was separated from the other forbs, and the material was oven dried at 60 ^oC for 24 hours and weighed. The aboveground biomass (dry weight) (Y) was related to percent cover (X) using least-squares regression techniques. The equations for the June and July collection periods respectively were:

$Y = 2.22238 + 2.76828X$ (r^2=0.96, p<0.001);

$Y = 22.09868 + 1.56925X$ (r^2=0.85, p<0.0001)

Because the correlation between percent cover and dry weight was not sensitive to monthly changes, in 1986, individual pinegrass tillers were measured each month. Grass growth measurements included height, number of leaves, and number of connected tillers. Ten tillers in each of ten patches per treatment were monitored for the 1986 growing season. Least-squares regression analysis was used to predict aboveground biomass of the individual tillers (Y) from tiller height (X) according to the formula:

$Y = -0.010144 + 0.002582X$ (r^2=0.88, p<0.0001)

In addition, leaf area of the individual tillers (Y) was predicted from height (X):

$\ln(Y) = 2.57807 + 1.39216X$ (r^2=0.92, p<0.0001)

In 1986 and 1987, percent cover of each treatment was estimated at the time in the growing season when leaf extension was greatest.

Neighbourhood design

Interference between plants is affected both by stand and individual plant characteristics. Whereas the replacement series design enables a determination of dominance or species shifts on a stand basis, the neighbourhood approach is useful to examine the response of individual plants to their neighbours. The neighbourhood design uses the space available to a plant as an integrator of resource availability (cf. Mack and Harper 1977, Waller 1981, Liddle *et al.* 1982, Weiner 1982, Goldberg and Werner 1983). In this neighbourhood study, performance of individual Douglas-fir seedlings was compared on the basis of abundance of neighbouring pinegrass-dominated vegetation.

In the middle of May 1986 approximately 230 Douglas-fir seedlings (seedlot 2439, stocktype 1+0 PSB 313)[1] were planted into undisturbed dense pinegrass dominated vegetation. Dense areas of pinegrass were chosen to minimize the effect of environmental differences (Goldberg and Werner 1983). Each seedling represented the centre of a 1.25 m radius circular sample plot (4.9 m^2 neighbourhood). Eleven treatments to manipulate leaf area index were randomly assigned to the sample plots and replicated at least 20 times. The eleven treatments are summarized in Table 1.1.

Goldberg and Werner (1983) stress that competition measured on a per-amount basis (e.g. biomass) will provide a better indicator of resource use than numbers of individuals. Because Petersen (1985b) found pinegrass leaf area index (LAI) to be a sensitive indicator of critical competition levels in young ponderosa pine plantations, LAI was chosen to quantify the

Table 1.1 Neighbourhood experiment treatment descriptions

Treatment 1: no vegetation removal (control).

Treatment 2: complete vegetation removal within a 30 cm radius of the plot centre (6% reduction in neighbouring plants).

Treatment 3: complete vegetation removal within a 60 cm radius of the plot centre (25% reduction in neighbouring plants).

Treatment 4: complete vegetation removal within a 90 cm radius of the plot centre (50% reduction in neighbouring plants).

Treatment 5: complete vegetation removal (100% reduction in neighbouring plants).

Treatment 6: vegetation cover reduced to 25% (vegetation removed in a chess-board pattern of approximately 2 cm x 2 cm squares to ensure an evenly distributed 25% reduction in neighbouring plants).

Treatment 7: vegetation cover reduced to 50% (vegetation removed in a chess-board pattern of approximately 2 cm x 2 cm squares to ensure an evenly distributed 50% reduction in neighbouring plants).

Treatment 8: vegetation cover reduced to 75% (vegetation removed in a chess-board pattern of approximately 2 cm x 2 cm squares to ensure an evenly distributed 75% reduction in neighbouring plants).

Treatment 9: vegetation clipped to a height of 15 cm (vegetation clipped to maintain neighbouring plants at a height of 15cm).

Treatment 10: vegetation clipped to a height of 8 cm (vegetation was clipped to maintain neighbouring plants at a height of 8 cm).

Treatment 11: vegetation clipped to a height of 2 cm (vegetation was clipped to maintain neighbouring plants at a height of 2 cm).

amount of neighbouring vegetation. LAI was measured using a point intercept frame consisting of four spokes with 14 pins each placed at 4 cm intervals beginning 9 cm from the tree (Mueller-Dombois and Ellenberg 1974). The spokes were placed around the tree oriented to the north, east, west and south. The number of times a pin intercepted a green plant part represents a measure of the LAI. A number of variables incorporating distance and leaf area were calculated to act as indices of the level of neighbourhood interference experienced by the individual seedlings. These competition indices included:

(1) **AvLA**=Average leaf area index for the entire 1.25 m radius circular neighbourhood.

(2) **AvLA1**=Average leaf area index for the centre 0.30 m radius circular neighbourhood.

(3) **AvLA2**=Average leaf area index for the neighbourhood starting at a distance of 0.30 m and extending to approximately 0.60 m.

(4) **AvLA3**=Average leaf area index for the neighbourhood starting at a distance of 60 cm and extending out to approximately 0.90 m.

(5) **AvLAD123**=Average leaf area index of each of the three concentric rings (numbers 2-4 above) divided by the median distance to each ring squared.

$$AvLAD123=AvLA1/13.25^2 + AvLA2/44^2 + AvLA3/69^2.$$

(6) **AvLAD**=Average leaf area index at 0.04 m intervals divided by the distance to the pin squared.

Douglas-fir survival, vigour and growth performance were measured as described for the replacement series experiment. Mortality and condition were assessed monthly throughout the two growing seasons. All growth measurements were taken in the late summer after leaf extension and height growth were complete but before the grass had begun to senesce.

Data Analyses

Data were analysed using Statistical Analysis System programs (SAS Institute 1985). The results of both the replacement series and neighbourhood experiments are based on the 1987 data.

Replacement series experiment

The replacement series analyses followed procedures described in Harper (1977) and Jolliffe *et al.* (1984). Growth rates of Douglas-fir and pinegrass were calculated as described in Hunt (1982).

Neighbourhood experiment

For the neighbourhood experiment planned contrasts were examined to compare effects of different qualitative treatment combinations on both seedling size and vigour (Petersen 1985a). Analyses addressed the following questions.

(1) Does no removal differ from complete removal? (Treatment 1 versus 5)

(2) Does any amount of vegetation removal differ from no removal? (Treatments 2-11 versus 1)

(3) Are partial removal treatments as effective as complete removal to a 1.25 m radius? (Treatments 2,3,4,6,7,8,9,10,11 versus 5)

(4) Do treatments where the vegetation is completely removed to varying distances from the seedling differ from other vegetation manipulation treatments? (Treatments 2-5 versus 6-11)

(5) Do treatments where vegetation is completely removed to either 0.30, 0.60 or 0.90 m from the seedling differfrom complete removal to a 1.25 m radius? (Treatments 2-4 versus 5)

(6) Do treatments where vegetation is completely removed to varying distances differ from the treatments where the vegetation cover is evenly reduced around the seedling? (Treatments 2-5 versus 6-8)

(7) Do clipping treatments differ from non-clipping treatments? (Treatments 9-11 versus 2-8)

(8) Does clipping to the ground differ from partial clipping treatments? (Treatment 11 versus 9,10)

Categorical analyses involving a maximum likelihood fit of proportions were used to examine the probability of vigour classes at various competition levels (McCullagh and Nelder 1983). The data was fit to the following functions:

$$\log (p_0/p_3)=a_0+b_0\mathrm{AvLA1}$$
$$\log (p_1/p_3)=a_1+b_1\mathrm{AvLA1}$$
$$\log (p_2/p_3)=a_2+b_2\mathrm{AvLA1}$$

where p is the probability of each vigour class denoted as 0,1,2 and 3 respectively referring to good, fair, poor and moribund and AvLA1 is a competition index. Linear regression models were used to select the most sensitive conifer growth variables and the most predictive interference indices (Neter *et al.* 1983). In order to measure prediction bias, the predictive value of the neighbourhood model was tested on a separate data set. The test data set was obtained using approximately 65 of the Douglas-fir seedlings planted in 1986 into the replacement series experiment; the same seedling measurements and neighbourhood interference variables outlined above were made.

RESULTS AND DISCUSSION

Growing Season Weather Observations

The spring of 1985 was hot and dry, followed by a cool, wet June, a hot, very dry July, and a cool, dry August. At Williams Lake Airport, which has similar topography as the study site and is the nearest long term data source (approximately 50 km north of the study site, in the IDFb), May precipitation was 42% of the average, June 139% of average and July and August 34% of average. The mean air temperature in May was 1.5 ^{o}C above average and July mean air temperature was 2.3 ^{o}C above average. At the study site an extended dry period occurred from June 25 to August 2 during which less than 10 mm of rain fell. High temperatures (maxima ranged from 16.9 to 31.3 ^{o}C) and low relative humidities resulted in a mean July vapor pressure deficit of 2.5 kPa with deficits frequently greater than 3.0 kPa and occasionally greater than 3.5 kPa (Figure 1.3).

In contrast to 1985, the spring of 1986 was cool and moist, June was warm and dry, July was cold and moist, and August hot and dry. At Williams Lake Airport May precipitation was 154% of average, June rainfall was 80% of average with mean daily air temperature 1 ^{o}C above average, July rainfall was 139% of average and mean daily temperature 1.4 ^{o}C lower than average and August had 59% of the normal precipitation while the temperature was 1.9 ^{o}C above average. During 1986 the summer dry period did not begin until August when the vapor pressure deficit averaged 2.0 kPa (Figure 1.4).

In 1987 the spring was warm and dry, followed by a hot, dry June and July and a cool dry August. At Williams Lake Airport, precipitation was 16%, 120%, and 44% of average for April, May and June respectively while mean monthly air temperatures were 1.9, 0.7 and 2.2 ^{o}C above average for the same respective months. July and August precipitation at Williams Lake Airport was slightly below normal and September was very dry with only 13% of the average precipitation. An extended dry period began at the site on August 6 and continued through to October during which time there was less than 10 mm of precipitation (Figure 1.5).

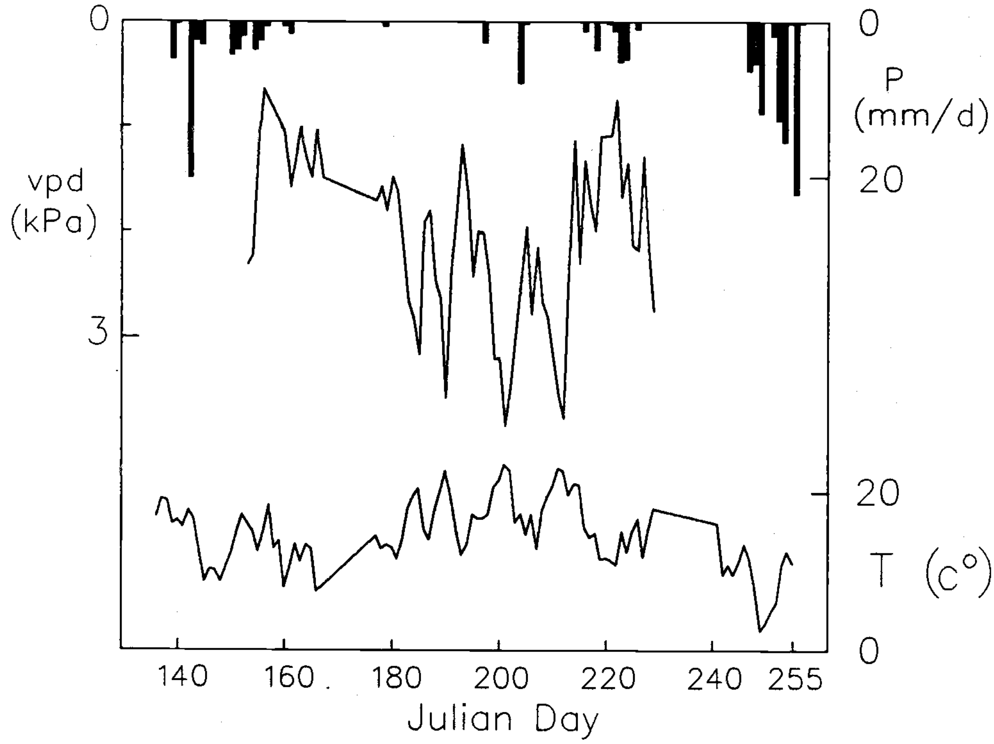

Figure 1.3 Average air temperature (T), maximum vapour pressure deficit (vpd) and precipitation (P) over the course of the 1985 growing season.

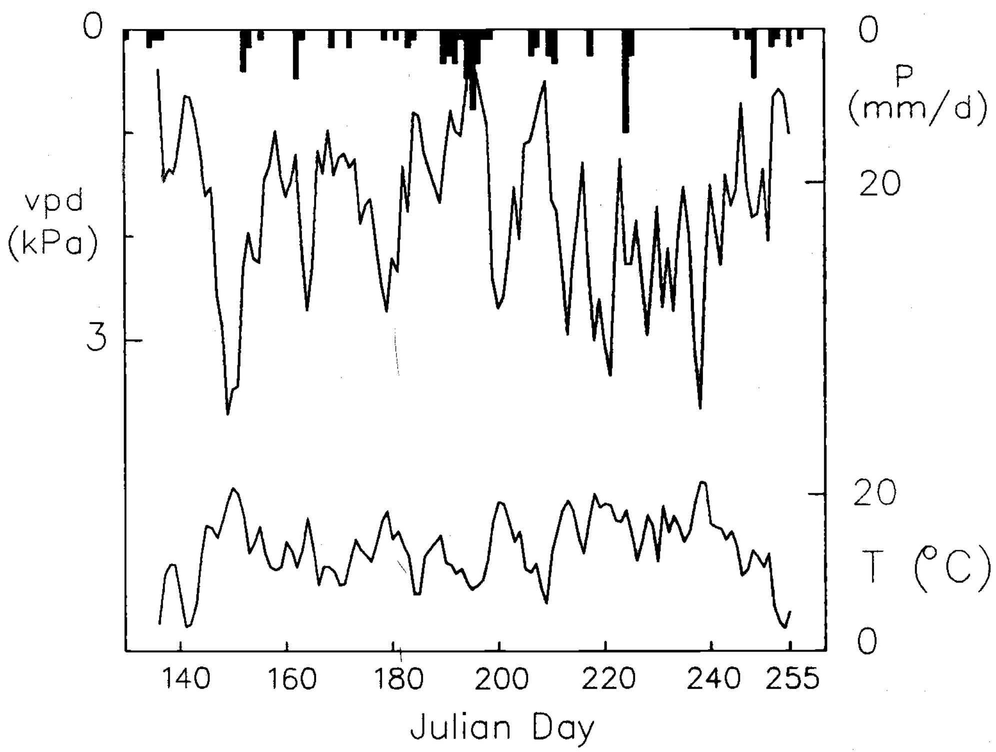

Figure 1.4 Average air temperature (T), maximum vapour pressure deficit (vpd) and precipitation (P) over the course of the 1986 growing season.

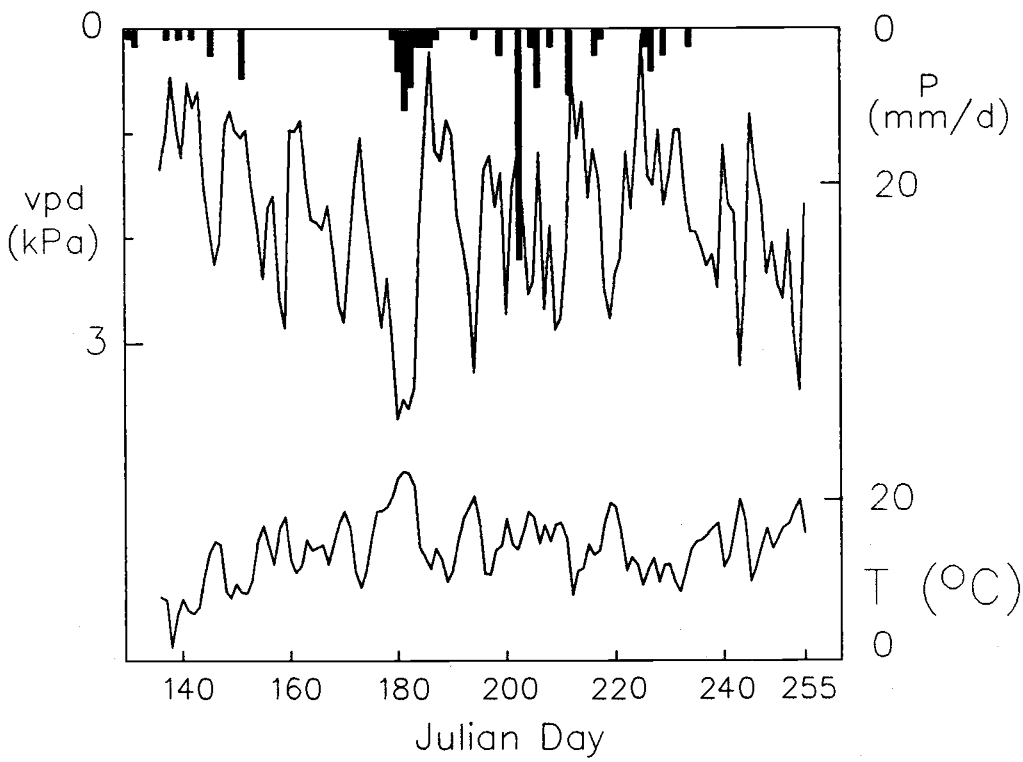

Figure 1.5 Average air temperature (T), maximum vapour pressure deficit (vpd) and precipitation (P) over the course of the 1987 growing season.

Replacement Series Experiment

The results of the replacement series experiment during the first three years after outplanting indicated that the densities of the mixed Douglas-fir:pinegrass populations were too low for individuals to interfere with one another (Table 1.2). Thus, the criteria of density-independant yield (i.e., constant final yield) has not yet occurred in this experiment (Harper 1977). This observation is not surprising since by choosing to examine a stand density similar to operational planting standards, the seedlings, as spaced, were too small to interact competitively. As a result, there was no difference in seedling growth, survival or vigour between treatments when the effect of planting density was considered (Table 1.2).

Although treatment yields were not significantly different, using sample blocks was highly effective in increasing the experiment's precision. Mean block Douglas-fir seedling yields, summarized in Table 1.3, suggest that Block 3 trees were much larger after the third growing season. Block differences are discussed further in terms of survival and vigour.

Douglas-fir survival

Overall survivorship of spring 1985 planted trees was 93% in the fall of 1985, decreasing to 68% in the fall of 1986, and 43% by the fall of 1987 (Table 1.4). More trees survived in Block 3 than in the other three blocks in the fall of 1985. This trend continued such that by the fall of 1987 mortality was only 3% in Block 3 compared to 13%, 16% and 11% in blocks 1, 2 and 4 respectively. Because Block 3 was planted with seedlings grown at a different nursery than the other three blocks, differences in seedling vigour due to cultural or storage conditions are suspected causes for the differences in tree mortality observed. In addition, it is possible that an underlying site difference exists or slight differences in the degree of accumulated stresses have become compounded over time. It was apparent that blocks 2 and 3 received less visible frost damage in 1985 than blocks 1 and 4. Furthermore, because Block 3 was the first planted seedlings planted there spent two to three fewer days in cold storage than those planted in the other blocks.

The survival of the seedlings planted in 1986 to replace those that had died followed similar trends as those planted in 1985 (Table 1.4). Survival in the fall of 1986 was 92%. After a second growing season survival had declined to 76%.

Table 1.2 Replacement series experiment treatment mean yields and relative yields of Douglas-fir and pinegrass (relative yield=yield in mixture/ yield in monoculture)

Year	Proportion	Monoculture Yield (g/m^2)	Mixture Yield (g/m^2)	Relative Yield
1985				
	100% Pinegrass	32.4	-	-
	50% Pinegrass	11.6	13.4	1.2
	25% Pinegrass	6.2	4.9	0.8
	10% Pinegrass	2.6	1.7	0.7
	100% Douglas-fir	0.99	-	-
	90% Douglas-fir	0.91	0.89	1.0
	75% Douglas-fir	0.80	0.83	1.0
	50% Douglas-fir	0.50	0.51	1.0
1986				
	100% Pinegrass	41.3	-	-
	50% Pinegrass	19.0	22.7	1.2
	25% Pinegrass	12.3	8.7	0.7
	10% Pinegrass	9.8	2.9	0.3
	100% Douglas-fir	1.54	-	-
	90% Douglas-fir	1.94	1.42	0.7
	75% Douglas-fir	1.38	1.65	1.2
	50% Douglas-fir	1.12	0.89	0.8
1987				
	100% Pinegrass	35.1	-	-
	50% Pinegrass	15.2	13.7	0.9
	25% Pinegrass	9.1	6.9	0.8
	10% Pinegrass	3.1	2.3	0.7
	100% Douglas-fir	2.50	-	-
	90% Douglas-fir	5.10	2.68	0.5
	75% Douglas-fir	2.83	3.25	1.1
	50% Douglas-fir	3.22	1.97	0.6

Table 1.3 Replacement series experiment 1987 mean yield Douglas-fir by block

Block	1	2	3	4
Mean Aboveground Biomass (g)	3.3	4.3	10.2	5.7
Number of Trees Measured	68	77	146	118

Table 1.4 Percent survival of trees planted in 1985 and 1986 in a replacement series experiment

Date	Survival Trees Planted 1985 (%)	Survival Trees Planted 1986 (%)
Fall 1985	93	-
Spring 1986	73	-
Fall 1986	68	92
Spring 1987	61	85
Fall 1987	43	76

Douglas-fir vigour

Seedling vigour over the first growing season (1985) after outplanting tended to decline corresponding to accumulated stresses (Table 1.5). Obvious environmental stresses included a severe mid-June frost that damaged 20% of the seedlings and subsequent water stress that resulted in 30% of the live seedlings wilting by September. Thus the 20% mortality which occurred over the first winter was not surprising. Probabilities of freezing temperatures after specific dates in June, predicted on the basis of longterm temperature data (1.5 m above ground level) from the Williams Lake Airport, are as follows: 50% of the time after June 3, 33% after June 11, and 25% after June 14 (Environment Canada 1982). Since seedlings typically begin flushing in early June on these sites, based on these data frost damage in at least one in three years would be expected. This estimate is conservative as temperatures at seedling height are typically cooler than at 1.5 m.

Table 1.5 Vigour of trees planted in 1985 and 1986 in a replacement series experiment (<5% chlorosis=good-moderate vigour, 5-30% chlorosis=poor vigour, >30% chlorosis=moribund)

Date	Vigour Class	Trees Planted 1985	Trees planted 1986
		(% of live trees)	
Fall 1985			
	Good-Moderate	61	-
	Poor	21	-
	Moribund	19	-
Spring 1986			
	Good-Moderate	74	-
	Poor	23	-
	Moribund	3	-
Fall 1986			
	Good-Moderate	76	80
	Poor	19	17
	Moribund	6	4
Spring 1987			
	Good-Moderate	36	36
	Poor	24	44
	Moribund	39	20
Fall 1987			
	Good-Moderate	55	50
	Poor	29	40
	Moribund	16	10

In addition to frost damage and drought stress, many seedlings developed signs of other stress. For example, five percent did not flush and one percent developed stunted needles. These symptoms suggest that tree seedling quality at the time of planting may have contributed to the mortality[3] .

Vigour of the 1985 and 1986 planted seedlings remained fairly constant over the 1986 growing season. There was no obvious evidence of frost damage, wilting, or seedling quality problems. The cooler, moister weather during the summer of 1986 likely contributed to improved seedling vigour. During the winter of 1986-87, however, vigour declined appreciably. For example, vigour of seedlings planted in 1985 declined from 75% good/moderate and 6% moribund to 36% good/moderate and 39% moribund over the winter (Table 1.5). Approximately 6% of the Douglas-fir seedlings showed evidence of rodent damage in the spring of 1987.

3 D. Deyoe, Department of Forest Science, Oregon State University, personal communication, October 1986.

Interestingly, 81% of the rodent damaged trees occurred in Block 3 where the majority of trees 70% were still classified as being in good/moderate condition. Damage generally consisted of one or more diagonal or vertical toothcuts on the lower stem exposing the sapwood. Approximately 15% of the trees were infected with Cooley spruce gall aphids (*Adelges cooleyi* Gillette); these infected seedlings also tended to be the healthier members of Block 3.

Minor frost damage was recorded in 1987. Minimum temperatures at 0.15 m above ground at the site were -0.6, -2.6,-0.1,-3.4 and 0 ^{o}C on June 1, 2, 7, 23 and 24, 1987 respectively (Figure 1.6). Typically the frost affected only a few of branches of new foliage and it was the healthier seedlings that tended to be affected. Obviously, timing of frost relative to flushing time was an important factor. Furthermore, flushing time may be tied to seedling vigour.

Douglas-fir and pinegrass growth rates

The average aboveground relative growth rate (RGR) of each species over the 1986 growing season is shown in Figure 1.7. The Douglas-fir tended to maintain a constant though low RGR throughout the summer whereas pinegrass RGR peaked rapidly in the spring and then declined in association with maturation and senescence. Because moisture is considered a limiting resource in these IDF ecosystems, rapid growth of the pinegrass early in the season when moisture is most available gives it a significant competitive edge over Douglas-fir seedlings that have not yet developed extensive root systems.

Mean RGRs of Douglas-fir seedlings were -0.0009 g/g/d (S.E. 0.0002), 0.0042 g/g/d (S.E. 0.0002), and 0.0005 g/g/d (S.E. 0.00002) during the 1985, 1986, and 1987 growing seasons respectively (early June through mid-August). These results are consistent with the survival and vigour data. In 1985 the seedlings did not grow, in fact many decreased in size due to declining vigour. The second summer was more favourable and seedling growth reflected improved moisture conditions. In 1987, growth rates were lower than 1986 presumably because conditions were drier than in 1986.

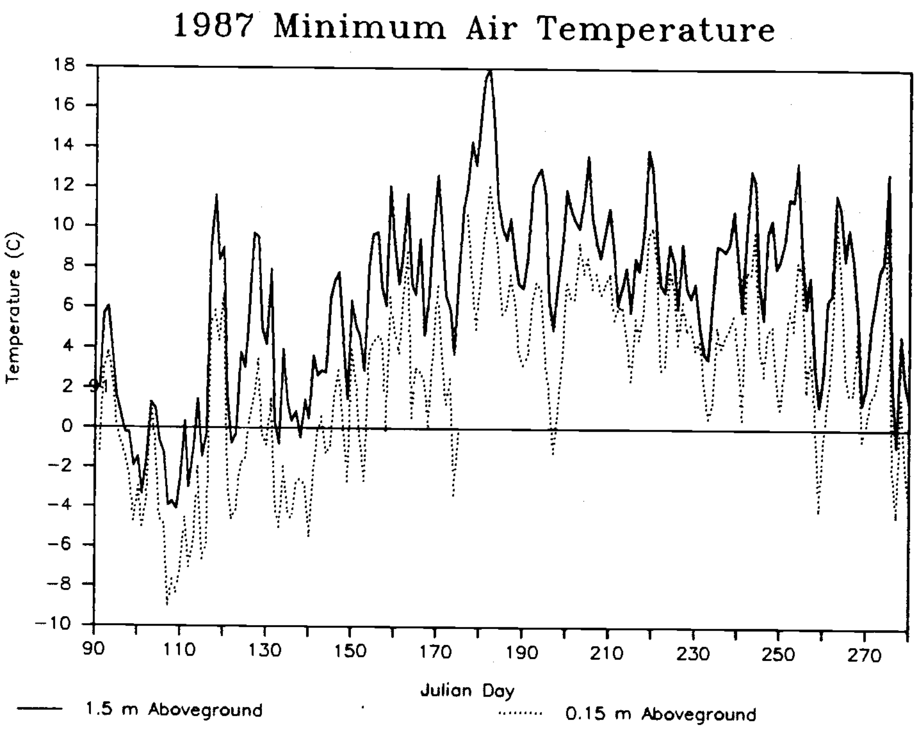

Figure 1.6 Minimum air temperature during the 1987 growing season at 1.5 m and 0.15 m above the ground.

Soil temperatures

Daily variations in soil temperature during the 1987 growing season at three depths in the seedling root zone are depicted in figures 1.8 to 1.10 for the 100% grass and 100% tree treatments. (Note the change in the scale of the graphs in figures 1.8 to 1.10.) Removing the native grass vegetation increased the diurnal flux and promoted soil warming earlier in the spring at the 0.05 m and 0.15 m depths. There was little difference between the two treatments at the soil surface (0.005 m). Figure 1.11 further illustrates the effect that removing native vegetation has on mean soil temperatures (0.05 m and 0.15 m).

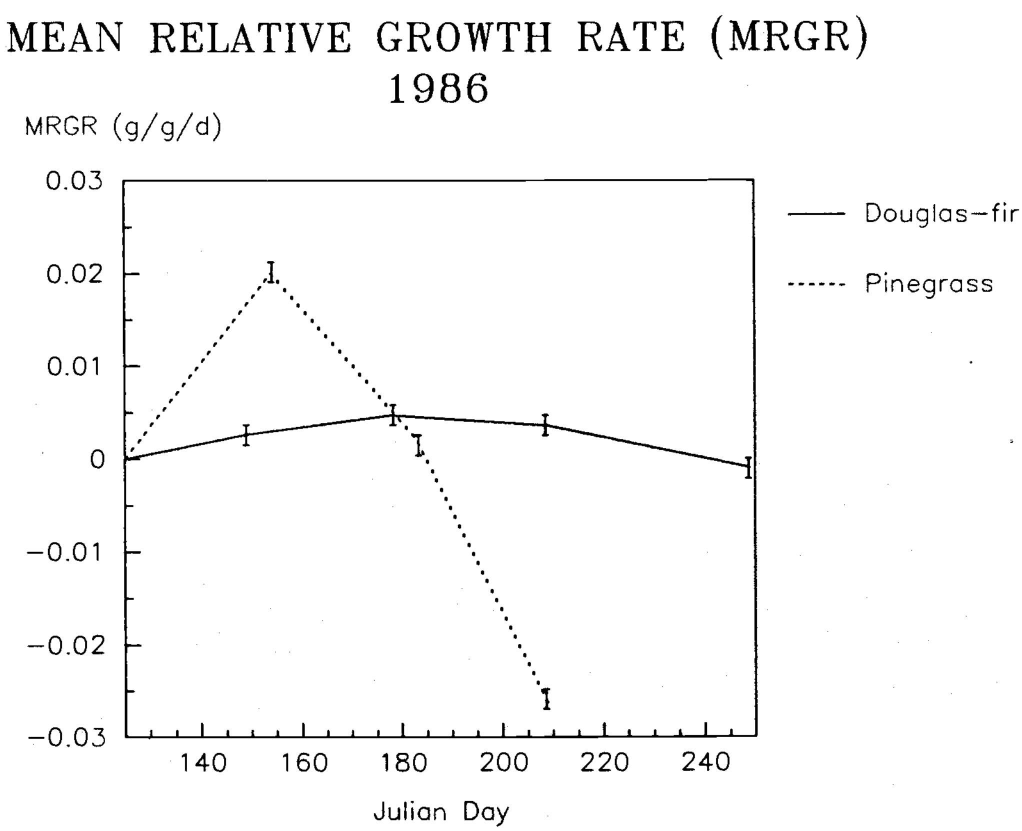

Figure 1.7 Mean relative growth rates of Douglas-fir and pinegrass over the course of the 1986 growing season. Error bars are 1 S.E.

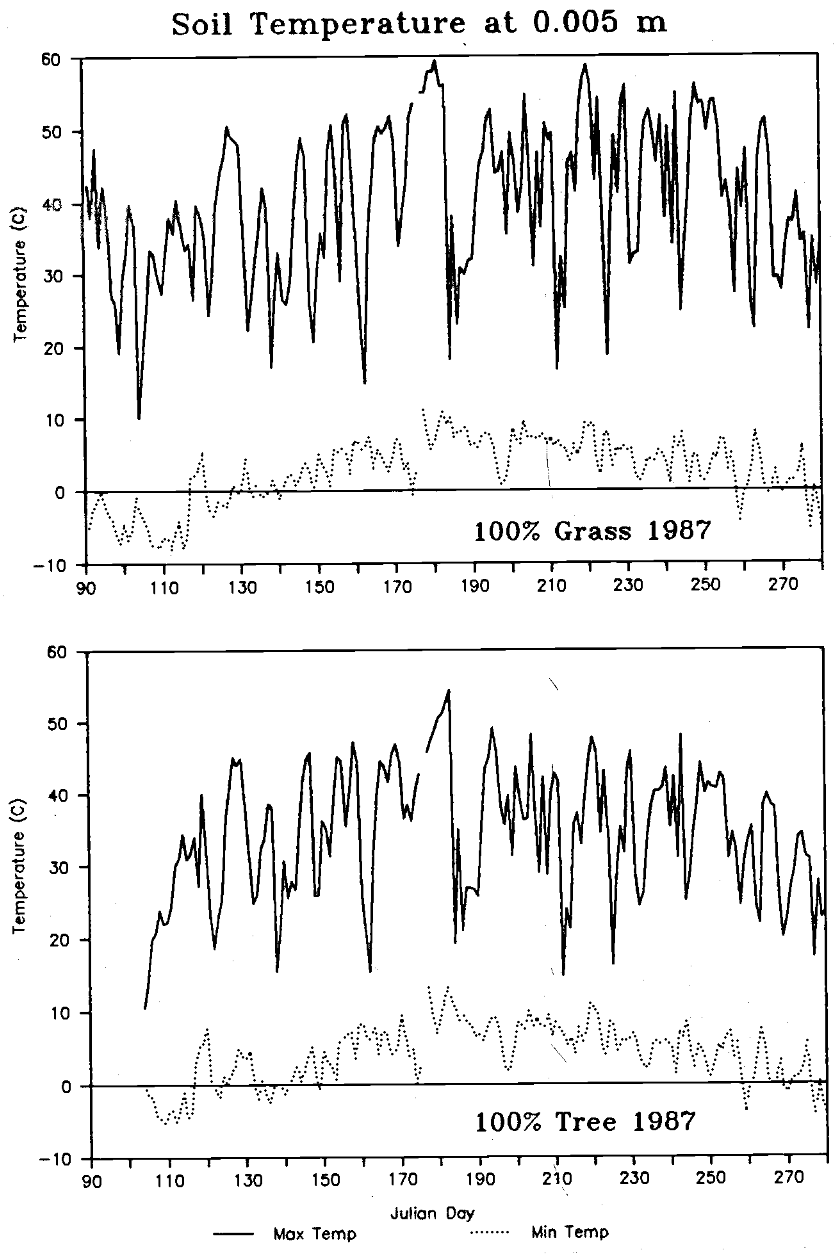

Figure 1.8 Maximum and minimum soil temperatures over the course of the 1987 growing season at 0.005 m below the surface in the 100% grass and 100% tree treatments.

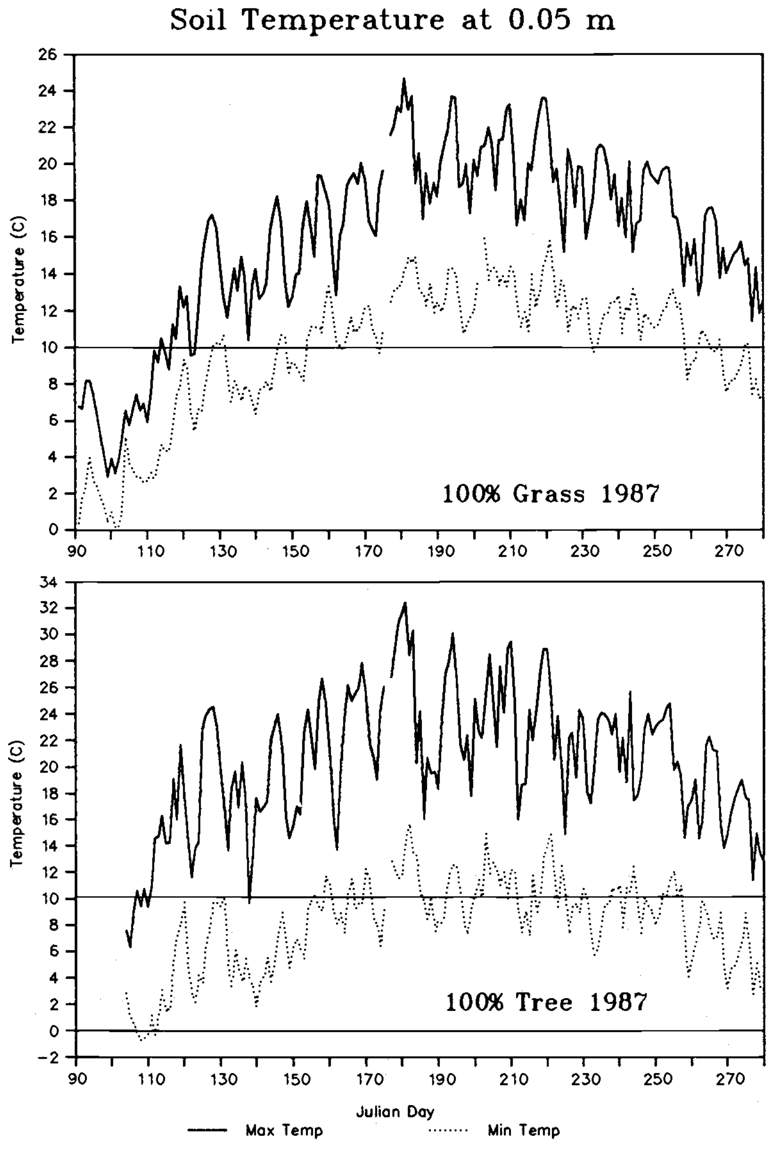

Figure 1.9 Maximum and minimum soil temperatures over the course of the 1987 growing season at 0.05 m below the surface in the 100% grass and 100% tree treatments. Note the temperature scale used differs for the two treatments.

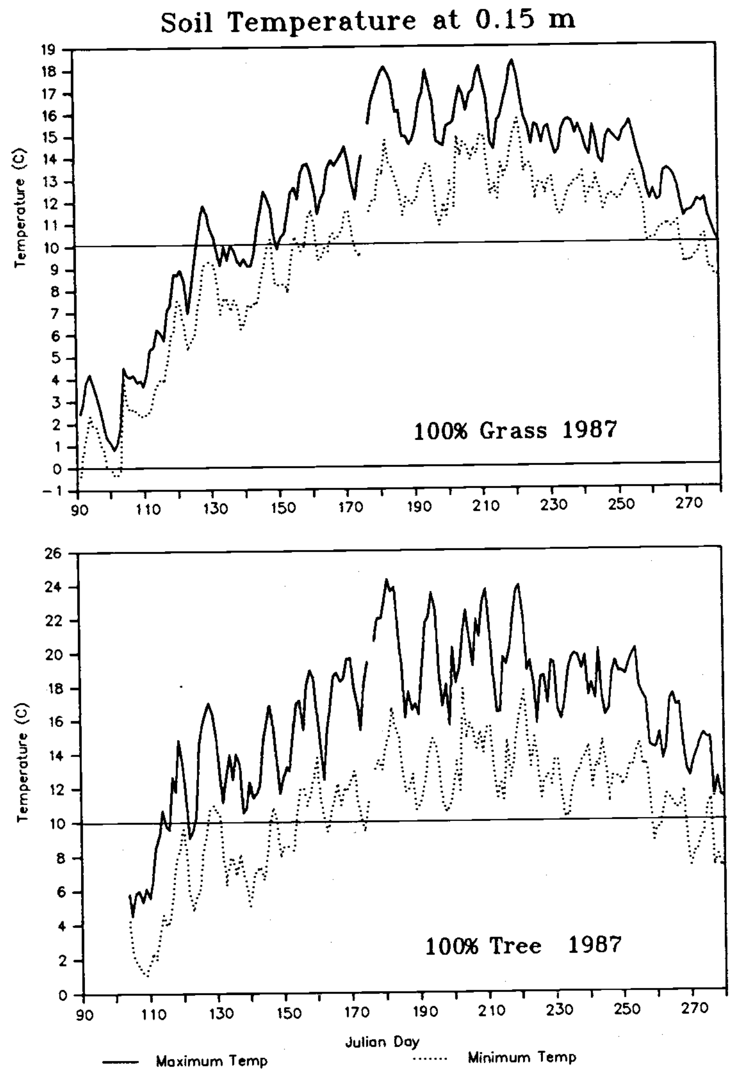

Figure 1.10 Maximum and minimum soil temperatures over the course of the 1987 growing season at 0.15 m below the surface in the 100% grass and 100% tree treatments. Note the temperature scale used differs for the two treatments.

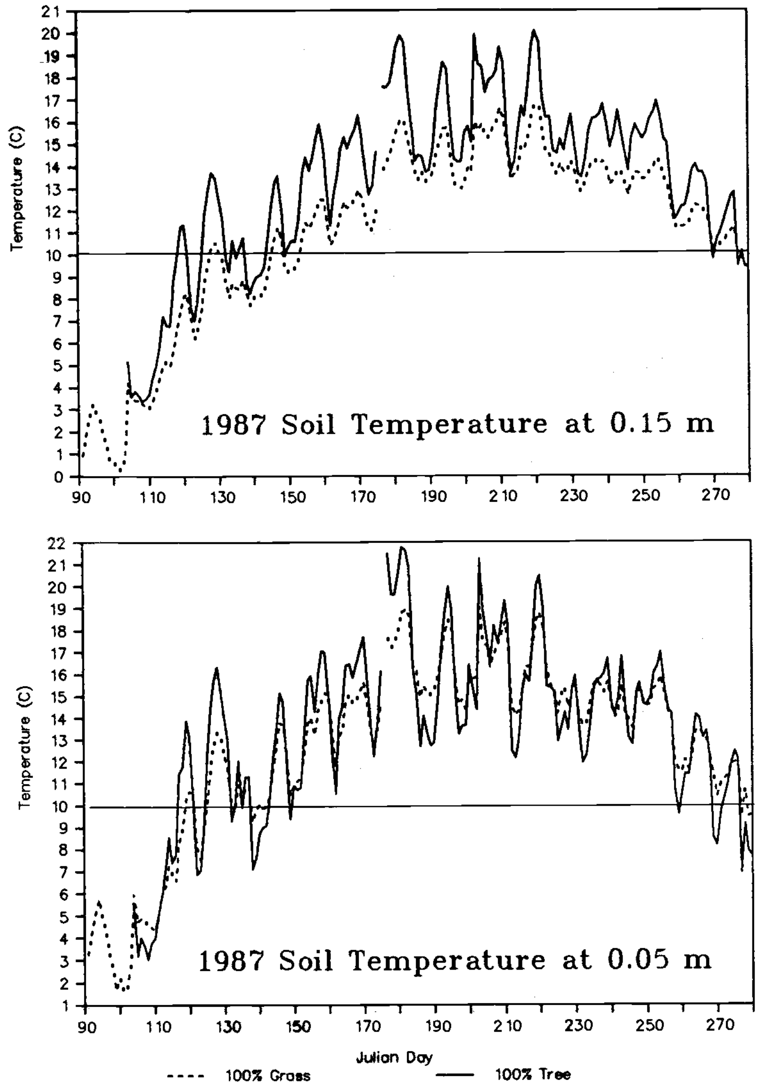

Figure 1.11 Comparison of the average soil temperature at 0.15 m and 0.05 m below the surface over the course of the 1987 growing season in the 100% grass and 100% tree treatments. Note the temperature scale used differs for the two treatments.

The above results indicate that the study site is dry and that moisture stress during the growing season can be expected to deter survival and growth of planted Douglas-fir seedlings. Because root proliferation and water uptake slows as the soil dries, it is critical that root extension into the deeper moister soil layers occurs quickly. In general conifers have two peak periods of root growth (Ritchie and Dunlap 1980). The main period occurs in the spring and continues until shoot growth begins. The second occurs in the fall after bud set and before true dormancy. The length of these periods depends on soil moisture and soil temperature (Running and Reid 1980). Input from snow at the study site likely ensures that root growth is not limited by soil moisture in early spring. However, lack of moisture is likely to be a concern in the fall when precipitation is unreliable and soils are typically very dry after the summer. The unreliability of September rainfall is exemplified by data for the 1961-87 period at the Williams Lake Airport. During that period, in 50% of the years, September rainfall was one standard deviation (≤11 mm) or more below the longterm monthly average (30 mm).

Soil temperature likely affects the duration of both spring and fall growth activity periods. Lopushinsky and Kaufman (1984) reported that cold soil temperatures impeded root growth and reduced water uptake in two year old Douglas-fir (var.*glauca*) seedlings. There is evidence that abrupt changes in root resistance are typical at low soil temperatures. Running and Reid (1980) reported that these changes are associated with a root membrane barrier to water uptake. Interestingly, van den Driessche (1984) found that under natural conditions root growth of two year-old Douglas-fir (var. *menziesii*) was best at soil temperatures of 20 °C. Ritchie and Dunlap (1980) reported that optimal soil temperatures for root growth of a number of species range from 18 to 25 °C. Heninger and White (1974) reported that Douglas-fir (var. *glauca*) seedlings during the first eight weeks after germination tolerated a wide range of soil temperatures with best growth occurring between 15 and 27 °C. Root penetration was greatest at 23 °C. Stone *et al.* (1962) similarly found root elongation of three year-old Douglas-fir seedlings to be best at 20 °C; very little growth occurred below approximately 15 °C. Marshall and Waring (1985), however, recorded significant root growth between progressive sampling dates for two year-old Douglas-fir (var.*menziesii*) seedlings grown at both 10 °C and 20 °C.

Despite these studies, it is difficult to determine specific soil temperature thresholds for minimum and optimum Douglas-fir root growth since many variables must be controlled. For example, the effect of soil temperature on root growth is complicated by soil moisture and carbohydrate status, and the relationships between physiological and ecological soil temperature optima must be considered (Lyr and Hoffmann 1967). However, if one assumes a soil temperature of 10-15 ^{o}C to be the threshold for measurable root extension then, during the 1987 growing season Douglas-fir root growth in the 100% tree plots likely began around the beginning of May and continued until the first week of June when flushing began (figures 1.9 and 1.10). Figure 1.11 provides a comparison of average soil temperatures at 5 cm and 15 cm depths for the 100% grass and 100% tree treatments. These graphs indicate that seedling root growth likely is more restricted in the 100% grass treatment than in the 100% seedling treatment due to lower spring and fall soil temperatures. Even with vegetation removal, in the spring favourable root growth conditions would be limited to only one month. Given this observation, it is likely that on this type of site forest managers face an extremely narrow planting window for Douglas-fir seedlings.

Finally, it should be noted that important and complex inter-relationships exist between soil temperature and soil moisture. This latter topic is discussed in detail in Chapter Three.

Neighbourhood Experiment

The results and discussion of the neighbourhood experiment are presented below. The neighbourhood experiment treatments are summarized in Table1.1.

Douglas-fir survival

After the two growing seasons Douglas-fir survival in the neighbourhood experiment ranged from 33% in treatment 9 to 95% in treatment 5 (tables 1.1 and 1.6). Although there was no obvious damage due to frost, wilting or stock quality problems in the first summer (1986), during the winter, survivorship declined. As in the replacement series experiment, rodent damage appeared to contribute to declining vigour and increased mortality.

Douglas-fir vigour

Table 1.7 shows that the distribution of seedlings by vigour class changed very little over the two growing seasons for those treatments involving complete vegetation removal around the seedling (treatments 2-5, Table1.1). Vigour, however, declined appreciably in the other vegetation removal treatments and the control (treatments 6-11 and 1, Table1.1).

Table 1.6 Neighbourhood experiment Douglas-fir percent survival (treatments are described in Table 1.1)

Date	Treatment										
	1	2	3	4	5 (%)	6	7	8	9	10	11
Fall 1986	95	82	95	95	100	90	95	85	81	85	100
Spring 1987	64	71	76	80	100	68	95	62	67	60	71
Fall 1987	36	62	62	75	95	45	85	52	33	35	43

Table 1.7 Neighbourhood experiment Douglas-fir vigour (<5% chlorosis=good-moderate vigour, 5-30% chlorosis=poor vigour, >30% chlorosis=moribund). (Treatments are described in Table 1.1)

Date		Treatment										
	Vigour Class	1	2	3	4	5 (%)	6	7	8	9	10	11
Fall 1986												
	Good-Moderate	52	78	85	84	100	74	76	65	47	47	57
	Poor	33	22	10	11	0	11	19	18	47	35	24
	Moribund	14	0	5	5	0	16	5	18	6	18	19
Spring 1987												
	Good-Moderate	50	80	88	94	95	80	74	85	57	58	53
	Poor	21	7	6	6	0	7	11	0	14	17	47
	Moribund	29	13	6	0	5	13	16	15	29	25	0
Fall 1987												
	Good-Moderate	38	77	92	87	90	30	41	27	43	14	22
	Poor	38	15	8	7	5	59	24	45	43	43	56
	Moribund	25	8	0	7	5	20	35	27	14	43	22

Table 1.8 Neighbourhood experiment contrasts for the effects of qualitative treatments on Douglas-fir seedling vigour (Treatments are described in Table 1.1)

Contrast	Degrees of Freedom	Chi-Square	Probability
Treatment 1 versus 5	3	16.34	0.0010
Treatment 1 versus 2-11	3	3.51	0.3198
Treatment 5 versus 2-4,6-11	3	16.01	0.0011
Treatments 2-5 versus 6-11	3	38.49	0.0001
Treatments 2-4 versus 5	3	5.26	0.1540
Treatments 2-5 versus 6-8	3	21.25	0.0001
Treatments 2-8 versus 9-11	3	19.39	0.0002
Treatment 11 versus 9, 10	3	0.83	0.8419

Table 1.9 Neighbourhood experiment contrasts for the effects of the qualitative treatments on Douglas-fir stem diameter (Treatments are described in Table 1.1)

Contrast	Degrees of Freedom	Chi-Square	Probability > F
Treatment 1 versus 5	1	8.04	0.0054
Treatment 1 versus 2-11	1	0.14	0.7120
Treatment 5 versus 2-4,6-11	1	23.46	0.0001
Treatments 2-5 versus 6-11	1	29.55	0.0001
Treatments 2-4 versus 5	1	4.49	0.0363
Treatments 2-5 versus 6-8	1	17.54	0.0001
Treatments 2-8 versus 9-11	1	10.48	0.0016
Treatment 11 versus 9, 10	1	1.48	0.2267

Overall there was a significant difference among treatments for the planned contrasts comparing the effects of different qualitative treatment combinations on seedling vigour (X^2=69.7, d.f. 30, p=0.0001). Table 1.8 lists the p-values for the significant contrasts of maximum likelihood estimates. From this table it can be seen that the pooled vigour ratios for complete vegetation removal to a distance of 1.25 m (100% reduction) are significantly different than any of the other partial vegetation removal treatments (treatment 1 versus 5, and treatment 5 versus 2-4, 6-11, Table 1.1). Furthermore, pooled vigour ratios of treatments where vegetation was completely cleared to various distances from the seedling were significantly different from all other vegetation manipulation treatments (treatments 2-5 versus 6-11, Table 1.1) and from treatments just involving evenly distributed vegetation reductions (treatments 2-5 versus 6-8) (Table 1.8). Warmer early spring soil temperatures associated with the complete removal treatments (treatments 2-5, Table 1.1) may account for this difference. Clipping treatments were significantly different from the other vegetation removal treatments (treatments 2-8 versus 9-11, Table 1.1) but there was not a significant difference among the clipping treatments (treatment 11 versus 9-10, Table 1.1) (Table 1.8). Although the vigour ratio satisfactory:dead was the major contributor to treatment differences, the poor, moribund and dead classes are likely interrelated as well.

To provide an estimate of the proportion of the sample occurring in each vigour class at various levels of interference, vigour ratios, (i.e., good:moribund, fair:moribund, and poor:moribund), were compared to competition indices using a categorical analysis. This analysis revealed that most sensitive competition indices were AVLA, AVLA1, AVLAD123, and AVLAD. The indices were very similar and for purposes of illustration AVLA1 (the simplest one) is depicted in Figure 1.11. This figure, depicting the predicted probabilities at various levels of AvLA1, clearly illustrates that vigour is sensitive to competition. Furthermore, high levels of vegetation control and the associated environmental conditions, at least immediately adjacent to the seedling, are closely associated with the satisfactory vigour class.

In summary, it appears that manipulating vegetation has some impact on seedling vigour; complete removal of vegetation around a seedling to a distance of 1.25 m is most favourable.

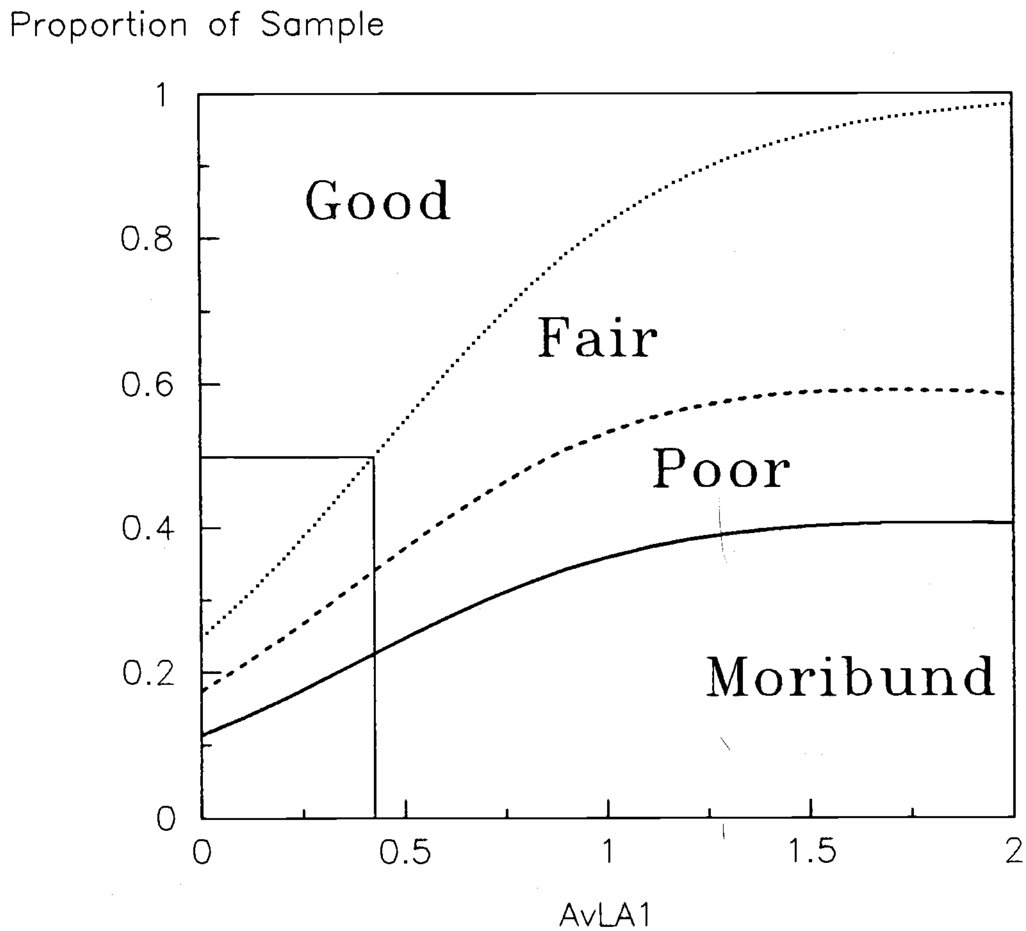

Figure 1.12 Influence of AvLA1 (the leaf area index within a 0.30 m radius of the seedling) on the proportion of seedlings per vigour class.

Douglas-fir growth

When planned contrasts were applied to assess the effect of the qualitative treatment combinations on seedling growth as measured by stem diameter similar trends to those discussed above for vigour were observed (tables 1.8 and 1.9). When D^2H and height:stem diameter ratio were substituted as indicators of growth somewhat weaker relationships were found. Other researchers have similarly found these variables to be useful growth indicators (Zutter *et al.* 1986, and Coates 1987). Both height and canopy volume measurements were insensitive.

In attempting to develop a neighbourhood regression model for predicting Douglas-fir growth from a competition index, first the most sensitive Douglas-fir growth variables were selected. As in the planned contrasts stem diameter was found to be the most sensitive Douglas-fir seedling size variable when regressed against the interference indices. It was followed by D^2H and height:stem diameter ratio. Increasing neighbourhood leaf area may be negatively related to seedling size (Figure 1.13).

The next step in developing a neighbourhood, single variable, regression model was selecting functions to fit the data (e.g., linear, inverse and quadratic (Table 1.10)). Although based on the reciprocal yield law, one would have expected the hyperbolic model to provide the most appropriate description of the relationship between individual plant growth and quantity of neighbours, in this experiment the inverse function provided only a marginally better fit than the linear model (Weiner 1982, Goldberg and Fleetwood 1987). In fact the inverse function improved the fit by less than 1% and the residual distribution only slightly. The fit and residual distribution associated with the quadratic function showed similar trends.

The r^2 values for all of the models tested to predict seedling size from the leaf area interference indices were small, acounting for only 6% to 12% of the variability in seedling size. These results are within the range of r^2 values reported in the literature for similar studies (Waller 1981, Watkinson *et al.* 1983, Weiner 1984, Silander and Pacala 1985, Goldberg 1987, Wagner and Radosevich 1987, Goldberg and Fleetwood 1987).

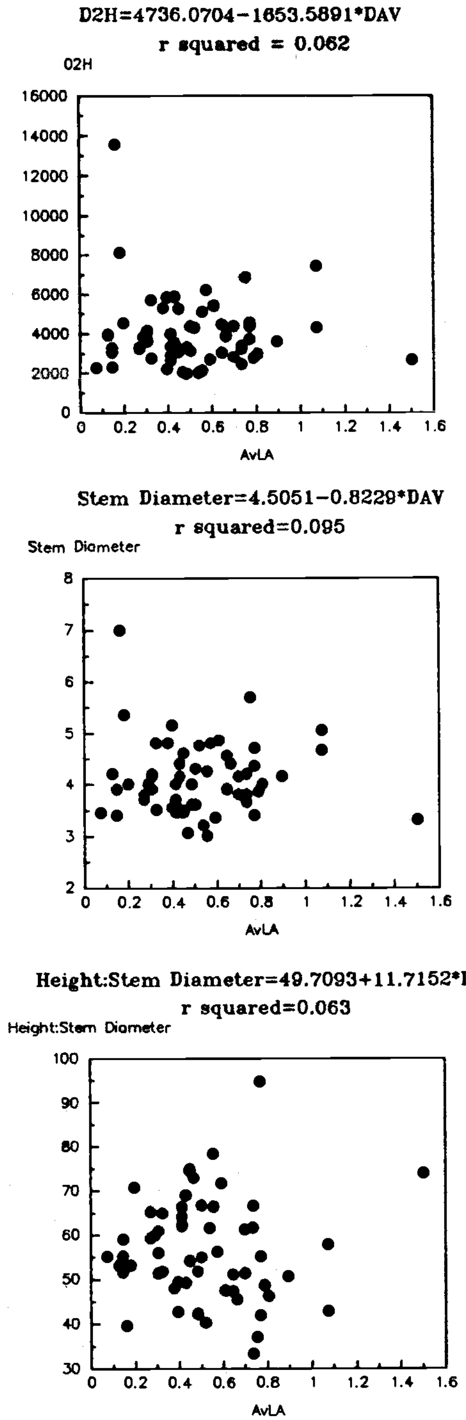

Figure 1.13 Influence of AvLA (the leaf area index within a 1.25 m radius of the seedling) on Douglas-fir D^2H, stem diameter and height:stem diameter.

Table 1.10 Comparison of linear, reciprocal and quadratic models of several measures of competition for stem diameter, height:stem diameter and D^2H of individual Douglas-fir seedlings

Measure of Interference	Linear Model r^2	Linear Model p-value	Inverse Model r^2	Inverse Model p-value	Quadratic Model r^2	Quadratic Model p-value
			STEM DIAMETER			
DAV	0.09	0.0004	0.08	0.0009	0.12	0.0005
DAV1	0.11	0.0002	0.12	0.0001	0.11	0.0008
DXAV	0.11	0.0001	0.12	0.0001	0.11	0.0060
DXLL	0.12	0.0001	0.12	0.0001	0.12	0.0003
			HEIGHT:STEM DIAMETER			
DAV	0.06	0.0042	0.05	0.0107	0.07	0.0125
DAV1	0.06	0.0048	0.04	0.0315	0.06	0.0189
DXAV	0.06	0.0038	0.04	0.0253	0.06	0.0159
DXLL	0.07	0.0023	0.04	0.0168	0.07	0.0102
			D^2H			
DAV	0.06	0.0045	0.01	0.1859	0.08	0.0066
DAV1	0.06	0.0073	0.04	0.0177	0.06	0.0276
DXAV	0.06	0.0054	0.04	0.0212	0.06	0.0214
DXLL	0.07	0.0028	0.04	0.0295	0.07	0.0101

The more complex competition indices, e.g., those incorporating distance such that a neighbour's effect decreases with the square of its distance to the sample tree, only accounted for up to 3% more of the variation. Furthermore, the mean leaf area of the 0.30 m radius area immediately adjacent to the seedling was as predictive as the mean leaf area of the entire 1.25 m radius plot. Given this result the simpler AVLA1 was chosen as the interference variable for the subsequent regression analyses.

Finally a multiple regression neighbourhood model was selected that predicted growth measured as the inverse of stem diameter from seedling vigour, original height and AVLA1. It was selected from a variety of multiple regression models and accounted for substantially more variation (R^2=0.28, p-value=0.0001) than the single variable model discussed above. As one would expect, seedling vigour accounted for a major proportion of the variation. However, original height of seedlings also reduced the variation in seedling size significantly. On the other hand, the competiton index only reduced the variation marginally when the original height and seedling vigour variables were included in the model (p-value=0.058).

The predictive power of this multiple regression model was tested using the second "test" data set and was found to be adequate (p-value=0.048 F=2.446 df 4,183). The test data set was very similar to the original data set since: the tree seedlings were from the same seedlot, planted at the same time and at the same site. Based on this observation, one would expect the independant variables to follow similar patterns of multicollinearity.

CONCLUSIONS

This chapter quantified the influence of environmental conditions and pinegrass on the survival and growth of Douglas-fir seedlings. Several conclusions are presented below:

1. In the replacement series experiment, over the three study years seedlings planted in a relatively competition free situation suffered 57% mortality.

2. Seedling vigor declined over the three study years (1985-1987) corresponding to accumulating stresses of drought, frost, and rodent damage. Poor seedling quality at the time of planting is also suspected to have contributed to mortality.

3. A comparison of the RGR of the Douglas-fir with the pinegrass shows that Douglas-fir tended to maintain a constant though low RGR throughout the summer whereas pinegrass RGR rapidly peaked in the spring then declined in association with maturation and senescence.

4. Pinegrass' rapid growth when moisture is least limiting early in the season may give it a considerable competitive edge over the Douglas-fir seedlings.

5. Removing native vegetation improves soil temperature conditions in early spring when conifer seedling root growth is critical.

6. The neighbourhood experiment results indicate that the presence of neighbouring vegetation reduces growth and raises risk of death to the Douglas-fir seedlings.

7. One can expect that reducing the leaf area of the neighbouring vegetation by approximately one half (i.e., to LAI=0.5) may help maintain up to 50% of the surviving seedlings in satisfactory condition.

8. Treatments that were most effective at improving seedling performance were those in which neighbouring vegetation surrounding seedlings was completely removed.

Response of Douglas-fir and Pinegrass to Moisture Deficits

Chapter Two

INTRODUCTION

A plant becomes water stressed when it can no longer maintain adequate plant water potential and turgor for optimal growth and development (Hsiao 1973). Water stress affects plant functioning through many physiological and metabolic processes including reduced cell growth and division, reduced cell wall and protein synthesis, reduced chlorophyll accumulation, altered enzyme levels, increased abscisic acid synthesis, inhibited photosynthesis, and reduced xylem conductance (Hsiao *et al.* 1976). Water moves from the soil through the plant and into the atmosphere along a water potential gradient. Resistance to water movement along that gradient results in a replacement lag, thus all terrestrial plants develop some degree of water deficit on a daily basis (Turner and Begg 1981). Because evaporative demand and water availability to the roots control degree and length of a water deficit, water stress is strongly tied to both atmospheric and soil-water conditions.

Conifer regeneration in the dry southern interior of British Columbia is believed to be controlled by moisture availability. For example, the amount and distribution of moisture significantly affects germination, survival, and growth of Ponderosa pine (Noble *et al.* 1979), lodgepole pine (Shepperd and Noble 1976), and Douglas-fir (Noble *et al.* 1978). Furthermore, increased rates of evaporation and transpiration associated with high temperatures may exacerbate drought conditions.

An understanding of the drought responses of conifer seedlings and the dominant understory species is critical to ensuring successful reforestation efforts in the Interior Douglas-fir (IDF) Biogeoclimatic Zone (Kramer 1986). Differences in species responses to moisture deficit may be an important factor in the suppression of one species by another (Conard and Radosevich 1981). This information is therefore important for both predicting plantation success relative to climatic variability and prescribing suitable silviculture strategies to favour conifer establishment.

Mechanisms for surviving drought often are divided into two categories. These are: (i) *stress avoidance mechanisms* whereby plants typically complete their reproductive cycle before the dry season and (ii) *stress tolerance mechanisms* which include adaptations to postpone dehydration and adaptations to increase tolerance of dehydration (Kramer 1980). With respect to forest trees, Kramer (1986) suggests that two specific stress tolerance mechanisms warrant study:

(i) decreased transpiration and increased water use efficiency through stomatal closure at low water potentials (moisture conservation) and

(ii) osmoregulation to maintain high leaf conductances for continued photosynthesis at low water potentials (moisture expending).

This chapter presents the results of a three-year study directed at:

(1) quantifying and comparing the degree of diurnal and seasonal water stress experienced by Douglas-fir seedlings and pinegrass (*Calamagrostis rubescens* Buckl.);

(2) examining Douglas-fir seedling's diurnal and seasonal stomatal conductance;

(3) examining the ability of Douglas-fir seedlings to osmotically adjust during the course of the first growing season after outplanting; and

(4) relating the seasonal trends in soil water deficit, and surface resistance to plant water stress.

METHODS

Study Site and Experimental Design

The study site is described in detail in Chapter One. It is located in the IDF Very Dry Montane Biogeoclimatic Subzone, East Fraser Plateau Variant (IDFb2) in a 14 year old clearcut dominated by pinegrass. The elevation is 1150 m, aspect 300^o, slope 8%, and the soil is a deep, (1 m), well drained, silt loam textured Orthic Gray Luvisol over compact glacial till (Canada Soil Survey Committee 1978). Weather conditions including air temperature, relative humidity, precipitation, solar irradiance and wind speed were continuously monitored during the study period and are described in Chapter One.

A replacement series experiment was used to examine the relationships between temperature, soil-moisture conditions, and pinegrass to Douglas-fir seedling performance (de Wit 1960 and Harper 1977). Since the specifics of the design are not pertinent to the physiological measurements per se the experimental design is merely summarized in this chapter. A complete description is presented in Chapter One. The experiment included five treatments of varying proportions of pinegrass to Douglas-fir seedlings. Douglas-fir (seedlot 3087, stocktype 1+0 PSB 3-13)) were dibble planted into 0.25 m^2 hand cleared patches during the third week of May 1985. At the beginning of July 1985, and end of June 1987, 2 kg a.i. per ha of glyphosate (isopropylamine salt) was hand sprayed around each seedling to kill all the native vegetation within a 1.56 m^2 patch. Seedlings were covered with large cups to protect them from the herbicide.

Soil matric potentials were measured as outlined in Chapter Three. Direct measurements were made at depths of 0.05, 0.15, 0.30, and 0.50 m using: (i) Model 5201 Soilmoisture Blocks and a Model 5910-A Soilmoisture Meter (Soilmoisture Equipment Corp.) and (ii) Model PST-55-30 Soil Psychrometers and a HR33T Microvoltmeter (Wescor Inc.) on psychrometric and dewpoint modes. The average soil water potential of the profile was calculated for two treatments, the 100% tree and 100% grass, as the average of the measurements to a depth of 0.50 m.

Total twig/leaf xylem water potential, osmotic potential and transpiration resistance were monitored daily and seasonally as described in the following sections. Healthy seedlings and pinegrass tillers were randomly selected for measurement from blocks two and three of the replacement series experiment. Unlike blocks one and four, these two blocks were located beside one another and contained enough vigorous seedlings to sustain the destructive sampling.

Although the treatments within the replacement series were designed to provide varying levels of competition, the seedlings were too small relative to their allotted 1.56 m^2 of competition free space to experience measurable competition from adjacent 1.56 m^2 patches of pinegrass. For example, throughout the three growing seasons of the study there was no significant difference in growth parameters or total leaf/twig xylem water potential of the seedlings between treatment plots or blocks. Likewise the pinegrass was not measurably affected by the Douglas-fir seedlings. Thus I assumed both species to be growing in a comparatively interspecific competition free situation during the three study years.

Total Twig/Leaf Xylem Water Potential

Total leaf/twig xylem water potential was measured with a pressure chamber (PMS Inc.) (Scholander *et al.* 1965). Current years growth of Douglas-fir seedling twigs (ranging from 25 to 35 mm in length) and pinegrass tillers (of similar size and developmental stage) were 'straight cut' using surgical scissors, placed in plastic bags containing damp tissue and transported to the pressure chamber where measurements were made within two to three minutes following excision. No more than two twigs were removed from the same tree seedling during the course of a growing season.

Six to 10 randomly selected seedlings and grass tillers were selected for measurements at predawn and at two hour intervals on one day each month between May and September, 1985 and 1986. In 1987 measurements were limited to predawn and midday for one day during June, July, August and September.

Osmotic Potential

Osmotic potential was measured using the psychrometer method with Model C-52 thermocouple psychrometer chambers (Wescor Inc.) and an HR-33T dew point microvoltmeter

(Livingston 1986). During 1985 six to 10 samples were taken at predawn from the same seedlings measured for total twig xylem water potential. To obtain measurements turgor pressure was first decreased to zero by pressing 10-15 conifer needles on a 6.2 mm diameter filter paper disc between two metal plates using vice grips. To prevent chemical changes, the saturated discs were immediately wrapped in parafilm, placed in airtight vials and frozen in a thermos containing a solution of dry ice and acetone. Tissue sap was expressed before freezing to minimize dilution of the symplastic sap with apoplastic water. (Livingston (1986) compared this psychrometer technique to the pressure volume technique using conifer seedlings and found good agreement in results suggesting that sap dilution is minimal.)

Samples were analysed the following day in the laboratory. Discs were removed from the vials and allowed to thaw for two minutes. The parafilm was then removed and the disc placed in a calibrated psychrometer chamber encased in foam and allowed to equilibrate for a minimum of 15 minutes. The chamber was calibrated between each sample measurement using salt solutions of known osmotic potential. Osmotic potential was measured using the dew point mode after adjustng the thermocouple cooling coefficient for temperature.

Transpiration

Transpiration resistance and stomatal conductance were measured with a transient type porometer (Model CS-102, Micromet Systems Inc.). Livingston *et al.* (1984) describe the theory underlying its operation. Assuming transpiration rate is controlled by changes in stomatal aperature, this method measures transpiration resistance by the rate of change in relative humidity of air enclosed in the chamber with a transpiring plant. All of the foliage of the conifer seedling and clump of pinegrass tillers were enclosed in a stainless steel chamber for 40 seconds and 15 seconds respectively during the measurement. Diurnal transpiration cycles based on measurements at approximately two hour intervals were measured monthly for 10 randomly selected Douglas-fir seedlings and 10 randomly selected pinegrass clumps during 1985. In 1987, diurnal transpiration cycles were again measured on 10 randomly selected Douglas-fir seedlings. Total projected leaf areas of the Douglas-fir seedlings were determined using a leaf area meter (Model Li-3000, LiCor Inc.).

RESULTS and DISCUSSION

Diurnal and Seasonal Plant Water Potential

Figures 2.1 and 2.2 depict the course of daily minimum and maximum xylem water potential of Douglas-fir seedlings and pinegrass for the 1985 through 1987 growing seasons. The observed values are similar to those reported in the literature for Douglas-fir (Running 1976, Hallgren 1977, Kelliher *et al.* 1984, and Livingston 1986) and pinegrass (Svejcar 1986). Predawn xylem potential for both species tended to progressively decline throughout the summer (Figure 2.1). During the first part of the growing season pinegrass maintained higher (less negative) xylem potentials than Douglas-fir, however, by the end of August when pinegrass senesced it exhibited lower (more negative) values. Since root resistance to water uptake is a function of soil temperature as well as soil water content early in the season xylem potential values may be depressed by low temperatures. Soil temperatures at the study site are described in Chapter One.

Midday xylem water potentials for the two species are shown in Figure 2.2. Like the predawn xylem water potentials, the midday values tended to decrease over the course of the growing season. In 1985, midday values of the two species were similar and the lowest observed. For example, the most negative xylem water potential recorded for Douglas-fir was 2.82 MPa measured on August 29 while the most negative xylem water potential for pinegrass was 2.70 MPa measured on July 18. By 1987, the midday xylem water potential measured for the Douglas-fir remained consistently higher than the pinegrass values. This may be because the conifer seedling roots had grown out of the root ball and were therefore better able to absorb water. Differences between the two species in 1987 ranged from 0.21 MPa on June 18 to 0.43 MPa on September 12.

Some year-to-year variation in predawn and midday xylem potential also is evident in figures 2.1 and 2.2. The moister conditions of 1986 are reflected in higher predawn xylem potentials. During the hot dry summer of 1985, however, both species were under greater water stress than in 1986. The weather during the summer of 1987 was intermediate between that of 1985 and 1986. For example, in mid-July of 1985 average predawn xylem potentials of pinegrass were approximately 1.2 MPa more negative than in 1986 and 0.5 MPa more negative

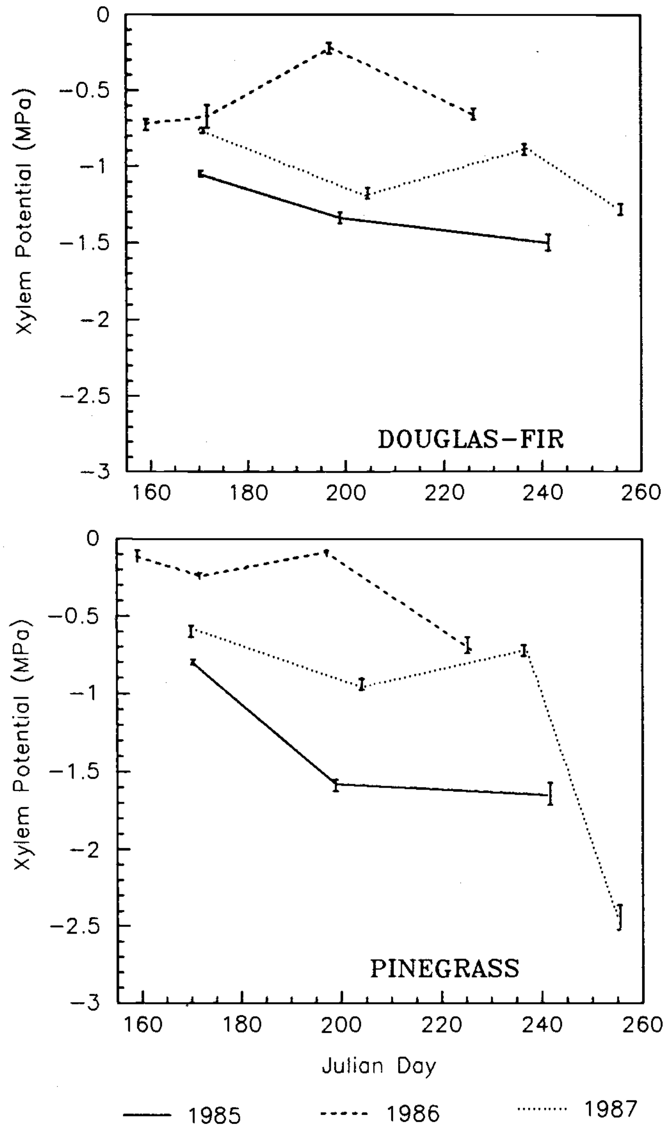

Figure 2.1 Douglas-fir and pinegrass predawn xylem water potential over the course of the 1985, 1986 and 1987 growing seasons. (Error bars are 1 S.E.).

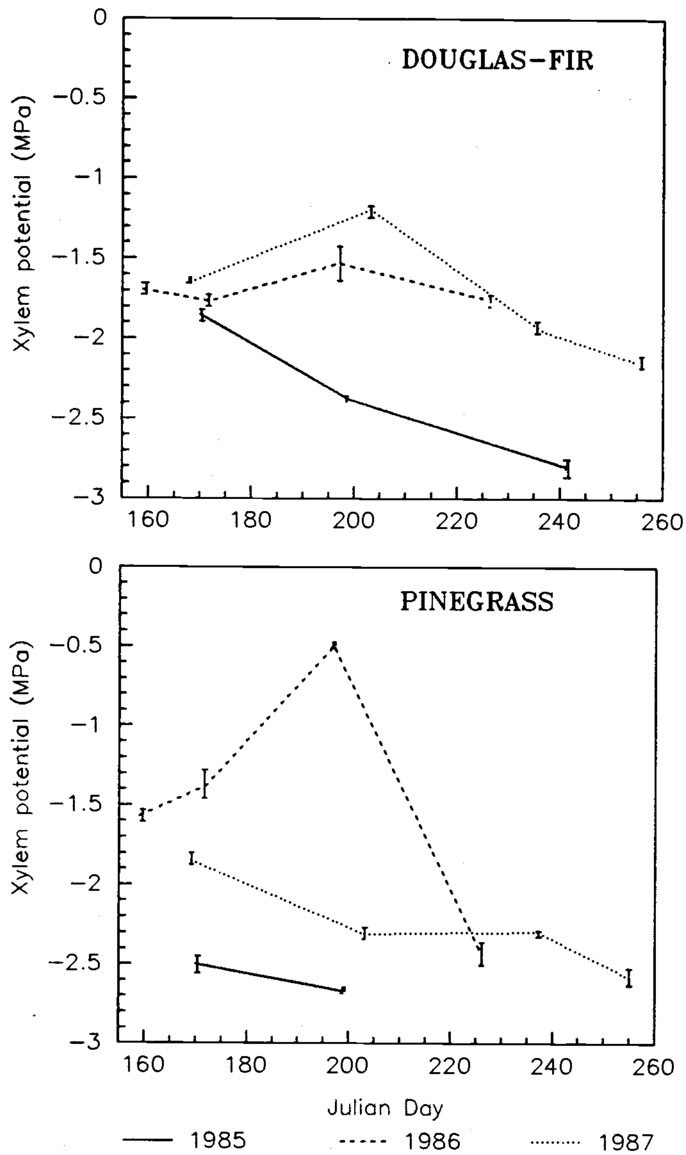

Figure 2.2 Douglas-fir and pinegrass midday xylem water potential over the course of the 1985, 1986 and 1987 growing seasons. (Error bars are 1 S.E.).

than in 1987. Predawn xylem potentials of Douglas-fir in mid-July of 1985 were approximately 0.9 MPa lower than in 1986 and 0.2 MPa lower than in 1987. Similar differences occurred among years with respect to pinegrass midday xylem water potential. Douglas-fir midday xylem water potential also was much lower in 1985 than either 1986 or 1987. There was, however, little difference between the 1986 and 1987 measurements which could be the result of root growth by the Douglas-fir seedlings. Excavation of roots of a number of seedlings at the end of each growing season revealed average values for longest new roots of 6, 15, and 30 mm in for 1985, 1986 and 1987 respectively. Thus, the greater rooting depth achieved by 1987 may have resulted from the moister conditions of 1986.

During 1985 and 1986, xylem potentials were measured diurnally for the Douglas-fir seedlings and pinegrass on seven dates (figures 2.3 and 2.4). All sample days were dry and sunny except for June 8 and July 16, 1986. July 18, 1985 most clearly represents the two species response to water stress conditions, since July 1985 was a particularly dry and warm and July 18 had a mean air temperature of 20.8 ^{o}C and relative humidities ranged from approximately 40% to 18% (Figure 2.3). Both species were characterized by a decline in xylem water potential during the morning with most negative values typically reached by noon or early afternoon (Figure 2.3). Figures 2.3 and 2.4 indicate that although recovery of xylem potential usually began by late afternoon, it was minimal. Only on July 13, 1986, which was very wet (10 mm precipitation) and cool (8.6 ^{o}C mean air temperature), was there a marked recovery of xylem potential before dark.

Svejcar (1986) reported little diurnal variation in pinegrass xylem water potential by late August which he attributed to senescence. Presumably senescence of the pinegrass by the end of August 1985 precluded the measurement of xylem water potential. In 1986, it appears that pinegrass senescence was delayed due to the moister growing season conditions, thus a diurnal variation of 1.75 MPa was measured into August.

In summary, predawn and midday xylem water potential of both Douglas-fir and pinegrass decreased through the growing season. Over the course of a day xylem water potentials of the two species also declined to a minimum by early afternoon. Pinegrass tended to reach lower xylem water potentials than Douglas-fir. Xylem water potentials of Douglas-fir and pinegrass reflected growing season weather conditions; 1985 was the most stressful and 1986 the least.

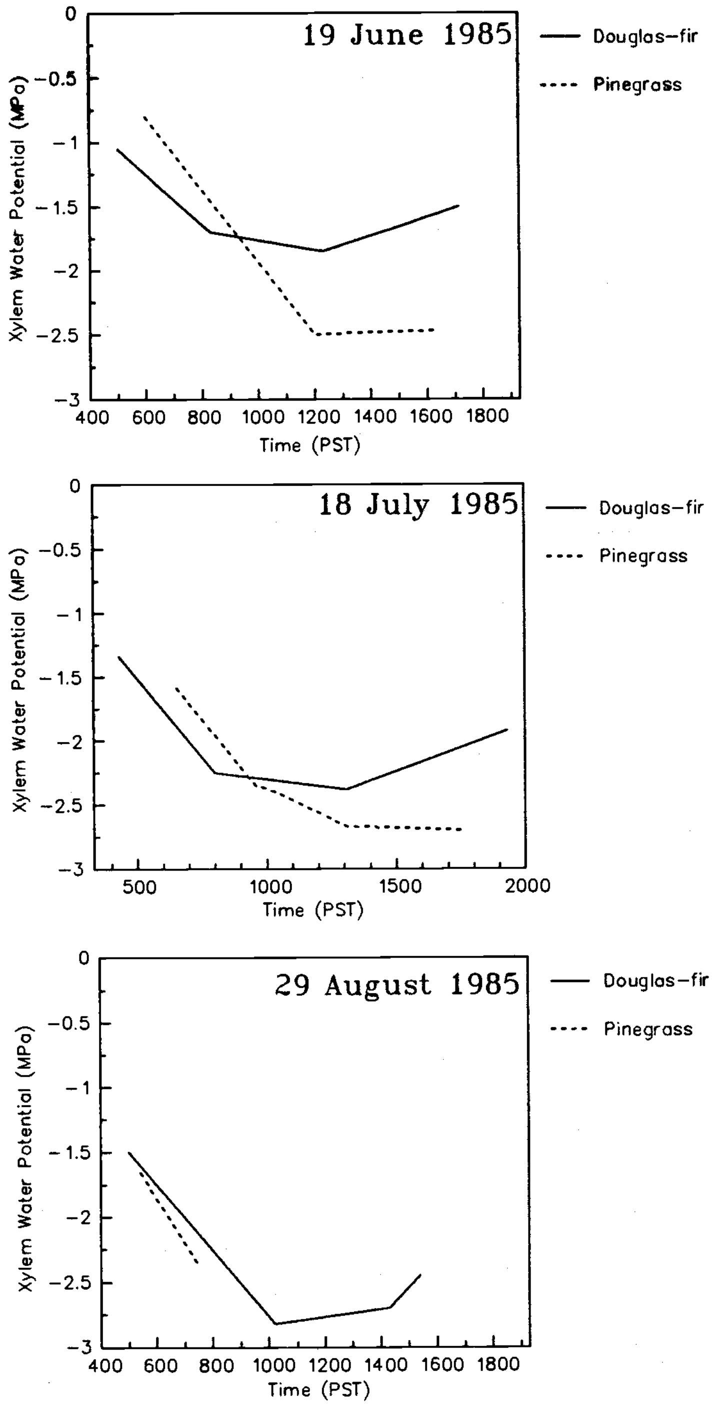

Figure 2.3 Courses of xylem water potential for Douglas-fir and pinegrass on 19 June 1985, 18 July 1985, and 29 August 1985.

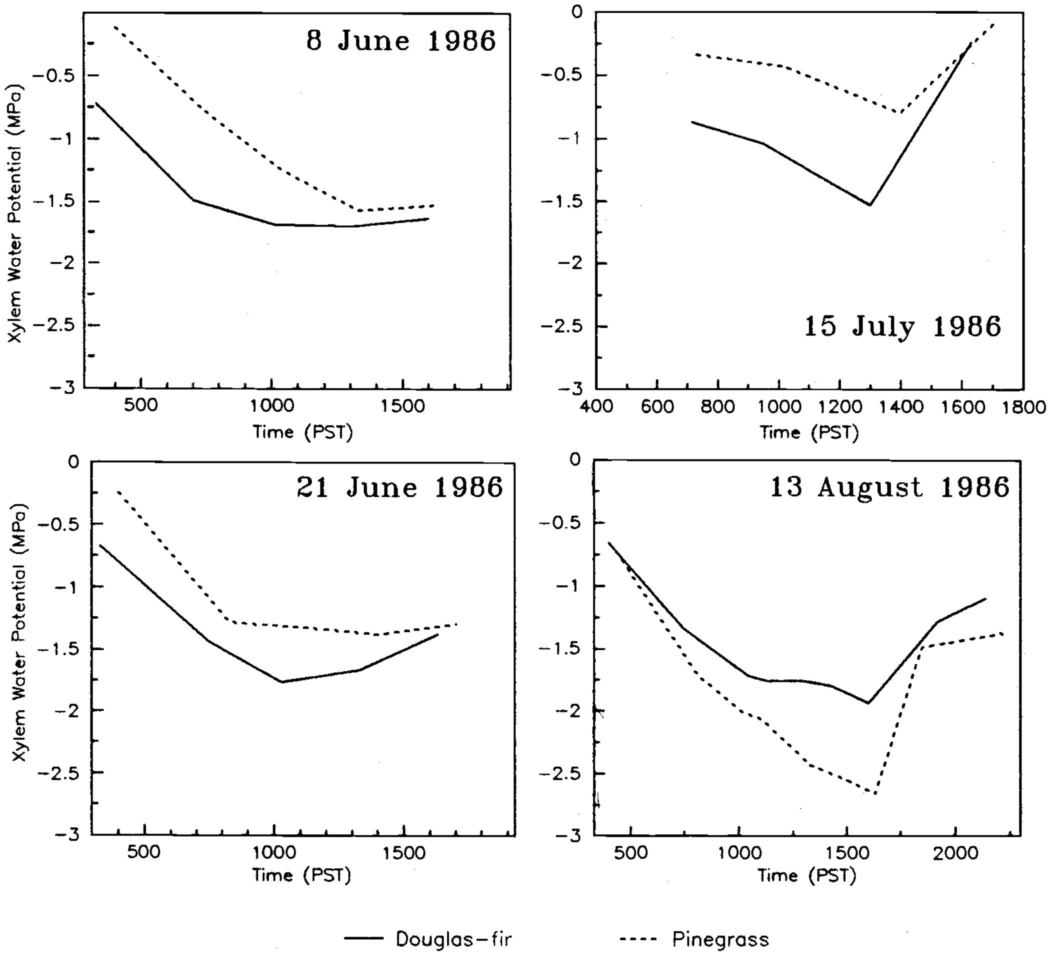

Figure 2.4 Courses of xylem water potential for Douglas-fir and pinegrass on 8 June 1986, 21 June 1986, 15 July 1986, and 13 August 1986.

However, by 1987, midday xylem water potential of Douglas-fir remained higher than in the previous years, likely due to seedling's greater rooting depth. Pinegrass xylem water potentials in 1986 indicated that it was the more responsive species to improved weather conditions.

Diurnal and Seasonal Transpiration and Stomatal Conductance

Water flow through plants is controlled by the vapour phase between the evaporating surface on the leaf and the surrounding air. Transpiration is affected by a number of environmental and biological factors for this reason. These factors include: irradiance, vapour pressure deficit, air temperature, wind, water supply, stomatal behaviour, leaf area, leaf structure, and root absorption (Kramer 1983). It is difficult to predict transpiration rate since a change in any factor does not necessarily change the transpiration rate proportionally. For example, Sandford and Jarvis (1986) noted for four conifer species that transpiration was not reduced as the vapour pressure deficit increased and stomatal closure occurred. Examining stomatal conductance, however, provides some insight into the relationship of plant water status and transpiration. Indeed, the sensitivity of stomata to vapour pressure deficit is an important determinant in stomatal adjustment versus stomatal closure. Furthermore, the ability of stomata to adjust to low plant water potentials may be limited by the plants ability to osmotically adjust (Turner and Begg 1981).

In this study, transpiration and stomatal conductance of the Douglas-fir were measured on two dates in 1985 and on four dates in 1987 (figures 2.5-2.7). In 1985, transpiration rates of the Douglas-fir rapidly reached a peak early in the morning and declined to a minima by midday. On June 19 recovery began in late afternoon; no recovery was measured on July 18 (Figure 2.5). By contrast, in 1987 stomata remained open throughout the day and transpiration rates rose to a plateau about midmorning falling again in midafternoon with decreasing maximum vapour pressure deficit. Although the data represent only four days of measurements, Table 2.1 suggests that total transpiration per day declined over the course of the 1987 growing season. This was largely attributed to decreasing irradiance, air temperature and soil water potential.

On each date that it was measured stomatal conductance peaked in early morning and declined in relation to increasing vapour pressure deficits. Sanford and Jarvis (1986) also reported decreasing stomatal conductance with increasing vapour pressure deficit under more controlled conditions where changes in temperature and plant water status were limited.

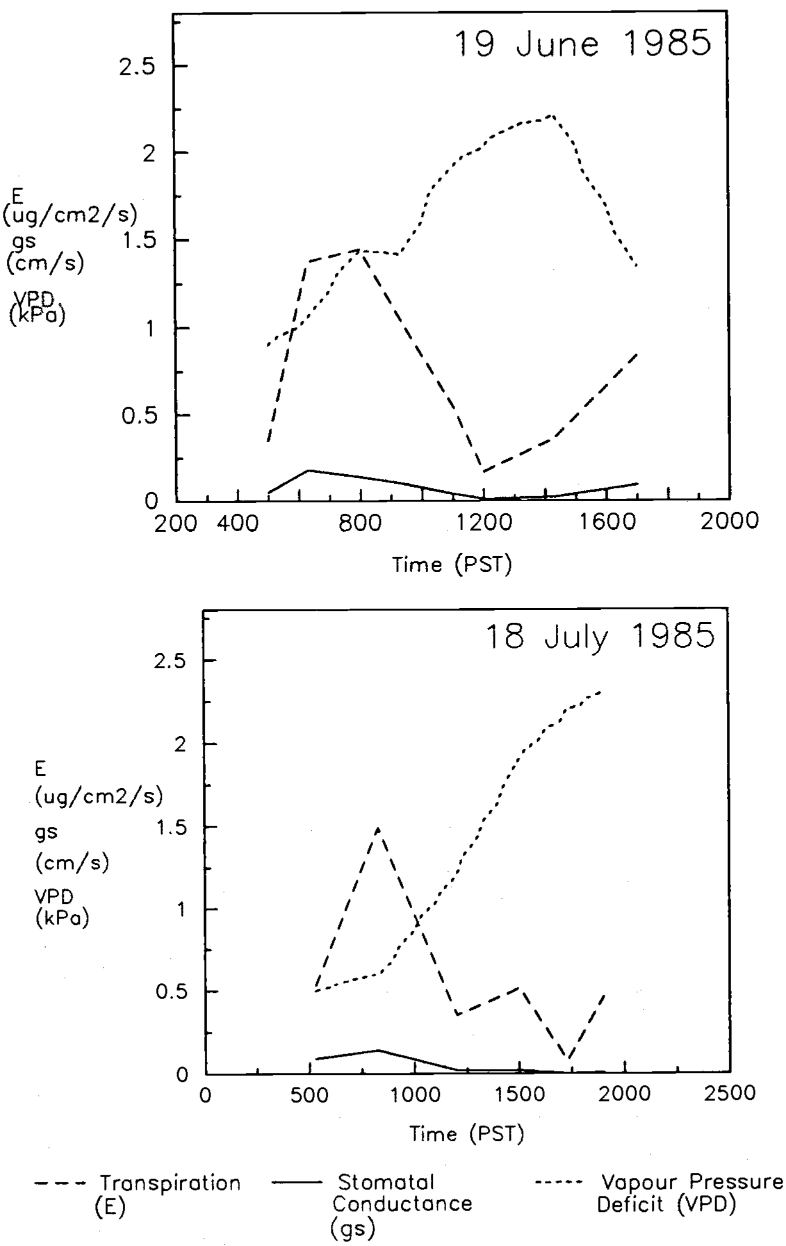

Figure 2.5 Course of vapour pressure deficit and Douglas-fir stomatal conductance and transpiration on 19 June 1985 and 18 July 1985.

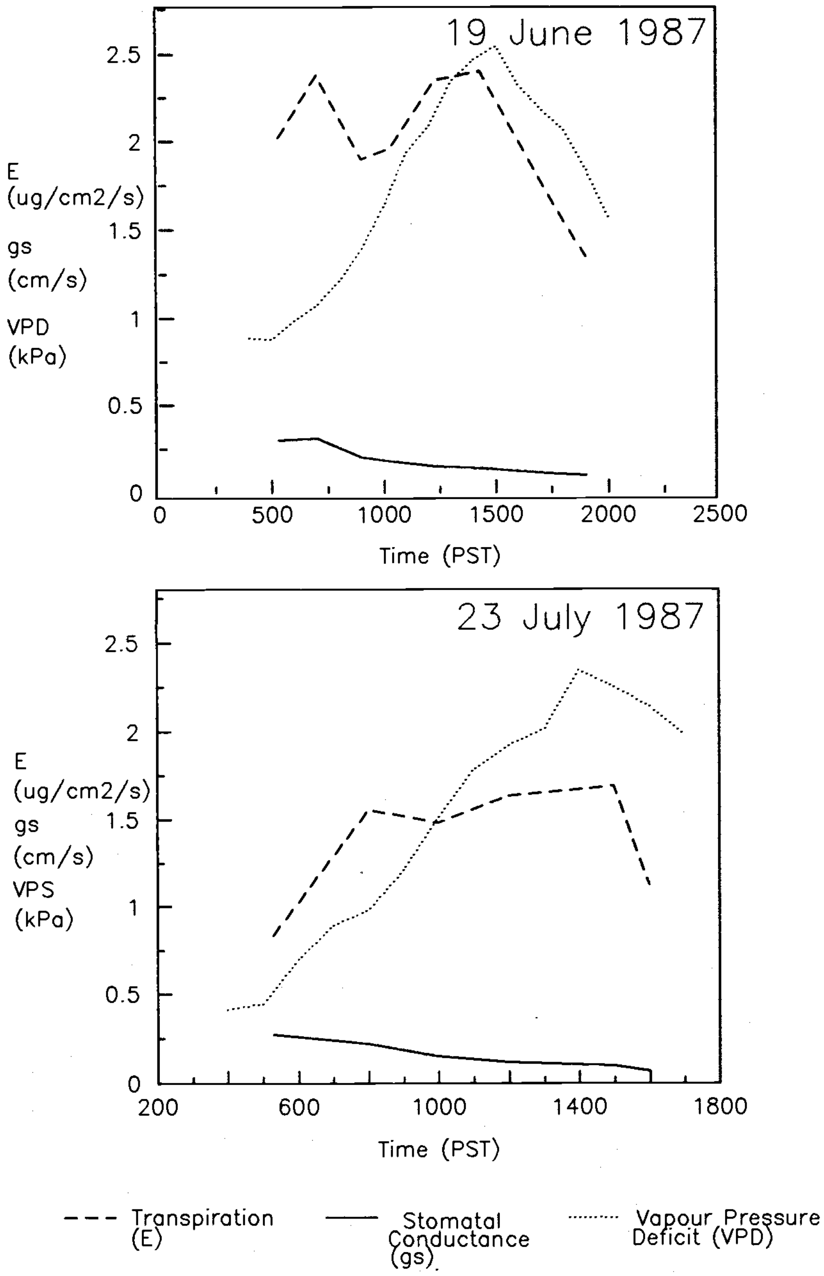

Figure 2.6 Course of vapour pressure deficit and Douglas-fir stomatal conductance and transpiration on 19 June 1987 and 23 July 1987.

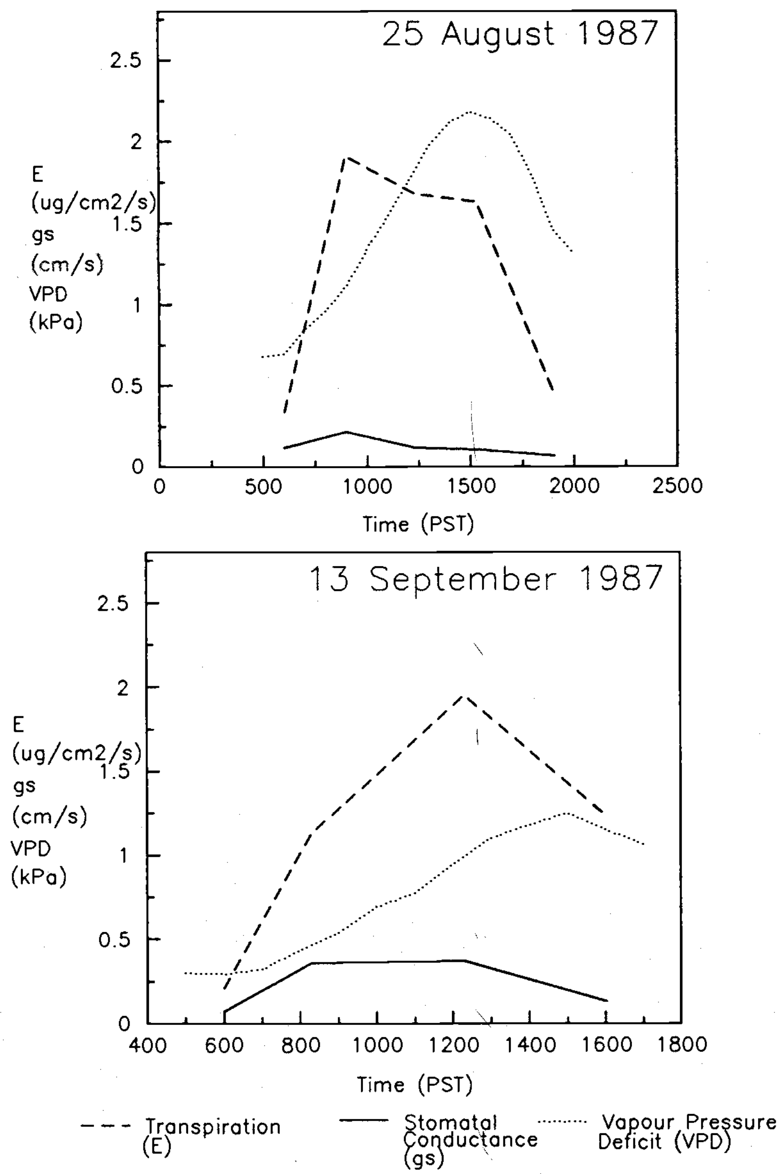

Figure 2.7 Course of vapour pressure deficit and Douglas-fir stomatal conductance and transpiration on 25 August 1987 and 13 September 1987.

Least-squares regression relating the square root of stomatal conductance (g_s) to vapour pressure deficit (v.p.d.) provided the equation: gs = 0.597 - 0.175(v.p.d.) (R^2=0.52, p<.0001). It was necessary to transform the data to obtain constancy of the error variance (Neter *et al.* 1983). Many researchers have similarly demonstrated the importance of vapour pressure deficit on Douglas-fir stomatal conductance (Running 1976, Hallgren 1977, Tan *et al.* 1977, Tan *et al.* 1978, Johnson and Ferrell 1983, Marshall and Waring 1984, and Livingston 1986). A vapour pressure deficit of approximately 1 kPa tends to be the threshold for stomatal closure in this species (Lopushinsky 1969, and Tan *et al.* 1978). This value is consistent with

Table 2.1 Course of 1987 growing season: soil water potential averaged for the entire profile and seedling rooting zone, Douglas-fir predawn xylem water potential, Douglas-fir total daily transpiration (E) and maximum transpiration rate, and maximum vapour pressure deficit (standard deviations are given in brackets.)

Date	Profile Soil Water Potential (MPa)	Root Zone Soil Water Potential (MPa)	Xylem Water Potential (MPa)	Total Daily E (g/cm^2/d)	Max. E (ug/cm^2/s)	Max. VPD (kPa)
19 June 1987	-1.0	-1.5	-0.76 (0.08)	0.11	2.4 (0.5)	2.50
23 July 1987	-1.0	-1.3	-1.19 (0.16)	0.06	1.7 (0.6)	2.30
25 Aug. 1987	-1.1	-1.6	-0.88 (0.23)	0.07	1.7 (0.5)	2.15
12 Sept. 1987	-1.6	-2.0	-1.27 (0.28)	0.05	2.0 (0.6)	1.70

the conditions measured on June 19 of both 1985 and 1987. On these dates, vapour pressure deficits were high all day long and stomatal conductances were correspondingly low (figures 2.5 and 2.6). Tan *et al.* (1977) reported that the decline in stomatal conductance with increasing vapour pressure deficit tends to become more rapid as the soil dries and Running (1976) and Tan *et al.* (1977) reported that Douglas-fir stomata begin to close at leaf water potentials of approximately -2.0 MPa, depending to some extent on stress prehistory.

The data obtained on 18 July 1985 are particularly interesting in that stomatal conductance decreased sharply corresponding to high leaf water potentials early in the day despite the fact that the vapour pressure deficit had not yet reached 1 kPa (Figure 2.5). This observation is consistent with the findings of Tan *et al.* (1977).

Interestingly, the average maximum stomatal conductance values of Douglas-fir measured at the beginning of the growing season (June) ranged from 0.18 cm/s (s=0.09) in 1985 to 0.31 cm/s (s=0.08) in 1987. Maximum stomatal conductance values for Douglas-fir seedlings reported in the literature are somewhat higher. For example, Livingston (1986) reported a maximum stomatal conductance of 0.44 cm/s and Hallgren (1978) reported a maximum stomatal conductance of 0.43 cm/s. Both authors note that leaf conductance decreases as plant water stress increases, thus, the lower conductance values measured in this study were likely due to greater water stress at the beginning of summer. Indeed, as the season progressed and predawn xylem water potentials decreased, mean maximum stomatal conductance declined by 31% to the end of August. It is not clear why the conductances measured in September were much higher than on the earlier dates (Table 2.2).

The apparent importance of Douglas-fir seedling root growth after two field growing seasons to xylem water potential is reinforced by the transpiration measures. In 1985, transpiration tended to peak sharply and decline (Figure 2.5). This observation suggests that the rate of water uptake limited transpiration. In 1987, transpiration peaked then levelled, only declining in late afternoon when vapour pressure deficits were highest (figures 2.6 and 2.7). This plateau type response suggests that seedlings had developed more and deeper roots enabling them to maintain a water uptake rate sufficient to offset that being lost through transpiration.

On two dates in 1985, pinegrass transpiration was measured on a per unit ground area basis rather than on a per unit foliage basis (Figure 2.8). Based on the leaf area index (LAI) of the site of 1.1 (LAI was calculated as the average LAI for Treatment 1 of the neighbourhood experiment, see Chapter One), the transpiration rate per unit ground area is approximately equal to the transpiration rate per unit foliage. Comparison of the transpiration rates of the pinegrass and Douglas-fir on the two dates clearly shows pinegrass to be superior to the newly planted Douglas-fir at coping with drought. Indeed, pinegrass maintained a higher transpiration rate throughout the day. Even assuming a more conservative estimate of water use by substituting an overall site LAI of 0.5 indicates that pinegrass would utilize twice as much water per unit of foliage as the Douglas-fir during its peak growing period.

Table 2.2 Douglas-fir mean maximum stomatal conductance (standard deviations are given in brackets.)

Date	Maximum Stomatal Conductance (cm/s)	
19 June 1985	0.14	(0.07)
18 July 1985	0.18	(0.09)
18 June 1987	0.31	(0.08)
23 July 1987	0.27	(0.07)
25 August 1987	0.21	(0.05)
13 September 1987	0.35	(0.06)

Clearly, the results indicate the two species employ different strategies with respect to drought conditions. Pinegrass grows guickly during a shorter period and appears to expend more water during this process than the Douglas-fir. In contrast, Douglas-fir seedlings seem more conservative, using less water per unit of foliage. However, their development period is longer so their water requirement occurs over a longer period. Therefore, it appears that pinegrass could potentially deplete the soil moisture at the expense of Douglas-fir even after seedings have established a well developed root system.

Seasonal Osmotic Adjustment

In many plants turgor maintenance by osmotic adjustment through solute accumulation is an important mechanism to tolerate water stress. Because planting shock will exacerbate water stress conditions, it is particularly useful to examine osmoregulation in conifer seedlings during the first season after outplanting. Measurements during the 1985 growing season indicated that Douglas-fir seedlings exhibited osmotic adjustment of approximately 1.2 MPa (Table 2.3). The observed values of osmotic potential are similar to those reported for Douglas-fir by Ritchie and Shula (1984) and Livingston (1986). Livingston attributed Douglas-fir's osmotic adjustment primarily to environmental stress as opposed to a seasonal response, since he observed less adjustment by irrigated versus non-irrigated seedlings. However, it is of interest to note that osmotic adjustment also may be affected by the maturing of the plant tissue (Hsiao *et al.* 1976).

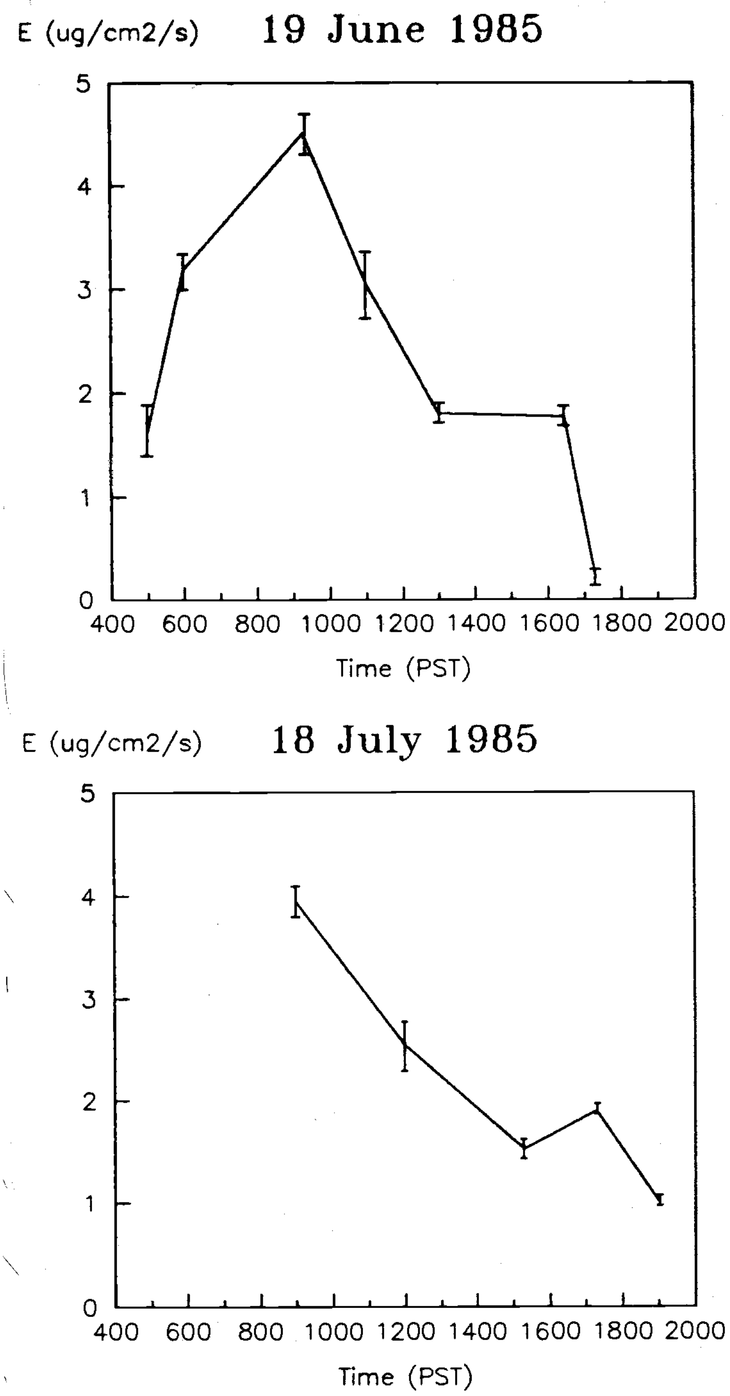

Figure 2.8 Course of pinegrass transpiration per unit ground area on 19 June 1985 and 18 July 1985.

Table 2.3 Douglas-fir osmotic potential and minimum turgor potential during the first growing season after outplanting (standard deviations are given in brackets.)

Date	Osmotic Potential (MPa)		Minimum Turgor Potential
19 June 1985	-1.6	(0.2)	-0.25
18 July 1985	-2.5	(0.3)	0.12
29 August 1985	-2.8	(0.2)	0.03
15 November 1985	-2.9	(0.3)	-

The course of the Douglas-fir seedlings minimum turgor potential during the first growing season after outplanting is shown in Table 2.3. Turgor potential was calculated by subtracting osmotic potential from predawn twig xylem water potential (Slavik 1974). Although the decline in osmotic potential observed did not prevent loss of turgor on July 18 1985 which was a hot and dry day, the results suggest that osmotic adjustment is likely an important stress tolerance mechanism in Douglas-fir seedlings (Table 2.3).

In 1985 attempts to extract pinegrass xylem sap and measure osmotic potential were unsuccessful because insufficient quantities of sap could be obtained to make reliable measures. The method used to obtain sap was the filter paper/vice grips technique (Livingston 1986). Svejcar (1986) used a dewpoint hygrometer to measure osmotic potential of pinegrass leaf discs killed by freezing rather than expressed sap. He reported osmotic adjustment in pinegrass of about 0.7 MPa over the course of the growing season, the reduction being most pronounced toward the end of the summer coinciding with senescence. Svejcar also reported good agreement of those results with measures obtained using the pressure bomb technique to construct pressure-volume curves. Those observations suggest that an increase in cell solute concentration, i.e., osmotic adjustment, may be an important mechanism for enabling pinegrass to maintain turgor and thus low xylem water potentials. However, it is not clear what role the developmental stage of the tissue played in the osmotic potential measured and thus it is difficult to compare the relative advantages of osmoregulation to Douglas-fir versus pinegrass.

The Seasonal Relationship of Environmental Conditions to Plant Water Status

The water stress that develops in a plant depends on atmospheric demand and availability of soil moisture. The rate of water lost through transpiration reflects the leaf water potential. When leaf water potential is high transpiration is a function of atmospheric demand. When leaf water potential is low transpiration is reduced in order to maintain leaf water potential at a tolerable level. In general, at the beginning of the growing season when moisture is least limiting, atmospheric conditions control water loss. As the growing season progresses, the accompanying increase in the soil water deficit results in a slowing of the rate at which water moves into the roots. Thus, soil water status becomes the effective control of water loss. The same relationship holds on a daily basis. In the early morning when leaf water potential is least negative, the vapour pressure deficit sets the transpiration rate. As the day progresses and the soil water around the roots is depleted increasing resistance to water uptake results in lower leaf water potentials which in turn controls the transpiration rate.

Transpiration rate may be a useful measure from which to infer plant water status if atmospheric demand and soil water potential also are known. For example, if evaporative demand and soil water potential are high and transpiration also is high, then the plant can not be considered stressed. If, on the otherhand, the transpiration rate is low while the evaporative demand and soil water potential are both high, then the plant clearly would be stressed. The possible combinations of the three conditions resulting in stress are presented in Table 2.4.

Table 2.4 Qualitative relationships of the combined effect of transpiration rate, evaporative demand and soil water potential on plant water stress (H=high water stress, L=low water stress)

Transpiration Rate	Evaporative Demand	Soil Water Potential	Inferred Water Stress
H	H	H	-
L	H	H	+
H	L	H	- (may not exist)
L	L	H	-
H	H	L	would not exist
L	H	L	+
H	L	L	-
L	L	L	?

A disadvantage of using transpiration measurements to infer plant water status is that they are only single measurements whereas water- use should be integrated over a season. An estimate of the resistance to water vapour transfer from the surface (soil and leaf) (r_c) provides a method for integrating water supply rate over the season. If one assumes the ground to be operating as a large exchange surface, then r_c is equivalent to stomatal resistance of individual leaves for a vegetated surface plus soil surface resistance for a bare soil.

Surface resistances were estimated over the growing seasons of the three study years. The surface resistance calculations are outlined in Appendix I. Seasonal changes in r_c ranged from about 200 to 3000 s/m and are shown in Figure 2.9. These data are comparable to canopy resistance estimates of Ripley and Redmann (1976) and Parton *et al.* (1981) for grassland ecosystems. Surface resistance in the 100% tree treatment tended to be higher and peak earlier in the first half of the growing season than in the 100% grass treatment. The 100% grass treatment, however, tended to have a higher surface resistance by mid August. The dramatic mid-season drops in r_c relate to precipitation. The dry year of 1985 produced higher values of r_c for both the 100% tree and 100% grass treatments. Comparable end-of-season maxima were reached in 1987 and in 1985. The much lower values in 1986 correspond to the moist conditions that year.

In general, the magnitude of seasonal change in surface resistances relates to both changing green leaf area and soil water status. Although the leaf area index at the site was relatively low (approximately 1.1 in the 100% grass treatment as compared to 0.3 in the 100% tree treatment) it appears to have had a significant effect on surface resistance. For example, at the beginning of all three growing seasons when the grass was just beginning to grow, the soil was the main exchange surface in both treatments. Thus, as long as the soil surface remained wet, surface resistance was low (approximately 300 s/m).

By mid-June the leaf area in the 100% grass treatment was much higher than in the 100% tree treatment, and the open stomata maintained a lower surface resistance later into the growing season. As the season progressed, soil surface drying combined with the effect of drought on stomatal opening and senescence on leaf area contributed to the dramatic increase in surface resistance.

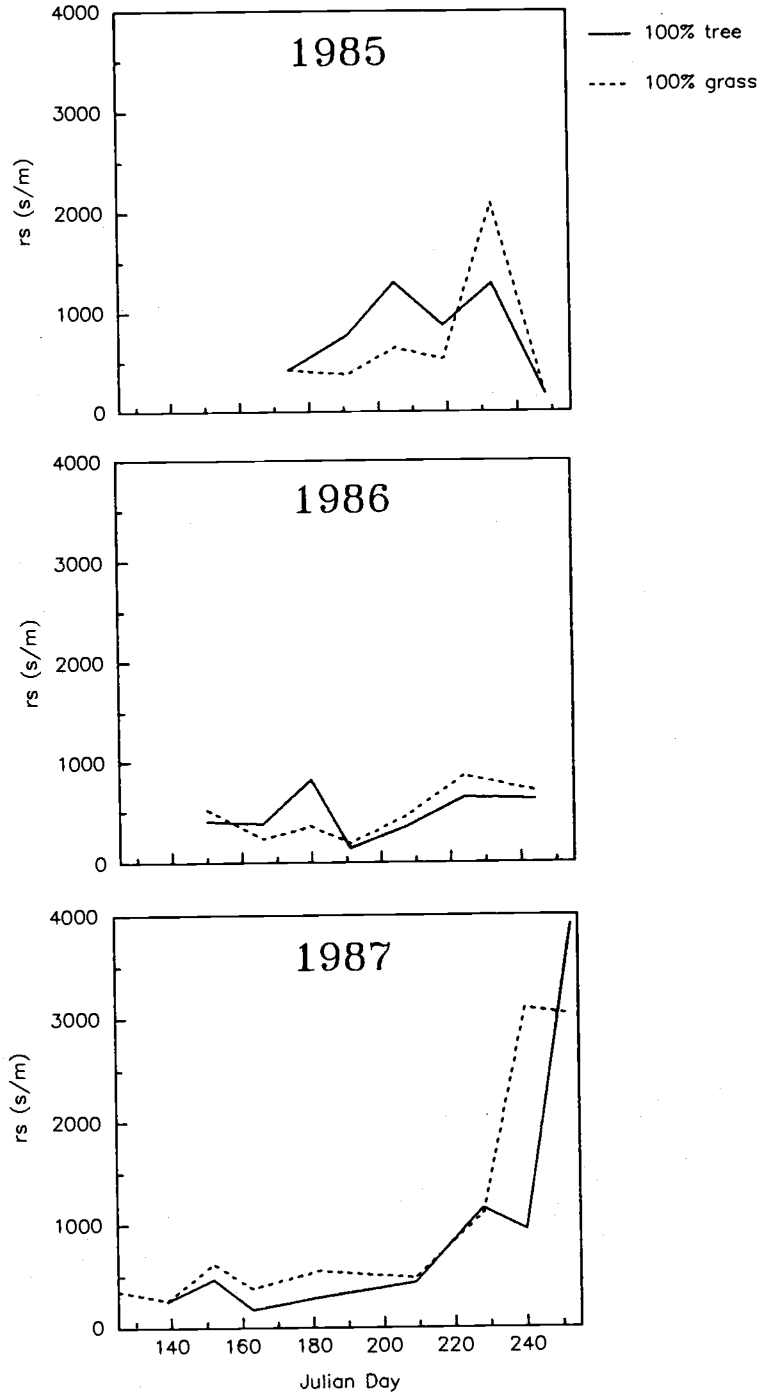

Figure 2.9 Comparison of surface resistance over the 1985, 1986 and 1987 growing seasons for the 100% grass and 100% tree treatments.

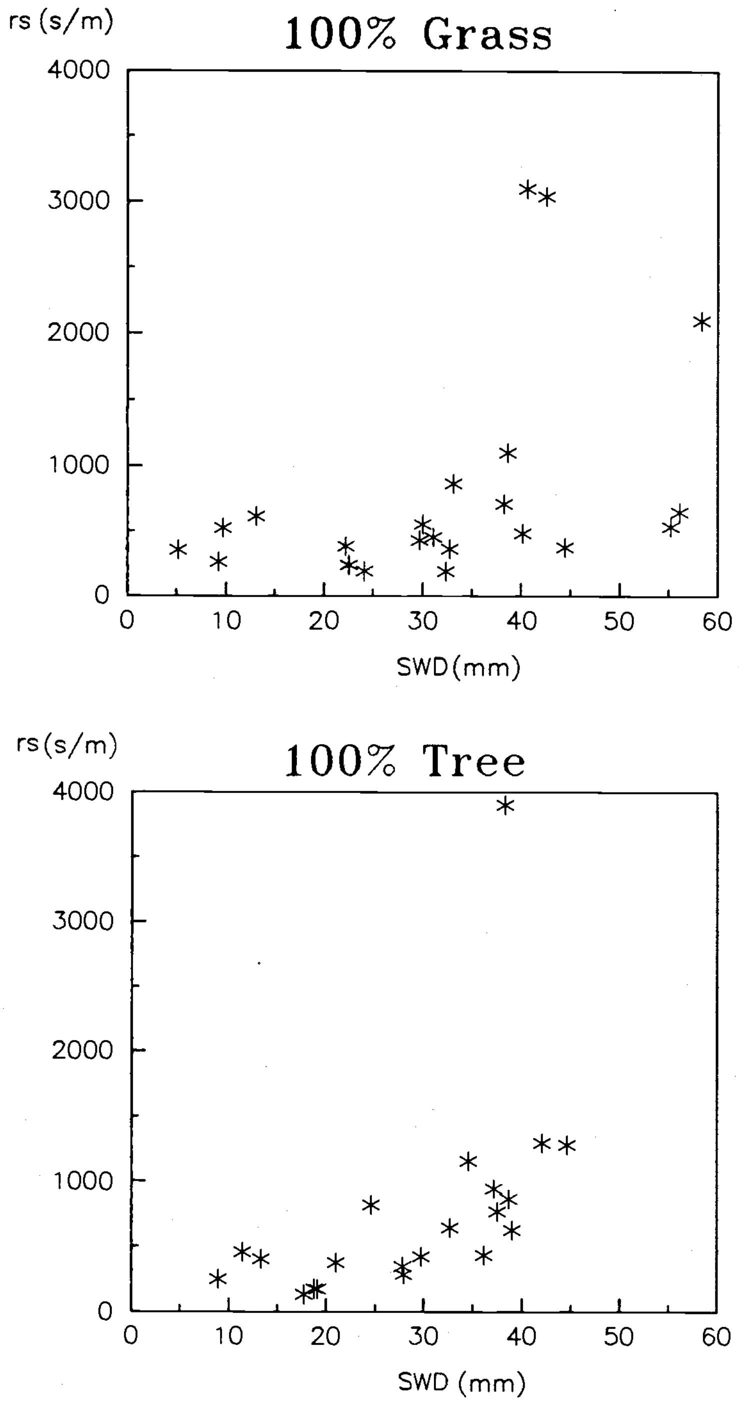

Figure 2.10 Relationship of surface resistance and soil water deficit in the 100% grass and 100% tree treatments.

Calculated values of r_c are plotted against soil water depletion deficit in Figure 2.10. Only measurements between June and mid-August were included for the 100% grass treatment to avoid the effect of changing green leaf area. Periods with low precipitation are marked. This figure suggests patterns for both treatments. For the 100% tree treatment r_c remained approximately 300 s/m until the soil water deficit reached about 35 mm (Figure 2.10). After that point r_c increased rapidly. The results for the 100% grass treatment were similar although more variable (Figure 2.10). Surface resistance remained constant at about 300 s/m at soil water deficits below about 45 mm but then increased sharply. These results further suggest the importance of leaf water status in controlling surface resistance, and the importance of the pinegrass on site water balance discussed further in Chapter Three.

CONCLUSIONS

The results and discussion are summarized below:

1. Predawn water potential values in this study suggest that the Douglas-fir seedlings, in the absence of competition, were moderately stressed by mid-June in all three years.

2. During the first growing season at the site the seedlings experienced severe water stress throughout most of the summer, whereas in 1986 and 1987 the seedlings remained only moderately stressed.

3. The stomata of the Douglas-fir seedlings appear to be correlated to increasing vapour pressure deficit. In 1985, stomata had closed by midday, whereas in 1987 transpiration did not decline until midafternoon. The high vapour pressure deficits of 1985 combined with the low rooting volume of the seedlings likely resulted in the early stomatal closure.

4. Osmotic adjustment appears to be an important mechanism enabling newly planted seedlings to tolerate their typical water stressed condition. Seedlings were less water stressed in 1987 presumably because of their greater root volume and thus, by maintaining turgor, were able to maintain relatively high stomatal conductances as soil water potential declined.

5. Pinegrass was severely water stressed throughout most of the hot dry 1985 growing season. In contrast, during the moist 1986 growing season, pinegrass appeared to be only under mild water stress up until the time it senesced.

6. Douglas-fir did not show as strong a response as pinegrass to the increased moisture availability in 1986. It is speculated that this was because seedlings had not yet developed adequate rooting systems after one growing season.

7. During the summer of 1987 (the most typical of the three years) pinegrass was moderately stressed by mid-June and remained so until it senesced.

8. Based on the two summers in which it was measured, the magnitude of change in surface resistance values over the growing season appear to be tied to both soil water status and changing green leaf area. Thus pinegrass appears to play a major role in the water balance of the site.

Water Balance of an Interior Douglas-fir Zone Site

Chapter Three

INTRODUCTION

Moisture stress has been considered to be a major factor determining tree survival in plantations in the Interior Douglas-fir (IDF) Zone of south-central British Columbia (Clark 1967, and Clark and Elmes 1979). In dry climates the rate of soil moisture depletion is controlled to a large extent by the vegetation present (Anderson *et al.* 1987). The potential, therefore, exists to control the soil water balance on IDF zone plantations by manipulating the vegetation. Investigations of soil moisture, and in particular measurements of water balance and soil water potential are a prerequisite for understanding the possible role of vegetation management on these sites.

The specific objectives of this portion of my study are listed below:

(1) quantify growing season soil water deficits and rates of water loss for an IDF site dominated by pinegrass;

(2) determine how removal of the native ground cover (pinegrass) affects site water balance; and

(3) examine year-to-year variation in seasonal water stress using the long-term weather data from nearby Williams Lake Airport.

METHODS

Site Description

The study site is described in detail in Chapter One. Briefly, the site is dominated by pinegrass. It lies within the IDF Very Dry Montane Biogeoclimatic Subzone, East Fraser Plateau Variant (IDFb2). In addition to pinegrass, soopolallie (*Shepherdia canadensis* (L.) Nutl.), rose (*Rosa acicularis* Lindl.), twinflower, (*Linnaea borealis* L.), and bluegrass (*Poa pratensis* L.) are common. The elevation of the site is 1150 m, the aspect is 300^{o}, the slope is 8% and the soil is a a deep (1m), well drained, silt loam textured Orthic Gray Luvisol over compact glacial till (Canada Soil Survey Committee 1978).

Micrometeorological measurements, including air temperature, precipitation, relative humidity, solar irradiance and wind speed, were made throughout the three study years as described in Chapter One.

Experimental Design and Soil Moisture Measurements

Two experimental designs, a replacement series experiment (de Wit 1960, Harper 1977) and a neighbourhood experiment (Mack and Harper 1977, Goldberg and Werner 1983), were used to examine the relationships between soil-moisture conditions and pinegrass to Douglas-fir seedling performance. Because the designs were chosen specifically to quantify the effects of competition on seedling performance they are not pertinent to this chapter and are not described in detail here. Complete descriptions are presented in Chapter One.

Soil water content was measured during the three growing seasons in two treatments of the randomized block replacement series experiment. The treatments chosen (100% pinegrass and 100% Douglas-fir seedling treatment) were the two extremes, i.e., monoculture plots, within the series. Plots were 15 x 15 m, replicated 4 times. Ground cover within the 100% pinegrass treatment was approximately 25% pinegrass, 50% other forbs (*S. canadensis* was removed by hand) and 25% bare ground. Douglas-fir seedlings (seedlot 3087, stocktype 1+0 PSB 313) were planted in mid May 1985 into 0.25 m^2 scalped patches at 1.25 m spacing in the 100% Douglas-fir plots. In early July 1985 and late June 1987, the latter plots were treated with glyphosate (2.0 kg active ingredient per ha) to kill all other vegetation. Douglas-fir seedlings were protected with paper cups during the herbicide applications.

Soil water content was measured also in the neighbourhood experiment during the 1986 and 1987 growing seasons. In May of 1986, Douglas-fir seedlings (seedlot 2439, stocktype 1+0 PSB 313) were planted into the centre of 1.25 m radius plots randomly located across the study site. The treatments imposed involved monthly manipulation of the leaf area around the seedlings during the 1986 and 1987 growing seasons. Soil water content was measured in three of the treatments:(i) 100% removal of the vegetation by hand scalping (Treatment 5), (ii) 50% removal of the vegetation by hand scalping (Treatment 7), and (iii) clipping the vegetation to the ground (Treatment 11).

Soil water content of the root zone was measured approximately every two weeks during the growing season using: gravimetric sampling for the top 10 cm, and the neutron moderation method at 15 cm depth intervals to 60 cm (Douglass 1966). Evapotranspiration was calculated as the sum of the change in soil water content and precipitation that occurred during soil measurement intervals.

Gravimetric sampling is a direct and reliable method for determining soil water content although it involves destructive sampling and requires sufficient replication to reduce errors caused by soil variability (Cannell and Asbell 1974, Slavik 1974, Holmes *et al.* 1967). Problems related to soil variability are reduced with the neutron-moderation method when estimating moisture change over time since sampling occurs at the same location. The latter method is widely used for water balance studies and is considered a relatively accurate measure of soil water content below 10 cm (McGowan and Williams 1980, Spittlehouse and Black 1980, Visvalingam and Tandy 1972, Bowman and King 1965). McGowan and Williams (1980) discuss the main sources of error associated with the neutron probe method of measuring soil water, i.e., calibration, soil damage, damage to vegetation, random count error, soil variability, and relocation error. Absolute sampling error, is generally independant of the length of measurement period and may be up to ±5 mm. Spittlehouse and Black (1980) summarize the probable relative errors associated with the soil water balance method. The error in the soil water balance estimate of evapotranspiration, relative to the actual change in soil water content, decreases with increasing intervals between measurements and increases as the soil dries. Relative error is <20% over a two week measurement period.

In the replacement series, two gravimetric samples per treatment, replicated four times, were collected using a core sampler during 1985 and 1986. Five neutron probe access tubes were installed at least 1 m apart in a circular configuration around the plot centers. Two replicates per treatment were sampled in 1985 and four replicates per treatment were sampled in 1986 and 1987. In the neighbourhood exeriment, two gravimetric samples per treatment plot replicated five times, were collected in 1986. One neutron probe access tube was installed within 10 cm of the plot centre. In 1986 and 1987, five replicates per treatment were sampled.

The probe used in this study, a Troxler Depth Moisture Gauge Model 3333, was calibrated annually over a range of soil water contents using gravimetric samples collected adjacent to a calibration access tube. In order to convert gravimetric water content to a volumetric basis, bulk density and coarse fragment content were sampled at 10 cm intervals at four locations across the study site. In addition, soil water content was converted to soil matric potential with a soil-moisture-retention curve obtained in the laboratory using a pressure plate apparatus (Appendix III.I). These values were similar to measurements made in the field using soil moisture blocks and thermocouple psychrometers.

Soil matric potentials less than 0.1 MPa were measured directly at 0.05, 0.15, 0.30, and 0.50 m withmoisture blocks and soil hygrometers. These were: Model 5201 soil moisture blocks and a Model 5910-A soil moisture meter (Soil Moisture Equipment Corp.); and Model PST-55-30 soil hygrometers using a HR33T microvoltmeter (Wescor Inc.) on psychrometric and dewpoint modes. Soil hygrometer measures were used to calculate average root zone values of soil matric potential for the various treatments to a depth of 0.30 or 0.50 m. The moisture block measurements were used to indicate trends.

A total of 130 moisture blocks were installed within treatment plots in both the replacement series and neighbourhood experiments. They were monitored at a minimum of once every two weeks throughout the 1985, 1986, and 1987 growing seasons. Soil hygrometers were installed in the spring of 1986 and monitored at the same time as the moisture blocks were monitored during 1986 and 1987. Soil hygrometers were installed in a 100% grass and a 100% tree replacement series plot (one profile each). In addition, in the neighbourhood experiment, four replicates were installed at 5, 15, and 30 cm in each of the treatments 5, 7, and 11. To install the prewetted moisture blocks and thermocouple hygrometers, a hole approximately 0.15 m in diameter was excavated about 0.20 m from a seedling and small access holes for the leads were then made in the side of the hole at the various depths. After placement of moisture blocks and hygrometers thehole was filled with lightly packed stone free soil.

Water Balance Calculations

Because of its' importance to soil water balance equation, accurate estimates of evapotranspiration are fundamental to the evaluation of drought severity and thus the benefits of silviculture prescriptions. Spittlehouse and Black (1984) reviewed several models that predict evapotranspiration. They noted that the 'energy-soil limited evapotranspiration model' is appropriate for general forest water balance calculations since it does not require extensive weather data. For the purposes of this study, field-measured soil water and precipitation values were incorporated into the 'energy-soil limited evapotranspiration model' to estimate daily evapotranspiration.

Water balance calculations were confined to the two treatments described for the replacement series experiment. The root zone soil water balance equation for a period is defined as

$$W_i = W_{i-1} + (P_i - E_i) \quad (3.1)$$

where W_i (mm) is the root zone soil water storage at the end of the ith time period, P is precipitation in mm and E is the daily evapotranspiration in mm. Both runoff and interception are assumed to be negligible. Rearranging equation 3.1 allows calculation of E using W_{i-1}-W_i measured by means of the neutron probe. The water deficit over the growing season can be calculated by summing daily values of (E_{max}-E) where E_{max} and E are the modelled maximum and actual rates of evapotranspiration, respectively. The 'energy-soil limited evapotranspiration model' is outlined in Appendix III. Measured evapotranspiration data were used to calibrate the model.

Long-term Growing Season Weather Variability

Year-to-year growing season variability in air temperatures and precipitation was examined using climate data collected at Williams Lake Airport from 1961 to 1984[4].

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4 Environment Canada, Atmospheric Environment Service weather archives, Vancouver, B.C.

RESULTS and DISCUSSION

Estimating Evapotranspiration

Values of evapotranspiration were calculated, for periods ranging from 10 to 24 days, throughout the growing seasons of 1985, 1986, and 1987. Evaptranspiration values measured for the 100% grass and 100% tree treatments were similar both at the beginning of the growing season before the grass had grown appreciably and at the end of the growing season after the grass had senesced (Table 3.1, Figure 3.1). During the middle of the growing season, which was characterized by low precipitation periods, (< 10 mm), evapotranspiration was clearly higher in the 100% grass treatment, by approximately 1 mm/day, than in the 100% tree treatment. Unfortunately, measurements periods during the middle part of the growing season occurred at times when precipitation contributed significantly to evapotranspiration through soil surface evaporation. As a result treatment differences were masked. This is evident from Figure 3.2 which shows the cumulative evapotranspiration over the growing season in relation to precipitation.

Figure 3.1 depicts seasonal trends in measured and potential evapotranspiration for the 100% grass treatment. Since it has been shown that evapotranspiration is energy limited when soil water is not limiting, potential evapotranspiration was estimated from the energy-soil limited evapotranspiration model outlined in Appendix III (Giles *et al.* 1985, Wallis *et al.* 1983, and Spittlehouse and Black 1981). The soil limited phase predicts water deficits for both transpiration and soil evaporation. During all three years of the study, water deficits had developed by July and continued through the end of August. In addition, water deficits tended to occur at least each spring for short periods. Patterns of evapotranspiration clearly varied from year-to-year. In 1985, the rate of evapotranspiration began a sharp decline from the mid-July peak, whereas in both 1986 and 1987 the rate of evapotranspiration peaked earlier (mid-June) and gradually declined through the summer.

Table 3.1 Average daily evapotranspiration measured over the course of the 1985, 1986, and 1987 growing seasons.

PERIOD OF TIME (yr/m/d)	PRECIP (mm)	EVAPOTRANSPIRATION (mm) Replacement Series Treatments		Neighbourhood Experiment Treatments		
		100% Grass	100% Tree	5	7	11
85/06/12						
	20	1.87	1.87			
85/07/04						
	3	2.47	1.39			
85/07/17						
	8	2.11	1.16			
85/08/01						
	17	1.28	0.85			
85/08/13						
	4	0.63	0.99			
85/08/29						
	77	1.74	1.78			
85/09/12						
86/05/20						
	12	1.57	1.93			
86/06/08						
	9	2.46	1.74			
86/06/22						
	6	2.03	1.02	0.55	0.95	1.43
86/07/05						
	32	1.36	1.64	2.42	1.94	2.20
86/07/16						
	17	1.55	1.86	1.44	1.80	1.24
86/08/05						
	16	1.34	1.71	1.36	1.69	1.85
86/08/20						
	14	1.01	1.11	1.14	1.27	1.41
86/09/13						
87/04/28						
	14	1.86	1.93	1.52	1.75	1.94
87/05/11						
	20	1.77	1.66	1.62	1.67	1.64
87/05/27						
	2	0.96	0.69	0.37	0.55	0.78
87/06/06						
	6	2.02	1.79	1.66	1.97	2.35
87/06/18						
	29	1.72	1.80	1.89	1.78	1.74
87/07/14						
	25	1.67	1.53	1.93	1.78	1.68
87/08/10						
	9	0.55	0.54	0.68	0.63	0.59
87/08/21						
	0	0.30	0.40	0.47	0.31	0.29
87/09/03						
	0	0.29	0.16	0.25	0.27	0.19
87/09/17						

Figure 3.1 shows differences between actual and potential evapotranspiration in the 100% tree treatment. In this treatment, the water deficits primarily relate to soil surface evaporation since leaf areas were low. As expected, reduced leaf area led to lower rates of evapotranspiration in the 100% tree treatment than in the 100% grass treatment. In 1985, the rate of evapotranspiration peaked early and declined rapidly. In September 1985, the rate of evapotranspiration increased corresponding to a period of heavy rainfall, however, this sudden input of moisture was not reflected in the modelled maximum evapotranspiration values because moisture was lost to surface runoff (Figure 3.1). In the summer of 1986, which was cooler and moister, the rate of evapotranspiration was relatively consistent except for a short dry period during the latter part of June. In 1987 the pattern was essentially the same for the 100% tree and 100% grass treatments peaking in June and declining slowly until mid August when it decreased rapidly as a result of soil drying, senecscence of the grass (in the 100% grass treatment) and lack of precipitation to wet the soil surface in the 100% tree treatment.

Although the pattern of the evaporative demand seems variable from year-to-year, it is interesting that total evapotranspiration over the growing season was similar for the three years. For example, evapotranspiration for June 12 to August 15 in the 100% grass treatment was 121 mm, 110 mm, and 105 mm in 1985, 1986 and 1987 respectively. In 100% tree treatment corresponding values were 95 mm, 103 mm,and 102 mm. These results suggest that water is always limiting during the growing season at the site. However, the pattern and timing of depletion are important to consider with respect to plant water stress. Figure 3.3 depicts the pattern of soil water depletion. The soil water depletion deficit is defined as the amount of water required to return the soil to the water content at the beginning of the growing season (taken to be 180 mm in this study). Like the rate of evapotranspiration the depletion deficit varies from year-to-year and is likely tied to date of snow melt. The soil water depletion deficit appeared to begin earlier in 1985 than in 1986 or 1987 and increased rapidly (Figure 3.3). Depletion deficits in 1986 and 1987 were initially the same, however, in 1986 deficit development slowed considerably through July although by September the values were again similar. Figure 3.3 also shows a smaller soil water deficit in the 100% tree treatment where the grass has been removed than in the 100% grass treatment.

The above description of evapotranspiration at the site provides a useful indicator of the inherent variability in timing and duration of water deficits. Furthermore, it provides an indication of the impact of pinegrass on site water relations. However, to better characterize evapotranspiration it is useful to examine water depletion through the soil profile.

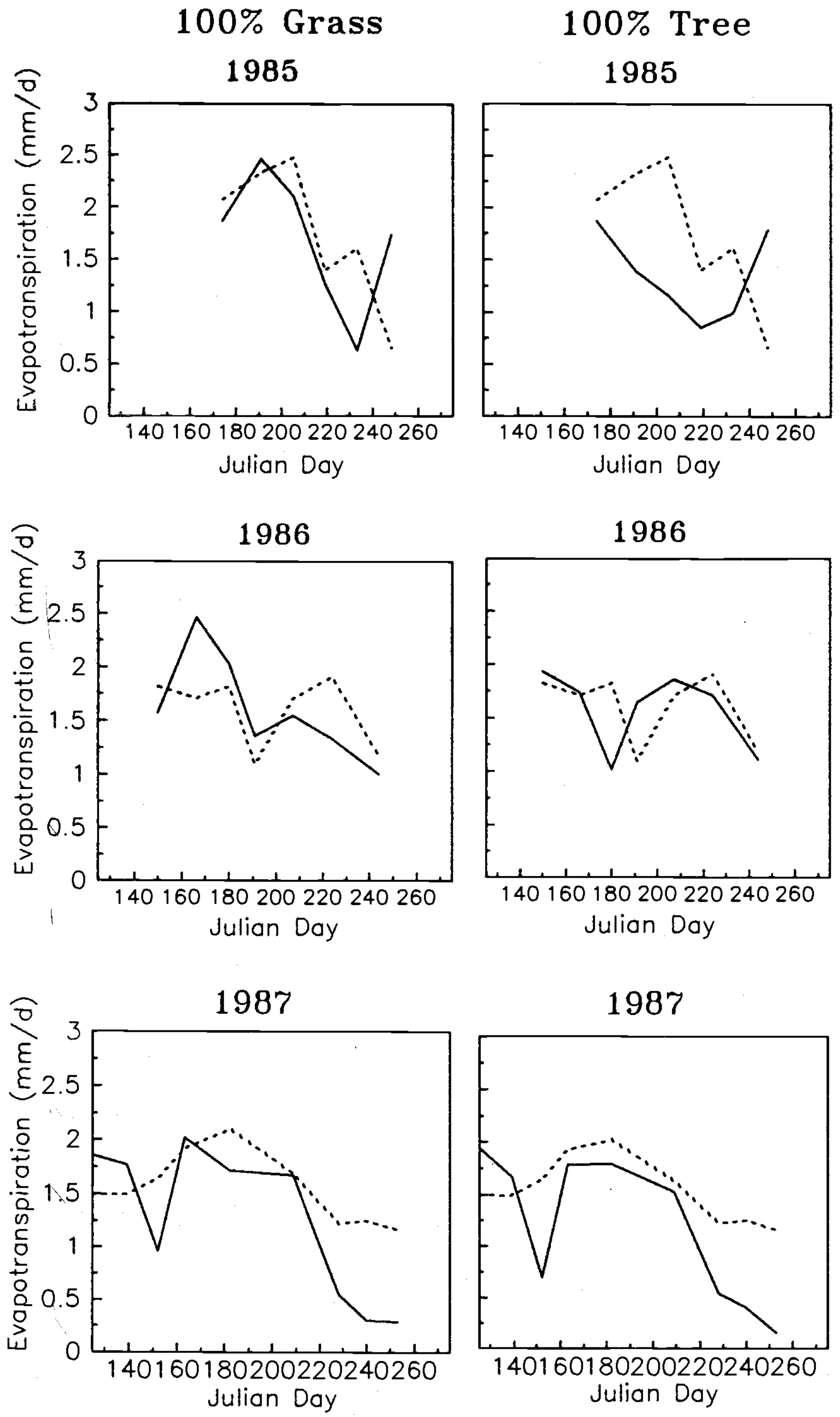

Figure 3.1 Modelled maximum (----) and actual (——) evapotranspiration rates for the 100% grass and 100% tree treatments over the 1985, 1986 and 1987 growing seasons.

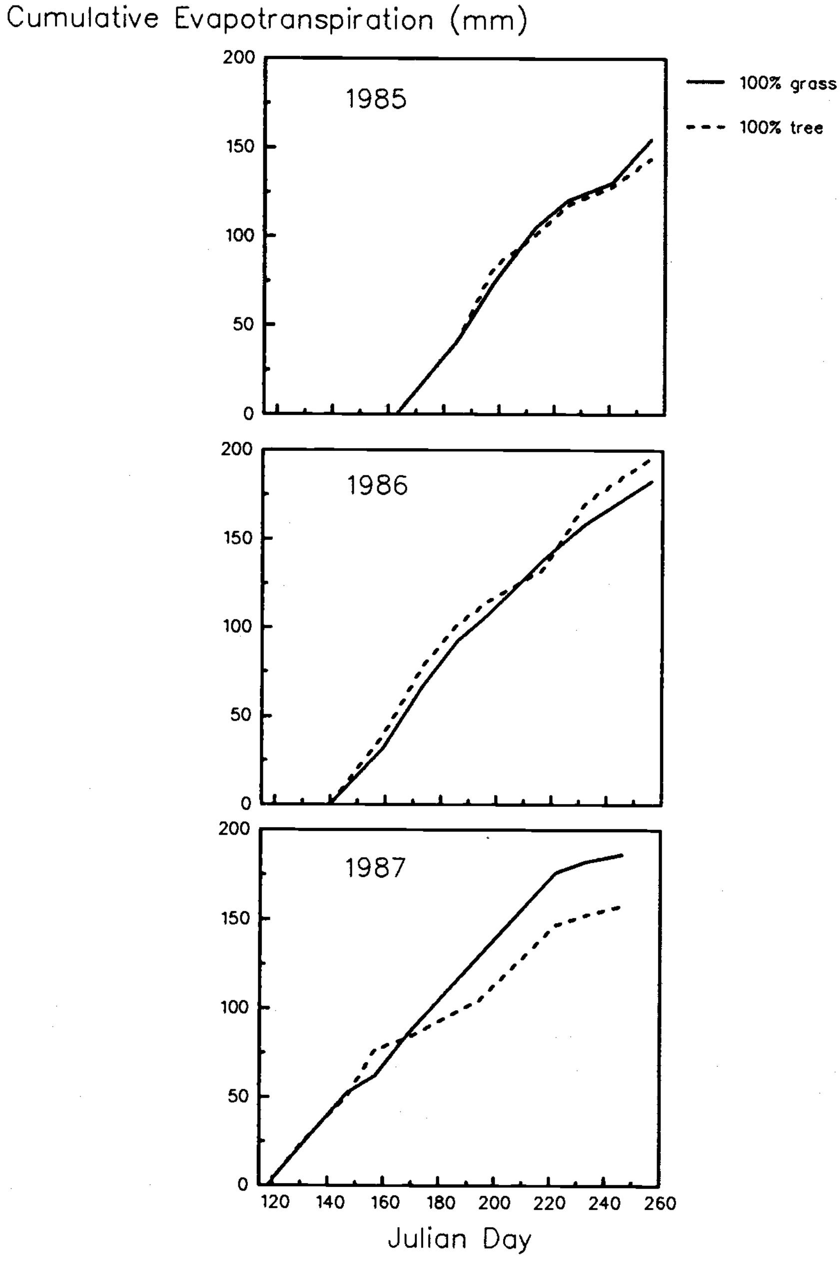

Figure 3.2 Comparison of cumulative evapotranspiration for the 100% grass and 100% tree treatments over the 1985, 1986 and 1987 growing seasons.

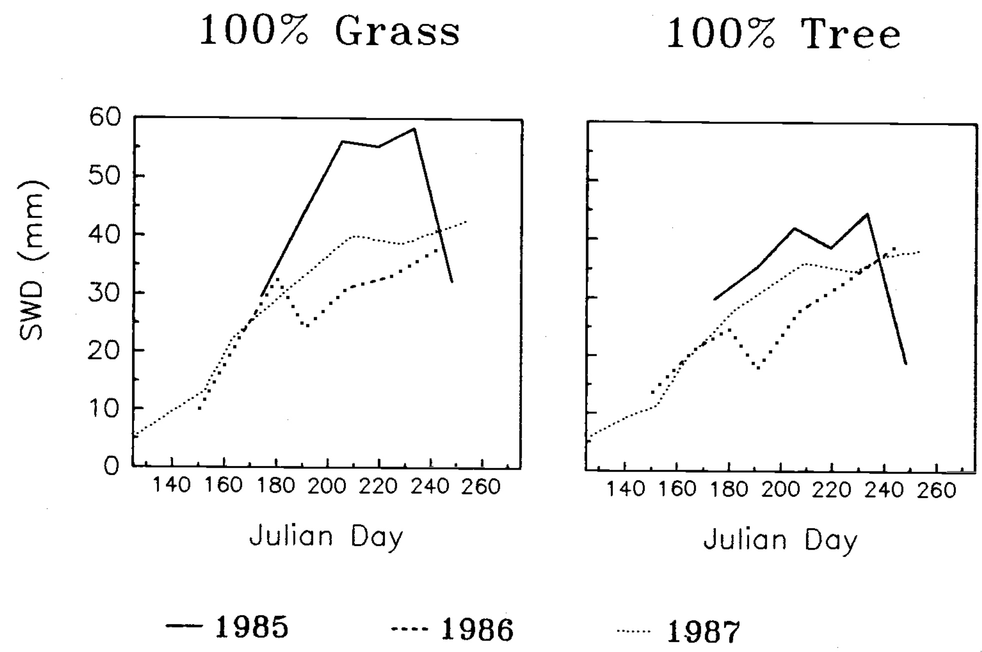

Figure 3.3 Soil water deficit over the 1985, 1986 and 1987 growing seasons in the 100% grass and 100% tree treatments.

Soil water content profiles for selected dates over the three growing seasons are shown in figures 3.4 to 3.6 for the 100% grass and 100% tree treatments. The 1987 growing season provided the clearest indication of rapid depletion over time (Figure 3.6). In particular, the dramatic decrease between March 19 and April 28, 1987 suggests the importance of late snow melt in maintaining maximum available soil water content for tree growth. As the growing season progresses, the top of the soil profile tends to become drier than the bottom as a result of greater root activity and surface evaporation. Patterns of water content for the two treatments indicate that below 0.15 m the 100% grass treatment generally has less water than the 100% tree treatment. This results from the greater rooting activity and subsequent transpirational loss from that portion of the profile. Above 0.15 m, however, the tree treatment tended to be drier presumably because of greater loss through soil surface evaporation. Figure 3.7 shows the average water retention curve for the soil sampled at the study site (Appendix II). The water content drops from approximately 30% at saturation to 25% at -0.03 MPa and 12% at -1.92 MPa. These values in conjunction with the water contents measured indicate that very early in the growing season significant water potentials have developed in the top 0.30 m and subsequently even soil water potentials at depths greater than 0.30 m rapidly drop to below -0.2 MPa (figures 3.4-3.6).

Soil water potential profiles for selected dates in 1986 and 1987 are shown in Figure 3.8 for both treatments. Again, 1987 shows typical depletion patterns, whereas, the 1986 growing season clearly was wetter than normal. In 1987, root zone soil water potential decreased throughout the growing season reaching a minimum of approximately -3.0 MPa by mid-September whereas in 1986 root zone soil water potential remained above -0.5 MPa until September. Comparisons of precipitation patterns with soil water potential at different soil profile depths through the growing season, demonstrate that once the top 0.05 m of soil dries they do not noticeably wet up again unless precipitation exceeds 10 mm. Furthermore, it takes approximately 30 mm of precipitation to wet the soil to a depth of 0.15 m. This suggests that although precipitation occurs throughout the growing season much of it is not available to the plants since it evaporates quickly. However, this lack of availability to plants is not reflected in the evapotranspiration values (Table 3.1).

On the basis of the above discussion it may be more appropriate to consider the root zone as a two layered system rather than a single layer as was done here. For example, dividing the root zone into a top 0.10 m and a layer below 0.10 m would allow one to partition surface evaporation from transpiration. If this were done then comparisons of actual and potential evapotranspiration would be more indicative of water stress severity and duration. Unfortunately, without additional soil moisture and root density measurements, this two-layered approach would require extensive extrapolation to develop effective models.

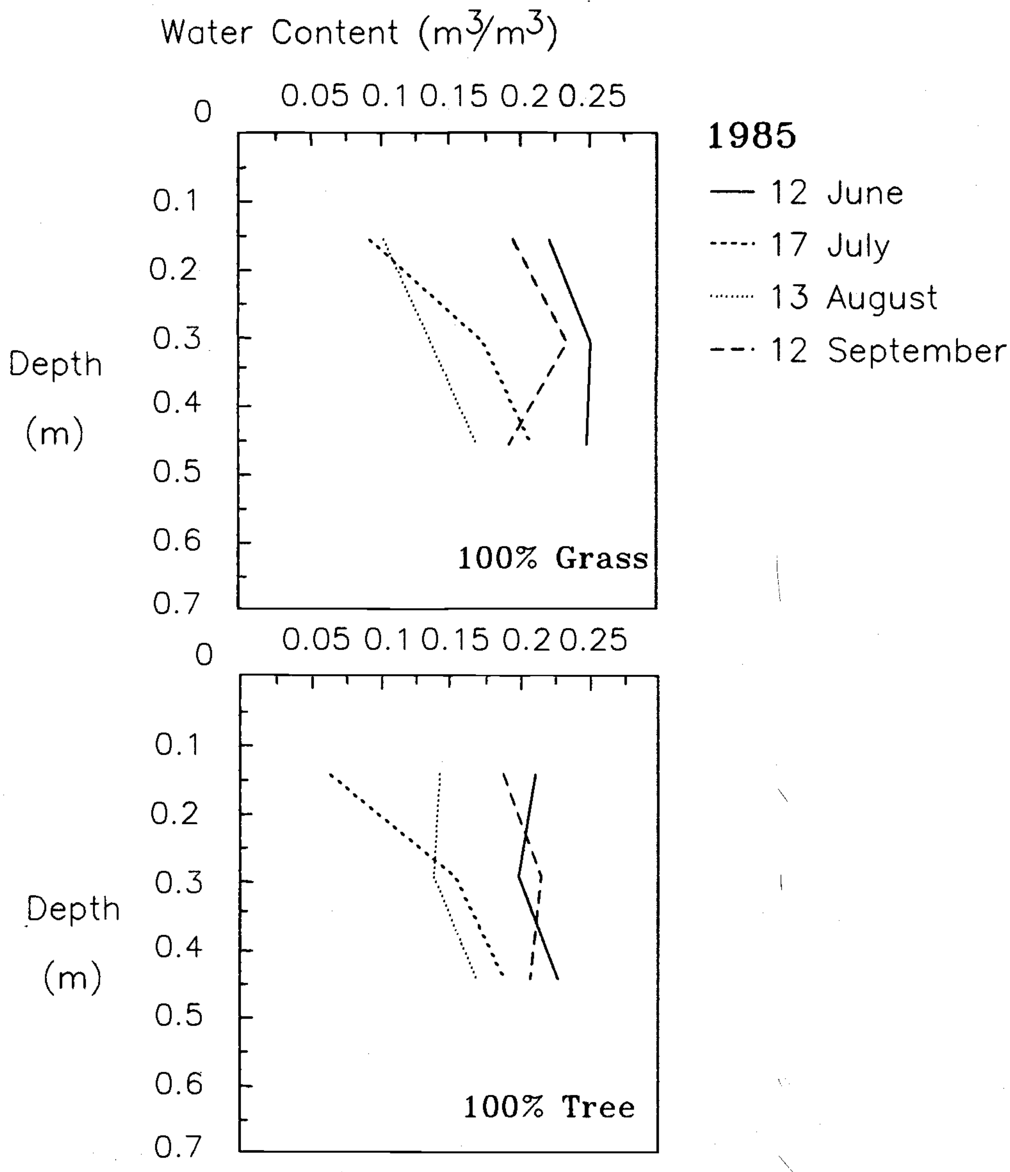

Figure 3.4 Soil water content in the 100% grass and 100% tree treatments at various depths over the course of the 1985 growing season.

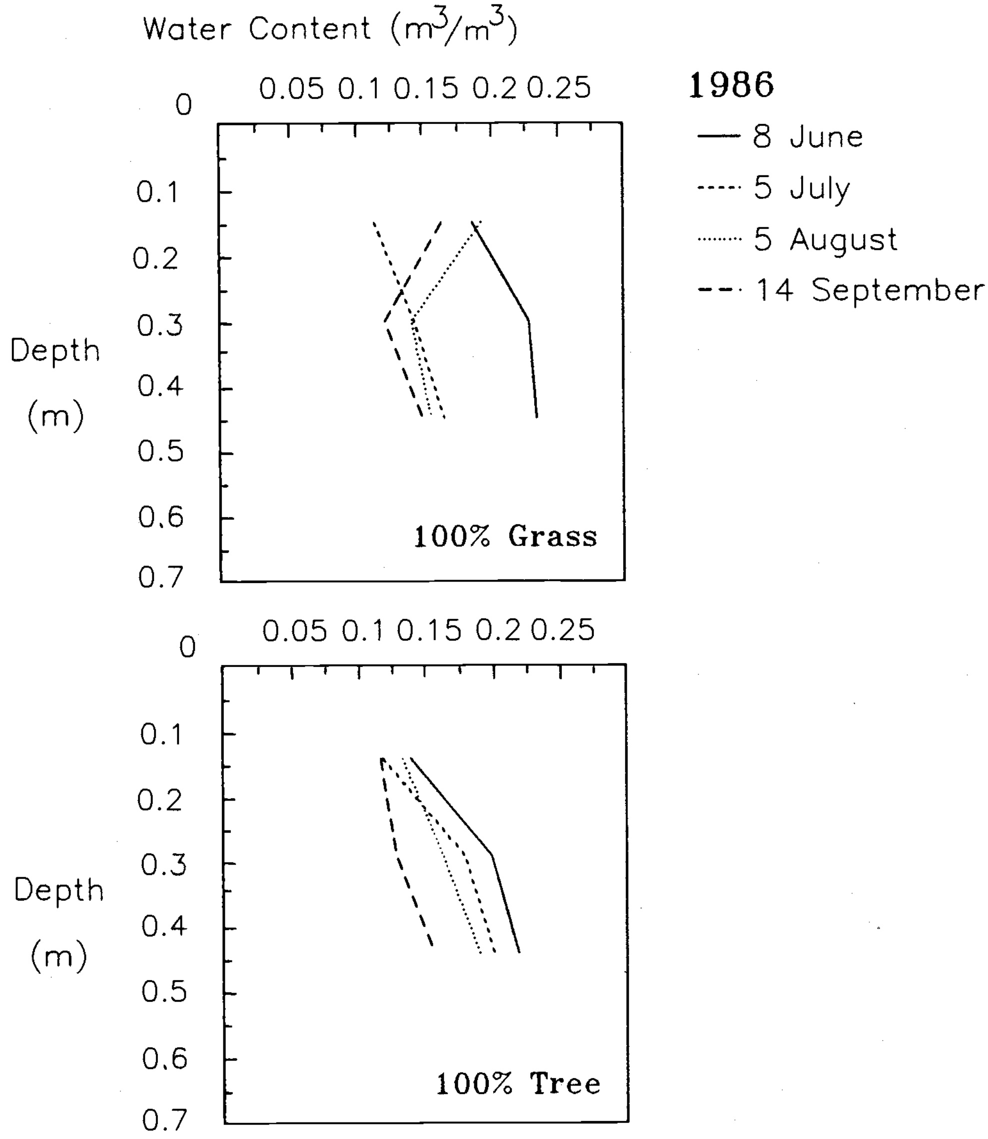

Figure 3.5 Soil water content in the 100% grass and 100% tree treatments at various depths over the course of the 1986 growing season.

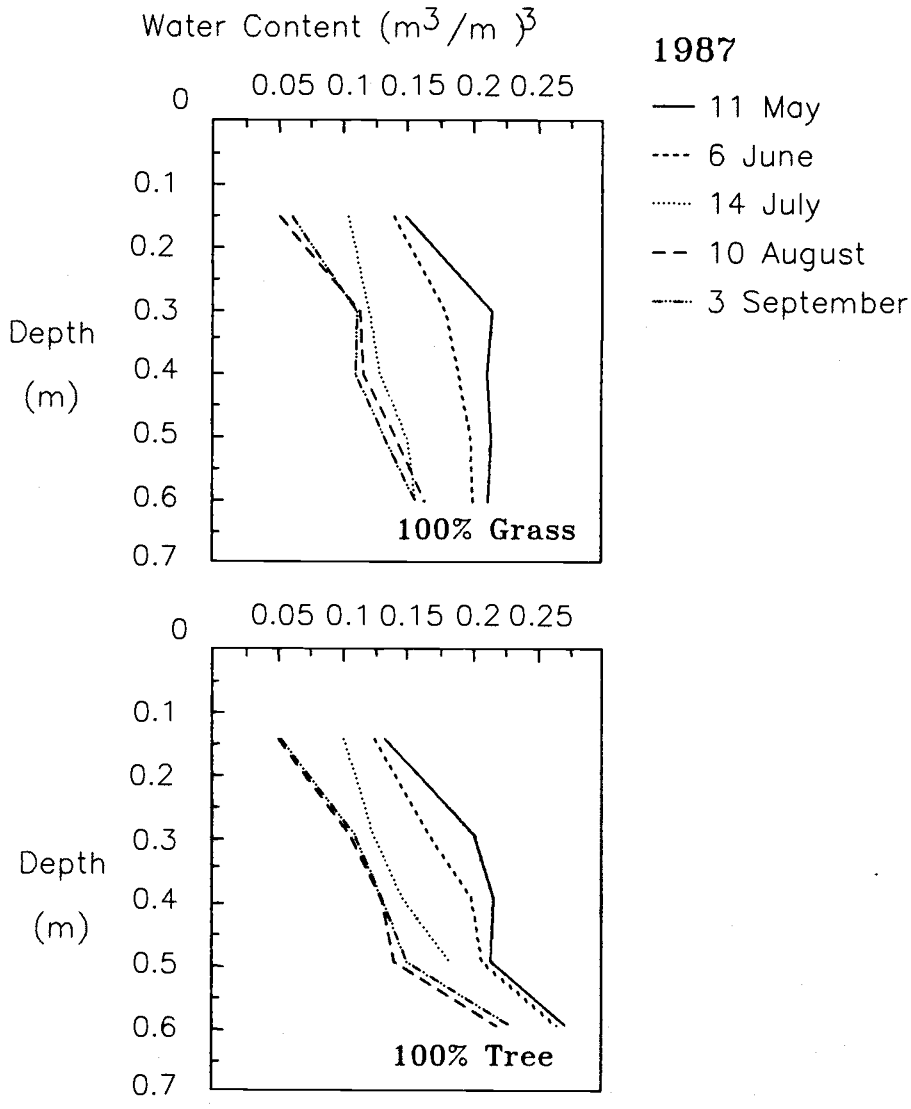

Figure 3.6 Soil water content in the 100% grass and 100% tree treatments at various depths over the course of the 1987 growing season.

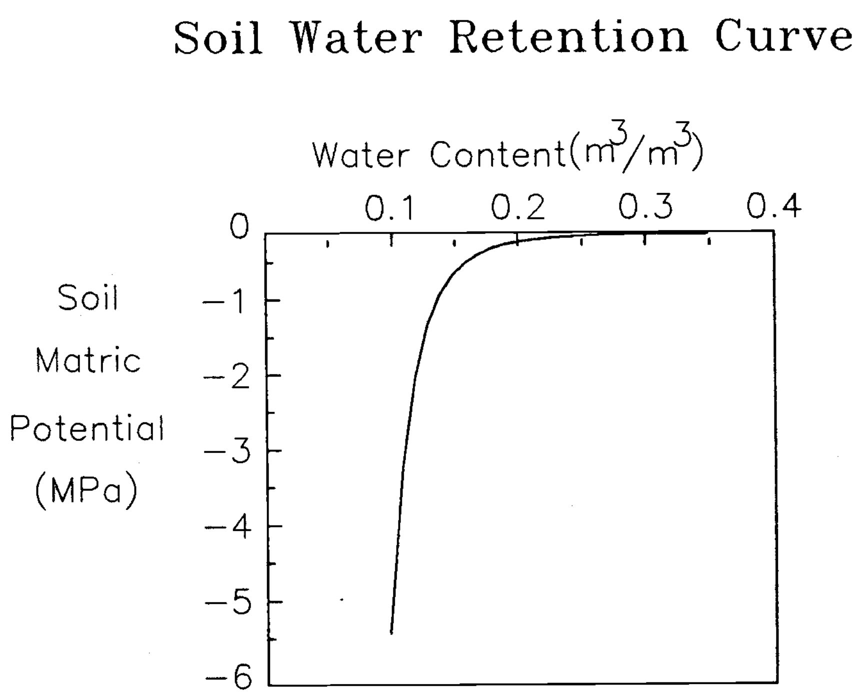

Figure 3.7 Average soil water retention curve for the study site silt loam soil.

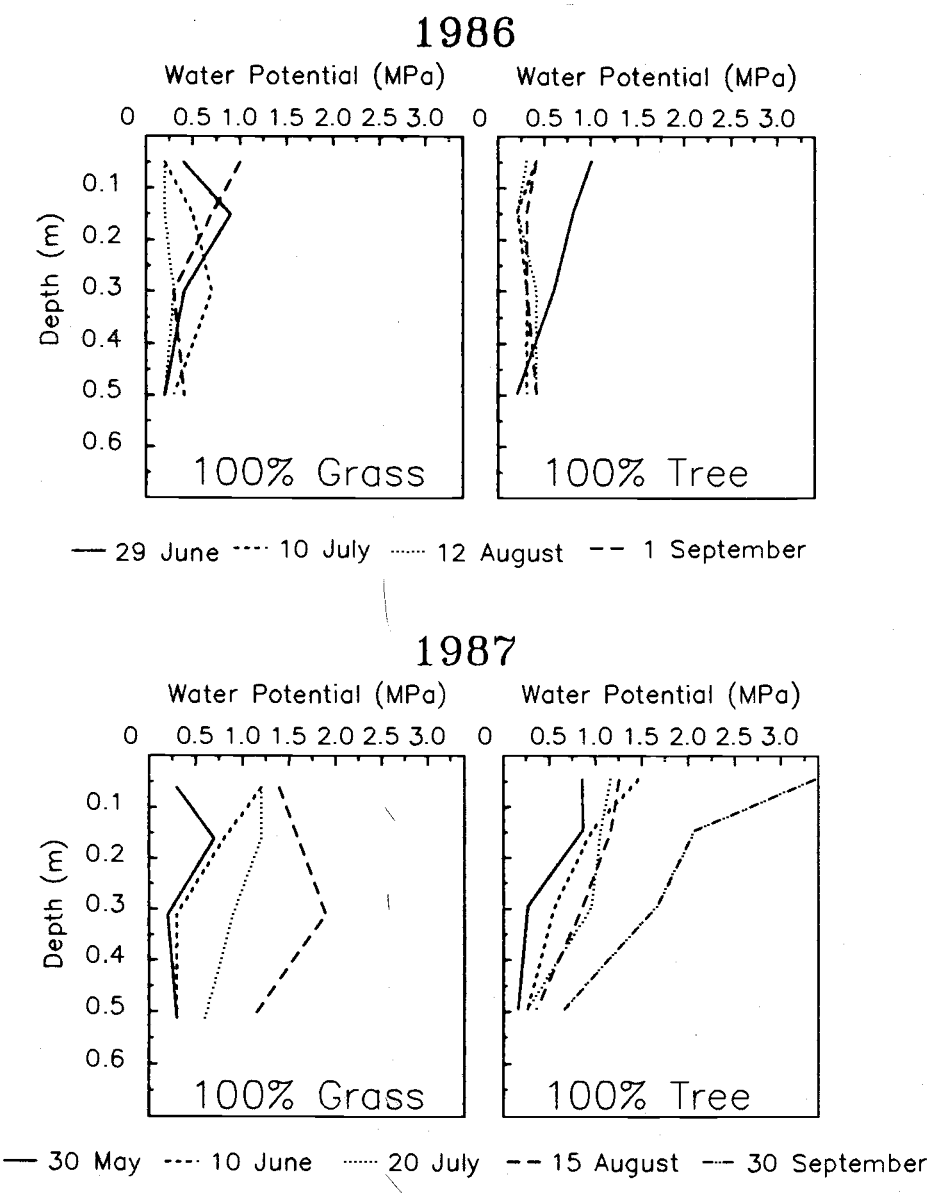

Figure 3.8 Soil matric potential in the 100% grass and 100% tree treatments at various depths over the course of the 1986 and 1987 growing seasons.

Long-term Variability in the Growing Season Weather

At Williams Lake Airport, long-term average total annual precipitation is 413 mm, 50% of which typically occurs from May through September (Environment Canada 1980). This long-term average, however, reveals little about the frequency of unfavourable growing season conditions for seedling establishment. A better indication of year-to-year growing season variabililty is obtained by examining monthly average temperature and moisture conditions over a number of years. Table 3.2 shows there was month to month and year to year variability for the years 1961-1987 at the airport.

Table 3.2 Monthly variation in May to August precipitation and temperature for the period 1961 to 1987 at the Williams Lake Airport (IDFb). Monthly precipitation classes are: Very Dry <20 mm, Dry 20-35 mm, Moist 35.1-50 mm, and Wet >50 mm. Monthly classes of average temperature are: Cold <10 ^{o}C, Cool 10.1-13 ^{o}C, Warm 13.1-17 ^{o}C, Hot >17 ^{o}C.

PRECIPITATION	PERCENTAGE OF YEARS			
	May	June	July	August
Very Dry	26	19	19	26
Dry	30	26	4	26
Moist	22	11	41	11
Wet	22	44	37	37
TEMPERATURE				
Hot	0	4	15	15
Warm	0	26	85	74
Cool	30	70	0	11
Cold	70	0	0	0

As noted in Chapter Two, conifer regeneration in the IDF is believed to be largely controlled by atmospheric and soil-water conditions. Furthermore, the timing and pattern of moisture depletion in the upper 15 cm of soil appear critical to seedling survival. Weather conditions in May and June are particularly critical because both precipitation and temperature during the first half of the growing season determine to a large extent the rate of soil water depletion. Of the three study years, 1985 had the largest water deficit early in the growing season yet June was wet and cool. This suggests that growing conditions for conifer seedlings would be favourable only if precipitation during May and June was sufficient to meet evaporative demand without severely depleting soil moisture.

A decision table was constructed to assess the risk of failure in seedling establishment, i.e., the probability of having unfavourable moisture conditions early in the growing season (Spittlehouse and Childs 1989). Four precipitation classes based on monthly totals were used: very dry (<20 mm), dry (20-35 mm), moist (35.1-50 mm), and wet (>50 mm). For example, in 26 percent of the years May had less than 20 mm of precipitation (Table 3.2). The classes were chosen using the following criteria:

(i) approximately 50 mm is sufficient to meet the monthly evapotranspiration requirement without depleting soil water storage (Figure 3.2);

(ii) approximately 15 mm is the amount of soil water that can be used without depleting the storage of water in the upper 15 cm soil layer below -0.2 MPa.; and

(iii) approximately 20 mm is the minimum amount of precipitation required to add to the amount of water stored (30 mm) in the upper 15 cm of the soil to balance the monthly evaporative demand.

A combination of May and June precipitation classes and a combination of June and July precipitation classes, were then categorized, on the basis of water availability to seedlings, as favourable (minimal moisture deficit) or unfavourable (moisture deficit) for seedling establishment (Table 3.3). The months were considered in combination because precipitation in one month may be ameliorated or exacerbated by the moisture conditions in the next month. A probability value for each individual category in the matrix was then obtained by multiplying the probabilities for each month (Weldon 1986). This assumes the monthly means are independant. For example, the probability of combinations of May and June precipitation was obtained by multiplying the probability of occurrence of each May precipitation class with each June precipitation class (Table 3.4). These combined probabilities, for the categories that were classified as unfavourable for seedling survival, were summed to provide an overall risk estimate of 65% unfavourable for May and June and 60% unfavourable for June and July precipitation.

Table 3.3 Matrices of May versus June and June versus July precipitation classes depicting the two seedling establishment categories based on water availability to the seedling : X=unfavourable (moisture deficit), √=favourable (minimal moisture deficit).

PRECIPITATION		JUNE Very Dry	Dry	Moist	Wet
	Very Dry	X	X	X	X
MAY	Dry	X	X	X	√
	Moist	X	X	√	√
	Wet	X	√	√	√
			JULY		
		Very Dry	Dry	Moist	Wet
	Very Dry	X	X	X	X
JUNE	Dry	X	X	X	X
	Moist	X	X	X	√
	Wet	X	√	√	√

Table 3.4 Frequency of the four precipitation classes for May and June and June and July, Williams Lake Airport, 1961-87, and probabilities for the various combinations of classes. Based on the two seedling establishment categories, favourable and unfavourable depicted in Table 3.3, these probabilities suggest that in 65% of the years May/June moisture conditions will be unfavourable and in 60% of the years June/July moisture conditions will be unfavourable for conifer seedling establishment.

				JUNE		
			Very Dry	Dry	Moist	Wet
		Frequency	(0.19)	(0.26)	(0.11)	(0.44)
	Very Dry	(0.26)	0.049	0.067	0.029	0.114
MAY	Dry	(0.30)	0.057	0.078	0.033	0.132
	Moist	(0.22)	0.042	0.057	0.024	0.058
	Wet	(0.22)	0.042	0.057	0.024	0.058
				JULY		
			Very Dry	Dry	Moist	Wet
		Frequency	(0.19)	(.04)	(0.41)	(0.37)
	Very Dry	(0.19)	0.036	0.008	0.078	0.07
JUNE	Dry	(0.26)	0.042	0.010	0.107	0.096
	Moist	(0.11)	0.021	0.004	0.045	0.041
	Wet	(0.44)	0.084	0.018	0.180	0.162

Because high air temperatures exacerbate evapotranspiration, the analysis was taken one step further to combine, with the precipitation classes, four temperature classes based on mean monthly temperature: (1) hot (>17 ^{o}C), (2) warm (13.1-17 ^{o}C), (3) cool (10-13 ^{o}C), and (4) cold (<10 ^{o}C) (Table 3.2). A 16 by 16 matrix of probabilities for May and June weather conditions was constructed to subjectively assess the favourability of moisture-temperature conditions for seedling establishment (Table 3.5). Unfavourable early growing season conditions occurred 80% of the time over the 1961-1987 period.

Table 3.5 Frequency of the 16 moisture-temperature conditions for May and June, Williams Lake Airport, 1961-87, and the two seedling establishment categories: X=unfavourable, √=favourable, determined from the combination of the regimes for each month. For the condition categories: V=very dry, D=dry, M=moist, P=wet, H=hot, W=warm, K=cool, and C=cold.

				JUNE					
	Frequency	V-H (0)	V-W (.11)	V-K (.07)	V-C (0)	D-H (0)	D-W (.07)	D-K (.19)	D-C (0)
MAY									
V-H	(0)	X	X	X	X	X	X	X	X
V-W	(0)	X	X	X	X	X	X	X	X
V-K	(.15)	X	X	X	X	X	X	X	X
V-C	(.11)	X	X	X	X	X	X	X	X
D-H	(0)	X	X	X	X	X	X	X	X
D-W	(0)	X	X	X	X	X	X	X	X
D-K	(.07)	X	X	X	X	X	X	X	X
D-C	(.22)	X	X	X	X	X	X	X	X
M-H	(0)	X	X	X	X	X	X	X	X
M-W	(0)	X	X	X	X	X	X	X	X
M-K	(0)	X	X	X	X	X	X	X	X
M-C	(.22)	X	X	X	X	X	X	X	X
P-H	(0)	X	X	X	X	X	X	X	X
P-W	(0)	X	X	X	X	X	X	X	X
P-K	(.07)	X	X	X	X	X	X	X	X
P-C	(.15)	X	X	X	X	X	X	X	X

Table 3 continued

	Frequency	M-H (0)	M-W (.04)	M-K (.07)	M-C (0)	P-H (.04)	P-W (.04)	P-K (.33)	P-C (0)
V-H	(0)	X	X	X	X	X	X	X	X
V-W	(0)	X	X	X	X	X	X	X	X
V-K	(.15)	X	X	X	X	X	X	X	X
V-C	(.11)	X	X	X	X	X	X	X	X
D-H	(0)	X	X	X	X	X	X	X	X
D-W	(0)	X	X	X	X	X	X	X	X
D-K	(.07)	X	X	X	X	X	X	X	X
D-C	(.22)	X	X	X	X	X	X	X	X
M-H	(0)	X	X	X	X	X	X	√	√
M-W	(0)	X	X	X	X	X	√	√	√
M-K	(0)	X	X	X	X	X	√	√	√
M-C	(.22)	X	X	X	X	X	√	√	√
P-H	(0)	X	X	X	X	X	X	X	√
P-W	(0)	X	√	√	√	X	√	√	√
P-K	(.07)	√	√	√	√	X	√	√	√
P-C	(.15)	√	√	√	√	√	√	√	√

In summary, the probability that growing season moisture and temperature conditions will be unfavourable for conifer seedling establishment is approximately 80%. This estimate of the risk of unfavourable weather conditions may be useful information for forest management decisions involving site assessment and silviculture planning.

CONCLUSIONS

Based on the above one can conclude the following.

1. The amount and distribution of growing season precipitation varies substantially in the IDFb.

2. Of the total 1985 growing season evapotranspiration (early June to late August) measured at the study site, approximately 39% came from precipitation and 61% from soil moisture storage. In contrast in 1986 and 1987 more than half of the evapotranspiration came from precipitation, i.e., 62% and 55% in 1986 and 1987 respectively.

3. Precipitation events during the growing season never exceeded the soil water deficit suggesting significant drainage from the soil profile did not occur.

4. Although the pattern and timing of depletion was variable, total growing season evapotranspiration was similar in all three study years.

5. Soil water content profiles suggest water deficits typically develop rapidly at the beginning of the growing season. Longterm climate records indicate that unfavourable early growing season conditions can be expected about 80% of the time.

6. Although during periods of low precipitation evapotranspiration was higher for the 100% grass treatment than the 100% tree treatment, treatment differences were masked most of time due to small precipitation events. However, growing season precipitation likely evaporates quickly and is thus unavailable to plants. To better understand the role of pinegrass in site water balance it would be more appropriate to treat the root zone as a two layered system thus separating surface evaporation from transpiration.

Silvicultural Implications

Chapter Four

This study, described in the preceding chapters, was initiated in an attempt to determine the effects of pinegrass and several environmental factors on the survival and performance of Douglas-fir seedlings. The major conclusion and underlying theme of this thesis is that the high rate of mortality of planted Douglas-fir seedlings on these types of sites is the result of a combination of several factors including: drought, spring frost, poor vigour at the time of planting, and animal damage. Furthermore, pinegrass competition appears to exacerbate seedling moisture stress. The results lead to speculation about the impacts of several factors on the success of silvicultural techniques and practices in pinegrass dominated sites within the IDF zone.

Analysis of longterm weather trends indicates that unfavourable growing seasons are common and unfavourable spring conditions should be expected more than three quarters of the time in the IDFb. Furthermore, the planting window for these open, pinegrass dominated sites is, at most, one month which appears to vary from year-to-year. Therefore, planting must be timed to take full advantage of this short period and the seedlings planted must be vigourous.

Ensuring that seedlings are vigourous is not a straightforward task. For example, in this study a great deal of attention was paid to proper handling techniques of seedlings. However, prior to planting, the history of these seedlings is unknown. There is some evidence, though, that stock planted in 1985 was of questionable vigour[5]. Indeed, bottlebrushing and mortality were observed within the first month after planting. Root growth capacity measures indicated that the seedlings were in reasonable health while in storage but it is well known that vigour can deteriorate quickly.

Since IDF clearcut sites are recognized as difficult to regenerate it seems particularly important that the seedlings planted be as vigourous and well adapted as possible. Based on the fact that seedlings used in this study were standard operational stock, foresters may find it advisable to monitor the vigour of seedlings destined for these types of sites closely.

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[5] D. Deyoe, Department of Forest Science, Oregon State University, personal communication, October 1986.

Tree seedling suitability is a key aspect relating to the outcome of this study that was not specifically addressed earlier. Hobbs (1984) suggests that seedlings with shoot-root ratios of 2.0 or less, high root growth potential, and fibrous roots with many growing tips, are best adapted to dry sites. Because these vigour related characteristics may be affected by seedling age and whether seedlings have been containerized or planted with a bare root, seedling age and stocktype may be important determinants of plantation success. Although Helgerson (1985) reported survival figures which slightly favoured planting of bareroot Douglas-fir seedlings on dry sites, most authors including Hahn and Smith (1983), Hobbs and Wearstler (1983) and Arnott (1975) have reported that container Douglas-fir survived better than bareroot stock on dry sites. Although little or virtually no information is available with respect to the effect of seedling age and planting success it seems reasonable that increased root development of two year-old seedlings might be advantageous over the one year-old stock used in this study. Clearly work is needed to determine the relative advantages of planting various Douglas-fir stocktypes on dry sites within British Columbia's southern interior.

This study also raises the questions of matching stocktype to a site. Clearly seedlings used here (PSB 313 1+0 Douglas-fir) were unable to extend their roots enough within the first few years to escape significant moisture stress. Whether another stocktype or species would be better adapted for rapid root growth and/or drought resistance was not examined.

The question of what species is most appropriate for backlog IDF sites depends on understanding the ecological amplitude of the species that naturally grow in the area combined with a knowledge of past silvicultural experience. As the climax species in the IDF zone, Douglas-fir is obviously well adapted to the climate and site conditions. Furthermore the species is of considerable commercial value. On the otherhand, in this subzone lodgepole pine, the seral coniferous species, may be better suited to coping in the open, harsh site during the first few years after planting. In the Kamloops Region, successful Douglas-fir plantations in the IDFb are notably absent while lodgepole pine plantations have been reasonably successful (Mather 1986). The wisdom of converting Douglas-fir stands to lodgepole pine, however, may be questioned on the basis of pest management, as well as wildlife, recreation and economic values.

Recently a number of silviculturalists have been considering the feasibility of first planting lodgepole pine followed after establishment with an underplanting of Douglas-fir. This of course raises a completely new set of competition related questions. At what densities should pine be planted? When should Douglas-fir be underplanted and at what spacing? What harvesting strategy should be used? Would conversion from even to uneven-age Douglas-fir management be possible and practical?

A third silviculture topic which arises when discussing seedling establishment on these types of sites is how best to improve environmental conditions through site preparation. This study suggests that treatments which are most likely to improve survival include: increasing available soil moisture, increasing soil temperatures in early spring, and decreasing chances of frost damage.

To date, on open backlog IDFb sites, trenching has most improved seedling performance. Third year results of a site preparation trial conducted at the study site correlated Douglas-fir and lodgepole pine survival with increased soil disturbance (Sutherland and Vyse 1987). Recent work in the IDFb to quantify the effects of various site preparation strategies on the microenvironment suggests that trenching and ripping increases soil porosity and thus soil water content through the growing season (Black *et al.* 1988). Furthermore, Black *et al.* (1988) found trenching to increase mean monthly soil temperature and to reduce frost damage. Based on the findings reported here and those of Black *et al.*, it is not surprising that trenching is becoming recognized as a valuable treatment on these types of sites.

Ideas regarding effective silviculture techniques and indeed future areas of research can be gleaned from observing natural regeneration in the IDFb. Interestingly, adjacent to the study site, Douglas-fir has competed successfully. The key to its success, as in a climax forest, appears to be overstory protection from snags and heavy slash. It is likely that reduced nocturnal radiation cooling combined with shade during the day have aided the natural regeneration. In the case of a wildfire therefore it would seem advisable to leave remaining snags and slash on site and plant beneath them.

In addition to stock suitability, stocktype, site treatment, and site history, competition is clearly an important factor affecting seedling survival. The presence of neighbouring plants may affect resource availability or environmental conditions. Petersen (1985b), for example, illustrates this concept for ponderosa pine (*Pinus ponderosa* Laws.) growing in association with pinegrass and elk sedge (*Carex gereyi* Boott). Stem volume of the four year-old pine plotted against leaf area index of the understory vegetation indicated that the leaf area index of the understory vegetation must be decreased to at least 0.4 in order to improve pine growth.

In this study it appears that although during the first few years after planting competition was not the prime factor determining seedling performance it did affect seedling vigor. Although threshold levels of pinegrass competition were not identified for either survival or growth of the seedlings, one would suspect that once the Douglas-fir overcomes initial establishment problems, competition will still control subsequent growth and yield.

Clearly, in order to efficiently and effectively address the silvicultural challenges presented by NSR sites like the one described here foresters and forest ecologists must address the questions raised in this chapter.

A Strategy for Studying Vegetation Competition With Respect to Reforestation Problems

Chapter Five

INTRODUCTION

During the past five years foresters and forest science researchers in British Columbia have come to recognize vegetation competition as one of the problems affecting reforestation. Indeed much of the research currently directed toward the province's extensive NSR forest land is focussed on vegetation competition. This thesis was no exception. It was designed to address a specific competition problem. During the course of such a study, however, I could not help but gain numerous insights regarding directions for future research. This chapter represents a derivative of the experience gained from the study reported in the previous chapters. In it, I present a general strategy for studying vegetation competition problems in British Columbia. The strategy is discussed within the context of the strengths and weaknesses of the three year project.

DISCUSSION

When considering vegetation competition as one of the major problems affecting reforestation in British Columbia, forest scientists must think about three basic questions.

(1) How does one identify whether a significant reforestation problem is attributable to vegetation competition?

(2) Which ecosystems and management prescriptions are most likely to present vegetation competition problems?

(3) How can ecosystems be managed to avoid vegetation competition problems?

Many foresters can successfully respond to these three questions when considering regeneration of a specific site that is about to be harvested based on their field experience. Frequently, the greatest problem is logistical, i.e., supplying the most appropriate management prescription at the right time. The thousands of hectares of NSR backlog, however, are not solely attributable to logistical difficulties. Research directed at answering the three questions that are posed above is essential if provincial foresters are to cure and prevent NSR problems which plague many of British Columbia's forest ecosystems. This, unfortunately, is not a simple task. Below I discuss the kind of information needed to answer the three basic questions stated above. In addition, research approaches necessary to obtain that information are outlined.

How Can Foresters Identify When Vegetation Competition is a Significant Problem?

Foresters are looking for simple tools to help them identify when there is too much vegetation competing with conifers on a particular site. However, determining what is too much involves making economic as well as biological assessments. Therefore, the forester requires means of measuring losses in survival and growth associated with a range of competition levels. To this end, the most logical research approach provides a quantifiable assessment of the survival and growth response of conifer seedlings relative to varying degrees of competition imposed by associated 'weed' species. With this knowledge the forester can determine when competition is a significant problem and whether benefits of vegetation management warrant costs.

It is tempting to embark upon competition studies as follows. (1) Examine initial seedling survival and growth characteristics on an individual tree. The underlying assumption here is that newly planted seedlings are operationally spaced beyond the influence of each other. (2) Continue, assuming that seedlings will begin to interact with one another. (3) Then assess competition by separating the quantitaive effects of intra- and inter-specific competition. The latter is accomplished by manipulating competition levels and measuring effects on a whole stand basis.

Unfortunately the above approach proceeds on the assumption that plantation failure is solely the result of vegetation competition. This poses a major problem because unless one is sure that an area constitutes a 'safe' site for a specific seedling in the absence of competition it cannot be determined whether minimum seedling requirements could be met regardless of the associated vegetation. Indeed, in marginal environments conifer seedlings may be responding to environmental factors which are limiting irrespective of competition.

Based on the above, on certain types of ecosystems it may be prudent to focus research initiatives on considering seedling physiology and growth responses relating to field conditions. Only through this approach can one identify: (i) causes of vegetation competition problems, and (ii) cost effective solutions to competition related regeneration problems. Unfortunately, literature concerning minimum seedling resource requirements over a broad spectrum of field conditions is scarce. Thus, in many cases seedling trials may be required.

Which Ecosystems Are Candidates for Vegetation Competition Problems?

To accurately foerecast which ecosystems are likely to have competition related problems after harvesting, it is necessary to predict the post harvest vegetation complex, its abundance, and its pattern of establishment. The British Columbia Ministry of Forests Ecosystem Classification System provides much of the information necessary for identifying potential 'weeds' for various ecosystems. But actual vegetation complexes and species abundance are frequently controlled by harvest prescriptions and site preparation disturbance.

To develop greater predictive capability, autecological studies of weed species should be conducted to identify: (i) seed characteristics (e.g., longevity, seedbed requirements, dispersal mechanisms), (ii) recruitment strategies (e.g., seed production, vegetative reproduction, bud dormancy), and (iii) growth rates (e.g., effects of environmental factors on rate and extent of growth over the growing season and over several years). Furthermore, assessment of water, nutrient and light relations of 'weed' species related to growth analysis will allow a determination of how and at what rate the competitor will affect the requirements of the seedling. Autecological research may also, provide a basis for identifying groups of weeds which are 'functionally equivalent' competitors thus broadening the applicability of competition research results to more than one plant community.

What Management Strategies will Prevent or Alleviate Competition Problems?

Next, in order to formulate concrete vegetation management objectives the forester must determine maximum acceptable levels of competing vegetation and how those levels are correlated with disturbance. Clearly, if one is to determine what management strategies will prevent or alleviate competition problems, then prior to harvesting a site it is important to have determined when vegetation competition will become significant and which ecosystems are likely candidates for problems. Having determined this, the forester must: (i) determine if a specific management technique is appropriate, (ii) estimate the additional cost for rehabilitation if the preferred technique is not successfully applied, and (iii) design tools or approaches to create 'safe' sites. To meet these needs an understanding of the factors that limit a conifer species survival and growth is essential. Furthermore, one must determine how potential competitors would affect the seedlings environment and resource availability. Trials testing vegetation control techniques will be more efficient with an understanding of the 'weeds' autecology. For example, treatment efficacy is generally tied to the development stage of the weed and thus knowing the best time to apply the treatment will affect the outcome of the trial.

The study reported here attempted to identify the factors most strongly affecting seedling survival and growth on pinegrass dominated sites in the IDF zone. In effect it addressed question one, i.e., when is competition from pinegrass significantly limiting to seedling survival and growth? Moisture stress was assumed to be the main factor limiting growth and competition from pinegrass was assumed to have a strong affect on the soil moisture regime.

The study also assumed that without pinegrass competition, seedling survival would not be a problem. The latter assumption was a weakness in the study and relates directly to the discussion of question one above, i.e., in assuming seedlings would establish if given sufficient competiton free space I ignored the possibility that the environment itself was so extreme as to deter survival.

The study was designed to examine the stand growth response of Douglas-fir seedlings using a replacement series design. However, the results indicate that despite allowing several years for seedlings to establish in the absence of competition, survival in that environment was still a problem. This tendancy was somewhat apparent after observing the heavy toll both frost and moisture stress had on seedlings the first growing season. Therefore, during the following spring a the neighbourhood study was initiated with the objective of quantifying the amount of pinegrass that significantly reduces individual seedling survival and growth. Results were more promising after the first growing season of this experiment although extensive rodent damage the following winter further emphasized the complexity and harshness of the environment faced by the seedlings.

Although I feel the neighbourhood study was a more appropriate approach, it is clear that had I understood the limitations to outplanted Douglas-fir seedling stock and appreciated how little is known about the characteristics of a 'safe' site in this environment I would have placed much less emphasis on growth measures and more on seedling and stock suitability for the range of conditions that typically occur. The strength of the project was the emphasis on microclimate monitoring and seedling resource use. Certainly studying both the site's water balance and its year-to-year variability and the water stress responses of the Douglas-fir seedlings (grown without competition) in comparison to pinegrass provides a step towards understanding minimum moisture requirements on these sites.

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APPENDICES

APPENDIX I

Estimating Surface Resistance

Because a reduction in evapotranspiration below potential is the result of stomates closing and surface drying (increased surface resistance), it is the rate of water supply to the surface that determines the evaporation rate (E). The approach taken in Chapter Three to model evapotranspiration can be made slightly more mechanistic by estimating surface resistance (r_c, s/m) and including it in the evapotranspiration calculations as outlined by Russell (1980). To do this, a potential rate of evapotranspiration (E_o, g/m^2/s) is initially calculated by setting r_c to 0 in the Penman-Monteith equation (Monteith 1965)

$$E=(\Delta(Rn-G)+®cp(e_s(T)-e)/r_a)/(\Delta+\square(1+r_c/r_a)) \qquad (I-1)$$

where Δ is the rate of change of saturated vapour pressure with temperature (Pa/K), Rn is the net radiation flux density (W/m^2), G is the soil heat flux density (W/m^2), ® is the density of air (kg/m^3), cp is the specific heat of air at constant pressure (J/kg/K), e_s is the saturated vapor pressure (Pa) at air temperature (T), e is the water vapor pressure (Pa), and □ is the psychrometer constant. The aerodynamic resistance, r_a, can be calculated from the equation of Thom and Oliver (1977):

$$r_a=(4.72\ln(z/z_o)2)/1+.54u \qquad (I-2)$$

where u is the mean windspeed (m/s) measured at height z (m) and the roughness length, z_o (m), is approximately 0.13 times the height of the vegetation. By rearranging the Penman-Monteith equation r_c is then calculated from

$$r_c=r_a[1+(\Delta y)][(E_o/E)-1]. \qquad (I-3)$$

Values of surface resistance were calculated for the same periods used for the evapotranspiration calculations. z_o was approximated to be 0.024 using wind speed measurements at 0.6 m, 1.4 m and 2.1 m, (Figure I-1). This agrees closely with a z_o estimate of 0.023 assuming that the average height of the native vegetation was 0.18 m.

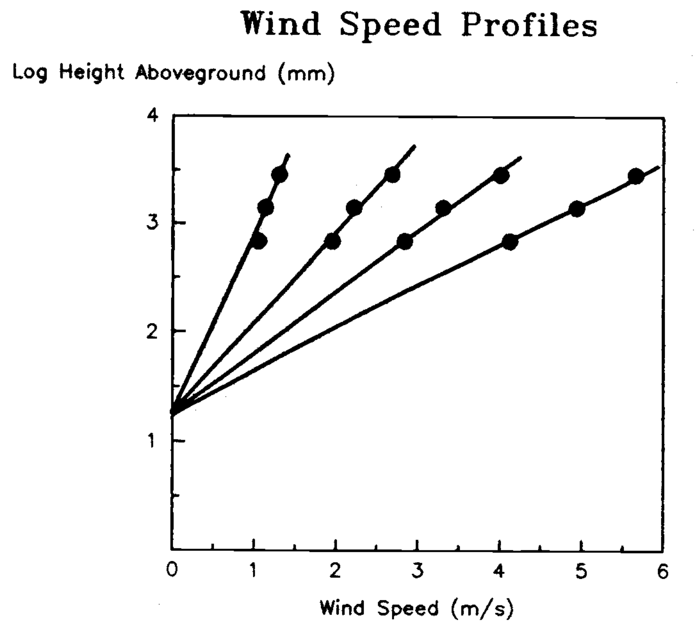

Figure I-1 Selected wind speed profiles. Anemometers compared favourably at the same height (r^2=0.996, s=0.04 and r^2=0.999, s=0.03) and corrections were made to wind speeds (u) using the anemometer at 1.4 m as the reference.

APPENDIX II

Soil-moisture-retention Characteristics

The relationship of soil matric potential (ψ_m) and soil water content is given by

$$\psi_m = \psi_e(\text{ø}/\text{ø}_s)^{-b} \qquad \text{(II.2)}$$

where ψ_e is the air entry suction (J/kg), ø is the water content, $ø_s$ is the saturated water content and b is a constant. ψ_e and b were determined by plotting moisture release data, for two soil profiles, on a log-log scale and fitting a straight line. The slope and intercept of the best-fit line were used to find b and ψ_e respectively (Campbell 1985). Values of ψ_e, $ø_s$ and b for the various soil depths are shown in Table II-1 below.

Table II-1 Average soil water retention characteristics.
Standard deviations are in brackets.

Depth (cm)	Air Entry Suction ψ_e (J/kg)	Water Content $ø_s$ (%)	Constant b
0-10	2.285	48.3	4.32
11-30	0.314	48.8	6.66
30-70	2.529	41.4	5.26
Profile Average	1.669 (1.86)	44.6 (5.21)	5.59 (1.37)

APPENDIX III

Evapotranspiration Model

Spittlehouse and Black (1981) describe the equilibrium evapotranspiration/soil water supply approach to evapotranspiration modelling. The rate of evapotranspiration (E) from a dry canopy (no intercepted water) can be estimated as the lesser of the energy limited and soil limited rates. The energy-limited rate (E_{max}, mm/day) is calculated from the Priestley and Taylor (1972) equation

$$E_{max}=\mathring{a}E_{eq} \qquad \text{(III-1)}$$

where å is an experimentally determined coefficient, and E_{eq} is the equilibrium evapotranspiration rate (mm/d). The soil water supply limited rate (E_s, mm/day) is given by

$$E_s=\beta\o_e \qquad \text{(III-2)}$$

where ß is an experimentally determined constant (mm/day), and $\o_e$ (m^3 water/m^3 soil) is the fraction of extractable water in the root zone (McNaughton *et al.* 1979). When the canopy is wet the rate of evaporation can be assumed to be equal to the energy limited rate for a surface such as grass or a bare soil (Spittlehouse and Black 1984). The specific procedure for calculating E_{max} and E_s is detailed below.

1. For the energy limited rate, given by equation III-1 above, å is an experimentally determined constant (dimensionless) and E_{eq} is approximated from

$$E_{eq}=(s/((s+\gamma)L\ \rho_w))(Rn-G) \qquad \text{(III-3)}$$

where s, γ, L, are respectively, the slope of the saturation vapor pressure curve (kPa/ °C), the psychrometric constant (kPa/ °C) and the latent heat of vaporization (MJ/kg), all at mean daily air temperature. ρ_w is the density of water (Mg/m^3), Rn is the daily net radiation (MJ /m^2/d) and G is the daily soil heat flux (MJ /m^2/d). I assume G to be 15% of Rn (Campbell 1977, Ripley and Redmann 1976); Rn is given by:

$$Rn=(1-\alpha)K+L^* \qquad \text{(III-4)}$$

where α is the albedo, K is the daily solar radiation (MJ /m^2/day), and L^* is the longwave radiation balance (MJ /m^2/day). I assumed α to be approximately 0.24 (Campbell 1977). L^* is given by

$$L^*=(0.1+(0.9K/K_{max}))(\varepsilon_a-\varepsilon_v)\partial T \qquad \text{(III-5)}$$

where K_{max} is the clear sky solar radiation, ε_a is the effective emissivity of the atmosphere calculated from Idso and Jackson (1969) equation

$$\varepsilon_a= 1-0.261\exp(-7.77*10^{-4}(273-T)^2)) \qquad \text{(III-6)}$$

ε_v is the emissivity of the vegetation which I assumed to be 0.96 (Jarvis *et al.* 1976), ∂ is the Stephan-Boltzmann constant ($4.9*10^{-9}$MJ/m^2/d/K), and T is the mean daily air temperature (K).

2. The soil limited rate is given by equation III-2 where ß is an experimentally determined constant (mm/day) and $ø_e$ is

$$(ø-ø_{min})/(ø_{max}-ø_{min}) \qquad \text{(III-7)}$$

where ø is the volumetric water content, and $ø_{max}$ and $ø_{min}$ are respectively, the volumetric water content at field capacity and at permanant wilting point. For silt loam textured soils, $ø_{max}$ is approximately 0.30 m^3 water/m^3 soil and $ø_{min}$ is approximately 0.11 m^3 water/m^3 soil (Campbell 1985, Clapp and Hornberger 1978). I also estimated $ø_{min}$ by plotting all of the calculated values of E against the corresponding average root zone soil water content and extrapolating to E=0. This approach gave a value for $ø_{min}$ of approximately 0.1 m^3 water/m^3 soil.

To determine whether evapotranspiration was energy or soil limited, E/E_{eq} was plotted against $ø_e/E_{eq}$ following the procedure of Spittlehouse and Black (1981) (Figure III-1). The value of $ø_e$ was calculated as shown above with $ø_{max}$=0.3 and $ø_{min}$=0.1. To minimize inconsistencies due to changing leaf area I used only values obtained during the height of the growing season, i.e., mid-June through mid-August. High precipitation periods tended to fall out as extreme points on the graph and were not used to calculate å. For values of $ø_e/E_{eq}$ > å/ß (estimated as 0.17 in this study), $E=E_{max}$, while for $ø_e/E_{eq}$ < å/ß $E=E_s$. For the energy limited rate å was found to be 0.71 (s=0.1, n=20). This is much lower than an å value of 1.27 Wallis *et al.* (1983) reported for a hay field in the Peace River area and for the å value of 1.2 I calculated for data collected on the Matador Project for a Mixed Prairie grassland (Ripley 1974, and Ripley and Redmann 1973). This discrepancy highlights the problem inherent in attempting to apply this model to a site with a relatively low leaf area. The model assumes that there is a uniform depletion of moisture through the profile and thus under a smooth continuous grass surface one can expect å>1 (Spittlehouse and Black 1981). At the study site, however, there is a large percentage of bare soil resulting in a high soil surface resistance component that suppresses evapotranspiration and thus lowers the value of å. As discussed above, because of rain during many of the mid-growing season periods, there were not enough evapotranspiration values for the soil limited phase to reliably calculate ß. However, using the above criteria of an initial value of $ø_e/E_{eq}$=0.17 for the transition from energy to the soil limiting evapotranspiration phases results in ß=4.2.

The equilibrium evapotranspiration soil water supply approach provides for an empirical comparison of actual to potential evapotranspiration. Reduction of the evapotranspiration rate below potential indicates the severity of stress. Duration of stress can be estimated by summing the difference (deficit) over the growing season.

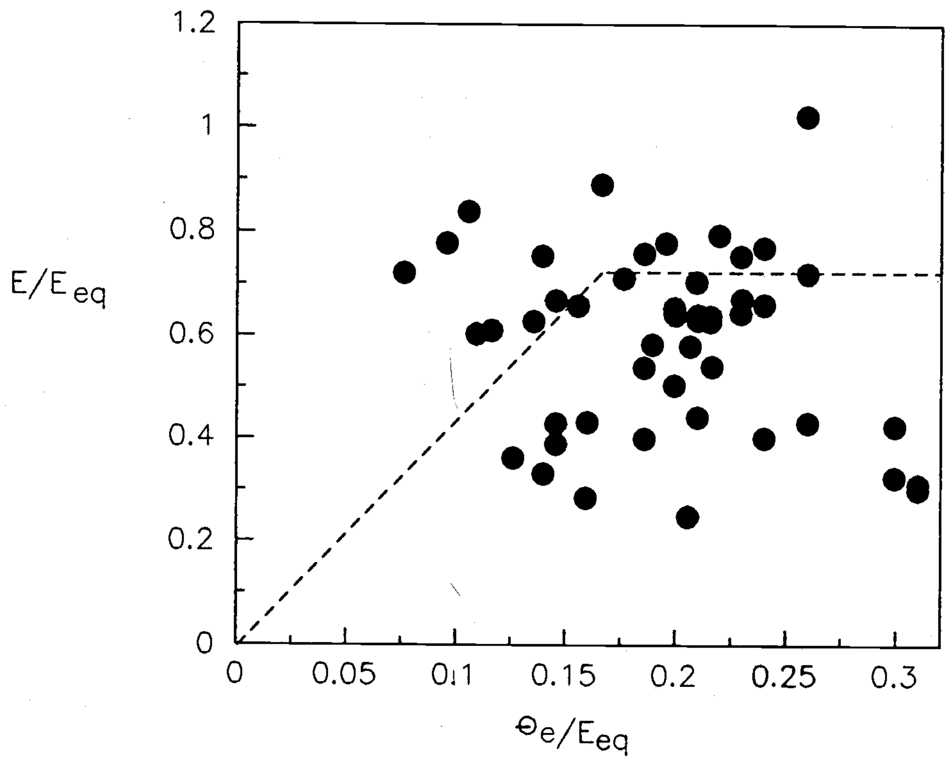

Figure III-1 Determination of the evapotranspiration model parameter å from the ratio of evaporation rate (E) to equilibrium evapotranspiration rate (E_{eq}) versus the ratio of the extractable water in the root zone ($ø_e$) to E_{eq}