THE ECO-PHYSIOLOGY OF GROWTH, NEEDLE PHOTOSYNTHETIC PIGMENT AND WATER CONTENTS, AND PHOTOSYNTHETIC PARTIAL PROCESSES IN FIVE POPULATIONS OF *PSEUDOTSUGA MENZIESII* (MIRB.) FRANCO.

by

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B.Sc. (Hons.), Simon Fraser University, 1977

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OF THE REQUIREMENTS FOR THE DEGREE OF
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The eco-physiology of growth, needle photosynthetic pigment and water contents, and photosynthetic partial processes in five populations of Pseudotsuga menziesii (Mirb.) Franco.

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ABSTRACT

The eco-physiology of
growth, needle photosynthetic pigment and water contents,
and photosynthetic partial processes in five populations of
Pseudotsuga menziesii (Mirb.) Franco.

Leaf variations were examined for two years in five populations of Douglas-fir, two of coastal and three of interior variety, growing under different light regimes (reduced light intensities and altered ultra-violet radiation levels), at two sites (one at the wet coastal region and the other in the dry interior region of British Columbia). Fluorescence induction (F_V) analyses were conducted simultaneously to relate any changes in leaf properties to changes in photosynthetic partial processes. Carbon dioxide exchange rate determinations were done at the end of the study.

Populations of interior variety had the greatest growth increases, pigment contents, chlorophyll *a* (Chl), Chl *b*, carotenoids (Car), Chl *a/b* and Chl/Car ratios, F_V levels and apparent rates of photosynthesis, at both sites. Coastal origin populations had the greatest needle water contents. Except for growth increases, for all parameters examined, all populations grown at the coastal site had greater values than those grown in the interior. Growth appeared to be negatively correlated with light intensity, as were Chl *a* and Chl *b*, Chl *a/b* ratios, and F_V levels, while Car and Chl/Car ratios increased with increased light intensity. Two year old needles had greater pigment contents and ratios than new needles.

Needle water content declined to a minimum in the spring after the initial flush, then increased rapidly when that year's new needles flushed. Water content was greatest in new needles. New needles at both sites had seasonal Chl *a* and Chl *a*/*b* ratio trends with summer and winter minima and fall and spring maxima, while two year old needles had a spring minimum and a fall maximum. Chl *b* had a spring minimum and a fall maximum for all needle ages. Seasonal Car and Chl/Car ratio trends had summer-fall minima and winter maxima, while F_V behaved in the opposite manner.

The data indicate that the main function of the Car is to protect Chl *a* from photo-destruction. Even though light regime rankings change considerably, the relationship of the populations to each other is very stable.

A mechanism for the winter inactivation of the photosynthetic apparatus in conifers is proposed.

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Special thanks are due to my wife, Shari, for her understanding and encouragement throughout this project, especially, after the arrival of Trevor and then Jocelyn.

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1)	A	: Absorbance
2)	ANOVA	: Analysis of variance
3)	Car	: Carotenoids
4)	Chl	: Chlorophyll (s)
5)	F_V	: Fluorescence induction
6)	IRGA	: Infrared gas analyzer
7)	LHCP	: Chl *a/b* - protein light harvesting complex
8)	O,I,D,P,S,M,T	: Features of the fluorescence induction transient (described in Figure V-1, page 133)
9)	PAR	: Photosynthetically active radiation (400-700nm)
10)	PS	: Photosystem
11)	PSU	: Photosynthetic unit
12)	p/r	: Photorespiration
13)	p/s	: Photosynthesis
14)	Ap/s	: Apparent photosynthesis
15)	Q	: The primary electron accept of PS II
16)	Γ	: CO_2 compensation point
17)	RuBP	: Ribulose-5 bi phosphate
18)	UV	: Ultra-violet
19)	% WC	: Percentage needle water content

CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Section 1: Introduction

Conifers are economically important in many areas of the world, yet compared to agricultural crop plants, little interest has been shown in the eco-physiology of their photosynthetic processes. In North America for example, the available biochemical, ultrastructural and organizational data describing the photosynthetic process in trees is scattered and limited (Schaedle, 1975). An understanding of the intraspecific variability of a species, basic to its evolutionary biology, is necessary before developing programs for tree improvement (Rehfeldt, 1978). Any species examined should be of economic importance, occupy a diversity of habitats, and have a wide geographic distribution so that transplants and provenance test trials could be initiated that would provide meaningful data for reforestation recommendations.

Provenance studies are initiated to detect the presence of interactions between the source population's genetic effects and the environmental effects at the planting site (Heslop-Harrison, 1964 for a review; Mergen et al. 1974). For example, an interaction exists if population A performs better than population B in environment I but B outperforms A in environment II (Wright, 1973). Interactions can be viewed as adaptations to geographic provinces (locales) which increases or enhances a population or species' ability to survive in a multitude of environments (Rehfeldt, 1978).

Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) is one of the most economically important trees in western North America (Scora, 1981) and it is widely used in reforestation programs. It ranges from the Pacific Ocean to the eastern slopes of the Rocky Mountains (Wright et al. 1971), and in British Columbia it grows well both in the mild humid coastal valleys and in the drier interior valleys (Tusko, 1963). Its natural north south distribution range extends from north central British Columbia to Baja California, Mexico, a distance of over 5000 kilometers (Scora, 1981). Survival for this species or any other gymnosperm occupying such a wide range in growing conditions requires that its annual developmental cycle or rhythm be attuned to local climatic conditions (Senser and Beck, 1977). For the Pinaceae in general, the annual developmental cycle is initiated with shoot elongation in the spring followed by leaf/needle maturation, and then stem unit initiation that will predetermine shoot growth in the following year (Rehfeldt and Wykoff, 1981). The last phase of the cycle must be completed before the process of cold acclimation prepares the tree for winter. Any study should examine the tree's responses to their environment over one or more developmental cycles.

The light environment during growth and development has been shown to have a greater influence on photosynthesis and plant growth than changes in temperature, water availability or other environmental factors (Clough et al. 1979). Changes in the light environment can result in adjustments to the leaves' internal structure and pigment composition (Hawkins et al. 1981; Del Rio and Berg, 1979). Therefore, when setting up provenance studies, as many different light regimes as possible should be utilized. In this study different levels of photosynthetically active radiation [PAR: defined as 380 to 710 nm radiation in the USSR and 400 to 700 nm light elsewhere (Stanhill and Fuchs, 1977)] were utilized to simulate different coastal and interior light regimes, and different qualities of ultra-violet (UV) radiation simulated increases in altitude and/or decreases in latitude (Caldwell, 1971; Johnson et al. 1976). Douglas-fir responses were observed under a wide range of light environments at the two experimental sites.

The responses of partial photosynthetic processes (see section 2 for a comprehensive overview) should be examined over the entire year because often variations in photosynthetic capacity, and eventually growth, have been shown to be due to short-term variation in a particular partial process (Lewandowska et al. 1977). Partial processes that will be observed are the potential of photosystem I (PS I) and PS II to transport electrons and CO_2 fixation and respiration. Additionally, variations in leaf properties such as photosynthetic pigment contents and their ratios, needle or leaf water contents, and tree or leader growth will be discussed.

This study was initiated to determine the response(s) of Douglas-fir to a variety of environments because of its economic importance and its wide use in reforestation in this region. Leaf variations were examined for two years in five populations of Douglas-fir, two of coastal and three of interior variety. The plants were grown under a series of light regimes, PAR reduced and altered ultra-violet radiation levels, at two sites, one in the wet coastal region and the other in the drier interior region of British Columbia. Fluorescence induction (F_V) curve analyses were conducted simultaneously to try and relate observed changes in leaf properties to changes in the photosynthetic partial processes, particularly PS I and PS II electron transport. Finally, near the end of the study, CO_2 exchange determinations were conducted to check the rates of apparent photosynthesis (Ap/s) in all of the populations at both sites.

Section 2: Literature review

Associated with the annual developmental cycle in the Pinaceae are many other annual patterns, trends and rhythms. The first annual rhythm which was clearly outlined in temperate region conifers was the photosynthetic rhythm, comprising carbon fixation and respiration. Carbon fixation starts at a low level in the spring, gradually increases to a maximum in the late summer or early fall, then declines rapidly until the winter depression is reached. It rapidly increases in the following spring to attain levels it had the previous late summer (Bamberg et al. 1967; Fuchs et al. 1977; Larcher, 1969; McGregor and Kramer, 1963; Waring and Franklin, 1979; among others). The seasonal respiration pattern closely parallels the CO_2 fixation annual rhythm (Krueger, 1967).

The annual pattern of translocation to the roots rapidly reaches high levels in the spring, declines to low levels during the period of shoot flush and rapid growth in early summer, increases to a fall maximum and then declines rapidly to zero or negligible levels in late fall or early winter. In the spring it again increases rapidly (Drew and Ledig, 1981; Shiroya et al. 1966). Root respiration parallels the annual pattern of translocation (Shiroya et al.1966).

Other seasonal trend studies followed these, and perhaps the most important was to observe the changes in chloroplasts of various conifer species because here is where the photosynthetic reactions occur. During summer and early fall, the chloroplast is symmetrical and full of starch. Then in late fall, the amount of starch begins to decrease coinciding with a decrease in the rate of CO_2 fixation (Martin and Öquist, 1979; Senser and Beck, 1978; among others). As the starch content is depleted the chloroplasts either swell and aggregate in one part of the cell (Chabot and Chabot, 1975; Senser et al. 1975), do not swell and aggregate (Fry and Phillips, 1977; Parker and Philpott, 1961), or they breakdown completely (Perry and Baldwin, 1966). All these different phases were found to occur during the winter depression or cessation of CO_2 fixation and respiration. During late winter, thylakoids can become damaged and the chloroplast envelope may disappear (Martin and Öquist, 1979). In spring, chloroplasts migrate to the cell wall and the thylakoid membrane system becomes reorganized (Martin and Öquist, 1979; Perry and Baldwin, 1966). At this time starch accumulation begins anew when the CO_2 fixation rate increases rapidly (Martin and Öquist, 1979; Senser and Beck, 1978).

Observed wintertime differences in chloroplasts could be due to:

(1) improved techniques in the late 1970's suggesting that details were overlooked or mis-interpreted in the 1960's (Martin and Öquist, 1979);

(2) winter temperatures determine the degree of disruption observed, the colder the temperature and higher the level of insolation, the greater the degree of disturbance or destruction (Fry and Phillips, 1977; Martin and Öquist, 1979).

Therefore, in areas with milder winter climates the only alteration that would probably occur to the chloroplast is the fall depletion of the starch reserve and a winter depression of photosynthesis (Waring and Franklin, 1979, Fig. 3). The winter depression of photosynthesis has been attributed to an annual rhythm or to the changing quality and quantity of light in winter (Bamberg et al. 1967).

Martin et al. (1978 a,b) and Öquist et al. (1978 a) have studied seasonal chloroplast structural changes in an attempt to correlate chloroplast changes with changes in photosynthetic electron transport and photosynthetic pigment moieties. Their analyses utilized the Butler tripartite model of the photochemical apparatus (Butler, 1978; Butler and Strasser, 1977). This model consists of:

(1) PS I made up of its antenna Chl a and the reaction center Chl with its electron acceptor molecule;

(2) PS II made up of its antenna Chl a and the reaction center Chl with its electron acceptor molecule;

(3) the photochemically inactive light harvesting Chl a/b protein

complex (LHCP), which contains all of the Chl b (Thornber, 1975) and about half of the Chl a.

This model assumes that excitation energy flows freely back and forth between the LHCP and PS II but that energy transfer between PS II and PS I via intersystem electron transport, or from LHCP to PS I occurs only in a unidirectional manner. The Z scheme of photon absorption and electron flow as discussed by Govindjee and Jursinic (1979) complements and reinforces the tripartite model of the photochemical apparatus.

Gymnosperm chloroplasts have the same constituents, spectral characteristics and function as equivalent complexes isolated from other classes of plants (Alberte et al. 1976). The primary difference between gymnosperm chloroplasts and agricultural crop plants is that their photosynthetic units (PSU) are 1.6 to 3.8 times larger. Consequently, they have fewer but larger chloroplasts which may account for the lower photosynthetic rates found in conifers compared to crop plants (Alberte et al. 1976).

The studies of Martin et al. (1978 a,b) and Öquist et al. (1978 a) indicate that the following occurs during the winter. In the fall when cold hardiness induction is initiated and the rates of photosynthesis and respiration decrease, there is a parallel decrease in the capacity of intersystem electron transport. With the onset of winter there is a destruction of Chl and it appears to be mainly the antennae Chl a associated with the two photosystems and to some extent in the LHCP. Intersystem electron transport is inhibited even though partial electron transport reactions showed low but fairly constant rates. In late winter, if temperatures are low and irradiance is high enough the destruction of the LHCP can become more pronounced than the destruction of the antennae Chl a. Antennae Chl a destruction can be greater than the destruction of LHCP in the spring if increased levels of insolation are accompanied by freezing temperatures. These processes are reversed and intersystem electron flow is re-established in the spring. It appears that these alterations are completely reversible because never or only rarely is the reaction center Chl destroyed. The duration and degree of inactivation and the time for system recovery is proportional to the duration of low temperatures and the radiation load received during the inactive period.

The processes just discussed are often refered to as photosynthetic partial processes.

Seasonal studies have also been done on the photosynthetic pigments of conifers (Khodasevich et al. 1978; Lewandowska and Jarvis, 1977; Linder, 1972, 1971; Bourdeau, 1959; Zacharowa, 1929; among others). Only with the aid of ultrastructural and biochemical studies have pigment content changes been related to actual thylakoid membrane functional changes.

Of the three primary photosynthetic pigments (Chl a, Chl b and the Car group), light energy is only transfered to the reaction centers from the antennae Chl a (Butler, 1978). The Car are the primary accessory pigments of green plants (Burnett, 1976), the carotene sub-group is thought to prevent photo-destruction of Chl a (Krinsky, 1968) and is primarily located around PS I (Grumbach, 1979), while the xanthophyll sub-group is thought to transfer absorbed light energy to Chl a (Burnett, 1976). The efficiency of energy transfer is about 100 % between Chl b and Chl a and ranges from 25 to 50 % between xanthophylls and Chl a (Gasanov et al. 1979).

Carotenes are thought to prevent Chl a photo-destruction by quenching the excess energy of singlet oxygen (Halliwell, 1978) which has become excited by receiving energy from an excited Chl a triplet (Britton, 1979). An excess of photons striking the LHCP may result in the formation of the Chl a triplet. The carotenes can also quench the excited Chl a triplet directly and prevent the production of the highly destructive singlet oxygen (Britton, 1979). When quenching singlet oxygen or triplet Chl a the carotene molecule becomes a carotene triplet which loses its excess energy harmlessly as heat (Britton, 1979). The carotenes are also capable of quenching Chl a fluorescence (Mathias et al. 1979)

With the advent of a portable fluorometer (Schreiber et al. 1975), F_V could be easily utilized as an intrinsic probe of the thylakoid membrane because F_V responds to changes in membrane structure and composition (Schreiber and Berry, 1977). It is now possible to detect seasonal membrane changes concomitantly with the determination of the annual photosynthetic pigment trend.

The Kautsky effect of Chl a F_V primarily eminates from the antenna Chl a of PS II (Butler, 1978). The rise of fluorescence emission in several phases to a maximum and the subsequent decline to a low steady state value, is a very complex phenomenon, and its normal course depends on undisturbed electron flow through PS II (see Papageorgiou, 1975 for a review, and Fig. V - 1 for a typical conifer F_V curve with description of the curve features). F_V curves are indicators for PS II activity and in intact leaves in the presence of CO_2, they are indicators for complete photosynthesis (Lichtenthaler and Grumbach, 1975).

Leaf variation is a term which has been given by Lewandowska and Jarvis (1977) to indicate changes in photosynthetic pigment content and their ratios (see above), needle or leaf water contents (Pharis, 1967; Zavitkovski et al. 1981; among others), and tree leader growth (Griffin and Ching, 1977; Tusko, 1963; among others). A study which combines F_V analyses concurrently with leaf variation analyses allows inferences to be made as to the status of the entire photosynthetic apparatus.

Since photosynthesis is the only source of energy for plant growth, understanding its environmental control is basic to understanding the relationship between the productivity of vegetation and the environment (Berry, 1975). Therefore, without a sound understanding of the long term physiological processes related to photosynthesis and their differences between populations, tree improvement projects cannot be initiated with any degree of confidence.

CHAPTER II

MATERIALS AND METHODS

Section 1: Plant Material

Bare root, 2-0 stock seedlings of five British Columbia populations of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were obtained in late March 1977 from the British Columbia Forest Service. Two populations were of coastal variety (var. *menziesii* Franco) and the other three populations were of the interior variety (var. *glauca* (Beissn.) Franco). Population origins, designations and codes are shown in table II - 1.

Approximately 700 trees from these populations were potted out in 20 by 15 cm black plastic pots in early April 1977 and were coded by source as shown in table II - 1. A locally obtained clay loam topsoil mix utilized by the Simon Fraser University Greenhouse was used as the potting medium for all trees.

One month after potting, one hundred seedlings from each population were selected on the basis of uniform height and growth as the experimental material. The five populations were each divided into ten sub groups.

Two experimental sites were selected and established in early May 1977. Simon Fraser University (SFU) was selected in the coastal region of B. C. (49.17' N. lat., 123.55' W. long., elev. 325 m) and the Summerland

Table II - 1. Population origin, latitude, longitude and elevation of population origin, and population designation and color code with abbreviations for the five populations of Douglas-fir.

Population Origin	Latitude	Longitude	Elevation	Designation		Color Code	
Bella Coola	52.25' N.	126.15' W.	185 m	coastal low	CL	red	R
Squamish	49.50' N.	123.15' W.	640 m	coastal high	CH	orange	O
Quesnel	52.25' N.	121.20' W.	1250 m	interior high	IH	green	G
Lac la Hache	51.50' N.	120.45' W.	1065 m	interior medium	IM	blue	B
Nelson	49.35' N.	117.45' W.	975 m	interior low	IL	yellow	Y

Agricultural Research Station (SRS) was chosen in the dry interior region of B. C. (49.34' N. lat., 119.40' W. long., elev. 340 m). The SFU site had an open exposure, from the ENE to the WSW, of at least 50 m and for at least 10 m from the WSW on around to the ENE. The clear exposure at the SRS site was at least 15 m from the WSW to the NW and at least 50 m from the NW on around to the WSW.

At SFU, nine trees of each coastal population and ten trees of each interior population were placed under each of the following light regimes:

(1) Open - control, full ambient light;

(2) UVT (ultra violet light total) - plexiglass control, 93 +% transmission (angle of incidence 90° for all plexiglass specifications) of ambient light in ultra violet, visible and near infrared spectral regions, shorter wavelength limit of 255 nm (Rohm and Haas Canada Ltd., Toronto, Ont., Plexiglass (R) II UVT);

(3) UVA - UV_A present, same spectral characteristics as UVT except shorter wavelength limit of 335 nm with 70 % transmission at 350 nm (Rohm and Haas Canada Ltd., Toronto, Ont., Plexiglass (R) II UVA);

(4) UVO - no UV radiation present, same spectral characteristics as UVT except shorter wavelength limit of 385 nm with 70 % transmission at 400 nm (Rohm and Haas Canada Ltd., Toronto, Ont., Plexiglass (R) UF - 1 in Canada and UF - 4 in USA);

(5) 60 % - 62 % transmission of ambient light, one layer of grey fiberglass screening, a second layer of screening was added 09 March 1978, hereafter called 30 %;

(6) 30 % - 29 % transmission of ambient light, two layers of grey fiberglass screening. A third layer of screening was added 09 March 1978, reducing transmission to 11 %, hereafter called 10 %.

The spectral characteristics of the light filters used are shown in Figure II - 1. Each light regime was replicated and the plants from each population were established in each (Figure II - 2).

At SRS, 12 trees of each coastal population and six trees of each interior population were placed under the following light regimes:

(1) Open - as at SFU;

(2) UVT - as at SFU;

(3) UVO - as at SFU;

(4) 60 % - as at SFU except a second layer of grey fiberglass screening was added 05 December 1977, hereafter called 30 %.

Again, each light regime was replicated and the population sub groups were divided between the replicates (Figure II - 3).

All potted trees were buried in 15 cm trenches and surrounded with the local topsoil to the top of the pot at both SRS and SFU.

Canopies supporting the various light filters were placed over the trees (Figure II - 4). The plexiglass screens and the grey fiberglass screening were fixed over the top and down the south sides of the frames to within 40 cm of the ground surface. These openings together with the open north side of the frame provided free air circulation. Thus even during winter, direct solar radiation had to pass through the light filters before

Figure II - 1

Spectral light characteristics of the various light filters utilized in the study. Spectra A, E, F and G were obtained on a Perkin Elmer model 450 spectrophotometer. Spectra B, C and D were obtained from Rohm and Haas Canada Ltd., specifications for ultra violet filtering and transmitting formulations of Plexiglass $^{(R)}$ acrylic plastic. A, open no filter; B, UVT; C, UVA; D, UVO; E, 60 %; F, 30 %; and G, 10 %.

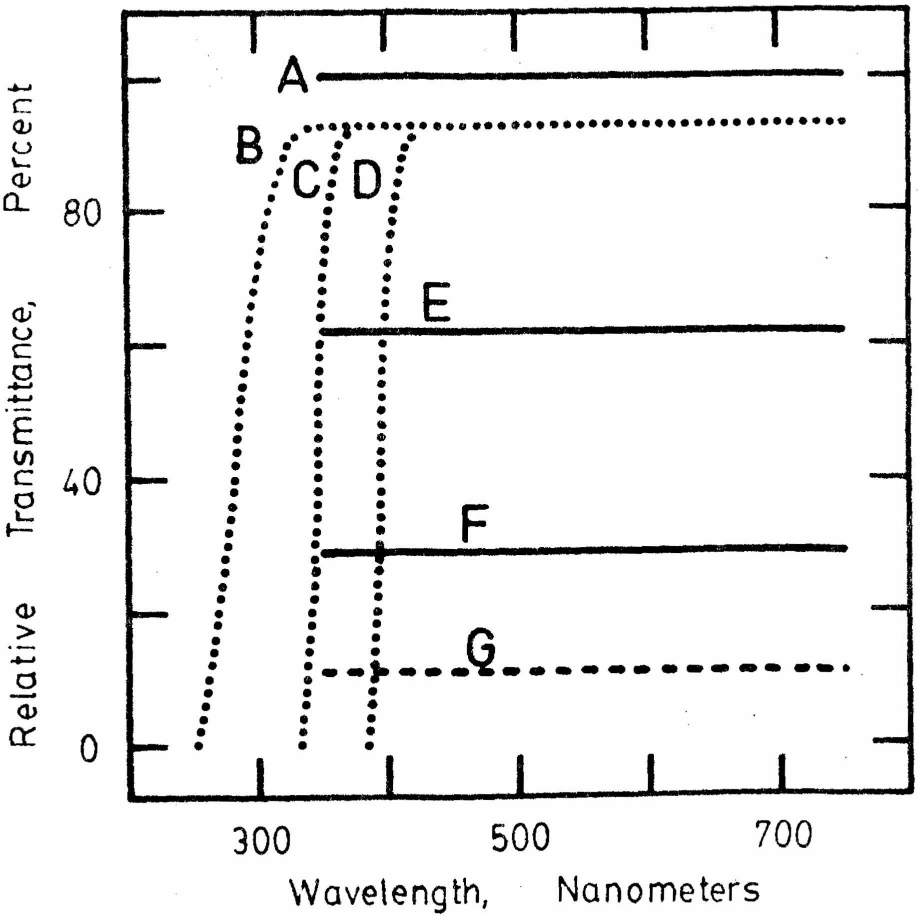
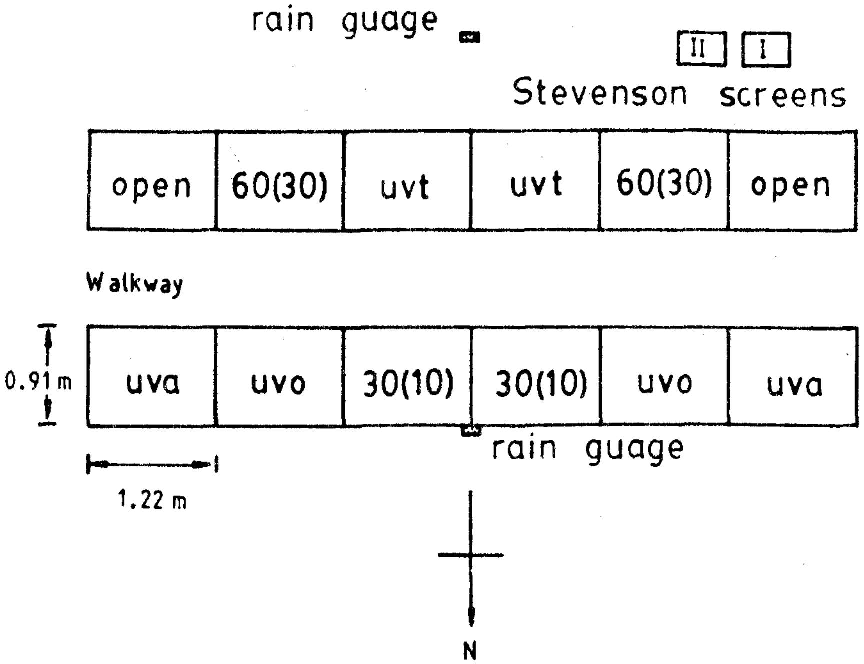

A
B
C
D
E
F
G
0
40
80
Relative Transmittance, Percent
300
500
700
Wavelength, Nanometers

Figure II - 2

The experimental site at SFU including location of the weather station (A) and tree layouts (B) in each replicate pair of plots. High (I) and low (II) Stevenson screens are described in the text. Rain guages were placed one meter above the ground surface. Tree layout in the replicate plot on the right is the mirror image of the plot illustrated. Tree layout in the lower group of plots is identical to the layout in the six plots above them. Tree abbreviations are given in Table II - 1.


rain guage
II
I
Stevenson screens
open
60(30)
uvt
uvt
60(30)
open
Walkway
0.91 m
uva
uvo
30(10)
30(10)
uvo
uva
rain guage
1.22 m
N

A

B

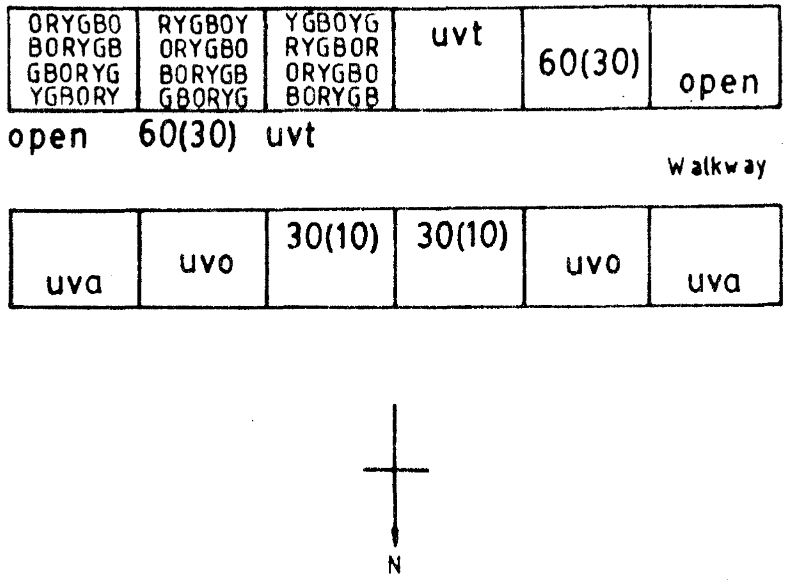

ORYGBO
BORYGB
GBORYG
YGBORY
RYGBOY
ORYGBO
BORYGB
GBORYG
YGBOYG
RYGBOR
ORYGBO
BORYGB
uvt
60(30)
open
open
60(30)
uvt
Walkway
uva
uvo
30(10)
30(10)
uvo
uva
N

Figure II - 3

The experimental site (A) at SRS and tree layouts (B) for each replicate pair of plots. Tree layout in the replicate plot on the right is the mirror image of the plot illustrated. Tree layout in the lower group of plots is identical to the layout in the four plots above them. Tree abbreviations are given in Table II - 1.

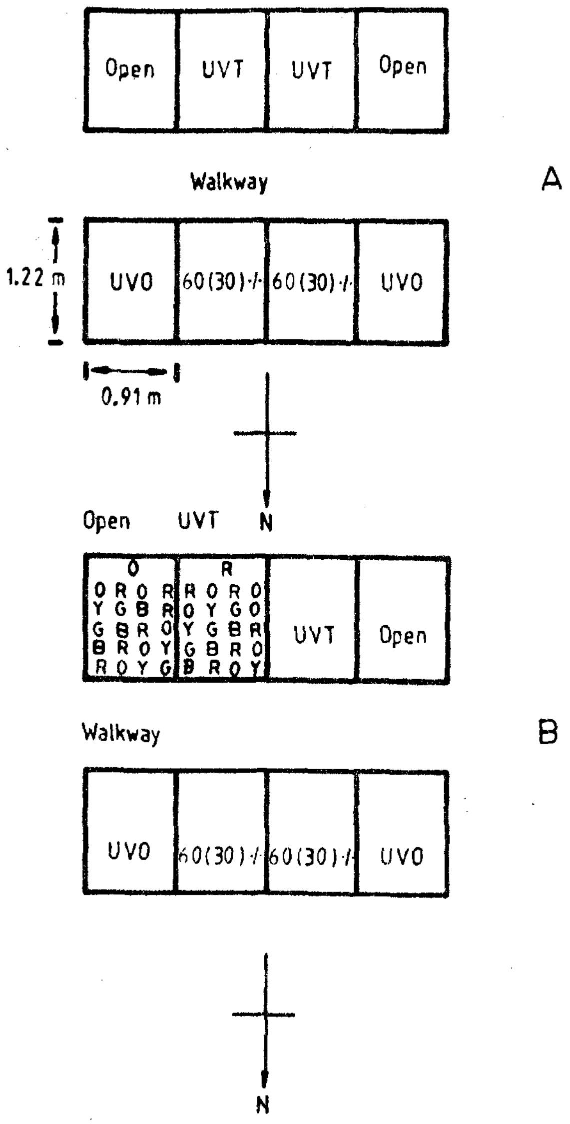
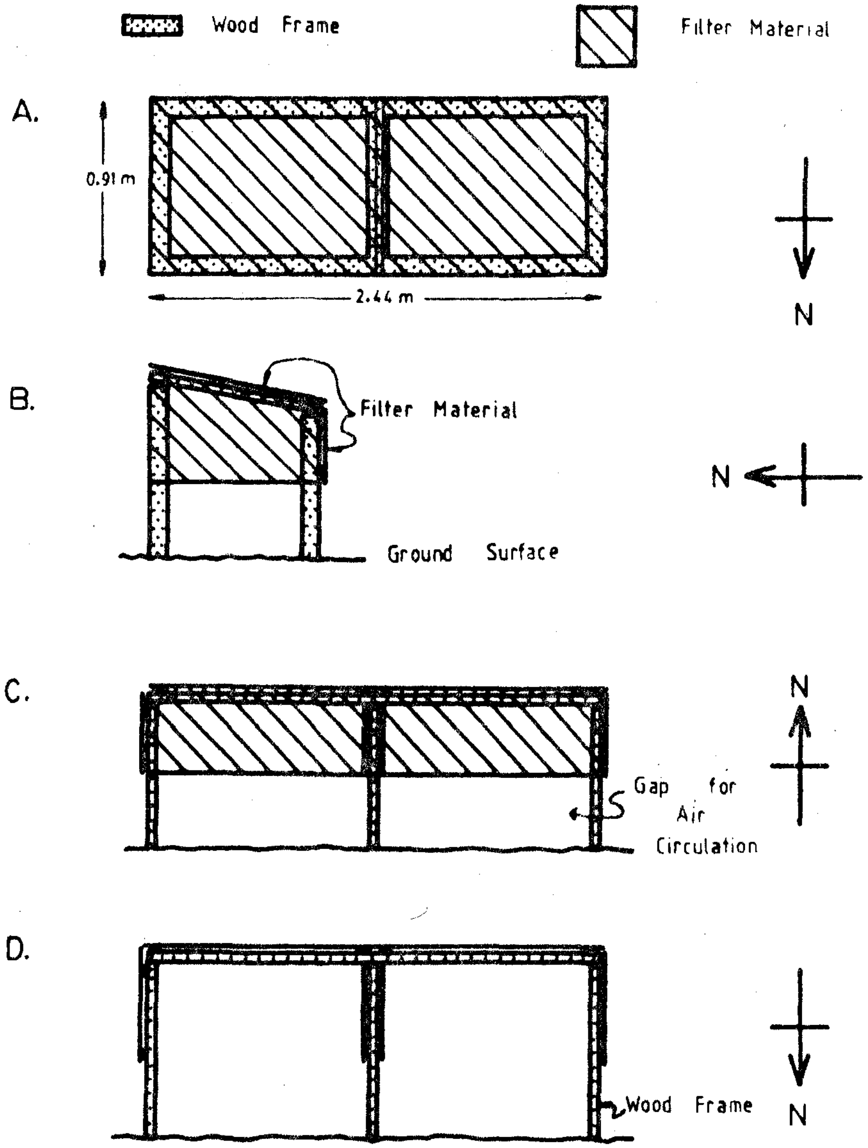

Open
UVT
UVT
Open
Walkway
A
1.22 m
UVO
60(30)·/·
60(30)·/·
UVO
0.91 m
N
Open
UVT
N
O
R
O Y G B R
R G B R O
O B R O Y
R R O Y G
R O Y G B
O Y G B R
R G B R O
O O R O Y
UVT
Open
Walkway
B
UVO
60(30)·/·
60(30)·/·
UVO
N

Figure II - 4

The canopy construction for two side by side plots at SFU. Views shown are A, plan; B, lateral; C, frontal; D, rear. Canopy construction at SRS was identical except the long axes of the plots were reversed (compare figures II - 2 & 3).


Wood Frame
Filter Material
A.
0.91 m
2.44 m
N
B.
Filter Material
N
Ground Surface
C.
N
Gap for Air Circulation
D.
Wood Frame
N

reaching the tree foliage. Trees at both experimental sites were only watered after at least 14 days without rain during the dry summer months. For the remainder of the year, the plants received the precipitation and run off / ground water normally occurring at each experimental site. Each tree was fertilized quarterly with 75 ml of 1 normal modified for Douglas-fir Hoaglands solution (Ross, 1977).

Section 2: Environmental Measurements

For the center pot of each plot, a gypsum KS-1 Soil Moisture Tester (Delmhorst Instrument Co., Boonton, N. J.) was placed in the root space and a shaded Model 8510-20 thermister temperature probe (Cole-Parmer Instrument Co., Chicago, Ill.) was placed at two-third seedling crown height above the soil to monitor these environmental parameters at regular intervals. Solar radiation was measured periodically in each plot using a Licor Model LI - 185A radiation sensor (Lambda Instruments Corp., Lincoln, Neb.). Spectral distribution under the various light regimes was measured near the spring equinox using an ISCO Model SR spectroradiometer (Instrument Specialties Co., Lincoln, Neb.).

Daily temperature, precipitation and sun hours were obtained for SRS from the Environment Canada weather station on site. Daily temperature and precipitation were obtained at SFU from the Environment Canada reporting station on campus and a station established on site. The on site station consisted of Stevenson screens located at 122 cm and 20 cm above ground level. Each screen contained a hygrothermograph (Casella Instruments Ltd., London, U. K.) and a maximum-minimum thermometer (Sybron 5458, Taylor Instruments Ltd., Toronto, Ont.). Rain guages (Tru-Chek, Edwards Manufacturing Co., Albert Lea, Minn.) were located on the north and south sides of the site (Figure II - 2). Daily sun hours were obtained from Environment Canada for several greater Vancouver stations and averaged to give an approximation of the SFU sun hours (Hawkins et al. 1981).

Section 3: Morphological Measurements

For each light regime, leader shoot elongation was measured on eight trees of each population at SFU and six trees of each population at SRS at regular intervals during the course of the growing season. Leader length was defined or measured as the distance from the leader's apical bud tip to the upper surface of the first lateral whorl of branches. Needle lengths of the leader and last whorl of lateral branches were determined concurrently. Ten needles on each shoot were measured on all trees for all populations and light regimes at SRS and SFU.

Differences between means for populations and treatments were calculated using ANOVA (Mendenhall, 1971).

Section 4: Photosynthetic Pigment Determinations

Individual current year needles were collected from terminal ends of lateral and leader branches in the mid to upper crown region from five trees in each population growing under each light regime, and then pooled (Sestak,

1971) and divided into three groups. The three groups were utilized for photosynthetic pigment, water content and F_V determinations. Needle collections were made at three week intervals during the growing season and at four to six week intervals during the winter. All collections were made as near as possible to the same time of day to minimize daily pigment fluctuations (Hawkins et al. 1981). In the following year, the new current year needles were collected at the same time intervals but the now year old needles were collected about every eighth week. No trees from the south row of the plots at SFU or the south two rows at SRS were sampled (see figures II - 2B & 3B).

The groups of needles for pigment and water content determinations were stored on dry-ice in the dark (Sestak, 1971) until five samples for pigment analysis and three samples for water content determination were prepared from each collection. The needles for F_V measurements were placed between moist paper towels and stored in the dark. F_V methodology will be discussed in the next section.

Pigment analysis was done on 30 to 100 mg fresh weight of tissue extracted in 10 to 25 ml of acetone at -70° C (Sestak, 1971), following homogenization at maximum speed until the residue was colorless, about 30 to 60 s in a Willems Polytron $^{(R)}$ homogenizer (Brinkman Instruments, Montreal, P. Q.). The supernatant was filtered into Büchner flasks wrapped in aluminium foil and containing a pellet of dry-ice to produce an inert atmosphere thus preventing photo-oxidation of the pigment solution (Vaisberg and Schiff, 1976). Aliquots of the pigment solution were then placed in vials on ice in light tight containers until spectophotometry was done (Linder, 1974). All of the above procedures were carried out under green safe light and/or low level indirect light to prevent pigment photo-oxidation.

Continuous absorption spectra were obtained for each pigment solution aliquot between 350 and 750 nm on a double beam model 450 spectrophotometer (Perkin Elmer Corp., Norwalk, Conn.). Chl a, Chl b, and total Car were estimated using Holm's (1954) equations (results in mg liter^{-1}):

$$\text{Chl } \underline{a} = 9.78 \times A_{662} - 0.99 \times A_{644};$$
$$\text{Chl } \underline{b} = 21.4 \times A_{644} - 4.65 \times A_{662};$$
$$\text{Car} = 4.69 \times A_{440.5} - 0.267 \times (\text{Chl } \underline{a} + \text{Chl } \underline{b}).$$

Calculations of means, standard deviations and absolute errors were after Bukatsch and Rudloph (1963).

Determinations of % WC were made on 10 to 50 mg fresh weight of tissue which was oven dried at 90° C ± 2°C for 24 hours, after which further water loss was insignificant (Hawkins et al. 1981).

Section 5: Fluorescence Determinations

The needles collected for F_V were allowed to dark adapt for at least 30 min at 20° C ± 2° C before conducting F_V determinations (Fink, 1978). F_V measurements were done at 20° C ± 2° C on the abaxial (stomatal) surfaces of detached dark adapted needles with a version of the portable fluorometer developed by Schreiber et al. (1975), see Fink (1978) for details. During the experimental period, fluorometer excitation was kept constant at four units which was approximately 1.5×10^3 erg cm^{-2} s^{-1} as measured with a Model 65 YSI Radiometer (Yellow Springs Instrument Co., Yellow Springs, Ohio). Fluorometer output was displayed on a dual beam storage oscilloscope (model 214, Tektronix Inc., Beaverton, Ore.) and/or recorded on a Speed Servo (R) recorder (model S-601-S, Esterline Angus Instrument Co., Indianapolis, Ind.). Standardization of the technique was after Fink (1978).

Sample assay sequence for F_V determinations were always the same at both experimental sites.

Section 6: CO_2 Gas Exchange Measurements

CO_2 gas exchange was determined on four trees of each population growing under all light regimes at both experimental sites in July and August of 1978. One tree of each population under a given light regime was analyzed to complete a trial. The order and protocol of the trials for both SRS and SFU were similar (Appendix I).

A closed system was used containing a Model 4K pump (Neptune Dyna-pump, Fisher Scientific Co., Pittsburgh, Pa.) a Model 604 flowmeter (Matheson Co., Whitby, Ont.), a Model IR 215 infrared CO_2 gas analyzer (Beckman Instrument Co., Fullerton, Ca.), and a brass water cooled cuvette (Clark and Lister, 1975). Lighting was provided by quartz-iodide bulbs with near infrared restricting front and rear mirrors (Dicrolite Co., Everett, Wa.). Further near infrared filtering was provided by a 10 cm pathlength water bath placed between the lamps and the plant cuvette.

Gases with concentrations of CO_2 of about 330 ul/liter and of O_2 of around 2 and 21 % (Union Carbide Canada Ltd., Vancouver, B. C.) were used for IRGA (infrared gas analyzer) calibration and to check for the presence or absence of photorespiration. Cuvette temperature was regulated to 21° C ± 3° C by adjusting the flow rate of water through the cuvette's water jacket and was monitored using a copper-constantan thermocouple inside the cuvette and recorded on a Labograph (R) Model E478 Metrohm recorder (Brinkman Instruments Ltd., Montreal, P. Q.). IRGA output was also read off a Labograph (R) recorder.

The attached terminal two to three cm of a mid to upper crown branch was sealed in the cuvette along with the thermocouple and illuminated with three different intensities of white light, approximately 400 to 700 nm waveband, as measured with a Licor Model LI-185A radiation sensor (Table II - 2). The three light intensities were obtained by placing none, one and five layers of white cheese cloth between the water bath and the cuvette.

A standard protocol for CO_2 gas exchange determinations was followed for each tree examined:

(1) Trees were pre-conditioned under a similar lighting arrangement for at least 15 minutes prior to any measurement;

(2) CO_2 gas exchange rate determinations were always done under high light first, followed by **medium**, and finally under low intensity light;

Table II - 2.

Light intensities utilized for the photosynthetic gas exchange determinations at both SRS and SFU (expressed in quantum, radiometric and photometric units). Figures in parentheses are the percentages of light transmitted by the different layers of cheese cloth.

Light Condition	Number of Cheese Cloth	Quantum uE m^{-2} s^{-1}	Radiometric W m^{-2}	Photometric Lux
High	0	1260 (100)	340 (100)	80,500 (100)
Moderate	1	925 (73)	247 (73)	56,000 (70)
Low	5	430 (34)	124 (36)	30,500 (38)

(3) Successive determinations at each light level were made until three consecutive determinations gave approximately the same result. This indicates a steady state following a period of light induction (Clark and Lister, 1975).

Photorespiration was determined by comparing the rates of CO_2 gas exchange at 21, 2 and again at 21 % O_2 under only the high light intensity. After gas analysis, the tested needles were removed from the twig, placed on dry-ice, and then analyzed for photosynthetic pigments and % WC determinations.

Section 7: Duration of the Study

The time period covered by this study is from late May 1977 to late May 1979, which is two complete growing seasons.

A one season extension to the study would have meant an additional 3,000 morphological measurements, 5,500 needle collections, 5,500 pigment extractions and determinations, 3,300 water content analyses, and 2,500 F_V measurements. The additional one years work would have added an extra two years to the collection, assay, and computation of the data to an analyzable form. Therefore, the study was terminated after the second year.

CHAPTER III

ENVIRONMENTAL PARAMETERS, MEAN LEADER GROWTH AND NEEDLE WATER CONTENT RESULTS AND DISCUSSION

Section 1: Environmental Parameters

Soil moisture content did not vary significantly between the 12 plots at SFU during the period that the soil moisture probes were in place (data not shown). It is assumed that the soil moisture content of the various SRS plots were similar to each other since the SFU plots were and because the supplementary watering regimes were similar at both experimental sites. Seasonal trend differences between light regimes at SRS or SFU, likely cannot be attributed to soil moisture content differences between the plots at a site but there maybe between-site soil moisture content differences that affected the observed results. Air temperature differences between the plots at one experimental site would be expected to be similar to between plot differences at the other site because construction and orientation of the plots were similar between sites (Figures II - 2 & 3). This does not imply that there could not be seasonal trend differences between SRS and SFU.

Random temperature checks in the plots showed that plot air temperature was up to two to three degrees C higher under the plexiglass screens and down to one degree C lower under the grey fiberglass screening than in the

Open plot during the summer months at SFU (data not shown). During the winter months air temperatures were similar between the Open and fiberglass screened plots but were about one degree C higher for the plexiglass screened plots (data not shown). These temperature differences could be reflected in any experimental differences observed between light regimes.

The difference between the relative light spectral distribution on 16 March 1978 at SFU (Figure III - 1) and the spectral characteristics of the various light filters (Figure II - 1) occurs because figure II-1 data were obtained with the light source at an angle of 90° to the filter, while the figure III-1 data were obtained with the light source, the sun, at a solar angle of 38.8° to the filter (calculation from Hay, 1977). The maximum percentage of light received by the trees under the filters never reaches the values cited in figure II-1 and is often lower than the values listed in figure III-1. This occurs because at solar noon on 21 June the solar angle is 63.8° and on 21 December the solar angle is only 17.8° at this latitude. Therefore, the Open light regime had a considerably higher light flux than the plexiglass light regimes as transmission was greatly reduced in these plots. The seasonality of the light flux under the light filters could play an important role in the observed seasonal trends.

The annual mean daily temperature from May 1977 through May 1978 was 9.0° C at SRS and 9.4°C at SFU and these temperatures were respectively 0.1 and 0.3° C below the long term annual mean daily temperature for these sites (Anon. 1977-1978). This could be considered a normal year temperature wise at both sites (Table III - 1) because they both had about the same

Figure III - 1

Relative spectral distribution under the various light regimes at SFU on 16 March 1978 as recorded with an ISCO Model SR spectro radiometer. Abbreviations as in text.

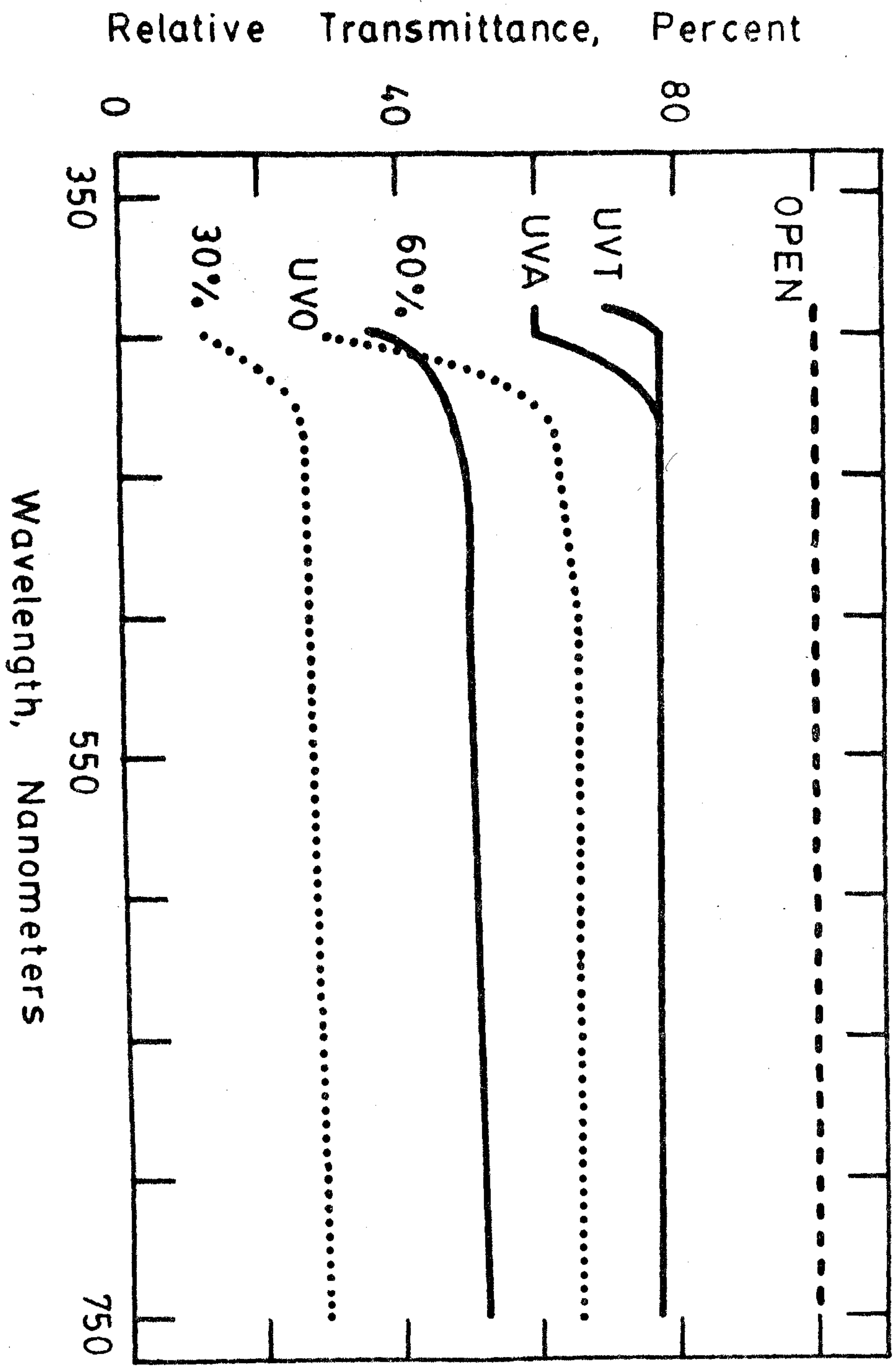

Relative Transmittance, Percent
0
40
80
350
550
750
Wavelength, Nanometers
OPEN
UVT
UVA
60%
UVO
30%

Table III - 1.

Monthly mean maximum, minimum and mean temperatures, in degrees C, for SRS and SFU during the entire study period.

Time		Location					
		SRS			SFU		
Year	Month	Maximum	Minimum	Mean	Maximum	Minimum	Mean
1977	May	17.3	6.1	11.7	13.6	6.3	10.0
	Jun	25.5	12.3	18.9	18.8	9.7	14.3
	Jul	27.0	12.6	19.8	18.9	15.0	17.0
	Aug	28.8	15.2	22.0	23.7	14.8	19.3
	Sep	18.8	8.6	13.7	15.7	9.7	12.7
	Oct	14.0	3.4	8.7	11.9	6.7	9.3
	Nov	4.8	-1.6	1.6	6.8	1.8	4.3
	Dec	0.0	-5.2	-2.6	4.4	0.0	2.2
1978	Jan	-0.6	-5.0	-2.8	5.6	1.6	3.6
	Feb	3.4	-2.2	0.6	8.3	2.7	5.5
	Mar	9.5	0.7	5.1	9.8	4.3	7.1
	Apr	12.9	3.5	8.2	11.3	4.9	8.1
	May	18.5	7.9	12.7	14.8	6.8	10.8
	Jun	24.7	11.3	18.0	19.6	11.8	15.7
	Jul	28.7	15.1	21.9	21.9	13.2	17.6
	Aug	24.8	13.4	19.1	20.4	12.5	16.5
	Sep	18.1	9.3	13.7	15.3	9.9	12.6
	Oct	13.9	3.9	8.9	13.2	8.0	10.6
	Nov	3.3	-3.7	-0.2	5.4	1.4	3.4
	Dec	-0.7	-8.3	-4.5	1.9	-1.4	0.3
1979	Jan	-6.0	-12.6	-9.3	1.7	-2.2	-0.3
	Feb	2.0	-4.6	-1.3	4.6	-0.1	2.3
	Mar	11.0	0.0	5.5	12.5	3.0	7.8
	Apr	14.8	1.6	8.2	12.6	3.5	8.1
	May	20.4	7.0	13.7	15.7	8.3	12.0

number of months with above and below normal mean daily temperatures (Anon. 1977-1978). Precipitation for this period (Table III - 2) was 125 % and 105 % of average at SRS and SFU respectively (Anon. 1977-1978). Most of the excess precipitation at SRS fell during the winter and early spring (Table III - 2). This possibly could be an important factor in tree survival during the first winter, as only one tree, a CH, died. Monthly bright sunshine hours (Table III - 3) for SRS and SFU were almost identical for the year and both received 41.4 % of the possible annual total (Anon. 1977-1978). Therefore, any differences observed in the experimental seasonal trends should not be correlated to different annual amounts of bright sunshine between the two experimental sites.

For the second year of the study, May 1978 through May 1979, the annual daily temperature was 8.2° C at SRS and 9.0° C at SFU and these were respectively 1.1 and 0.5° C below the long term mean annual mean daily temperature for the two sites (Anon. 1978-1979). The year could be considered much colder than normal at both sites (Table III - 1) because both had at least twice as many months with below than above normal mean daily temperatures (Anon. 1978-1979). Precipitation (Table III - 2) for this period was 82 % of normal at SRS and 88 % of normal at SFU (Anon. 1978-1979). Most of the precipitation decrease was observed during the winter and spring months at both sites (Table III - 2). This possibly accounts for the increased tree mortality at SRS, as two CH and two CL trees died. Daily bright sunshine hours (Table III - 3) were almost identical for the year between the two sites. SRS received 44.5 % and SFU 44.4 % of the possible annual total (Anon. 1978-1979). Annual bright sunshine hours are

Table III - 2.

Monthly precipitation, in mm, for SRS and SFU during the entire study period.

Time		Location	
Year	Month	SRS	SFU
1977	May	49.3	115.8
	Jun	9.4	30.0
	Jul	20.1	87.7
	Aug	13.5	80.8
	Sep	23.4	111.1
	Oct	8.2	173.0
	Nov	37.0	326.9
	Dec	60.5	255.6
1978	Jan	53.5	134.0
	Feb	28.3	124.0
	Mar	9.1	136.9
	Apr	57.7	139.5
	May	35.0	132.2
	Jun	20.4	54.7
	Jul	22.3	15.5
	Aug	40.6	92.0
	Sep	36.7	152.4
	Oct	6.4	55.5
	Nov	21.6	185.2
	Dec	15.0	166.3
1979	Jan	20.1	82.8
	Feb	10.1	247.7
	Mar	4.9	92.9
	Apr	13.4	128.8
	May	16.6	28.2

Table III - 3.

Monthly bright sunshine hours
for SRS and SFU during the
entire study period.

Time		Location	
Year	Month	SRS	SFU
1977	May	198.7	198.0
	Jun	318.4	300.4
	Jul	307.9	271.0
	Aug	309.1	313.0
	Sep	180.3	150.5
	Oct	161.1	125.9
	Nov	83.8	91.4
	Dec	27.5	79.6
1978	Jan	34.8	36.3
	Feb	78.9	77.9
	Mar	143.3	123.6
	Apr	112.9	126.5
	May	243.6	287.8
	Jun	274.3	261.2
	Jul	310.2	306.3
	Aug	194.5	229.6
	Sep	129.7	107.9
	Oct	184.6	156.9
	Nov	71.6	86.9
	Dec	72.3	89.7
1979	Jan	43.6	90.4
	Feb	98.1	74.7
	Mar	223.0	182.1
	Apr	210.6	194.1
	May	279.2	240.6

similar between the two sites because SRS is located in the bottom of a comparatively narrow north-south oriented valley and some of the summer sunshine hours are lost as the valley hills shade the floor from early morning and late evening sunshine. Any observed seasonal trend differences should not be correlated exclusively to different annual amounts of bright sunshine between SRS and SFU. Especially, if the Chabot et al. (1979) hypothesis that the total light energy received has a greater influence on the leaf than does the peak light energy, is correct.

From the meteorlogical data (Tables III - 1 to 3) it can be seen that the coastal climate at SFU is more moderate than the interior climate at SRS. The findings of Tusko (1963) confirm this observation.

The daily bright sunshine hours on collection days and for the three days preceeding them at SRS and SFU are shown in Tables III - 4 and 5 respectively. The short term light conditions can have a very pronounced affect upon needle pigment contents and ratios (Hawkins et al. 1981). This relationship will be examined in Chapter IV.

Section 2: Mean Leader Growth (Elongation)

Upon planting the coastal origin populations on average had the greatest mean tree heights, sometimes significantly (Tables III - 6 to 8) and often IL was significantly shorter than the other populations, especially at SFU (Table III - 8). These differences in mean tree height were probably due to inherent genetic differences. They also could be due

Table III - 4.

Daily bright sunshine hours on the collection days and for the three days preceeding them at SRS.

Collection Date	Bright Sunshine Hours Day Of	Day Before	Two Days Before	Three Days Before
26 May 77	1.5	14.2	2.2	0.0
16 Jun	15.0	12.0	10.4	12.5
05 Jul	9.7	9.0	4.5	5.3
02 Aug	13.4	12.9	13.4	12.3
22 Aug	11.3	6.5	12.5	12.7
13 Sep	11.0	11.2	9.8	10.3
13 Oct	8.1	0.9	8.9	3.6
05 Dec	1.9	2.0	5.9	0.3
04 Feb 78	0.0	2.3	0.0	0.0
21 Mar	9.2	9.4	6.5	8.2
16 May	8.4	0.1	3.4	2.9
27 May	5.6	5.5	4.5	0.0
15 Jun	1.0	6.4	5.2	3.5
07 Jul	12.3	10.5	9.2	8.2
30 Jul	13.5	13.6	9.6	12.1
20 Aug	6.3	4.1	1.7	5.4
13 Sep	0.3	4.6	8.5	2.0
08 Oct	6.3	7.6	8.8	8.9
13 Nov	1.1	6.8	6.8	7.4
13 Dec	0.3	6.2	3.8	0.0
13 Jan 79	0.0	0.1	0.0	0.0
16 Feb	0.0	6.1	7.7	6.2
20 Mar	10.6	10.8	10.0	9.9
25 Apr	11.9	12.2	8.4	12.6
28 May	8.4	6.3	8.3	10.9

Table III - 5.

Daily bright sunshine hours on the collection days and for the three days preceeding them at SFU.

Collection Date	Bright Sunshine Hours Day Of	Day Before	Two Days Before	Three Days Before
01 Jun 77	9.1	0.0	3.9	8.0
29 Jun	14.1	9.3	7.5	2.2
21 Jul	10.6	10.9	13.9	13.5
07 Aug	13.5	13.6	13.1	12.5
16 Sep	2.0	0.0	6.2	9.4
20 Nov	8.1	8.4	3.0	7.0
10 Feb 78	8.6	3.9	1.5	0.0
11 May	4.7	0.2	12.2	3.3
01 Jun	14.3	14.3	14.3	14.0
19 Jun	11.7	13.9	12.8	0.0
13 Jul	14.1	14.1	0.0	0.0
01 Aug	13.5	13.5	13.4	13.6
21 Aug	12.8	13.6	0.5	0.0
07 Sep	1.9	6.3	1.7	1.7
03 Oct	4.7	7.9	6.9	4.8
30 Oct	5.1	5.3	1.6	0.5
05 Dec	7.9	3.5	0.0	0.0
11 Jan 79	1.7	0.0	3.9	5.7
14 Feb	8.4	0.2	0.0	0.0
14 Mar	5.4	9.3	8.5	0.5
20 Apr	12.4	10.2	0.0	8.2
24 May	10.1	1.8	9.0	13.9

Table III - 6.

Initial mean tree heights (in mm) for all the populations under all of the light regimes at SRS. Light regime and population abbreviations as in the text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for the row numbers, followed by lower case letters, and the column numbers, followed by upper case letters.

Light Regime	Population IL	IH	IM	CH	CL
Open	224 a A	236 a B	193 a C	239 a D	248 a E
60 %	237 b A	224 b B	204 b C	249 b D	271 b E
UVT	223 c A	231 c B	195 c C	265 c D	210 c E
UVO	240 d A	210 d B	259 d	269 d D	246 d E

Table III - 7.

Initial mean tree heights (in mm) for all the populations under all of the light regimes at SFU. Light regime and population abbreviations as in text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for the row numbers, followed by lower case letters, and the column numbers, followed by upper case letters.

Light Regime	Population				
	IL	IH	IM	CH	CL
Open	249 a A	237 a C	222 a D	303 a E	253 a F
60 %	212 b A	212 b C	211 b D	310 c E	275 c F
30 %	166 d B	202 d C	187 d D	295 e E	252 e F
UVT	195 f B	208 f C	263 g D	283 g E	274 g F
UVA	153 h B	233 i C	190 h D	290 i E	268 i F
UVO	154 B	213 j C	200 j D	269 j E	250 j F

Table III - 8.

Initial mean tree height s (in mm) for all the populations under all the light regimes at SRS and SFU. Light regime and population abbreviations as in text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for row numbers, followed by lower case letters, and the column numbers, followed by upper case letters.

Site	Light Regime	Population				
		IL	IH	IM	CH	CL
SRS	Open	224 a A	236 a C	193 a D	239 a E	248 a F
"	60 %	237 b A	224 b C	204 b D	249 b E	271 b F
"	UVT	223 c A	231 c C	195 c D	265 c E	210 c F
"	UVO	240 d A	210 d C	259 d	269 d E	246 d F
SFU	Open	249 e A	237 e C	222 e D	303 e E	253 e F
"	60 %	212 f A	212 f C	211 f D	310 g E	275 g F
"	30 %	166 h B	202 h C	187 h D	295 i E	252 i F
"	UVT	195 j B	208 j C	263 k D	283 k E	275 k F
"	UVA	153 l B	233 m C	190 l D	290 m E	268 m F
"	UVO	154 B	213 n C	200 n D	269 n E	250 n F

to environmental differences as the seedlings were established at different forest service nurseries or a combination of the two differences described above. The differences in mean tree heights under the various light regimes (Tables III - 6 to 8) are due to the reasons cited above. As neither site had all trees being significantly taller than those at the other site, comparisons are made between rates of shoot elongation at SRS and SFU as well as within experimental site comparisons between the light regimes.

That interior populations IM and IH should have the greatest and the CL populations have the smallest 1977 mean leader increase at both sites (Tables III - 9 to 11) is surprising because Griffin and Ching (1977) and Tusko (1963) reported that coastal varieties of Douglas-fir grow more and for a longer seasonal period of time than interior varieties. Rehfeldt and Wykoff (1981) reported decreased leader growth with increased altitude of the seed source origin in two year old pine seedlings, which if applicable to Douglas-fir, would also indicate that the coastal populations should have the greatest growth. Most of the growth occurring before mid June (Figures III - 2 & 3) is also in contradiction of Griffin and Ching's (1977) observation. These unexpected population differences could be a result of the transplanting of bare rooted stock because Thompson (1980) suggested that this can mask seedling growth rates for one or even two years.

The increased heights under the 60 (30) % light regime at SRS and the UVT light regime at SFU was anticipated, as was the increased growth under UVO at SRS and the decreased growth under UVO at SFU (Table III - 11)

Table III - 9.

1977 mean leader growth (in mm) for all the populations under all the light regimes at SRS. Light regime and population abbreviations as in text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for the row numbers, followed by lower case letters, and the column numbers followed by upper case letters.

Light Regime	Population				
	IL	IH	IM	CH	CL
Open	101 a A	81 a B	87 a C	73 a D	57 E
60 %	93 A	88 b B	89 b C	71 b D	73 b
UVT	64 c	82 d B	90 d C	69 c D	56 c E
UVO	79 e A	80 e B	78 e C	75 e D	62 E

Table III - 10.

1977 mean leader growth (in mm) for all the populations under all the light regimes at SFU. Light regime and population abbreviations as in text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for the row numbers, followed by lower case letters, and the column numbers followed by upper case letters.

Light Regime	Population				
	IL	IH	IM	CH	CL
Open	83 a A	112 b B	106 b C	75 a E	64 a F
60 %	85 c A	103 c B	111 c C	92 c E	65 F
30 %	76 d A	93 d B	106 d C	96 d E	84 d F
UVT	93 e	97 f B	120 f C	86 e E	73 e F
UVA	66 g A	81 h B	85 h D	83 h E	64 g F
UVO	64 i A	86 j B	83 j D	72 i E	62 i F

Table III - 11.

1977 mean leader growth (in mm) for all the populations under all the light regimes at SRS and SFU. Light regime and population abbreviations as in text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for row numbers, followed by lower case letters, and the column numbers, followed by upper case letters.

Site	Light Regime	Population IL	 IH	 IM	 CH	 CL
SRS	Open	101 a A	81 a C	87 a E	73 a G	57 H
"	60 %	93 A	88 b C	89 b E	71 b G	73 b H
"	UVT	64 c B	82 d C	90 d E	69 c G	56 c H
"	UVO	79 e B	80 e C	78 e E	75 e G	62 H
SFU	Open	83 f B	112 g D	106 g F	75 f G	64 f H
"	60 %	85 h B	103 h D	111 h F	92 h G	65 H
"	30 %	76 i B	93 i D	106 i F	96 i	84 i
"	UVT	93 j A	97 k D	120 k F	86 j G	73 j H
"	UVA	66 l B	81 m C	85 m E	83 m G	64 l H
"	UVO	64 n B	86 o C	83 o E	72 n G	62 n H

Figure III - 2

Mean leader growth in 1977 (mm) for the five populations growing under the 60 (30) % light regime at SRS. Abbreviations as in text. This pattern of growth is representative of that found under the other three light regimes at SRS.

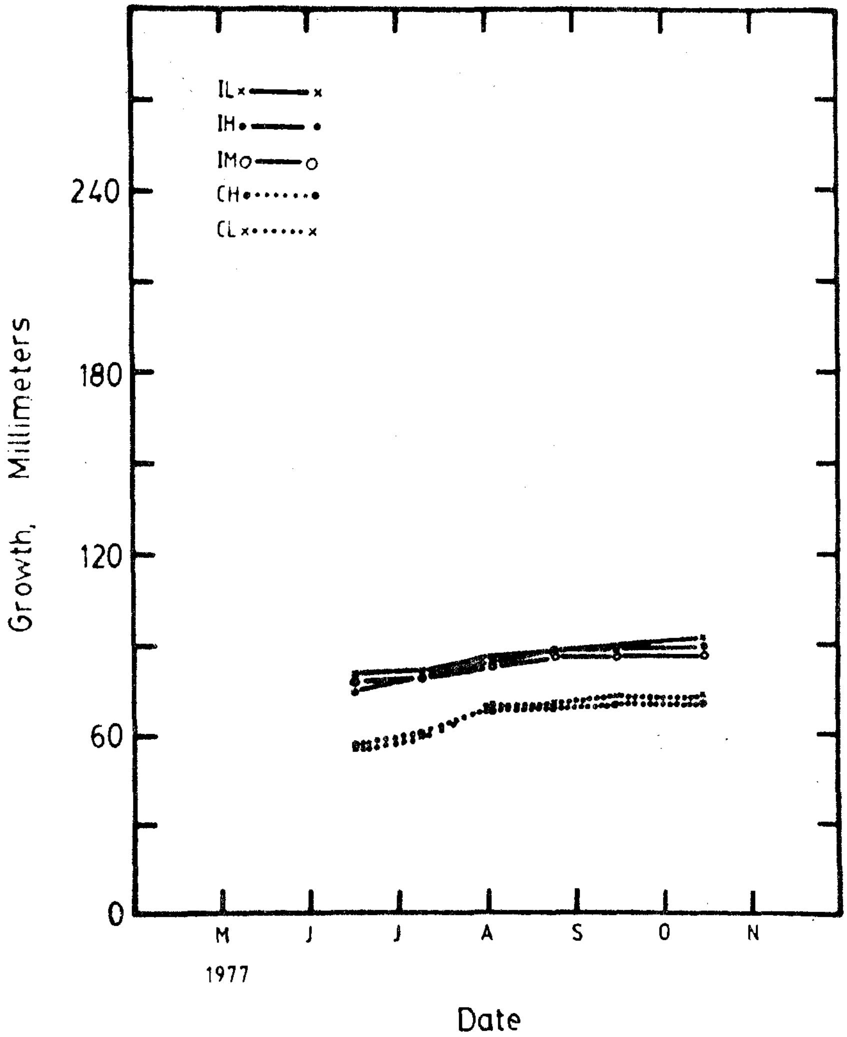
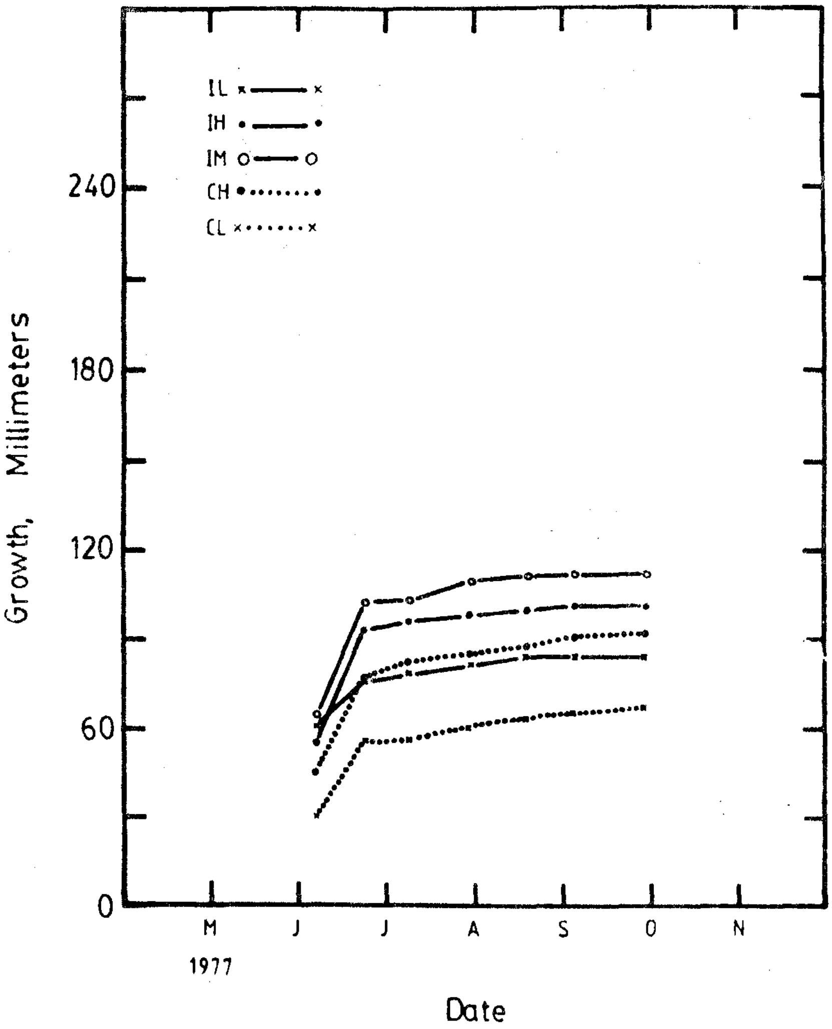

IL×——×
IH•——•
IMo——o
CH•······•
CL×······×
Growth, Millimeters
240
180
120
60
0
M
J
J
A
S
O
N
1977
Date

Figure III - 3

Mean leader growth in 1977 (mm) for the five populations growing under the 60 (30) % light regime at SFU. Abbreviations as in text. This pattern of growth is representative of that found under the other five light regimes at SFU.


IL ×———×
IH •———•
IM o———o
CH •·······•
CL ×·······×
Growth, Millimeters
0
60
120
180
240
M
J
J
A
S
O
N
1977
Date

because previous experiments have shown such responses (below). Kossuth and Biggs (1981) reported that Douglas-fir growth was unaffected by increased UV radiation, Chassagne et al. (1981), Fox and Caldwell (1978), Sisson and Caldwell (1977) and Vu et al. (1981) all reported decreased growth with increased UV irradiation, Logan and Krotkov (1969) observed that increased PAR had no effect on sugar maple growth, and Jarvis (1964) suggested that oak growth increased with decreased levels of PAR. The small increase in tree growth at SFU over that found at SRS would be expected for seedlings re-establishing themselves in a coastal climate instead of in the less moderate interior climate. However, Owston and Kozlowski (1981) reported greater growth in Douglas-fir seedlings grown under a hot climatic regime similar to that of SRS than under one similar to that found at SFU.

The 1978 mean leader growth ranking order at SRS was IL, CH, CL, IM, and IH (Table III - 12). These data agree with Farr and Harris (1979), Malcolm and Pymar (1975), Mergen (1963), Rehfeldt (1979b) and Zavitkovski et al. (1981) observations and Zavitkovski et al. (1981) hypothesis that shoot elongation is negatively related to the latitude of seed source origin. The data also confirm the observations of Griffin and Ching (1977) and Tusko (1963) that coastal varieties have greater growth rates than interior varieties. Zavitkovski et al. (1981) hypothesis did not hold at SFU in 1978 (Table III - 13) but Griffin and Ching (1977) and Tusko's (1963) relationship did. Growth continued through to the end of July for all populations at SRS (Figure III - 4) but only until mid June for the interior populations and into August for the coastal populations at SFU (Figure III - 5). The SRS data did not support Griffin and Ching's (1977) observation

Table III - 12.

1978 mean leader growth (in mm) for all the populations under all the light regimes at SRS. Light regime and population abbreviations as in text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for the row numbers followed by lower case letters, and the column numbers, followed by upper case letters.

Light Regime	Population				
	IL	IH	IM	CH	CL
Open	127 a A	85 a B	112 a C	122 a D	123 a E
30 %	266 b	188 b	197 b C	204 b D	219 b
UVT	132 c A	111 c B	111 c C	142 c D	139 c E
UVO	172 d A	132 d B	147 d C	223 d D	123 d E

Table III - 13.

1978 mean leader growth (in mm) for all the populations under all the light regimes at SFU. Light regime and population abbreviations as in text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for the row numbers followed by lower case letters, and the column numbers, followed by upper case letters.

Light Regime	Population				
	IL	IH	IM	CH	CL
Open	98 a A	109 a B	93 a C	132 a D	157 a F
30 %	96 b A	86 b B	103 b C	173 E	140 b F
10 %	107 c A	98 c B	94 c C	235 d E	162 d F
UVT	102 e A	96 e B	119 e C	209 f E	172 f F
UVA	91 g A	107 g B	98 g C	119 g D	150 g F
UVO	95 h A	93 h B	128 h C	217 i E	208 i F

Figure III - 4

Mean leader growth in 1978 (mm) for the five populations growing under the 30 (60) % light regime at SRS. Abbreviations as in text. This pattern of growth is representative of that found under the other three light regimes at SRS.

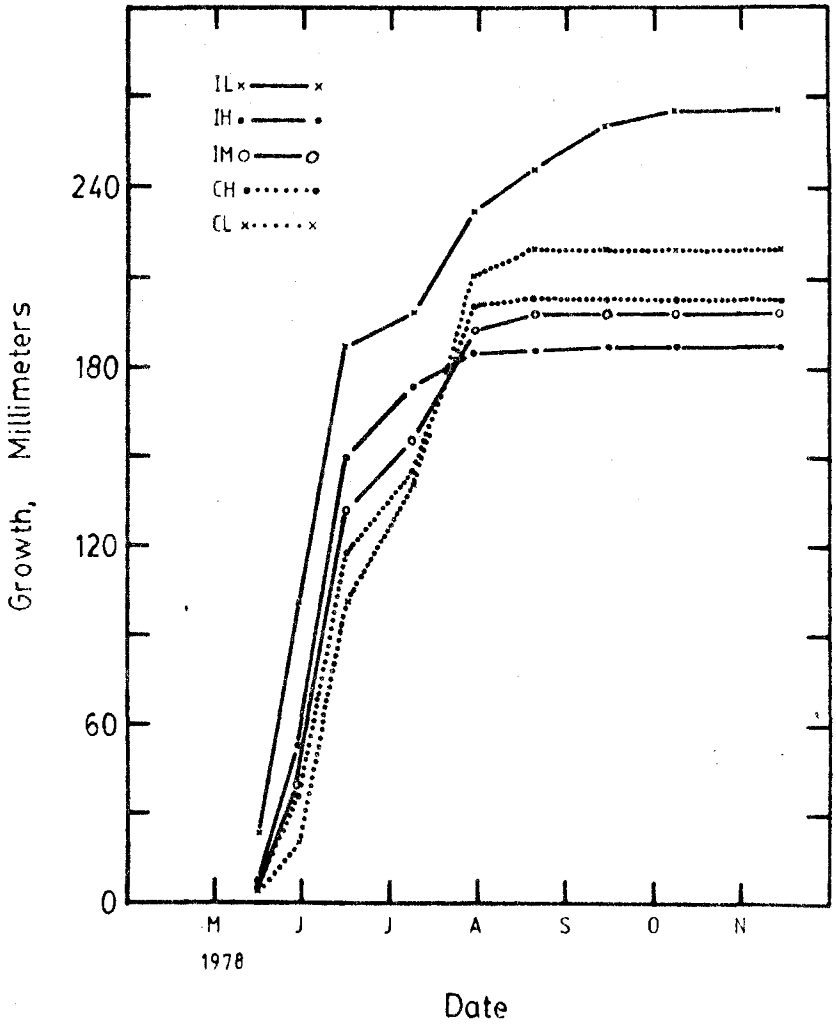
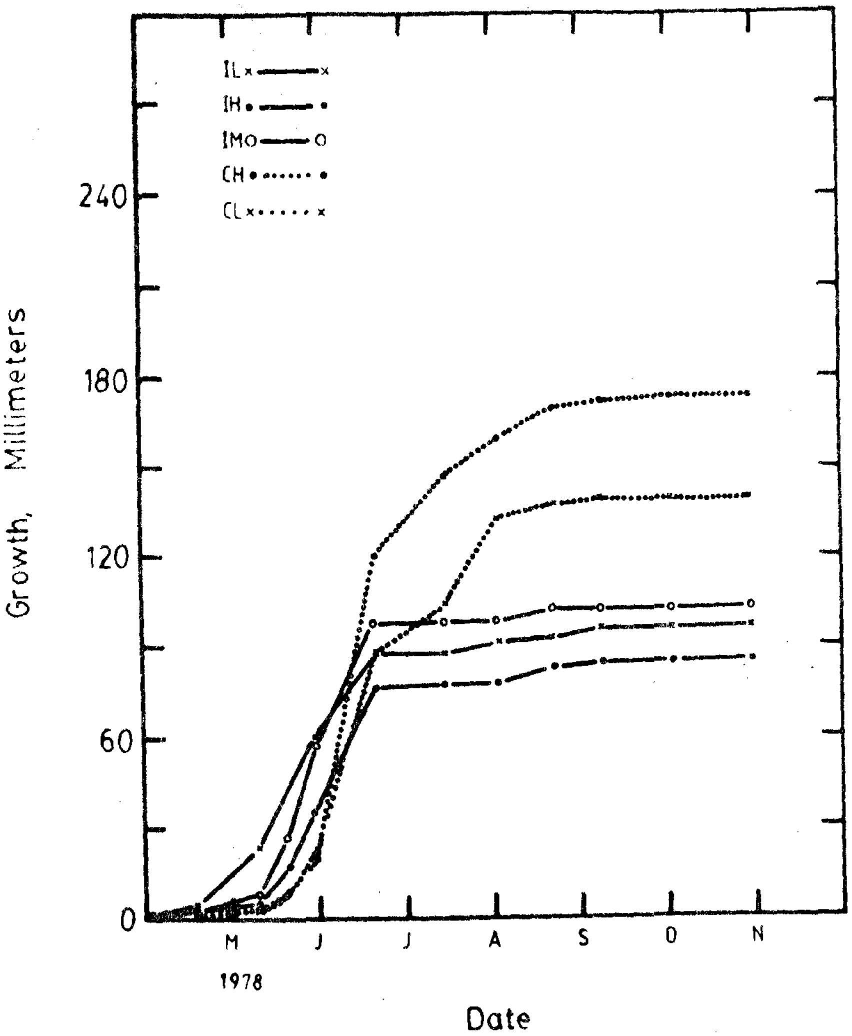

IL ×——×
IH •——•
IM o——o
CH •······•
CL ×······×
Growth, Millimeters
0
60
120
180
240
M
1978
J
J
A
S
O
N
Date

Figure III - 5

Mean leader growth in 1978 (mm) for the five populations growing under the 30 (60) % light regime at SFU. Abbreviations as in text. This pattern of growth is representative of that found under the other five light regimes at SFU.


IL × —— ×
IH • —— •
IMo —— o
CH • ······ •
CL × ······ ×
Growth, Millimeters
0
60
120
180
240
M
J
J
A
S
O
N
1978
Date

that coastal populations grow more and for a longer seasonal period of time but the SFU data did (Figures III - 2&3). A possible reason for this is that SRS grown trees encounter temperature stresses and possibly water stresses through July and August while SFU grown trees would only encounter these stresses early in August, if at all.

Again, as for the 1977 mean leader growth, the 1978 growth did not show any correlation for growth and light regime between SRS and SFU (Table III - 14), except that usually more growth occurred at the lowest light intensity at both sites. Also, growth at SRS was inversely related to light intensity (Table III - 12) and this agrees with Jarvis' (1964) observation for oak. The scatter of the light regime growth data at SRS and SFU (Table III - 14) likely validates the previously noted observations of Fox and Caldwell (1978), Jarvis (1964), Kossuth and Biggs (1981) and others that growth responses to light quality can be highly variable. SRS grown populations had more 1978 mean leader growth than the SFU populations for this period which supports the observations, based on temperature of Owston and Kozlowski (1981). A possible reason for this is that temperatures were warmer earlier in the growing season at SRS (Table III - 1) so that for this period, SRS grown trees would have higher rates of net photosynthesis (p/s) than those at SFU. This would result in more early season growth at SRS. Later in the season, increased temperatures, possibly causing stress to the photosynthetic apparatus, would result in less growth at SRS. SFU grown trees did not overcome the headstart of the SRS grown ones (Figures III - 4 & 5).

Table III - 14.

1978 mean leader growth (in mm) for all the populations under all the light regimes at SRS and SFU. Light regime and population abbreviations as in text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for row numbers, followed by lower case letters, and the column numbers, followed by upper case letters.

Site	Light Regime	Population				
		IL	IH	IM	CH	CL
SRS	Open	127 a A	85 a C	112 a D	122 a E	123 a G
"	30 %	266 b B	188 b	197 b	204 b E	219 b G
"	UVT	132 c A	111 c C	111 c D	142 c E	139 c G
"	UVO	172 d B	132 d C	147 d D	223 d F	123 d G
SFU	Open	98 e A	109 e C	93 e D	132 e E	157 e G
"	30 %	96 f A	86 f C	103 f D	173 E	140 f G
"	10 %	107 g A	98 g C	94 g D	235 h F	162 h G
"	UVT	102 i A	96 i C	119 i D	209 j E	172 j G
"	UVA	91 k A	107 k C	98 k D	119 k E	150 k G
"	UVO	95 l A	93 l C	128 l D	217 m F	208 m G

The final mean tree heights at SRS (Table III - 15) conform to latitude and variety differences predicted by Zavitkovski et al. (1981) and Griffin and Ching (1977) and Tusko (1963) respectively because the large 1978 increases contributed most to final tree height. The observation of Griffin and Ching (1977) and Tusko (1963) that coastal populations grow more rapidly is confirmed at SFU for final tree height (Table III - 16) but the hypothesis of Zavitkovski et al. (1981) that growth is negatively correlated to the latitude of seed source origin is not because the large 1978 increases followed the same patterns and were most responsible for final mean tree height. Tree height was inversely related to light intensity at SRS (Table III - 15) as it had been for 1978 growth. However, there was no correlation for light regime and final tree height between SFU and SRS and at SFU, supporting the observation that growth responses to light quality can be highly variable (Fox and Caldwell, 1978; Jarvis, 1964; Kossuth and Biggs, 1981; among others). There was little difference between the final mean tree heights at the two sites (Table III - 17) because growth was greatest at SFU in 1977 and at SRS in 1978. If the study had been carried on, tree heights would reflect 1978 growth increases because the trees had become established in their new environments.

The growth at SRS appeared to follow both Zavitkovski et al. (1981) and Griffin and Ching (1977) and Tusko's (1963) hypotheses but at SFU it appeared to follow only the later hypothesis. Tree growth appeared to be inversely related to light intensity at SRS but there did not appear to be any correlation between light intensity and growth at SFU. The observed differences between populations, light regimes and sites could be due to:

Table III - 15.

Final mean tree heights (in mm) for all the populations under all the light regimes at SRS. Light regime and population abbreviations as in text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for the row numbers, followed by lower case letters, and the column numbers, followed by upper case letters.

Light Regime	Population IL	 IH	 IM	 CH	 CL
Open	436 a A	402 a B	391 a C	433 a D	398 a E
30 %	595 b	501 b B	488 b C	523 b D	561 b
UVT	393 c A	423 c B	396 c C	476 D	404 c E
UVO	477 d A	422 d B	470 d C	578 D	408 d E

Table III - 16.

Final mean tree heights (in mm) for all the populations under all the light regimes at SFU. Light regime and population abbreviations as in text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for row numbers, followed by lower case letters, and the column numbers, followed by upper case letters.

Light Regime	Population				
	IL	IH	IM	CH	CL
Open	430 a A	456 a C	409 a D	510 E	465 a F
30 %	404 b A	400 b C	426 b D	563 E	480 b F
10 %	350 c A	370 c C	386 c D	614 d E	497 d F
UVT	390 e A	388 e C	503 f	578 f E	519 f F
UVA	298 B	420 g C	371 g D	461 g E	483 g F
UVO	306 h B	391 h C	394 h D	530 i E	520 i F

Table III - 17.

Final mean tree heights (in mm) for all the populations under all the light regimes at SRS and SFU. Light regime and population abbreviations as in text. No significant difference between the means [test ANOVA (alpha = 0.05)] is indicated for row numbers, followed by lower case letters, and the column numbers, followed by upper case letters.

Site	Light Regime	Population				
		IL	IH	IM	CH	CL
SRS	Open	436 a A	402 a C	391 a D	433 a F	398 a G
"	30 %	595 b	501 b C	488 b E	523 b F	561 b G
"	UVT	393 c A	423 c C	396 c D	476 F	404 c G
"	UVO	477 d A	422 d C	470 d D	578 F	408 d G
SFU	Open	430 e A	456 e C	409 e D	510 F	465 e G
"	30 %	404 f A	400 f C	426 f D	563 F	480 f G
"	10 %	350 g A	370 g C	386 g D	614 h F	497 h G
"	UVT	390 i A	388 i C	503 j E	578 j F	519 j G
"	UVA	298 B	420 k C	371 k D	461 k F	483 k G
"	UVO	306 l B	391 l C	394 l D	530 m F	520 m G

(1) The higher summer daily mean temperatures at the interior site (Table III - 1) could result in longer periods of and higher rates of p/s at SRS;

(2) The interaction between the tree and the environment could alter the growth between the two experimental sites, eg. IL at SRS and SFU (Tables III - 11 & 14);

(3) There is a great variability among plants in their response to UV_A radiation (Caldwell, 1971) and this could account for the growth differences seen under the plexiglass light regimes;

(4) The temperature differences between the plexiglass plots and the other light regimes could also be responsible for the growth differences; and

(5) The supplementary water regime at SRS could have increased growth rates because native interior Douglas-fir grow slowly and in much more shade than was available at SRS, except under the 30 (60) % light regime (Tusko, 1963).

The growth differences cannot be attributed to different soil types as all trees were planted in the same soil or to spacing differences, which can cause growth differences (Timmis and Tanaka, 1976), because spacing distance was similar under all the light regimes.

Leader needle and lateral whorl branch needle lengths were found to vary greatly within populations in the same growing season and between the same populations in different growing seasons (data not shown). Therefore, detailed statistical analysis is not warranted at this time.

Section 3: Needle Water Content

The % WC in 1977 to 1979 needles at SRS ranged from 30.1 to 76.0 % and was greatest in newly flushed needles. It then declined until November, peaked in December 1977, declined to a March-May 1978 minimum, increased through June-July, declined until March-April 1979 and then increased in May (Figure III - 6). Exceptions to this trend were that 60 (30) % grown populations did not have the first December peak and Open grown populations had a December 1978 peak too. The 1977 to 1979 % WC at SFU ranged from 40.6 to 77.5 %. The seasonal trend at SFU (Figure III - 7) was similar to that described for the 60 (30) % grown populations at SRS.

The decline in % WC to a March-May minimum in 1978 at SRS and SFU (Figures III - 6 & 7) and a March-April 1979 minimum at SRS and an April 1979 minimum at SFU has been previously reported in the mid-western USA for jack pine (Zavitkovski et al. 1981) and juniper (Brett and Singer, 1973) and in the western USA for several conifer species (Pharis, 1967). The increased % WC following the spring minimum at both sites has also been reported for juniper (Brett and Singer, 1973) and two year old spruce needles (Gary, 1971). This corresponds to the period immediately after the new year needles had flushed in their studies, as it did here. The December 1977 increase at SRS (Figure III - 6) could be due to an increase in the frost tolerance of the needles because eastern white pine tolerates freeze dessication by increasing the interfacial water binding capacity of the lamella (De Yoe and Brown, 1979). This increase is usually preceeded by a period of moderate water stress (Blake et al. 1979; Parsons and Li, 1979)

Figure III - 6

A representative example of the seasonal trend for % WC in 1977 to 1979 needles at SRS. The light regime used is UVT and all five populations are presented. Abbreviations as in text.

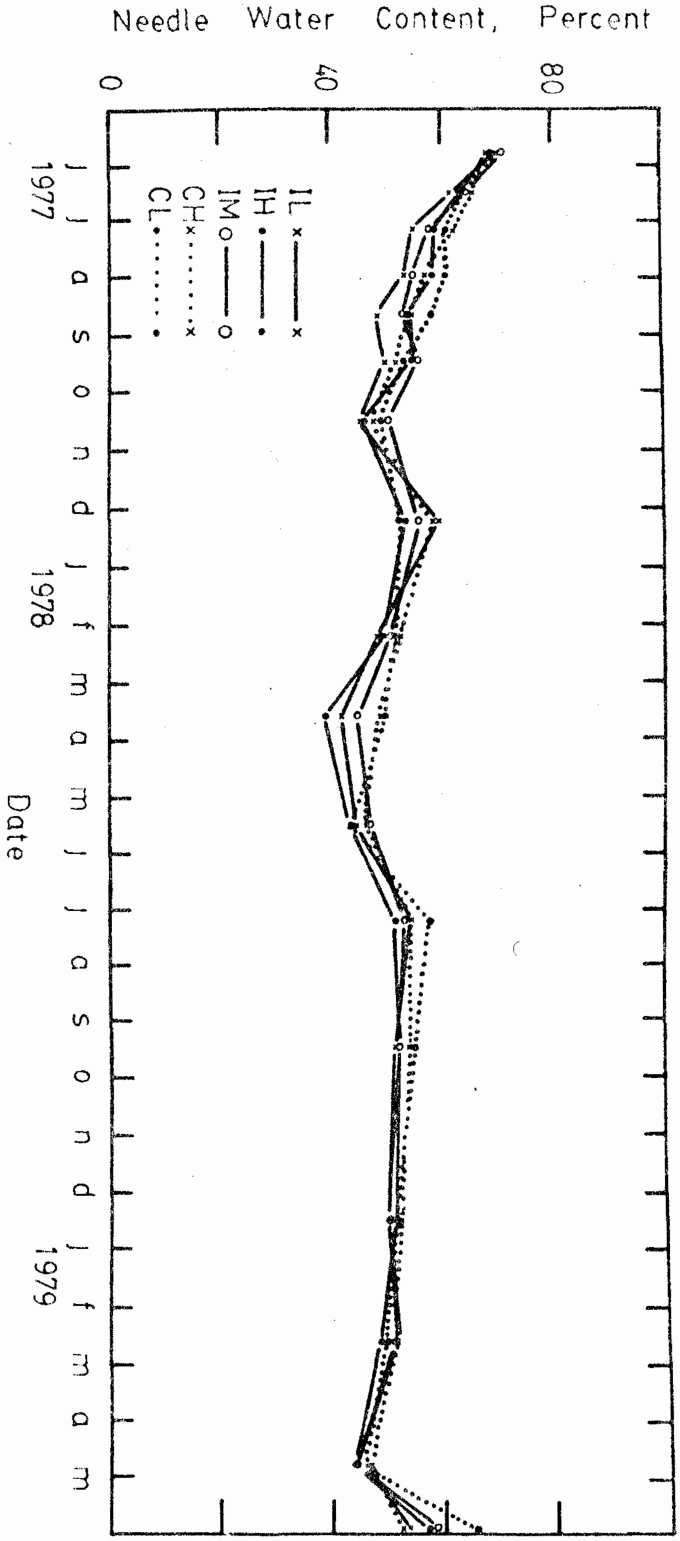
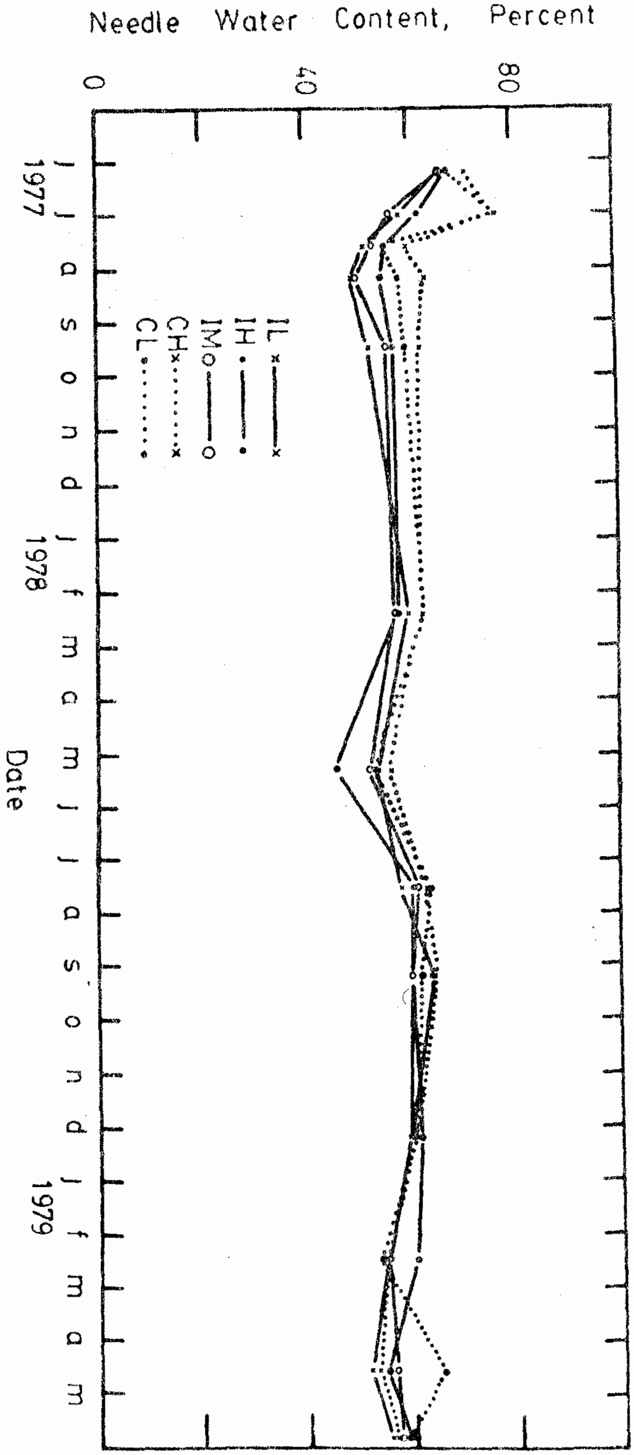

Needle Water Content, Percent
0
40
80
IL x——x
IH •——•
IM o——o
CH x·······x
CL •·······•
j j a s o n d j f m a m j j a s o n d j f m a m
1977
1978
1979
Date

Figure III - 7

A representative example of the seasonal trend for % WC in 1977 to 1979 needles at SFU. The light regime used is 60 (30) % and all five populations are presented. Abbreviations as in text.


Needle Water Content, Percent
0
40
80
Date
j
j
a
s
o
n
d
j
f
m
a
m
j
j
a
s
o
n
d
j
f
m
a
m
1977
1978
1979
IL ×——×
IH •——•
IMo o——o
CH× ········×
CL• ········•

and this may have occurred in November. Similar results have been reported for needles (chloroplasts) of Scots pine in Sweden (Öquist et al. 1978a,b). There was no increase in % WC for SRS - 60 (30) % grown seedlings and for all of the SFU grown ones. This data indicates several things could have occurred:

(1) Light is an important component in inducing frost hardiness as Christersson (1978) suggested from his experiments and Martin and Öquist (1979) reported that high light and low temperature induce greater hardiness than low light and low temperature;

(2) The environmental cues at SFU were not severe enough to bring on the indicators of frost hardiness induction; and

(3) There could have been December 1977 peaks under many of the light regimes but there was no December collection at SFU that year.

The amount of membrane bound water (unfreezable) in plants does not appear to have any relationship to the degree of frost hardiness that is attained (Burke et al. 1976). The only trees at either site to have a December 1978 peak in % WC were the SRS Open grown ones. This peak probably occurred because this is the only regime with sufficiently high light intensities and low temperatures to bring on some of the indicators of frost hardiness induction or two year old tissue does not require or is unable to undergo the degree of induction that new tissue does.

Coastal varieties had the greatest and interior populations the lowest and the same rankings for % WC in 1977 to 1979 needles at SRS and SFU (Table III - 18; the remaining tables are ranked by the numerical index ranking method). This may have occurred because coastal populations are genetically

Table III - 18.

Ranking of light regimes and populations for % WC in 1977 to 1979 needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes			
CL	30 %	Open	UVT	UVO
CH	30 %	UVO =	Open	UVT
IL =	Open	UVT =	UVO =	30 %
IH	30 %	Open	UVT	UVO
IM	30 %	UVT	Open =	UVO
Mean	30 %	Open	UVT	UVO

B. SFU

Population	Light Regimes					
CH	10 %	UVO =	UVA =	30 %	Open =	UVT
CL	30 % =	UVO =	Open	10 %	UVA	UVT
IL =	UVA	10 %	Open	UVT =	UVO	30 %
IH	10 %	30 %	UVA	UVT =	Open	UVO
IM	10 %	30 % =	UVT	UVA	UVO	Open
Mean	10 %	30 % =	UVA	Open =	UVT	UVO

programmed to high % WC, whereas interior varieties are not. The % WC decreased with increasing light intensity at both sites (Table III - 18). This result is consistent with the observations of Bourdeau and Laverick (1958) and Lewandowska and Jarvis (1976) who reported increased water contents with decreased light intensity. The anomaly observed under the UVO light regime (Table III - 18) is consistent with Caldwell's (1971) report that there is a high degree of variability in plant responses to UV_A radiation. SFU grown pspulations had higher % WC than SRS grown trees which correlates with the higher levels of precipitation and more moderate temperatures at SFU (Tables III - 1 & 2).

The % WC in 1978 to 1979 needles ranged from 47.4 to 80.0 % and was greatest in newly flushed needles. It then declined until November 1978, increased in December—January, declined until April—May 1979, and finally increased in late May (Figure III - 8). The exception to this trend was the 30 (60) % grown populations which did not have the December 1978 peak. At SFU, % WC was greatest in newly flushed 1978 to 1979 needles and ranged from 49.3 to 79.6 %. The trend in % WC then declined through July 1978, increased during August, declined for an April 1979 minimum and increased in May (Figure III - 9). Exceptions to this trend were that Open grown populations had an October minimum followed by a December 1978 maximum and declining to the April 1979 minimum and 10 (30) % grown populations declined until January 1979, increased in February and declined through April.

The decline in % WC to spring minima at SRS and SFU (Figures III - 8 & 9) for 1978 new needles corresponds to the spring minima observed in the

Figure III - 8

A representative example of the seasonal trend for % WC in 1978 to 1979 needles at SRS. The light regime used is UVT and all five populations are presented. Abbreviations as in text.

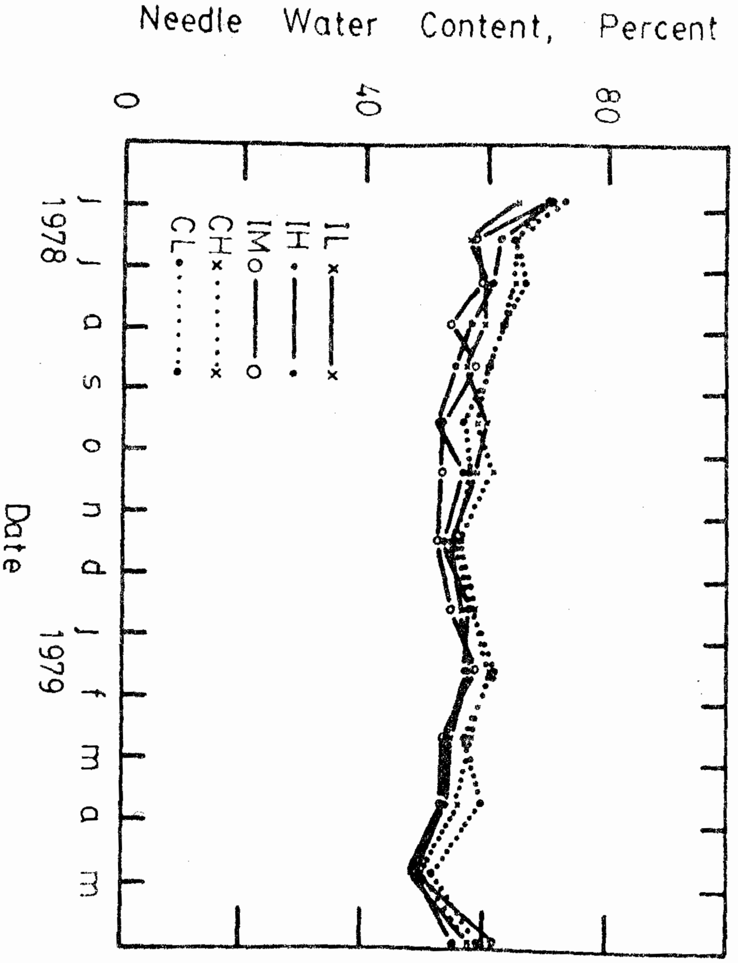
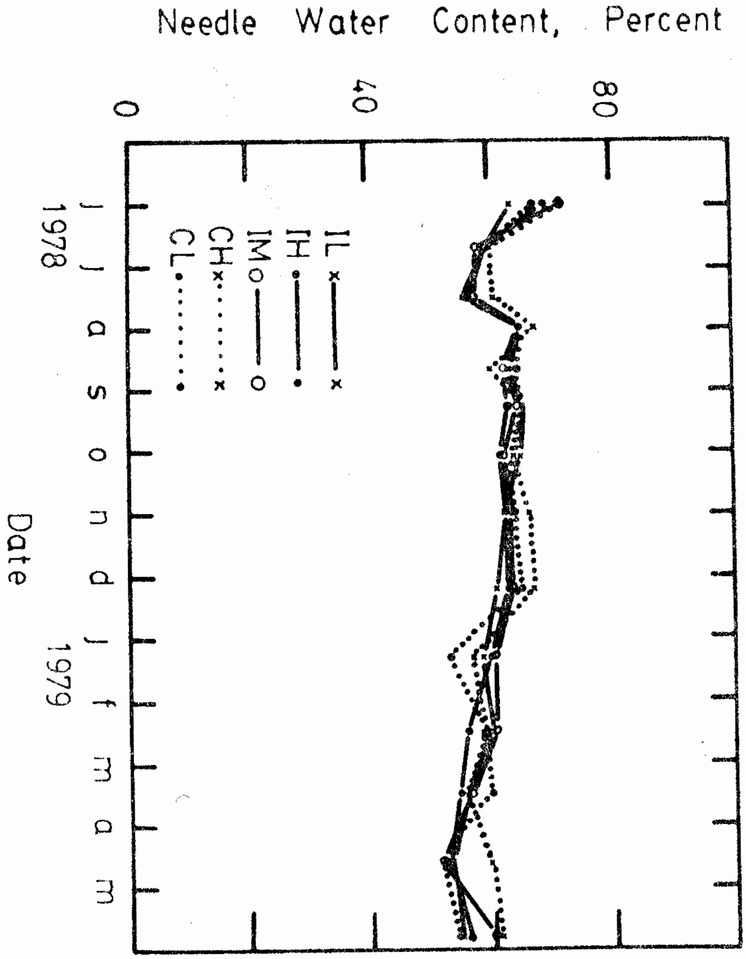

Needle Water Content, Percent
0
40
80
IL ×——×
IH •——•
IMo——o
CH ×·····×
CL •·····•
j
j
a
s
o
n
d
j
f
m
a
m
1978
1979
Date

Figure III - 9

A representative example of the seasonal trend for % WC in 1978 to 1979 needles at SFU. The light regime used is UVT and all five populations are presented. Abbreviations as in text.


Needle Water Content, Percent
0
40
80
IL ×——×
IH •——•
IMo o——o
CH ×·······×
CL •·······•
j
j
a
s
o
n
d
j
f
m
a
m
1978
1979
Date

1977 to 1979 needles and with the observations of Brett and Singer (1973), Gary (1971), Pharis (1967) and Zavitkovski et al. (1981). The increase following the spring minima at both sites (Figures III - 8 & 9) also occurred in the 1977 to 1979 needles . The December 1978 increase in % WC at SRS (Figure III - 8) is the first sign that frost hardiness induction is occurring in the 1978 new needles. The SRS 30 (60) % grown populations had the same response in 1978 as they had for 1977 new needles. Of the SFU grown populations, only the Open grown ones had a December 1978 maximum in % WC. This lends support to Martin and Öquist's (1979) observation that the response is greater if in the fall increased light intensity accompanies decreased temperatures (cf SRS 1977 to 1979 needles, December 1978 peak). Again, a period of apparent moderate water stress, October-November 1978, may have preceeded this % WC increase. The non winter peaks in the other SFU grown populations supports the hypothesis that decreased light intensity along with decreased temperatures results in decreased % WC compared to high light and low temperatures.

Coastal varieties had the greatest and interior populations the lowest rankings for 1978 new needles % WC at SRS and SFU (Table III - 19), and were the same as they had been for 1977 to 1979 needles at both sites (Table III - 18). This occurred for the reasons previously noted. % WC decreased with increasing light intensity at both sites for 1978 new needles when the PAR and UV plexiglass plots were examined separately. These results conform to Bourdeau and Laverick (1958) and Lewandowska and Jarvis' (1976) observation, especially when Caldwell's (1971) UV_A paradox, that growth responses to UV_A are highly inconsistent , and not understood. Again,

Table III - 19.

Ranking of light regimes and populations for % WC in 1978 to 1979 needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population		Light Regimes				
CL	=	30 %	UVO		Open	UVT
CH		30 %	Open		UVO	UVT
IL		30 %	UVO	=	Open	UVT
IM	=	30 %	UVO		Open	UVT
IH		30 %	UVO		UVT	Open
Mean		30 %	UVO		Open	UVT

B. SFU

Population	Light Regime							
CH	10 %	Open	UVA		30 %	=	UVT	UVO
CL	10 %	UVO	30 %		UVA	=	Open	UVT
IL	10 %	UVO	UVA	=	Open	=	30 %	UVT
IM	10 %	30 %	UVT		UVA		UVO	Open
IH	10 %	30 %	UVO		Open		UVT	UVA
Mean	10 %	30 %	UVO		Open	=	UVA	UVT

1978 new needle % WC was identical between SRS and SFU when the light regimes not common to both were excluded (Table III - 19). The above data suggests that % WC was largely under genetic control as populational % WC rankings were relatively unaltered by the different environments, even though there were fluctuations in % WC between the various light regimes at both sites (Table III - 18 & 19). SFU grown population's 1978 new needles had higher % WC than SRS grown ones. This is consistent with the moderate coastal climate at SFU (Tables III 1 to 3).

Population rankings for % WC were the same between 1977 and 1978 new needles at SRS and SFU (Tables III - 19 & 20), whereas only the lowest light intensity light regime maintained its ranking between the two years at both sites. The ranking similarities were due to the apparent rigidity of % WC. The light regime fluctuations may be attributed to a combination of the interaction of the populations with the environment and with different and variable responses to UV_A radiation (Caldwell, 1971). The 1977 and 1978 new needles had very similar trends at SRS (Figures III - 6 & 8) while the 1978 new needles' trend at SFU was quite different from the 1977 new needle trend (Figure III - 7 & 9) but it was quite similar to the 1977 two year old needle trend (Figure III - 7). The observed differences and similarities between the various seasonal % WC trends showed that while % WC was largely regulated by the plant, environmental parameters could alter % WC resulting in a different phenotypic expression in the new environment but with the same relationship between the five populations. Water content has also been observed to fluctuate through the year even under conditions of high soil moisture contents and between species with no apparent trend except for

Table III - 20.

Ranking of light regimes and populations for % WC in 1977 new needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Abbreviations as in text.

A. SRS

Population	Light Regimes				
CL	30 %	Open	UVT	=	UVO
CH	UVT	30 %	Open	=	UVO
IL	Open	UVO	30 %	=	UVT
IM =	30 %	Open	UVO	=	UVT
IH	30 %	Open	UVT		UVO
Mean	30 %	Open	UVT		UVO

B. SFU

Population	Light Regime										
CH	30 %		10 %		UVO		Open		UVT		UVA
CL	Open		30 %	=	10 %	=	UVA		UVO		UVT
IL	UVA		10 %		Open	=	UVT		30 %	=	UVO
IH	UVT	=	UVA	=	10 %		30 %	=	Open		UVO
IM	10 %	=	UVT		Open		30 %		UVO		UVA
Mean	10 %		Open		30 %	=	UVT	=	UVA		UVO

the three major features (Pharis, 1967), winter peak, spring minimum, and post flush increase, previously noted.

If water stress had occurred at SFU some of the growth increases observed there in the previous section (III.2) could be accounted for because water stress can result in reductions in growth and p/s comparable to UV_B stress (Lindoo et al. 1979). This was not the case because % WC and soil moisture content was greatest at SFU, therefore, the observed growth reductions at SFU are still due to the reasons postulated in the previous section (III.2).

CHAPTER IV

PHOTOSYNTHETIC PIGMENTS AND PIGMENT RATIO

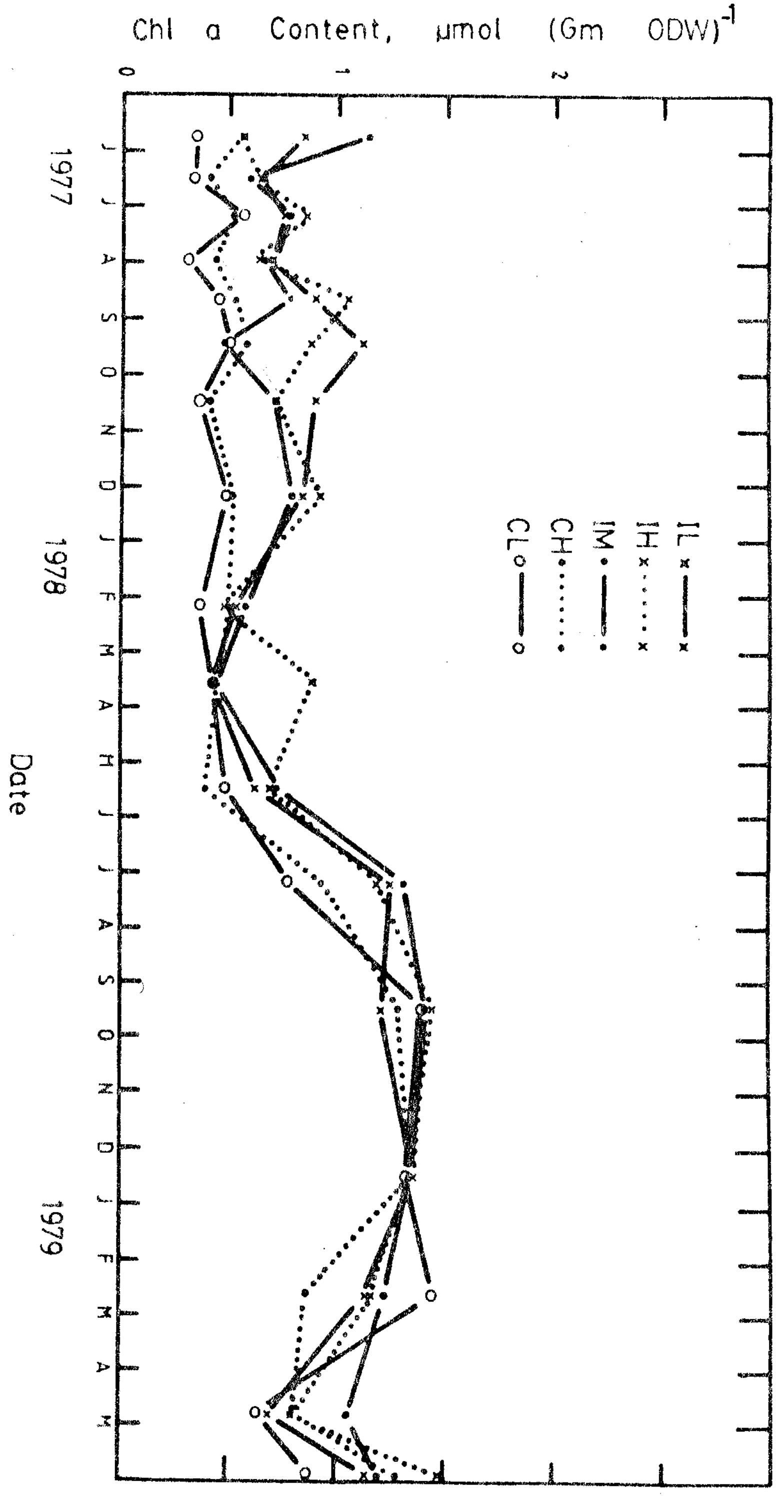
RESULTS AND DISCUSSION

Section 1: Chlorophyll a content

Chl a content ranged from 0.34 to 1.87 µmol (gm ODW)$^{-1}$ for 1977 to 1979 needles at SRS and from 0.31 to 2.51 µmol (gm ODW)$^{-1}$ at SFU. The seasonal Chl a trends show that at SRS and SFU, Chl a decreased from the spring flush through the early summer (July 1977), increased into the fall (Sept.-Oct. 1977), decreased to a spring minimum (Feb.-Mar. 1978), increased into the fall (Sept. and Dec. 1978), decreased into the spring (April 1979) and increased in late May (Figure IV - 1). The initial decrease into July paralleled the drop in % WC (Figures III - 6 & 7), both were probably due to increasing dry matter as the new needles matured, resulting in apparent pigment decreases with % WC decreases and dry matter increases. The longer term increase of Chl a into the fall of 1978 at SFU probably occurred because at SRS temperatures were lower, precipitation was much lower and daily sun hours were higher in September and October (Tables III - 1 to 3). This results in a reduction in Chl a in conjunction with frost hardiness induction. Similar seasonal trends to those observed here have been reported for different conifer species (Brett and Singer, 1973; Khodasevick et al. 1978; Lewandowska and Jarvis, 1977; Linder, 1971, 1972; Martin et al. 1978a; McGregor and Parker, 1963; Ollykainen, 1967, 1969a,b; Senser et al. 1975, 1978; Zacharowa, 1929). However, exceptions to this trend have been

Figure IV - 1

A representative example of the seasonal trend for Chl a content in 1977 to 1979 needles at SRS. The light regime used is Open and all five populations are presented. Abbreviations as in text.


Chl a Content, µmol (Gm ODW)$^{-1}$
0
1
2
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1977
1978
1979
Date
IL ×——×
IH ×·······×
IM •——•
CH •·······•
CL o——o

noted by Berner (1949) who found that there was no noticeable seasonal change in Chl a and Godnev et al. (1965) and Laurs (1935) both reported that Chl a inceased rather than decreased during the winter. The exception of SRS 60 (30) % to this trend could have occurred because the lower light intensity prevented the photo-destruction of Chl a during October and November. It was not until December that low temperarures induced the decrease of Chl a.

Chl a content at both sites was greater in two year old needles than in new needles as has previously been observed in conifers (Linder, 1972; Ollykainen, 1967). Interior populations had the greatest Chl a contents at both sites (Table IV - 1) for 1977 to 1979 needles. Chl a content was roughly proportional to altitude and inversely proportional to latitude of origin at both sites. Garrett (1969) reported a similar altitude-pigment relationship, whereas Baldwin (1955) and Linder (1972) reported an inverse altitude-pigment relationship. No reports of an altitude-latitude-pigment relationship have been found in the literature. Chl a decreased similarly with increasing light intensity at both sites when light regimes not common to both were excluded (Table IV - 1). Bourdeau and Laverick (1958), Jarvis (1964), Lewandowska et al. (1977) and Logan and Krotkov (1969) all reported the same response by Chl a to light intensity, while Sisson and Caldwell (1976) reported constant Chl a levels with increased UV and Vu et al. (1981) reported decreased Chl a with increased UV radiation. The UVA light regime being out of sequence at SFU (Table IV - 1B) could have occurred because of the variability of plant responses to UV_A radiation (Caldwell, 1971). Populations grown at SFU had the greatest Chl a content and this is

Table IV - 1.

Ranking of light regimes and populations for Chl a content in 1977 to 1979 needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes			
IH =	60 %	UVO	UVT	Open
IL =	60 %	UVO	UVT	Open
IM	60 %	UVO	UVT	Open
CH	60 %	UVO	UVT	Open
CL	60 %	UVO	UVT	Open
Mean	60 %	UVO	UVT	Open

B. SFU

Population	Light Regimes					
IL	30 %	60 %	UVA	UVO	UVT	Open
IH	30 %	60 %	UVA	UVO	Open	UVT
IM	30 %	UVO	60 %	UVA	UVT	Open
CH	30 %	UVT	UVA =	60 %	UVO	Open
CL	30 %	60 %	UVO =	Open	UVT =	UVA
Mean	30 %	60 %	UVA =	UVO	UVT	Open

consistent with SFU having a milder climate (Tables III - 1 to 3).

Seasonal Chl a content ranged from 0.54 to 3.32 µmol (gm ODW)$^{-1}$ at SRS and from 0.50 to 3.57 µmol (gm ODW)$^{-1}$ at SFU for 1978 new needles. The trend generally increased into the fall of 1978 after the initial decline, decreased into the early spring and then increased in the late spring of 1979 (Figures IV - 2 & 3). When the small oscillations, resulting from the sampling periods being closer together, are overlooked the seasonal trend for 1977 and 1978 new needles are very similar at both sites: summer minimum, fall maximum, winter minimum followed by a spring maximum. However, the two year old needles have only a spring minimum and a fall maximum. The initial spring decrease in new needle Chl a is probably due to the decrease in needle % WC. Contrary to the decline observed through the winter at both sites for 1977 to 1979 needles, in 1978 new needles Chl a remained relatively constant during this period which is similar to Berner's (1949) observation. The exceptions of SRS and SFU Open to the observed seasonal trend is probably due to increased light and lower temperatures over the other regimes during the fall and winter. The variation of the UVA light regime reinforces Caldwell's (1971) hypothesis that responses to UV_A radiation are highly variable.

The CL and CH populations had the highest Chl a content for 1978 new needles at SRS while the IH and IL populations had the highest at SFU (Table IV - 2). The altitude-latitude-pigment correlation observed between the two sites for 1977 to 1979 was not observed, probably because it takes a year or even two for seedlings to re-establish themselves when

Figure IV - 2

A representative example of the seasonal trend for Chl a content in 1978 new needles at SRS. The light regime used is UVT and all five populations are presented. Abbreviations as in text.

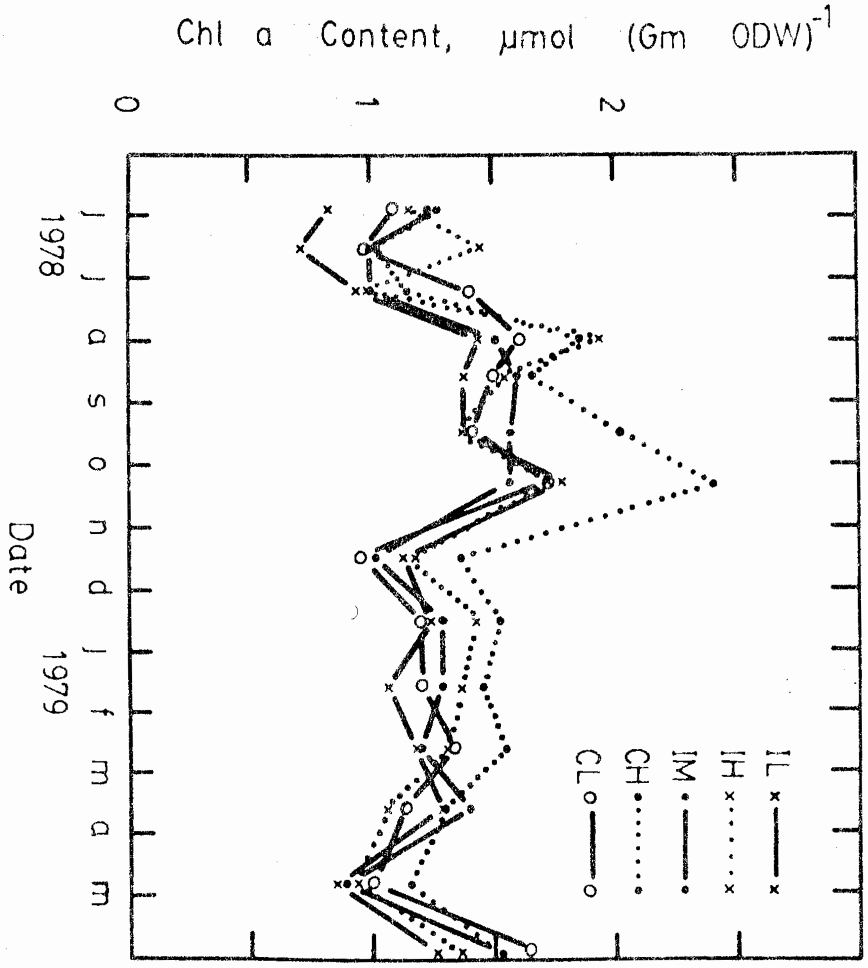

Chl a Content, µmol (Gm ODW)$^{-1}$
0
1
2
j
j
a
s
o
n
d
j
f
m
a
m
1978
1979
Date
IL
IH
IM
CH
CL

Figure IV - 2

A representative example of the seasonal trend for Chl a content in 1978 new needles at SFU. The light regime used is 10 (30) % and all five populations are presented. Abbreviations as in text.

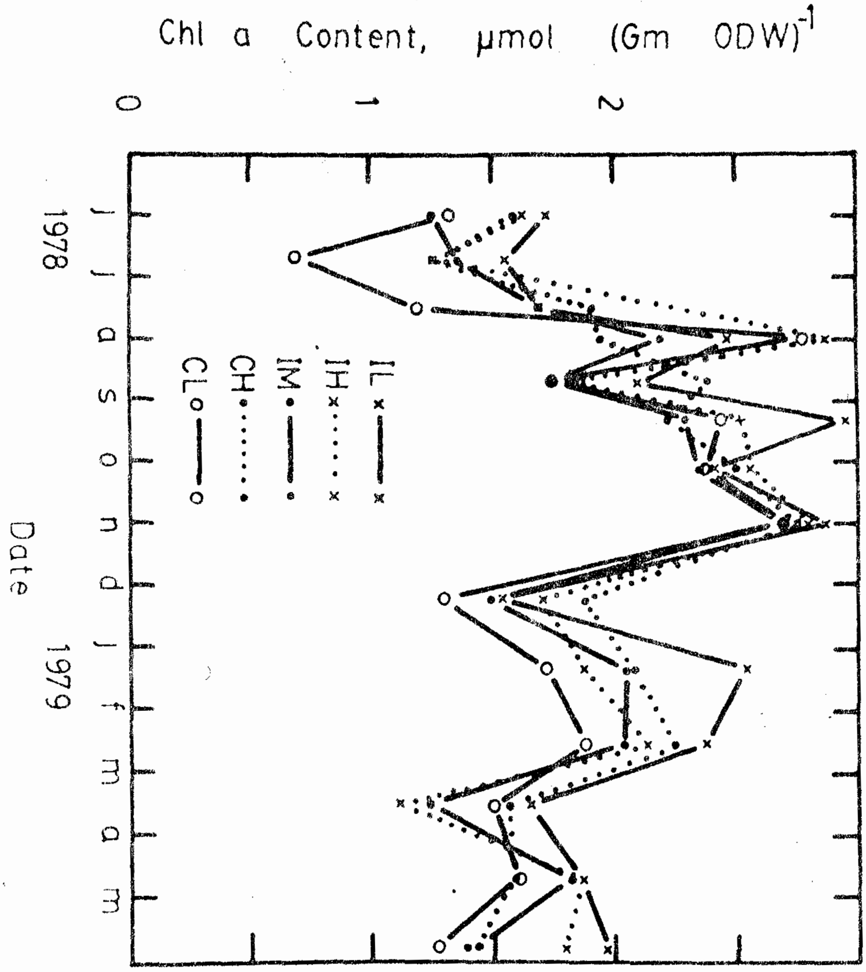

Chl a Content, μmol (Gm ODW)$^{-1}$
0
1
2
j
j
a
s
o
n
d
j
f
m
a
m
1978
1979
Date
IL x——x
IH x·····x
IM •——•
CH •·····•
CL o——o

Table IV - 2.

Ranking of light regimes and populations for Chl a content in 1978 new needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population		Light Regimes				
CL	=	30 %	UVO	Open	=	UVT
CH		30 %	UVT	Open	=	UVO
IH	=	30 %	UVT	Open		UVO
IM		30 %	UVT	UVO		Open
IL		30 %	UVO	UVT		Open
Mean		30 %	UVT	UVO		Open

B. SFU

Population		Light Regimes									
IH	=	30 %		10 %	Open	=	UVO		UVT	=	UVA
IL		10 %		30 %	UVO		UVT		UVA		Open
CH	=	10 %		30 %	Open	=	UVT		UVA		UVO
IM		10 %		30 %	UVA		UVT	=	UVO	=	Open
CL		30 %		10 %	Open		UVO		UVA		UVT
Mean		10 %	=	30 %	Open	=	UVO		UVA	=	UVT

transplanted (Thompson, 1980). The altitude-latitude-pigment relationship of the previous year was reversed at SRS (Table IV - 2A) so that the low altitude populations had the greatest Chl *a* levels. Similar results have been reported for conifers (Baldwin, 1955; Linder, 1972). The correlation between altitude-latitude-pigment content at SFU (Table IV - 2B) was with one exception in agreement with the previous year (Table IV - 1B). Chl *a* decreased with increased light intensity at both sites for 1978 new needles when the PAR and UV plexiglass plots were examined separately (Table IV - 2). The switch between UVO and UVT at SRS could again be due to Caldwell's (1971) UV$_A$ paradox. Increased Chl *a* with decreased light intensity is consistent with what was observed for the 1977 to 1979 needles (Table IV - 1). Populations grown at SFU had the greatest Chl *a* levels and this is likely due to the milder climate at SFU.

Populational differences observed between the two years new needles at both sites (Tables IV - 2 & 3) resembled those noted previously (Tables IV - 1 & 2)and presumably have the same causes as outlined there. The observed differences in light regime rankings between 1977 and 1978 new needles at SRS and SFU (Tables IV - 2 & 3) were similar to those between the 1977 to 1979 needles and the 1978 new needles at both sites (Tables IV - 1 & 2). These differences probably are due to the same causes noted above. However, the generality of increased Chl *a* with decreased light intensity still holds.

Two year old 1977 needles from the interior populations had the greatest Chl *a* content at both sites (Table IV - 4) as in 1977 to 1979

Table IV - 3.

Ranking of light regimes and populations for Chl a content in 1977 new needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population		Light Regimes						
IL	=	60 %		UVO		UVT		Open
IH		60 %		UVO		UVT	=	Open
IH		UVO		60 %		Open		UVT
CH		60 %		UVO		Open	=	UVT
CL		60 %		UVO		UVT		Open
Mean		60 %		UVO		UVT	=	Open

B. SFU

Population		Light Regime										
IL		30 %		UVA		60 %		UVT		UVO		Open
IH	=	30 %		UVA		60 %	=	UVO		UVT		Open
CH		30 %		UVT	=	60 %		UVA		UVO		Open
IM		30 %	=	UVO		60 %		UVT		Open	=	UVA
CL		30 %		Open	=	60 %	=	UVO		UVA		UVT
Mean		30 %		60 %		UVO	=	UVA		UVT		Open

Table IV - 4

Ranking of light regimes and populations for Chl a content in 1977 two year old needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes					
IH	30 %	UVT		UVO		Open
IM	30 %	Open		UVT	=	UVO
IL	30 %	UVT		UVO		Open
CH	30 %	UVT		UVO		Open
CL	30 %	UVT	=	UVO	=	Open
Mean	30 %	UVT		UVO	=	Open

B. SFU

Population	Light Regimes							
IL =	10 %	30 %	=	UVO		UVA	Open		UVT
IM	10 %	30 %		UVA	=	UVO	UVT	=	Open
IH	10 %	30 %	=	UVO		UVA	Open		UVT
CH	10 %	UVA		UVT		30 %	UVO		Open
CL	10 %	30 %		UVT		UVO	Open	=	UVA
Mean	10 %	30 %		UVO	=	UVA	UVT		Open

needles from both sites (Table IV - 1) and at SFU for 1978 new needles (Table IV - 2B). Chl a in 1977 two year old needles generally decreased with increased light intensity at both sites (Table IV - 4) and was similar to the rankings observed for the 1978 new needles (Table IV - 2). These results are consistent with those discussed previously. The similarities in ranking of light regimes and populations between the 1977 new and two year old needles indicate that the degree of needle plasticity decreased while the genetic control of physiological phenomena becomes increasingly more important and observable with age. The decreased number of features observable on the seasonal Chl a trend of the 1977 two year old needles compared to that of the 1977 and 1978 new needles' trend, one maximum and minimum versus two maxima and minima, also supports the hypothesis that needle plasticity decreases with increased needle age.

There does appear to be an inverse relationship between light intensity and Chl a content. There may also be a relationship between a populations original altitude and Chl a content, but it is not clear whether it is proportional as reported by Garrett (1969) or inversely proportional to altitude as reported by Baldwin (1955) and Linder (1972). Additional studies are required to clarify this. If a relationship exists between Chl a and original populational latitude much more data are required to establish it.

Section 2: Chlorophyll b Content

Chl b ranged in 1977 to 1979 needles from 0.17 to 1.21 µmol (gm ODW)$^{-1}$

at SRS and from 0.19 to 1.97 μmol (gm ODW)$^{-1}$ at SFU. The seasonal trend for Chl b decreased from the spring flush through the early summer, increased with small oscillations to a fall maximum (Dec. 1977), decreased to a spring minimum (May 1978), increased to a summer maximum (July 1978), gradually decreased to a spring minimum (April 1979) and then increased at SRS (Figure IV - 4), while at SFU, Chl b increased from the spring flush to a fall maximum (Sept. 1977), decreased to a spring minimum (June 1978) and then increased until the next spring (May 1979). Even though the short term trends were often anti-parallel between the two sites, overall Chl b trends similar to those observed for both years at SRS and the first year at SFU have been observed in conifers (Brett and Singer, 1973; Khodasevich et al. 1978; Lewandowska and Jarvis, 1977; Linder, 1972; Martin et al. 1978a; Ollykainen 1967, 1969a,b; Senser and Beck, 1978; Zacharowa, 1929). The increases observed in Chl b through the winter in the second year needles at SFU and in the SRS 60 (30) % populations has been reported by Godnev et al. (1965) and Laurs (1935). They both attributed this increase to a mild winter, but the winter in question is colder than the preceeding one, so this is not the reason for the increase. SRS UVO was an exception in the first year to the seasonal trend probably because of Caldwell's (1971) UV_A paradox that plant responses are highly variable to UV_A radiation.

Chl b content at both sites was greater in two year old needles than in new needles as has been observed in conifers by Linder (1972) and Ollykainen (1967). Interior origin populations had the greatest Chl b levels while the lowest was found in the CL population (Table IV - 5). Generally, Chl b was greatest in the high altitude origin populations as Garrett (1969) reported

Figure IV - 4

A representative example of the seasonal trend for Chl b content in 1977 to 1979 needles at SRS. The light regime used is 60 (30) % and all five populations are presented. Abbreviations as in text.

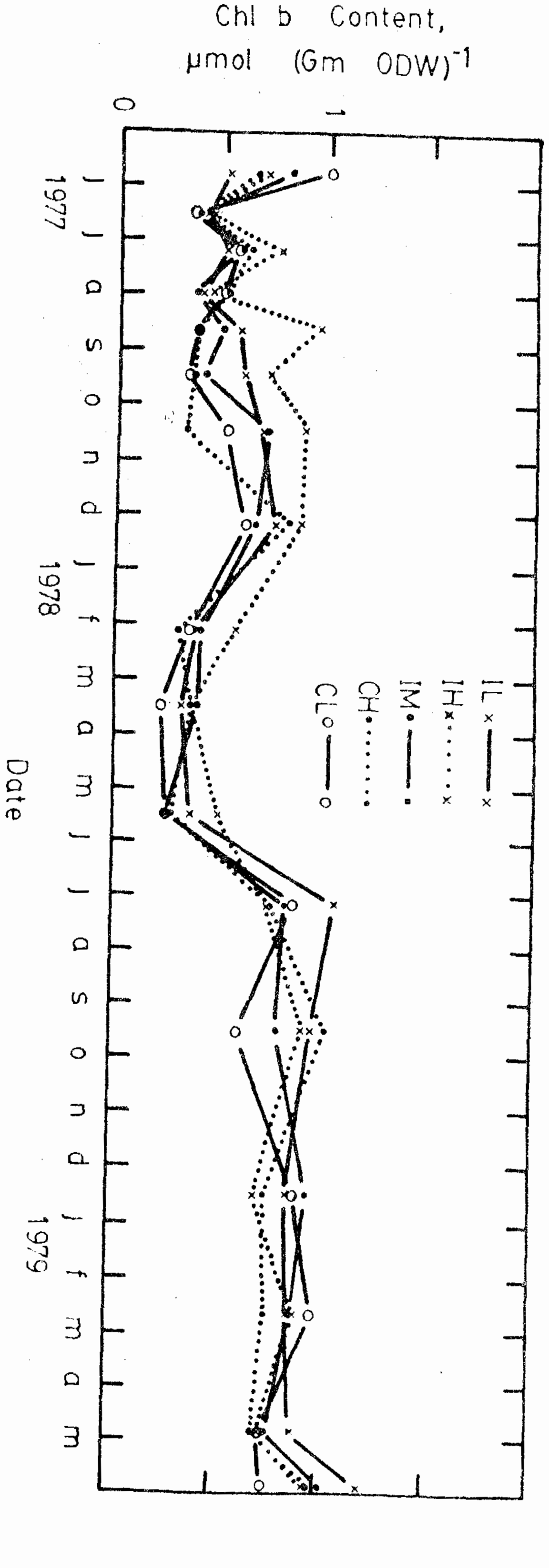

Chl b Content,
µmol (Gm ODW)$^{-1}$
0
1
j j a s o n d j f m a m j j a s o n d j f m a m
1977
1978
1979
Date
IL ×——×
IH ×·····×
IM •——•
CH •·····•
CL ○——○

Table IV - 5.

Ranking of light regimes and populations for Chl b content in 1977 to 1979 needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes			
IM =	60 %	UVO	UVT	Open
IH =	60 %	UVO	UVT	Open
IL	60 % =	UVO	UVT	Open
CH	60 %	UVO	UVT	Open
CL	60 %	UVO	UVT	Open
Mean	60 %	UVO	UVT	Open

B. SFU

Population	Light Regimes					
IL	30 %	UVO	UVA	60 %	UVT	Open
IH	30 %	60 %	UVO	UVA	UVT	Open
CH	30 %	UVT	60 % =	UVA	UVO	Open
IM	30 %	UVO	60 %	UVT	UVA	Open
CL	30 %	UVO	60 %	UVA	UVT	Open
Mean	30 %	UVO =	60 %	UVA =	UVT	Open

but there was not a good correlation between latitude and pigment content, as occurred with Chl a. Chl b decreased with increased light intensity at SRS and SFU for 1977 to 1979 needles (Table IV - 5) and was identical between the sites when light regimes not common to both were excluded. This result has been reported for Chl b in various tree species (Bourdeau and Laverick, 1958; Jarvis, 1964; Lewandowska et al. 1977; Logan and Krotkov, 1969). Populations grown at SFU had the greatest Chl b content for 1977 to 1979 needles and this is consistent with SFU having a milder climate (Tables III - 1 to 3).

Chl b in 1978 new needles ranged from 0.32 to 1.61 μmol (gm ODW)$^{-1}$ at SRS and from 0.23 to 1.60 μmol (gm ODW)$^{-1}$ at SFU. Chl b increased into the fall (Sept. & Oct. 1978) from the spring flush, decreased to November at SRS (Figure IV - 5) and until March 1979 at SFU (Figure IV - 6), increased gradually through the winter to February 1979 at SRS, decreased to April at SRS, and then increased to late May at both sites. The trend observed at SFU was the same as described for 1977 new needles at both sites and 1977 two year old needles at SRS. The overall trend at SRS for the 1978 new needles was the same as at SFU because the February peak is much lower than the October one (Figure IV - 5), therefore, the trend from fall to spring was downward even though there was an increase during the winter. Exceptions to the trend at SFU, UVO and 30 (60) %, appeared to be oscillating around the general trend, as did the SRS exception, 30 (60) %.

The CH population had the highest Chl b content at both experimental sites while IL had the lowest level at SRS and IM at SFU for 1978 new

Figure IV - 5

A representative example of the seasonal trend for Chl b content in 1978 new needles at SRS. The light regime used is UVT and all five populations are presented. Abbreviations as in text.

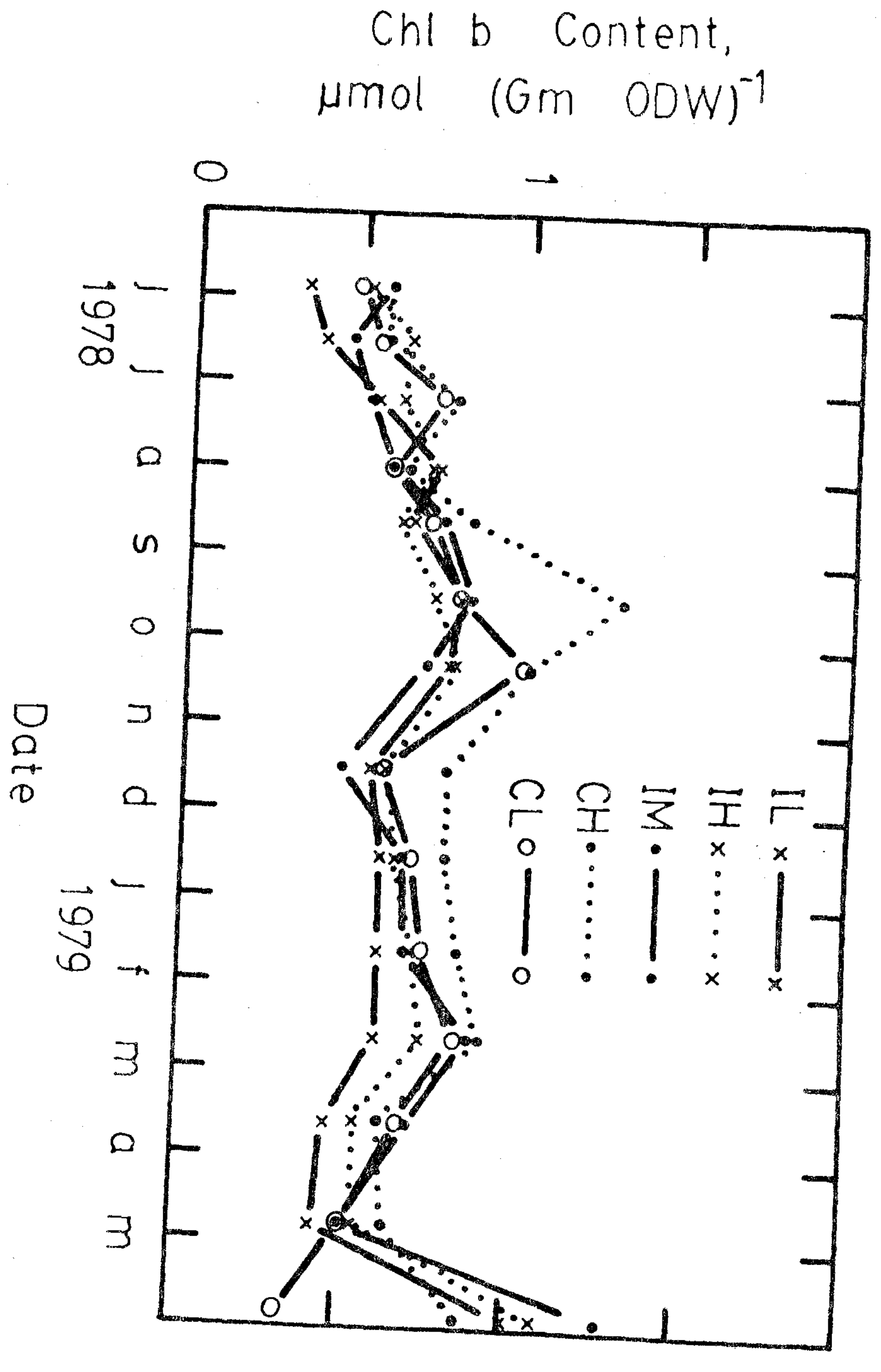
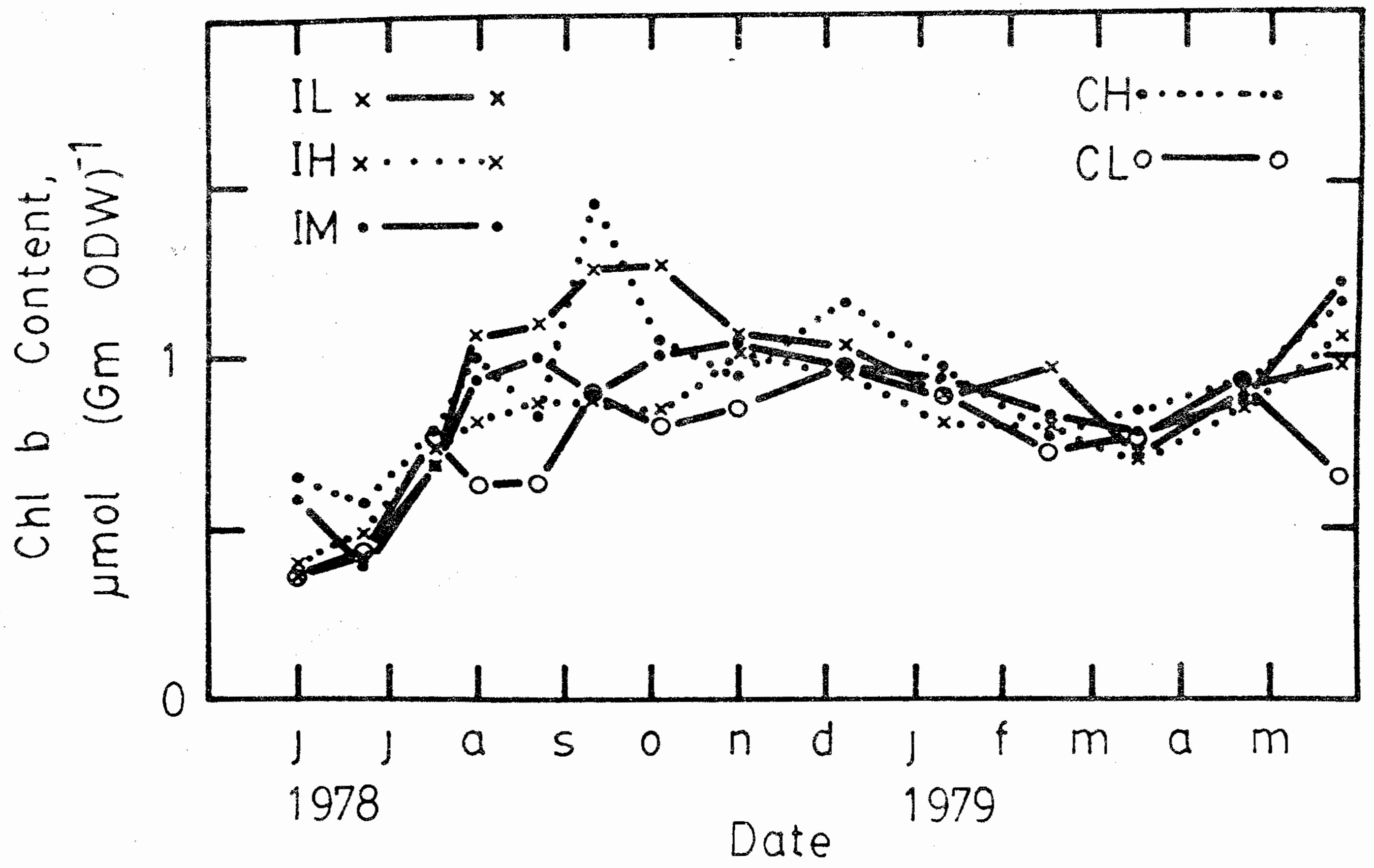

Chl b Content,
µmol (Gm ODW)$^{-1}$
0
1
j
j
1978
a
s
o
n
d
j
1979
f
m
a
m
Date
IL ×——×
IH ×·····×
IM •— —•
CH •·····•
CL ○——○

Figure IV - 6

A representative example of the seasonal trend for Chl b content in 1978 new needles at SFU. The light regime used is UVT and all five populations are presented. Abbreviations as in text.


Chl b Content,
μmol (Gm ODW)$^{-1}$
0
1
IL ×——×
IH ×·····×
IM •——•
CH•·····•
CL○——○
j
j
a
s
o
n
d
j
f
m
a
m
1978
1979
Date

needles (Table IV - 6). The altitude-pigment relationship appeared to be inversely related at SRS, contrary to the 1977 to 1979 needles (Table IV - 5A) but the same as Baldwin (1955) and Linder's (1972) observation. There did not appear to be any relationship between altitude and pigment content at SFU (Table IV - 6B), as there had been for 1977 new needles(Table IV - 5B). There did not appear to be any correlation between latitude and pigment content. Chl b decreased with increased light intensity at both sites for 1978 new needles, as it had for 1977 needles at both sites (Tables IV - 5 & 6). Chl b content was identical between SRS and SFU when light regimes not common to both were excluded (Table IV - 6). The switch between the UVA and UVO light regimes at SFU could be due to Caldwell's (1971) UV_A paradox or to the plots being next to each other and there being a cross over of light regimes every day as the sun moved across the sky (Figure II - 2). Again, SFU grown populations had the greatest Chl b content and this is consistent with SFU having a milder climate.

Populational differences observed between the 1977 and 1978 new needles at both sites (Tables IV - 6 & 7) resembled those noted previously (Tables IV - 5 & 6) and presumably have the same causes as outlined there. The observed similarities in light regime rankings between the two years new needles at SRS and SFU (Tables IV - 6 & 7) were similar to those between the two different year groups of needles at both sites (Tables IV - 5 & 6). Chl b increased with decreased light intensity as noted previously.

Two year old 1977 needles had the same populational differences as were observed for 1977 to 1979 needles at both sites (Tables IV - 5 & 8). The

Table IV - 6.

Ranking of light regimes and populations for Chl b content in 1978 new needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes					
CH	30 %	UVT		Open	=	UVO
CL	30 %	UVO		UVT		Open
IH	30 %	Open	=	UVT	=	UVO
IM	30 %	UVT		UVO		Open
IL	30 %	UVO		Open		UVT
Mean	30 %	UVO	=	UVT		Open

B. SFU

Population	Light Regimes								
CH	10 %	30 %		UVT		Open	=	UVA	UVO
IL	10 %	30 %	=	UVO		UVA		UVT	Open
IH =	10 %	30 %		UVA	=	UVO		Open	UVT
CL	10 %	30 %		UVA		UVO	=	Open	UVT
IM	10 %	30 %		UVT	=	UVA		UVO	Open
Mean	10 %	30 %		UVA		UVO		UVT =	Open

Table IV - 7.

Ranking of light regimes and populations for Chl b content in 1977 new needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes						
IL =	UVO		60 %		Open	=	UVT
IH =	60 %		UVO	=	Open		UVT
IM	UVO		60 %		Open	=	UVT
CH	60 %		UVO		Open		UVT
CL	60 %	=	UVO		UVT		Open
Mean	60 %	=	UVO		Open	=	UVT

B. SFU

Population	Light Regimes										
IL	30 %		UVA		UVT	=	UVO		60 %		Open
CH	UVT		30 %		60 %		UVA	=	UVO		Open
CL =	30 %		UVO		60 %		UVA		Open	=	UVT
IH	30 %		60 %	=	UVT	=	UVO		UVA		Open
IM	30 %		UVO		UVT		60 %		UVA	=	Open
Mean	30 %		UVO	=	UVT		60 %		UVA		Open

Table IV - 8.

Ranking of light regimes and populations for Chl b content in 1977 two year old needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population		Light Regimes				
IM		30 %	UVT		UVO	Open
IL		30 %	UVO		UVT	Open
IH	=	UVT	30 %	=	UVO	Open
CH		30 %	UVO	=	UVT	Open
CL		30 %	UVO	=	UVT	Open
Mean		30 %	UVT	=	UVO	Open

B. SFU

Population		Light Regimes									
IL		10 %	UVO		30 %	=	UVA		Open		UVT
IH	=	10 %	30 %		UVO	=	Open		UVA		UVT
IM		10 %	UVA	=	30 %	=	UVO		Open	=	UVT
CH		10 %	UVA		30 %		UVT	=	UVO		Open
CL		10 %	UVO		30 %		UVT	=	UVA		Open
Mean		10 %	30 %	=	UVO		UVA		Open	=	UVT

relationship between the 1977 two year old needles and the 1978 new needles (Tables IV - 6 & 8) was similar to that of the 1977 to 1979 and 1978 to 1979 needle groups at both sites (Tables IV - 5 & 6). Light regime rankings of Chl b for 1977 two year old needles was similar to all the other needle age groups (Tables IV - 5 to 8). Chl b increased with decreased light intensity. The number of observed primary features did not change for Chl b seasonal trends between new and two year old needles (Figures IV - 4 to 6). Both had one maximum and minimum overlain by a high degree of oscillation. There also was a great deal of similarity in the ranking of the light regimes between needle age groups (Tables IV - 5 to 8). These data probably indicate that the degree of plasticity of the Chl b response does not change with the age of the needle, as the Chl a response appeared to.

The relationship between light intensity and Chl b was the same as observed for Chl a. It increased with decreased light intensity. There was no indication of a latitude-pigment relationship but there was some indication of an altitude-Chl b correlation. Whether the relationship was proportional or inversely proportional to altitude was not clear because the data are not consistent and more data would be required to establish it.

Section 3: Carotenoid Content

Car content in 1977 to 1979 needles ranged from 0.40 to 1.44 µmol (gm ODW)$^{-1}$ at SRS and from 0.15 to 1.93 µmol (gm ODW)$^{-1}$ at SFU. Car increased to June from the newly flushed needles, decreased through August, increased to a December 1977 maximum, decreased to a May-June 1978 minimum, increased to a December 1978-January 1979 maximum, decreased to April and increased in late May at SRS (Figure IV - 7). At SFU, the general trend increased to July from the spring flush, decreased in August, increased to a December 1977 maximum, decreased to July 1978, increased to a December maximum and decreased until late May 1979. Seasonal Car trends were almost identical between SRS and SFU for 1977 to 1979 needles. The summer minimum and winter maximum trend for Car has been reported by Gerold (1959), Hellergren (1981), Kaloudin and Kaloudin (1967), Langlet (1942), Lewandowska and Jarvis (1977) and Ollykainen (1967) while a summer maximum and a winter minimum has been reported by Khodasevich et al. (1978), Linder (1972) and Ollykainen (1969a,b). The apparent degree of confusion surrounding the Car seasonal trend may occur because there are a large number of pigments in two different sub-groups that are being looked at as one group. This is because spectrophotometric separation of the various carotenoids from a mixed solution of pigments is not possible (Linder, 1972). Therefore, several different carotenoid pigment seasonal trends should be examined simultaneously to clarify this.

Car content was greater in two year old needles than in new needles at SFU as has previously been reported in conifers (Linder, 1972; Ollykainen, 1967). At SRS, Car content was about the same between new and two year old needles while Kaloudin and Kaloudin (1967) observed the highest Car levels in new needles. Car content was greatest in the interior populations at both sites (Table IV - 9). This can be generalized as increased Car with increased altitude of population origin. These results are consistent with those of Bukharin (1961) and Garrett (1969) but fail to confirm the data

Figure IV - 7

A representative example of the seasonal trend for Car content in 1977 to 1979 needles at SRS. The light regime used is 60 (30) % and all five populations are presented. Abbreviations as in text.

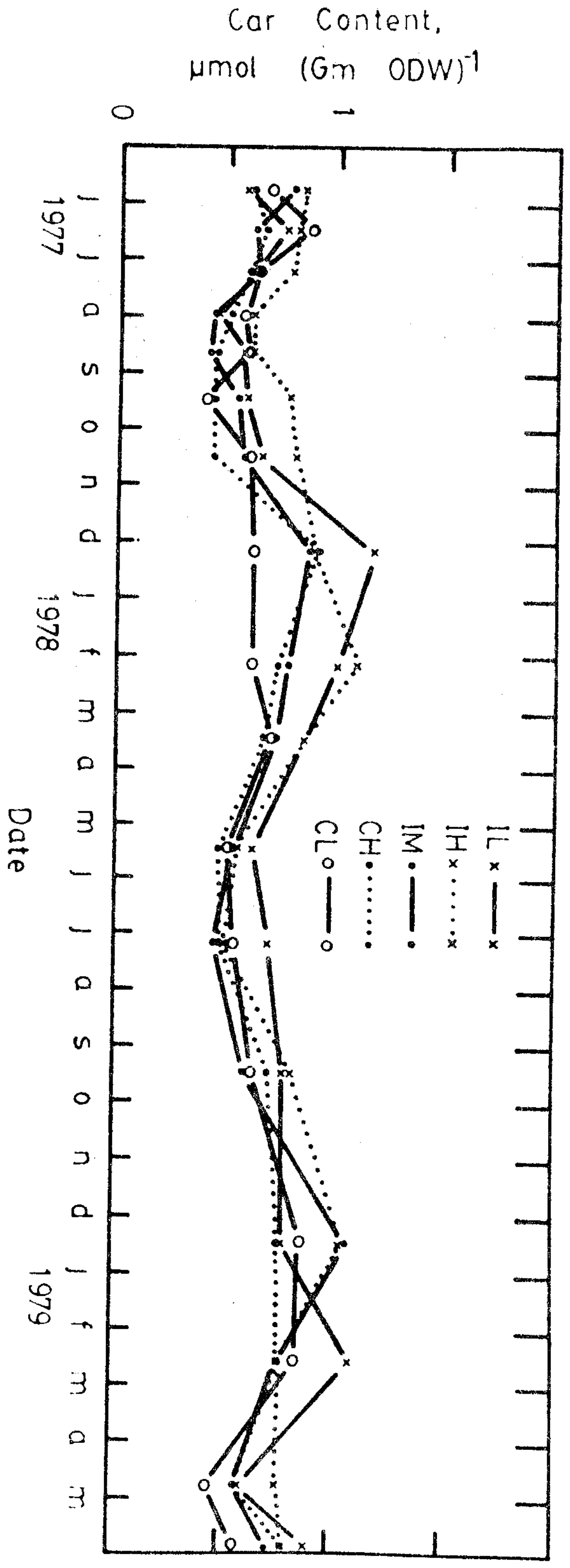

Car Content,
µmol (Gm ODW)⁻¹
0
1
1977
j j a s o n d
1978
j f m a m j j a s o n d
1979
j f m a m
Date
IL × —— ×
IH × ····· ×
IM • —— •
CH • ····· •
CL o —— o

Table IV - 9.

Ranking of light regimes and populations for Gar content in 1977 to 1979 needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes						
IH	Open	=	60 %		UVT		UVO
IL	UVT		UVO		60 %		Open
IM	Open	=	UVT		UVO		60 %
CL	Open		UVT		UVO	=	60 %
CH	UVO	=	60 %		Open		UVT
Mean	Open	=	UVT		60 %	=	UVO

B. SFU

Population	Light Regimes										
IL	UVA		Open		UVO		60 %		30 %		UVT
IH	Open	=	UVA		60 %		30 %		UVO		UVT
IM =	60 %		UVA		30 %	=	Open		UVT		UVO
CH	UVA		UVT		Open		60 %		UVO		30 %
CL	Open		60 %		UVA	=	UVO		30 %		UVT
Mean	UVA		Open		60 %		UVO	=	30 %	=	UVT

presented by Baldwin (1955) and Linder (1972) who reported increased Car with decreased altitude. There did not appear to be any relationship between latitude and Car content. There was not a strong correlation between light intensity and Car level at either site (Table IV - 9) but there may be a trend for increased Car with increased light intensity, especially in the PAR light regimes. Lewandowska and Jarvis (1977) reported decreased Car with increased light intensity. As with Chl a and b, populations grown at SFU had the greatest Car content and this is consistent with SFU having a milder climate (Tables III 1 to 3).

In 1978 new needles Car ranged from 0.26 to 1.99 μmol $(\text{gm ODW})^{-1}$ at SRS and from 0.26 to 1.65 μmol $(\text{gm ODW})^{-1}$ at SFU. Car increased with oscillations into the winter (Jan. 1979) at SRS (Figure IV - 8) and into the fall-winter (November 1978) at SFU (Figure IV - 9). It then decreased with oscillations until the spring of 1979 at both sites. This trend was similar to the summer minimum winter maximum discussed for 1977 to 1979 needles at both sites.

The IH population had the highest Car level at both sites while IM had the lowest at SRS and CL the lowest at SFU for 1978 new needles (Table IV - 10). The population that originated at the highest altitude had the greatest Car content at both sites but the altitude-Car relationship outlined for 1977 to 1979 needles was not clear. There did not appear to be latitude-pigment relationship at either site for 1978 new needles (Table IV - 10). Car generally decreased with decreased light intensity at SRS (Table IV - 10A), as was reported for 1977 to 1979 needles (Table IV - 9).

Figure IV - 8

A representative example of the seasonal trend for Car content in 1978 new needles at SRS. The light regime used is UVO and all five populations are presented. Abbreviations as in text.

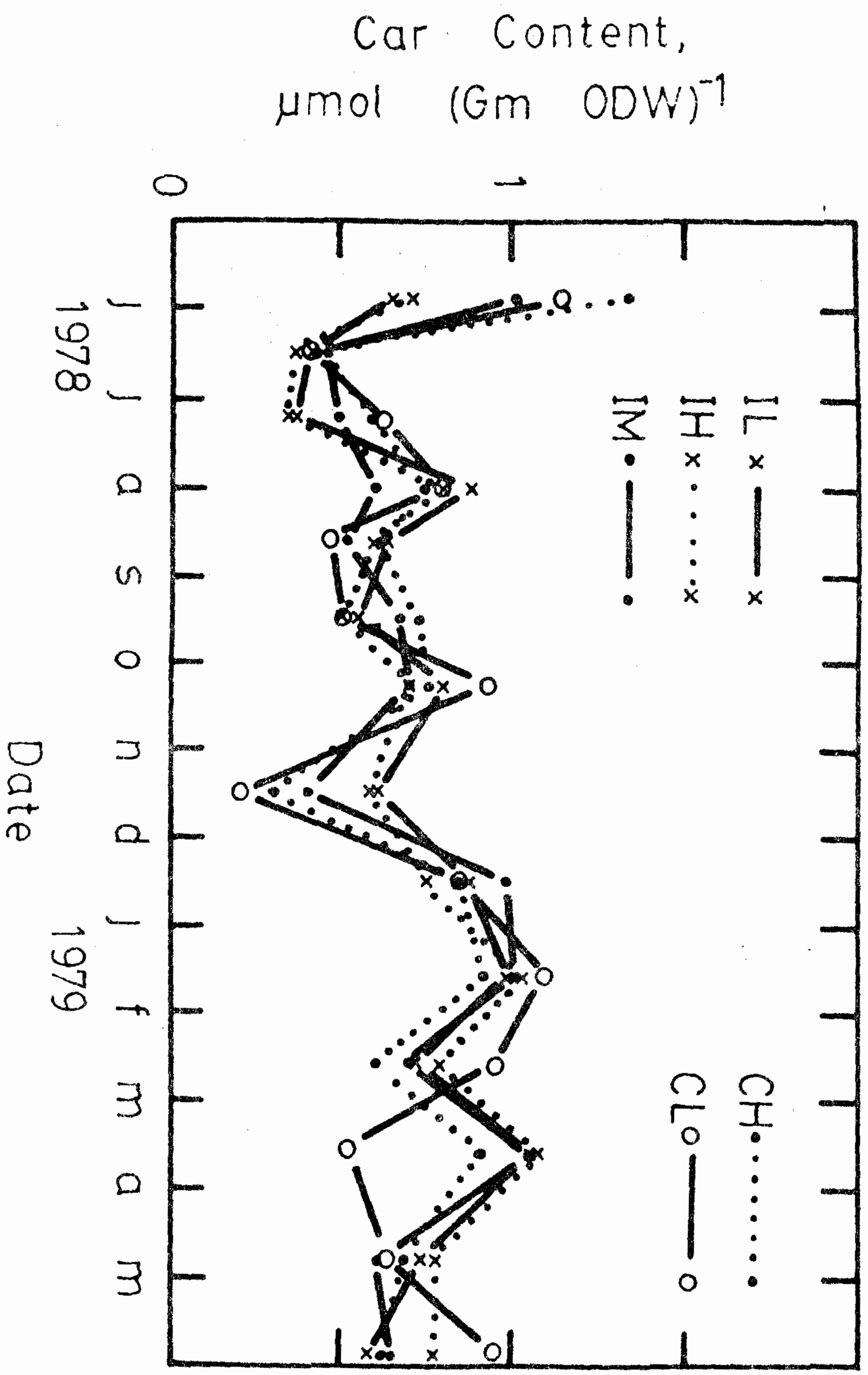

Car Content,
μmol (Gm ODW)-1
0
1
IL x —— x
IH x ····· x
IM • —·— •
CH • ······ •
CL o —— o
j
j
a
s
o
n
d
j
f
m
a
m
1978
1979
Date

Figure IV - 9

A representative example of the seasonal trend for Car content in 1978 new needles at SFU. The light regime used is 10 (30) % and all five populations are presented. Abbreviations as in text.

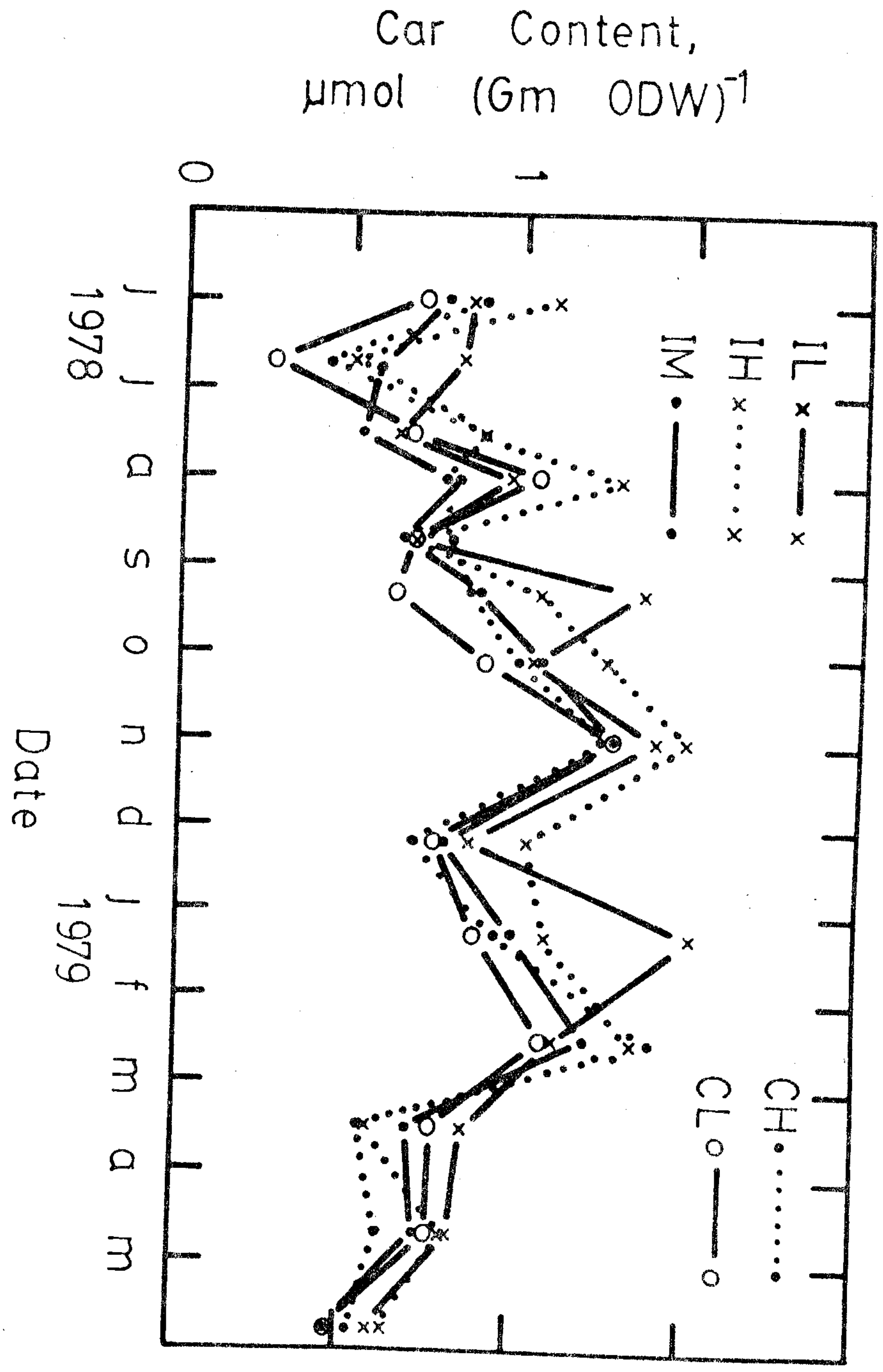

Car Content,
μmol (Gm ODW)-1
0
1
j
j
a
s
o
n
d
j
f
m
a
m
1978
1979
Date
IL
IH
IM
CH
CL

Table IV - 10.

Ranking of the light regimes and populations for Car content in 1978 new needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population		Light Regimes						
IH	=	Open		30 %		UVT		UVO
CL		30 %		Open		UVO	=	UVT
CH		UVT		Open		30 %		UVO
IL		UVO		Open	=	UVT	=	30 %
IM		Open	=	UVT		UVO		30 %
Mean		Open		UVT	=	30 %		UVO

B. SFU

Population		Light Regime										
IH	=	30 %		10 %		Open	=	UVO		UVT	=	UVA
IL		10 %		30 %		UVO		UVT		UVA		Open
CH		10 %		30 %		Open	=	UVT		UVA		UVO
IM	=	10 %		30 %		UVA		UVT	=	UVO	=	Open
CL		30 %		10 %		Open		UVO		UVA		UVT
Mean		10 %	=	30 %		Open	=	UVO		UVA		UVT

At SFU, Car decreased with increased light intensity (Table IV - 10B) when the PAR and UV plexiglass plots were examined separately. This confirms the findings of Lewandowska and Jarvis (1977). SFU grown populations had the greatest Car content and this is consistent with SRS having a more severe climate.

Populational differences between 1978 and 1977 new needles were the same at SRS and similar at SFU (Tables IV - 10 & 11) to those observed between the 1978 new and 1977 to 1979 needles (Tables IV - 9 & 10). Generally, the greater the altitude of origin, the greater the Car content. Light regime rankings for Car in 1977 new needles at SRS decreased with increased light intensity when the PAR and UV light regimes are viewed separately (Table IV - 11A). This had not been observed previously at SRS but had been at SFU for 1978 new needles (Table IV - 10B). Light regime rankings of 1977 new needles at SFU (Table IV - 11B) were the opposite of those observed for new needles at SRS (Table IV 11A) but the same as noted for 1977 to 1979 needles at SFU (Table IV - 9B).

Two year old 1977 needles at SRS and SFU have populational differences similar to those observed for 1977 to 1979 needles at both sites (Tables IV - 9 7 12). The relationship between 1977 two year old needles and 1978 new needles (Tables IV - 10 & 12) was similar to that described for 1977 to 1979 and 1978 new needles at both sites (Table IV - 9 & 10). Car were usually greater in populations from the highest altitudes. Light regime rankings of Car for 1977 two year old needles (Table IV - 12) were the same as for 1977 to 1979 and 1978 new needles at SRS (Tables IV - 9A & 10A) and

Table IV - 11.

Ranking of light regimes and populations for Car content in 1977 new needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes					
IH	60 %		UVO	=	Open		UVT
IL	UVO		60 %		Open	=	UVT
IM	UVO		60 %		Open	=	UVT
CL	60 %	=	UVO		UVT		Open
CH	60 %		UVO		Open		UVT
Mean	60 %	=	UVO		Open	=	UVT

B. SFU

Population	Light Regimes										
IL	Open	=	UVA		UVT		UVO		60 %		30 %
CH	Open	=	UVT	=	UVA		60 %		UVO		30 %
CL	Open		60 %	=	UVA		UVO		UVT	=	30 %
IH	UVA		UVT	=	Open		60 %	=	UVO		30 %
IM	Open		UVT		60 %	=	UVA		30 %		UVO
Mean	Open		UVA		UVT		60 %		UVO		30 %

Table IV - 12.

Ranking of light regimes and populations for Car content in 1977 two year old needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes			
IH	Open =	UVT	30 %	UVO
IL	UVT	UVO	Open =	30 %
CH =	UVO	Open =	UVT =	30 %
CL =	UVT	Open	UVO =	30 %
IM	Open	UVT =	UVO =	30 %
Mean	UVT =	Open	UVO	30 %

B. SFU

Population	Light Regimes					
IL	30 % =	UVA =	UVO =	10 %	Open	UVT
IH	10 %	Open	30 %	UVA	UVO	UVT
IM	30 %	UVA =	10 %	UVO =	Open	UVT
CH	UVA	10 %	UVT	Open	30 %	UVO
CL	10 %	Open =	30 % =	UVO	UVT =	UVA
Mean	10 %	30 % =	UVA	Open	UVO	UVT

for 1978 new needles at SFU (Table IV - 10B). At SRS, Car decreased with decreased light intensity while at SFU they decreased with increased light intensity. The number of observed primary features did not change for the seasonal trend between new and two year old needles but there were greater oscillations in the new needles (Figures IV - 7 to 9). There also was considerable switching in the rankings of the light regimes between needle age groups and sites. These data probably indicate that the degree of plasticity of Car content decreased with age, much like Chl a content.

The relationship between light intensity and pigment was reversed between the two sites. It decreased with decreased light intensity at SRS and with increased light intensity at SFU. There was no indication of a latitude-Car relationship but there was some indication of an altitude-Car correlation. The relationship appeared to be proportional (Bukharin, 1961; Garrett, 1969) not inversely proportional to altitude as suggested by Baldwin (1955) and Linder (1972). Much more data are required to establish this relationship.

Section 4: Photosynthetic Pigment Overview

The seasonal trends that have been described for Chl a (summer and winter minima with fall and spring maxima in new needles, and spring minimum with fall maximum in two year old needles) and Chl b (spring minimum with fall maximum for new and two year old needles, a gradual increase from the spring minimum was observed in two year old needles at SFU) were not due to the needles responding to the light conditions of the preceeding few days.

Hawkins et al. (1981) reported almost immediate Chl a and b increases in response to decreased bright sunshine hours. However, here, when maxima and minima were being approached, the pigment response to the light conditions was the opposite of what would have been predicted (compare sample day bright sunshine hours (Table III - 4 & 5) with the pigment trends (Figures IV - 1 to 9)). Therefore, the seasonal trends were actually occurring. Two maxima and minima in the annual Chl a and Chl b trend indicates that a disintegration of the thylakoid system is occurring during the cold season (Senser et al. 1975). If frost hardening was adequate, only one maximum and minimum would be observed. Two year old needles appear to have become less susceptible to temperature changes than new needles because the winter of 1978-1979 was much colder than the previous one (Table III - 1). It is difficult to correlate Car changes to bright sunshine hours because two different sub-groups of pigments, which have opposite responses to light (Burnett, 1976), were being observed as one. Likely, the Car trend is not due to the photosynthetic apparatus responding to the light conditions of the preceeding day or two, but is in fact an actual seasonal trend.

The decrease from the fall maximum in Chl a and Chl b could be due to decreased temperatures (Table III - 1), decreased day length (Table III -3), increased water stress (frozen ground or decreased precipitaton or any combination of them. Chl a and Chl b levels are known to decrease with:

(1) increased water stress (Alberte and Thornber, 1977; Beadle and Jarvis, 1977; Bengtson et al. 1978);

(2) decreased day length (Gerold, 1959; Hellergren, 1981; Linder,

1972); and

(3) decreased temperature (Alberda, 1969; Godnev and Hodasevic, 1965; Hellergren, 1981; Linder, 1972).

The Car trend lags behind the Chl trends and Robertson et al. (1966) suggested Chl concentrations will not increase above that level which can be protected by the Car. The shape of the Car trend curve would be similar to the Chl trend curve but would lag behind it in order to protect the Chl. Car also decrease in response to decreased day lengths (Hellergren, 1981), temperatures (Hellergren, 1981) and possibly even to water stress. The decrease in Chl a from the spring maximum in those needle age groups which had two maxima and minima, occurred in response to increased temperatures and solar radiation (Brett and Singer, 1973).

The increase in Chl a from both the summer and winter minima, if applicable, and in Chl b from the spring minimum likely occurred for similar reasons. The days begin to shorten in June, the cummulative radiation flux is decreased, and pigment content increases in response to shortened day length (Brett and Singer, 1973; Senser et al. 1975). Even though increased temperatures should decrease the Chl a and b levels the shortened day length apparently overrides this. As the fall maximum was approached, both day length and temperature were decreasing but not to sub-optimal levels, and the maximum value occurred. The spring increase indicated that the thylakoids were being functionally re-established, possibly in response to increased positive temperature and optimal levels of radiation (Senser et al. 1975). If Car pigments are present to protect Chl from photodestruction (Krinsky, 1968) and the level of Chl cannot rise above that which the Car can protect then the seasonal Car trend should be the same as the Chl trends but lag behind them. Unfortunately, the responses of Car pigments to specific environmental parameters are still not clearly defined.

For all three pigments, two year old needles had a greater pigment content than new needles, confirming the observations of Linder (1972) and Ollykainen (1967) but contradicting Kaloudin and Kaloudin's (1967) observation for Car. Two year old needles probably have the greatest pigment content because they are less susceptible to extremes in environmental parameters. This allows a higher pigment level to be maintained year round to optimize photosynthetic capacity.

Populations grown at SFU had greater pigment contents than those grown at SRS. This is because of the moderating coastal climate at SFU, probably the decreased temperature range and increased precipitation are mainly responsible for this.

The phenomenon of increased pigments with increased altitude of the seed source was in agreement with the observation of Garrett (1969) but was opposed to Baldwin (1955) and Linder's (1972) reports. However, Chl <u>a</u> and <u>b</u> did increase with decreased altitude of the seed source in 1978 new needles at SRS. The high degree of variability in this response as reported in the literature and here, indicates that this is a very complex relationship with many interacting factors. Increased pigment with increased altitude of the seed source indicates that these populations have a high capacity for pigment synthesis. As photo-destruction of pigments increases with altitude (Caldwell, 1971), higher altitude populations may require increased levels of pigment production to overcome the increased potential of pigment photo-destruction.

There appeared to be a negative correlation between Chl a and the latitude of the seed source. This is probable because in tree species with a long north-south range latitudinal ecotypes occur (Malcolm and Pymar, 1975). However, the interaction between latitude and altitude can obscure any latitudinal differentiation that occurs (Mergen et al. 1974) and this could be happening in this study.

Chl a and b decreased with increased light intensity and this confirms the observations of Brett and Singer (1973), Bourdeau and Laverick (1958), Jarvis (1964), Lewandowska et al. (1977) and Logan and Krotkov (1969). This may have happened because increased light intensity can cause photo-destruction of the pigments while decreased light intensity can result in increased Chl content, which increases the light gathering capacity in plants (Boardman, 1977). Therefore, increased light intensity probably results in lower Chl concentrations.

Car decreased with decreased light intensity at SRS and SFU for 1977 to 1979 needles and at SRS for 1978 new needles, while they increased with decreased light intensity at SFU for 1978 new needles. The latter result has been reported previously by Lewandowska and Jarvis (1977). Decreased Car with decreased light intensity, suggests the Car are primarly serving in a protective role rather than in an accessory role to the Chl pigments.

If they had been serving in an accessory role they would have increased with decreased light intensity or increased with decreased altitude of the seed source. Car values for SFU 1978 new needles indicate that they are serving in an accessory role. These observations do not invalidate the Robertson et al. (1966) hypothesis that Chl levels cannot rise above that level which can be protected by Car because two different Car sub-groups with opposing responses to light are being viewed as one group. The different responses of Car in 1978 new needles to light intensity is not contradictory, as it first appears to be. Because of extreme temperatures, reduced precipitation, and summer irradiance encountered at SRS, the photosynthetic apparatus is under a great deal of stress and it requires photo-protection, while at SFU the environment is less stressful and Car primarily serve in an accessory role. After the trees have become established at SFU, they are over their stress period and the photosynthetic apparatus increases its light gathering capacity.

Even though the environment plays a large role in altering the various physiological responses of conifers (Mergen et al. 1974), the pigment responses were not as plastic as was initially thought because of the high degree of similarity between the seasonal trends at both sites. The photosynthetic apparatus responses appeared to be contained within certain limits and the range of these responses decreased with increased needle age. Car appear to be more in tune to environmental cues than the Chl. This is not so, because we are observing the responses of the protective and accessory Car groups to different environmental cues, and not one group giving two different responses to a similar set of environmental cues.

Section 5: Pigment Ratios

Only Chl a/b and total Chl/Car ratios are considered because Hawkins et al (1981) have demonstrated them to be the important ratios when examining change over time.

Section 6: Chlorophyll a / Chlorophyll b Ratio

Chl a/b ratios ranged from 1.01 to 3.80 at SRS and from 1.01 to 3.82 at SFU for 1977 to 1979 needles. At SRS, it decreased into July from the newly flushed needles, increased in August, decreased to October 1977, gradually increased to a May 1978 maximum, gradually decreased until April 1979 and increased in late May (Figure IV - 10A). It decreased into July 1977 from the newly flushed needles, increased in August, gradually declined until February 1978, increased to a maximum in July and decreased until late May 1979 at SFU (Figure IV - 10B).

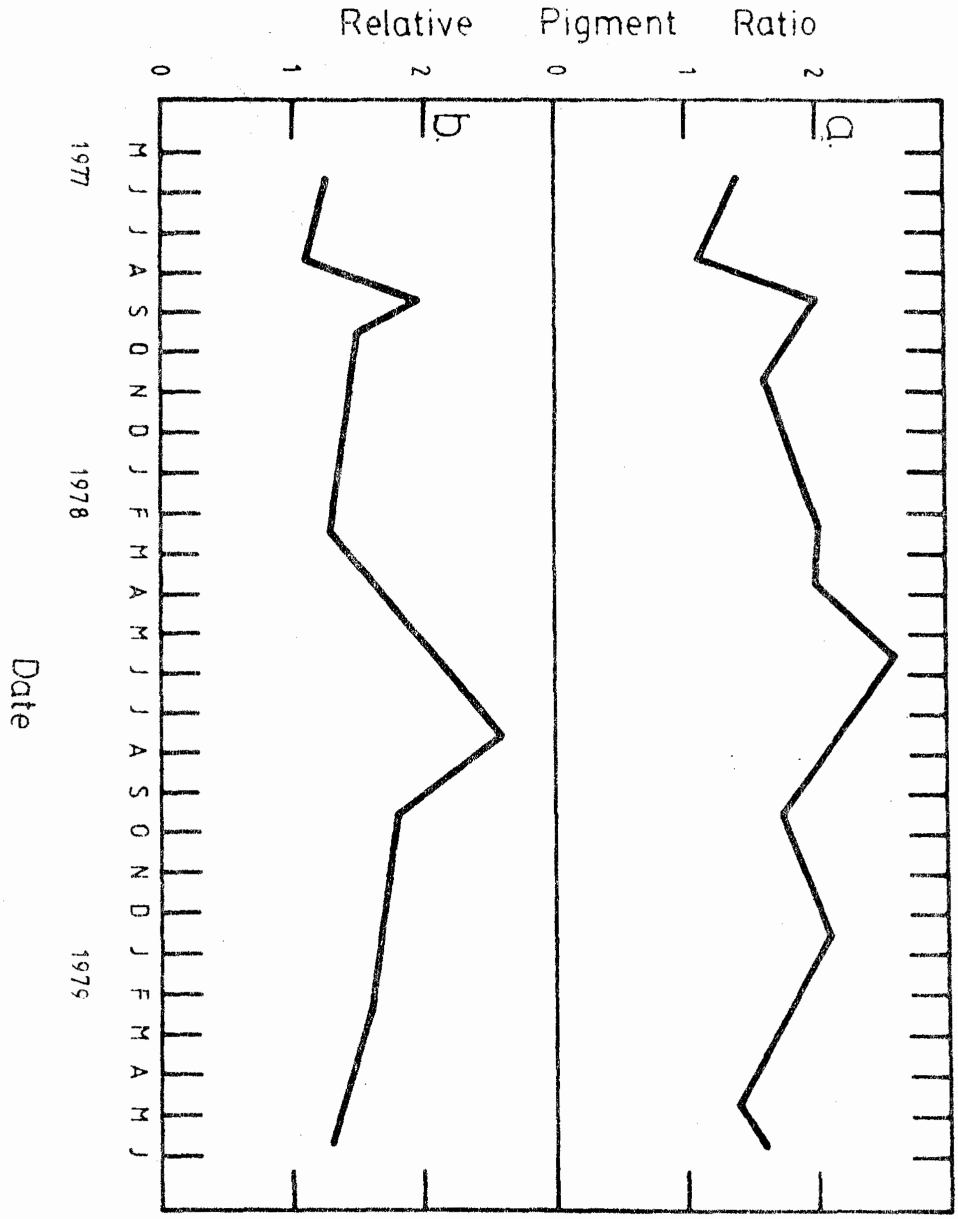
Chl a/b ratios were very similar between SRS and SFU, new needles had two maxima and minima and two year old needles had one maximum and minimum (Figure IV - 10). The two maxima and minima seasonal response has been reported by Senser et al. (1975) for new, two and three year old needles, while the maximum-minimum trend has been reported by Hellergren (1981). Lewandowska and Jarvis (1977) reported a rise in the ratio during the winter while Koch (1976) observed that the ratio did not change with the age of the needle.

Figure IV - 10

A representative example of the seasonal trend for Chl *a*/*b* ratios in 1977 to 1979 needles. The mean of the five populations under a light regime is presented. Abbreviations as in text.

A. SRS, Open light regime.

B. SFU, UVO light regime.


Relative Pigment Ratio
0
1
2
0
1
2
a.
b.
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1977
1978
1979
Date

Chl *a/b* ratios were about the same between 1977 new and two year old needles at SRS, while at SFU, the two year old needles had the highest ratio. This is consistent with the two year old needles having the greatest content, providing the relative increase was greater in Chl *a* than Chl *b*. The ratio generally decreased with decreasing altitude of the seed source (Table IV - 13). This was consistent with the individual pigment results providing Chl *a* decreased at a faster relative rate with altitude than Chl *b*. Chl *a/b* ratios decreased with decreased light intensity at both sites when the PAR and UV plexiglass plots were examined separately (Table IV - 13). The unusual ranking of the SFU 60 (30) % light regime cannot be explained. Decreased Chl *a/b* ratios in gymnosperms indicate the addition of LHCP to the PS II and I reaction centers and an increased size in the PSU (Alberte and Thornber, 1977). Decreased ratios with decreased light intensity confirms the observations of Alberte et al. (1976), Lewandowska and Jarvis (1977, 1978) and Wild (1979). Vu et al. (1981) reported decreased Chl *a/b* ratios with increased UV radiation and Tyszkiewicz et al. (1979) reported decreased ratios with increased levels of blue light. This could have some role in the displacement of the UVT light regime at SFU. SFU populations had larger ratios, as they had for individual pigment content, indicating a greater relative increase of Chl *a* to Chl *b* at SFU.

Chl *a/b* ratios ranged from 1.08 to 2.91 at SRS and from 1.11 to 3.43 at SFU for 1978 new needles. It decreased from the spring flush through a June-July 1978 minimum, increased in August, decreased through November, increased until January 1979, decreased into April and increased in late May at SRS (Figure IV - 11A). At SFU, it decreased with some oscillation

Table IV - 13.

Ranking of light regimes and populations for Chl a/b ratios in 1977 to 1979 needles. Abbreviations as in text. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally.

A. SRS

Population				
IH =	UVT	Open =	60 %	UVO
IL	UVT	UVO	60 %	Open
IM	Open	UVT =	60 %	UVO
CL =	60 %	UVT	Open	UVO
CH	Open =	UVO	UVT	60 %
Mean	UVT	Open =	60 %	UVO

B. SFU

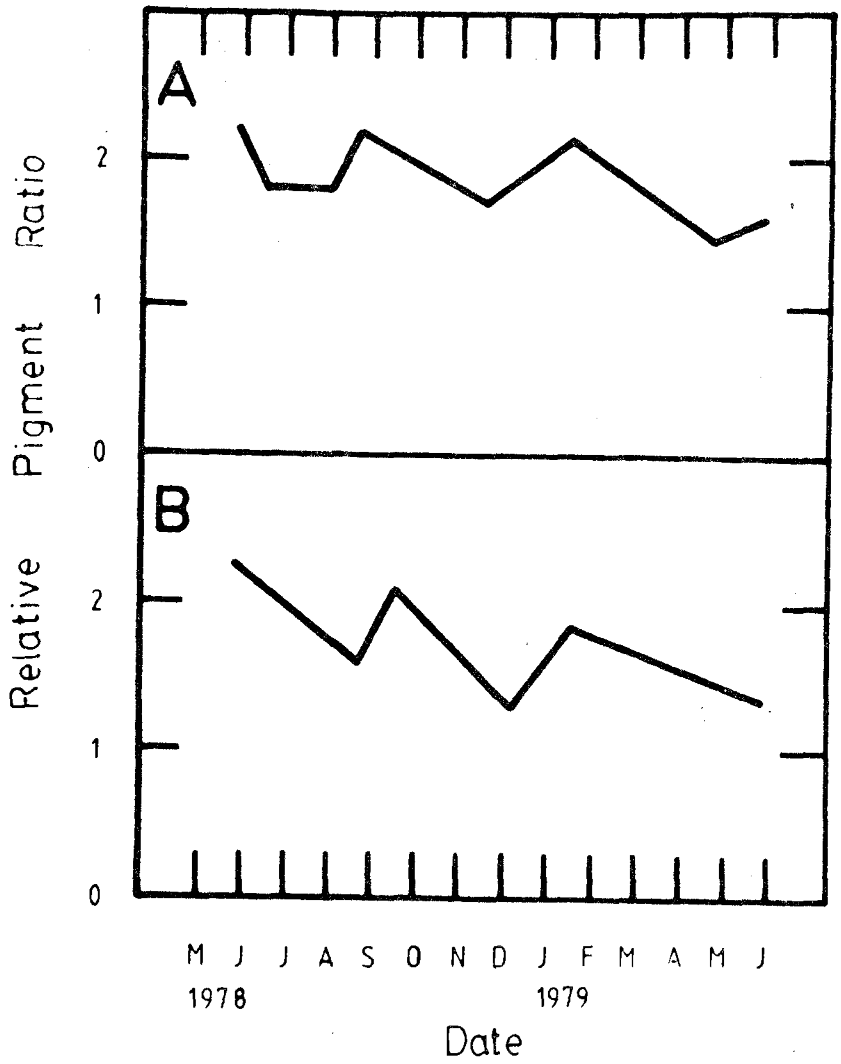
Population	Light Regimes					
IH =	Open =	UVA =	60 %	UVO	UVT	30 %
IL =	60 %	Open	UVA	UVT =	UVO	30 %
IM	60 % =	UVA	Open	UVT	30 %	UVO
CH	60 % =	Open =	UVA	UVT	UVO	30 %
CL	Open	60 %	UVA	UVT	30 %	UVO
Mean	60 % =	Open	UVA	UVT	UVO	30 %

Figure IV - 11

A representative example of the seasonal trend for Chl a/b ratios in 1978 new needles. The mean of the five populations under a light regime is presented. Abbreviations as in text.

A. SRS, Open light regime.

B. SFU, UVA light regime.


A
B
Relative Pigment Ratio
2
1
0
2
1
0
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1978
1979
Date

into August 1978 from the newly flushed needles, increased in September, decreased into December, increased in January 1979, and gradually declined untill late May (Figure IV - 11B).

The overall Chl a/b ratio trend for 1978 new needles was quite similar at both sites and to that described for the 1977 to 1979 needles (Figure IV 10 & 11).

The Chl a/b ratio was highest in the IH population at both sites and lowest in the CH population at SRS and the CL population at SFU for 1978 new needles (Table IV - 14). Again, there was a trend of decreased ratio with decreased altitude of the seed source. Chl a/b ratios decreased with decreased light intensity at both sites, as they had for the 1977 to 1979 needles (Tables IV - 13 & 14). There was a displacement of UVT and UVA ranking but these could be due to decreased ratios associated with increased shorter wavelength radiation (Vu et al. 1981; Tyszkiewicz et al. 1979). Again, Chl a/b ratios were greatest in the SFU populations.

Population rankings of 1977 new needles were almost identical to those of the 1978 new needles (Tables IV - 14 & 15). As occurred in the 1977 to 1979 and 1978 new needles at both sites, Chl a/b ratios decreased with decreased altitude of the seed source and light intensity in 1977 new needles (Tables IV - 13 to 15). There also was a displacement of the UVT populations at SFU (Table IV - 15B). Again, the unusual ranking of SFU 60 (30) % cannot be explained.

Table IV - 14

Ranking of light regimes and populations for Chl *a/b* ratios in 1978 new needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes			
IH	UVT =	UVO	30 % =	Open
IL	UVO	UVT	30 %	Open
CL =	Open	UVT	UVO	30 %
IM	UVT =	UVO	Open	30 %
CH	Open	UVT	UVO	30 %
Mean	UVT =	UVO	Open	30 %

B. SFU

Population	Light Regime					
IH	UVO	Open	30 %	UVT	10 %	UVA
IL =	30 %	Open	UVO	10 %	UVT	UVA
IM	Open	UVO	30 % =	10 % =	UVA	UVT
CH =	30 %	Open	10 % =	UVT	UVO	UVA
CL	Open =	UVO	30 %	UVT	UVA	10 %
Mean	Open	30 % =	UVO	10 %	UVT	UVA

Table IV - 15

Ranking of light regimes and populations for Chl a/b ratios in 1977 new needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population		Light Regimes						
IL	=	UVT	=	60 %		UVO		Open
IH		UVT		60 %		UVO	=	Open
IM		60 %		Open		UVT		UVO
CH	=	Open	=	UVO		UVT	=	60 %
CL		60 %	=	UVT		UVO	=	Open
Mean		60 %	=	UVT		Open	=	UVO

B. SFU

Population		Light Regimes										
IH		Open		UVA	=	UVO	=	60 %		UVT		30 %
IL	=	60 %		Open		UVA		UVT	=	30 %	=	UVO
IM		Open		UVA		60 %		UVO	=	30 %		UVT
CH		Open		UVA		60 %		UVO		UVT		30 %
CL		Open		60 %		UVA		UVT		UVO	=	30 %
Mean		Open		60 %	=	UVA		UVO		UVT		30 %

Two year old 1977 needles at both sites had similar populational and light regime rankings and relationships to all the other needle age groups previously examined for Chl *a/b* ratios (Tables IV - 13 to 16). There was no UVT population displacement at SFU but there was the unexplainable high ranking of the SFU 30 (60) % light regime populations.

The reduction in the number of maxima and minima in the Chl *a/b* ratio between new and two year old needles (Figures IV - 10 & 11) probably indicates that the degree of plasticity of this response decreased with increased needle age. Generally, Chl *a/b* ratios decreased with decreased altitude of the seed source and light intensity. These observations are:

(1) consistent with the individual pigment data;

(2) indirectly confirms Garrett's (1969) observation of increased pigment content with increased altitude and the observation of increased pigment content with decreased light intensity (Lewandowska et al. 1977); and

(3) directly confirms the previously reported responses of conifer Chl *a/b* ratios to light intensity (Alberte and Thornber, 1977; Wild, 1979).

Section 7: Total Chlorophyll / Carotenoid Ratio

Chl/Car ratios ranged from 0.95 to 4.72 at SRS and from 0.85 to 10.04 at SFU for 1979 needles. At SRS, it decreased from the spring flush until March 1978, increased to a September maximum, decreased to December, increased gradually to April 1979 and increased markedly in late May

Table IV - 16.

Ranking of light regimes and populations for Chl a/b ratios in 1977 two year old needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population		Light Regimes						
IH	=	Open		UVT	=	30 %		UVO
IL		UVT		UVO		Open	=	30 %
IM		Open	=	UVT		UVO	=	30 %
CH	≠	Open	=	UVT	=	UVO		30 %
CL		Open		30 %	=	UVT	=	UVO
Mean		Open	=	UVT		UVO		30 %

B. SFU

Population		Light Regimes										
IL		30		UVO	=	UVT	=	UVA		Open		10 %
IM	=	30 %	=	UVT		UVA		10 %	=	Open		UVO
CH	=	UVT		30 %		UVA		Open	=	UVO		10 %
IH		30 %	=	UVA		Open	=	UVO		UVT		10 %
CL		Open		UVT	=	30 %		UVA	=	10 %		UVO
Mean		30 %		UVT		UVA		Open		UVO		10%

(Figure IV - 12A). It decreased from the newly flushed needles until August 1977, increased in September, decreased to February 1978, increased to September, decreased to December, increased gradually until April 1979 and increased markedly in late May at SFU (Figure IV - 12B).

Chl/Car trends for 1977 to 1979 needles were similar at both sites, summer minimum, fall maximum, spring minimum, fall maximum, early spring minimum (Figure IV - 12). Similar Chl/Car trends have been reported by Hellergren (1981), Lakhanov (1978) and Linder (1972).

Chl/Car ratios were greater in 1977 two year old than in 1977 new needles at both sites.This is consistent with the two year old needles having greater pigment contents provided the relative increase of Chl was greater than that of Car. The ratio decreased with decreased altitude of the seed source at both sites (Table IV - 17). Again, this is consistent with the individual pigment data. The Chl/Car ratio decreased with increased light intensity for 1977 to 1979 needles at SRS and SFU when the PAR and UV plexiglass plots were examined separately (Table IV - 17). The changes in the ratio probably indicate that the Car are serving a protective function because Chl content decreased with increased light intensity, while the Car level increased. If the Car role had been as an accessory pigment the Chl/Car ratio would have increased with increased light intensity. As with the individual pigments, SFU populations had larger ratios than SRS ones, indicating there was a greater relative increase of Chl to Car at SFU and that the protective role of the Car was not as important at SFU.

Figure IV - 12

A representative example of the seasonal trend for Chl/Car ratios in 1977 to 1979 needles. The mean of the five populations under a light regime is presented.

Abbreviations as in text.

A. SRS, Open light regime.

B. SFU, UVT light regime.

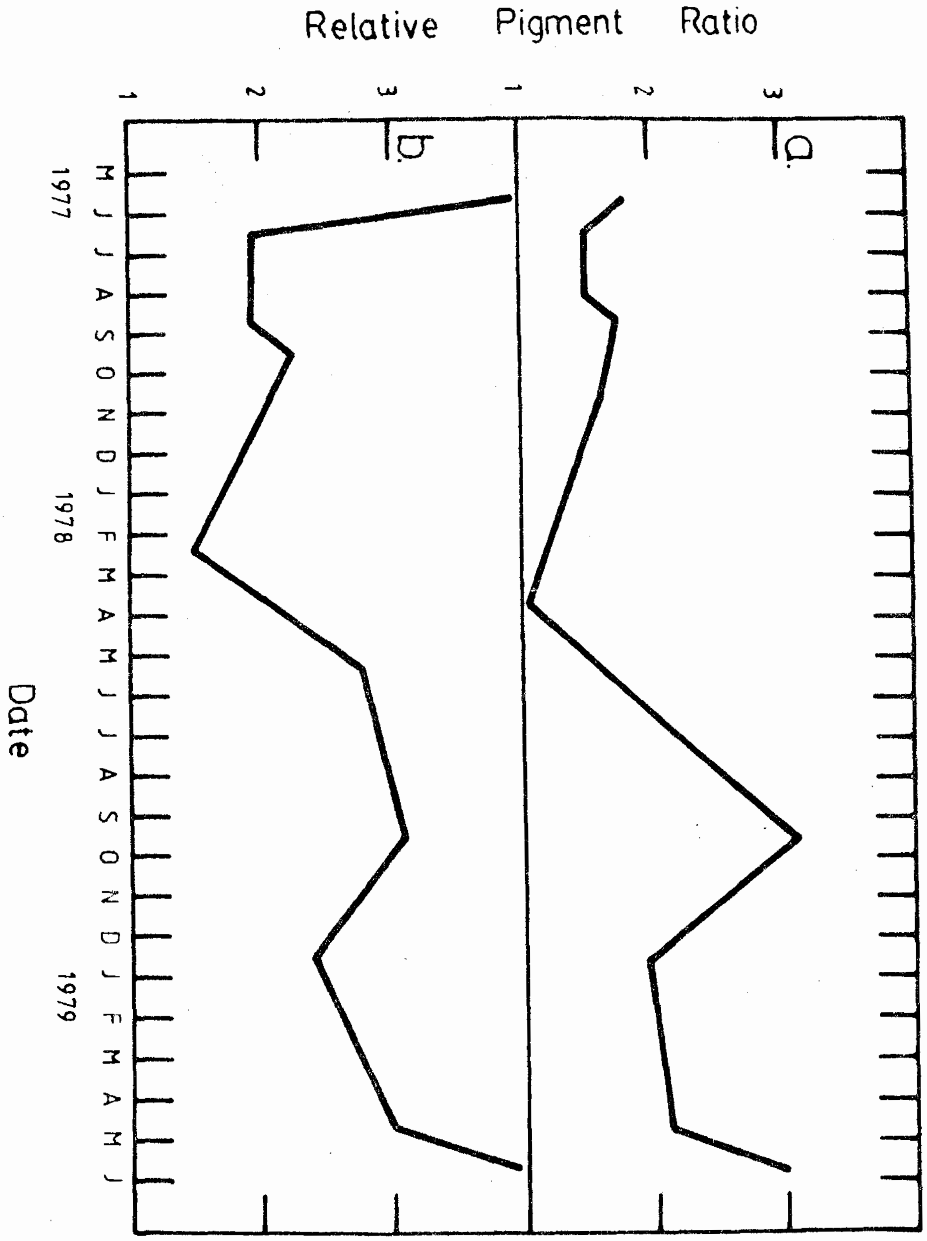

Relative Pigment Ratio
a.
b.
1
2
3
1
2
3
M J J A S O N D J F M A M J J A S O N D J F M A M J
1977
1978
1979
Date

Table IV - 17.

Ranking of light regimes and populations for Chl/Car ratios in 1977 to 1979 needles. Populations and light regimes are listed in descending order or ranking unless idicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes			
IM	60 %	UVO	UVT	Open
IL	60 %	UVO	UVT	Open
IH	60 %	UVO	UVT	Open
CH =	60 %	UVO	UVT	Open
CL	60 %	UVO	UVT	Open
Mean	60 %	UVO	UVT	Open

B. SFU

Population	Light Regimes					
IH =	30 %	60 % =	UVO	UVT	UVA	Open
IL	30 %	60 % =	UVO =	UVT	UVA	Open
IM	30 %	UVO	60 %	UVT	UVA	Open
CL =	30 %	UVO =	60 %	UVT	UVA	Open
CH	30 %	60 %	UVT	UVA =	UVO	Open
Mean	30 %	60 % =	UVO	UVT	UVA	Open

Chl/Car ratios ranged from 1.47 to 5.67 at SRS and from 1.53 to 7.02 at SFU for 1978 new needles. At SRS, it increased from the spring flush to an early July 1978 maximum, decreased in early August, increased in September, decreased rapidly to November, stabilized until January 1979, increased in February, decreased to April and increased in late May (Figure IV - 13A). At SFU, it increased to June 1978 from the newly flushed needles, decreased in July, increased in late August, gradually decreased with some oscillation to January 1979 and increased gradually with oscillations to late May (Figure IV - 13B).

Chl/Car seasonal trends were similar between the two sites for 1978 new needles (Figure IV - 13) and were similar to the trends discussed for the 1977 to 1979 needles (Figures IV - 12 & 13). The trend was for decreased ratios with increased altitude of the seed source, the opposite result to that reported for 1977 to 1979 needles. Chl/Car ratios decreased with increased light intensity at SRS and for the PAR plots at SFU but they increased for the UV plexiglas plot populations at SFU (Table IV - 18). The decreased ratio with decreased light intensity for the UV plot populations could have occurred because shorter wavelength radiation alters the Chl a and b contents which results in changed ratios (Tyszkiewicz et al. 1979; Vu et al. 1981). Again, Chl/Car ratios were greatest in the SFU populations.

Population rankings for 1977 new needles at both sites (Table IV - 19) were identical to the 1977 to 1979 needle rankings and essentially the opposite of the 1978 new needle rankings (Tables IV - 17 & 18). Chl/Car

Figure IV - 13

A representative example of the seasonal trend for Chl/Car ratios in 1978 new needles. The mean of the five populations under a light regime is presented. Abbreviations as in text.

A. SRS, UVT light regime.

B. SFU, UVO light regime.

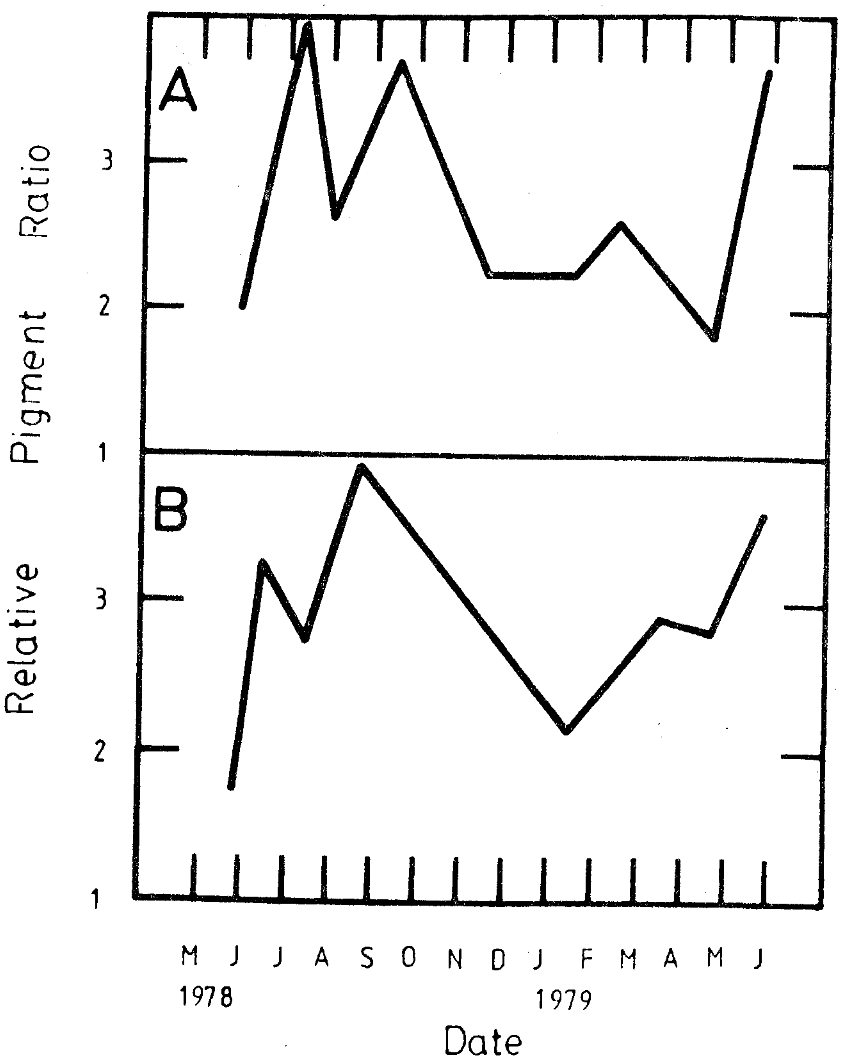

A
B
Relative Pigment Ratio
3
2
1
3
2
1
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1978
1979
Date

Table IV - 18.

Ranking of light regimes and populations for Chl/Car ratios in 1978 new needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population		Light Regimes				
CH		30 %	UVT		UVO Open	
IM	=	30 %	UVO	=	UVT	Open
CL	=	30 %	UVO		UVT	Open
IL	=	30 %	UVO		UVT	Open
IH		30 %	UVO		UVT	Open
Mean		30 %	UVO		UVT	Open

B. SFU

Population		Light Regimes								
CH	=	10 %	UVT		30 %		UVA	=	UVO	Open
IM		10 %	30 %		UVT	=	UVA		UVO	Open
IL	=	10 %	30 %		UVO		UVT		UVA	Open
CL		10 %	UVA		30 %		UVT		UVO	Open
IH		10 %	UVT	=	UVA		UVO	=	30 %	Open
Mean		10 %	30 %	=	UVT	=	UVA		UVO	Open

Table IV - 19.

Ranking of light regimes and populations for Chl/Car ratios in 1977 new needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population		Light Regimes					
IL	=	60 %		UVO	UVT	=	Open
IM		60 %		UVO	UVT		Open
IH		60 %		UVO	UVT	=	Open
CH	=	60 %		UVO	UVT		Open
CL		60 %	=	UVO	UVT		Open
Mean		60 %		UVO	UVT		Open

B. SFU

Population		Light Regimes							
IL		30 %	60 %		UVT	UVO		UVA	Open
IH	=	30 %	UVO		60 %	UVT	=	UVA	Open
IM	=	30 %	UVO		60 %	UVT		UVA	Open
CH		30 %	60 %		UVT	UVO	=	UVA	Open
CL		30 %	UVO		60 %	UVT		UVA	Open
Mean		30 %	60 %	=	UVO	UVT		UVA	Open

ratios decreased with increased light intensity at both sites for 1977 new needles as they had for 1977 to 1979 and 1978 new needles (Tables IV - 17 to 19). This indicates the probable role of the Car was as a protective pigment.

Two year old 1977 needles had similar populational rankings at both sites and to all other needle age groups except for the 1978 new needles (Tables IV - 17 to 20). Chl/Car ratios decreased with increased light intensity for 1977 two year old needles at both sites as they had for all the other needle age groups (Tables IV - 17 to 20). This indicates that the primary role of the Car is to protect the photosynthetic pigments rather than to assist in increasing the light gathering capacity.

The degree of similarity was high between new and two year old needles for Chl/Car ratios but the degree of oscillation was greatest in the new needles. This indicates that the Chl/Car ratio response decreases with increased needle age. Once the seedlings have become re-established the role of the Car appears to be protective at SRS and accessory at SFU. Car levels appear to increase at a faster rate than the Chl levels in response to seed source elevation, while Car levels increased and Chl levels decreased with increased light intensities. These data:

(1) directly and indirectly confirm Garrett's (1969) observation of the pigment content being proportional to the altitude of the seed origin;

(2) do not confirm Lewandowska and Jarvis' (1977) observation of decreased Car with increased light intensity; and

Table IV - 20.

Ranking of light regimes and populations for Chl/Car ratios in 1977 two year old needles. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

A. SRS

Population	Light Regimes					
IM	30 %		UVO	=	UVT	Open
IL =	30 %		UVO		UVT	Open
CH	30 %	=	UVT		UVO	Open
IH	30 %		UVO		UVT	Open
CL	30 %		UVO		UVT	Open
Mean	30 %		UVO		UVT	Open

B. SFU

Population	Light Regimes									
IH =	10 %		30 %		UVT	=	UVO		UVA	Open
IM	10 %		UVO		UVT		30 %		UVA	Open
CL =	30 %	=	UVO		10 %	=	UVA		UVT	Open
IL	10 %		UVO		30 %	=	UVT		UVA	Open
CH	10 %		30 %		UVA	=	UVT	=	UVO	Open
Mean	10 %		30 %	=	UVO		UVT		UVA	Open

(3) confirm the previously discussed Chl response of increased pigment levels with decreased light intensity.

Section 8: Photosynthetic Pigment Ratio Overview

The Chl a/b and Chl/Car ratios (Figures IV - 10 to 13) showed more oscillation than any of the individual pigment trends (IV - 1 to 9) because two and three parameters are being examined simultaneously. As the ratios are composed of individual pigment responses, their periods of up, down, and stabilization occur for the same reasons as outlined for the individual pigments (Section IV: 4). From previous experiments, the ratio trends can be correlated to changes in the structure and/or function of the photosynthetic membrane to provide an idirect view of the internal system. For instance in gymnosperms, increased Chl a/b ratios indicate a loss of the LHCP and a decreased PSU size (Alberte and Thornber, 1977) and this results in reduced light absorption or gathering capacity. This is because the photosynthetic apparatus is now high in PS I characteristics and low in PS II properties. A decreased ratio would indicate the opposite.

Unfortunately, such information is not extant for Chl/Car ratios. When examining these ratios, if Car are being reported as a group rather than individually, it is difficult to correlate ratio changes to the occurrence of specific phenomena. However, if Chl/Car ratios decrease and the Chl a/b ratio increases, likely there is an increase in the protective carotene pigments and a decrease in the photosynthetic accessory xanthophyll pigments. If the Chl/Car ratio decreased along with the Chl a/b ratio, likely there is an increase in the accessory and a decrease in the protective Car because energy transfer from the xanthophylls is facilitated by Chl b (Thorne and Boardman,1971). The data obtained for Chl a/b and Chl/Car ratios (Tables IV - 13 to 20) appear to support these hypotheses. Therefore, an indirect inference can be made as to which Car pigment subgroup is changing in response to a certain environmental parameter or parameters.

The high degree of similarity for both ratios over the various needle age groups occurred because of the high degree of similarity between the various seasonal pigment trends.

CHAPTER V

FLUORESCENCE INDUCTION AND
CO_2 GAS EXCHANGE
RESULTS AND DISCUSSION

Section 1: Fluorescence Induction

Only the F_V results from SRS are presented because this data clearly illustrates the seasonal trends, whereas, the SFU data illustrates the same trends but not to such a degree. Problems in initiating this new methodology were found and the first F_V curves done with any degree of confidence was in December 1977 at SRS. A sample F_V curve with nomenclature and interpretation are shown in Figure V - 1.

Trends for the winter-spring period were very similar between 1977 and 1978 new needles for the heights of, times to, and duration of the various F_V curve features (Figures V - 2 to 7). When features that did not occur in the second winter were accounted for, the trends for the two winter-springs are virtually identical.

The rapid fall-winter decline of P along with a slower decline of ID (Figure V -5, Sept. - Dec.) indicate that an alteration is occurring on the electron donor side of PS II or at its reaction center (Klosson and Krause, 1981b; Schreiber et al. 1978). As P continued to decline and ID remained relatively constant, ID was rising in relation to P, an inhibition of or

Figure V - 1

Representative F_V curve for conifer needles (after Hawkins et al. 1981). Curve nomenclature and interpretation after Papageorgiou (1975):

O = initial fluorescence level, indicator of the amount of Chl present;

O to I = Q oxidized;

I to D = reduction of Q;

D to P = oxidation of electron transport intermediates;

P to S = reduction of the intermediates by PS I and beyond;

S to M to T = membrane conformational changes.

One second on the figure is zero seconds in time.

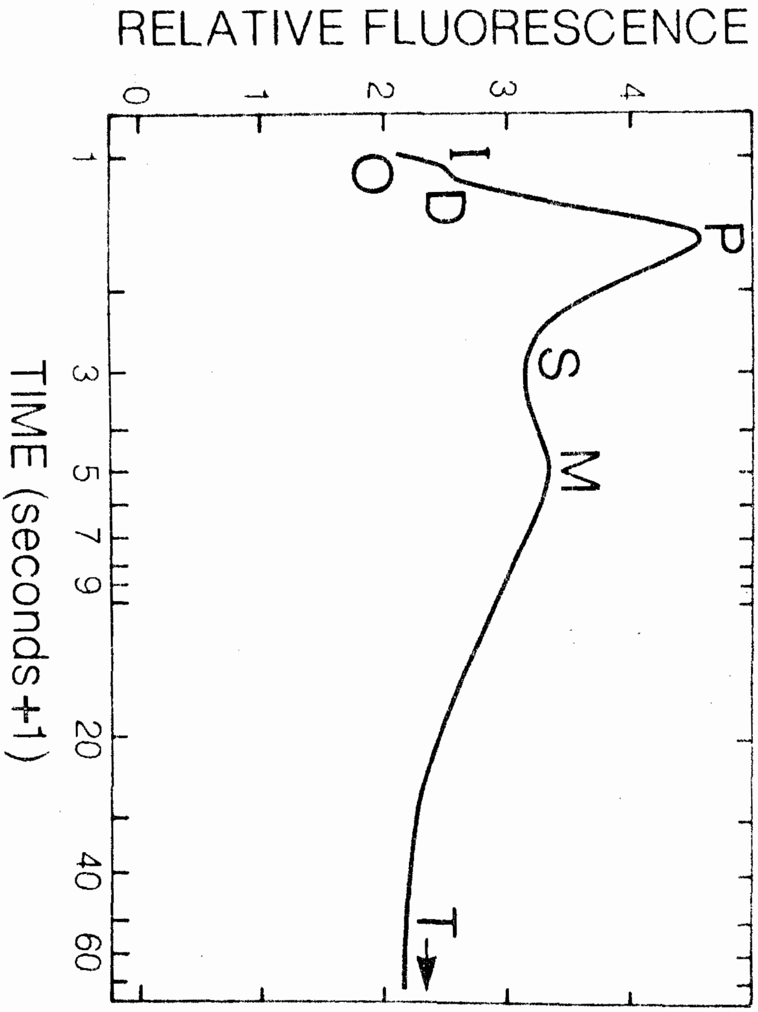

RELATIVE FLUORESCENCE
0
1
2
3
4
TIME (seconds+1)
1
3
5
7
9
20
40
60
O
I
D
P
S
M
T

Figure V - 2

Mean corrected heights (corrected height = feature height - 0 level height) of selected F_V features in 1977 new needles at SRS. Mean is of all five populations under each light regime.

A, Open; B, 60 (30) %; C, UVT; and D, UVO light regimes.

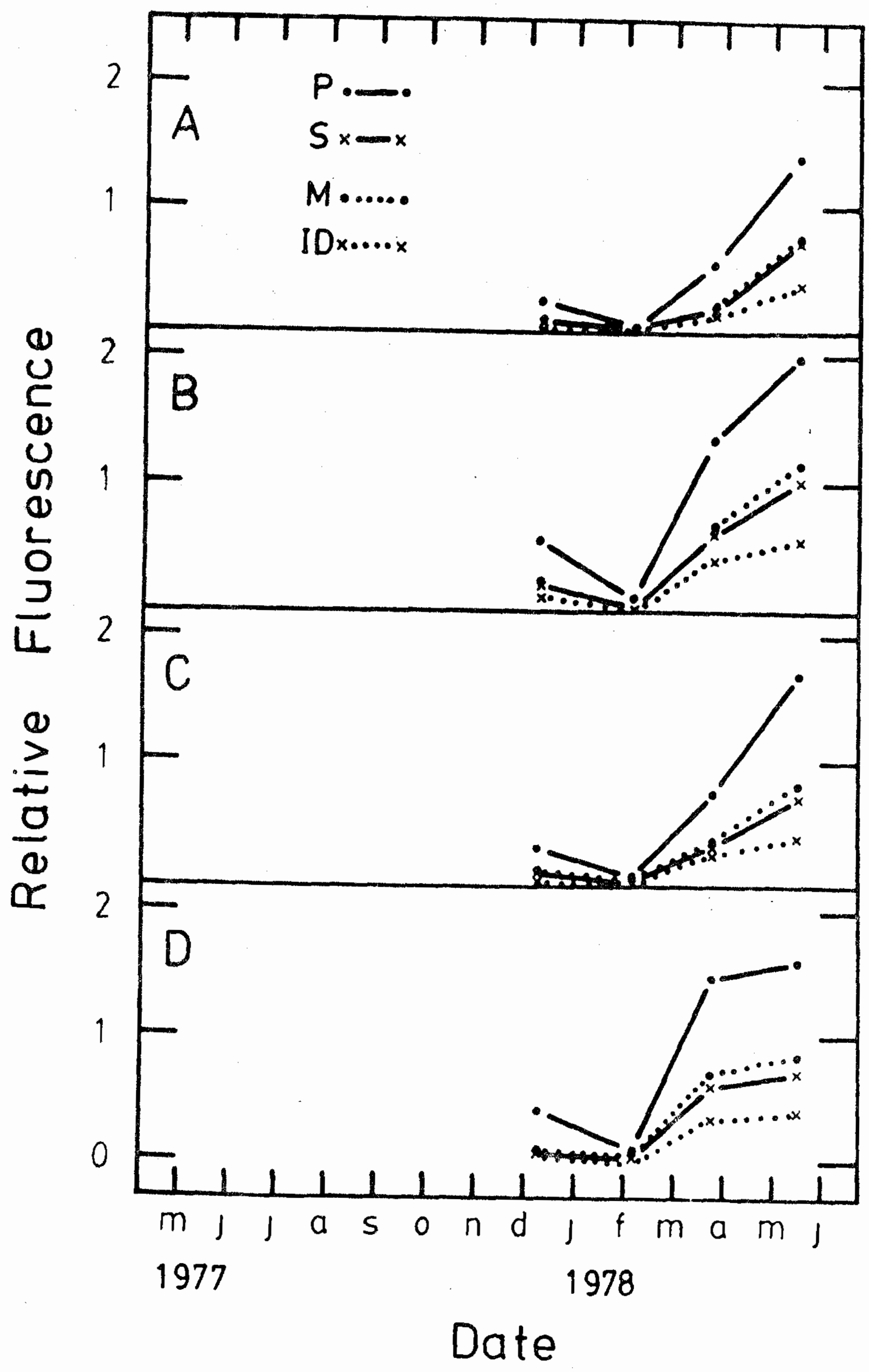

Relative Fluorescence
A
B
C
D
P •—•
S ×—×
M •·····•
ID ×·····×
2
1
0
m
j
j
a
s
o
n
d
j
f
m
a
m
j
1977
1978
Date

Figure V - 3

Mean time to P and time to and duration of ID in 1977 new needles at SRS. Mean is of all five populations under each light regime.

A, Open; B, 60 (30) %; C, UVT; and D, UVO light regimes.

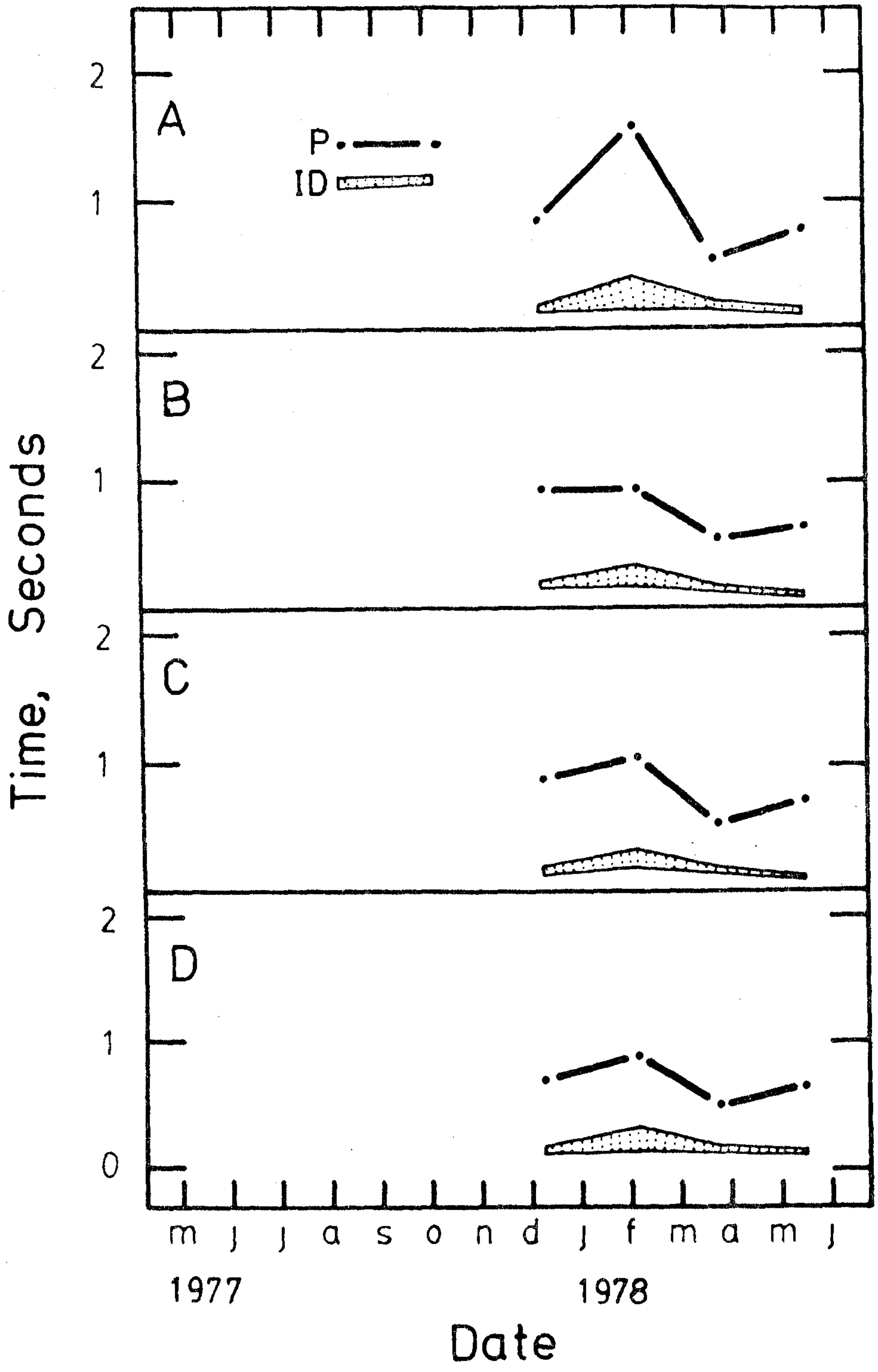

A
B
C
D
P
ID
2
1
0
Time, Seconds
m
j
j
a
s
o
n
d
j
f
m
a
m
j
1977
1978
Date

Figure V - 4

Mean times to S and M in 1977 new needles at SRS. Mean is of all five populations under each light regime.

A, Open; B, 60 (30) %; C, UVT; and D, UVO light regimes.

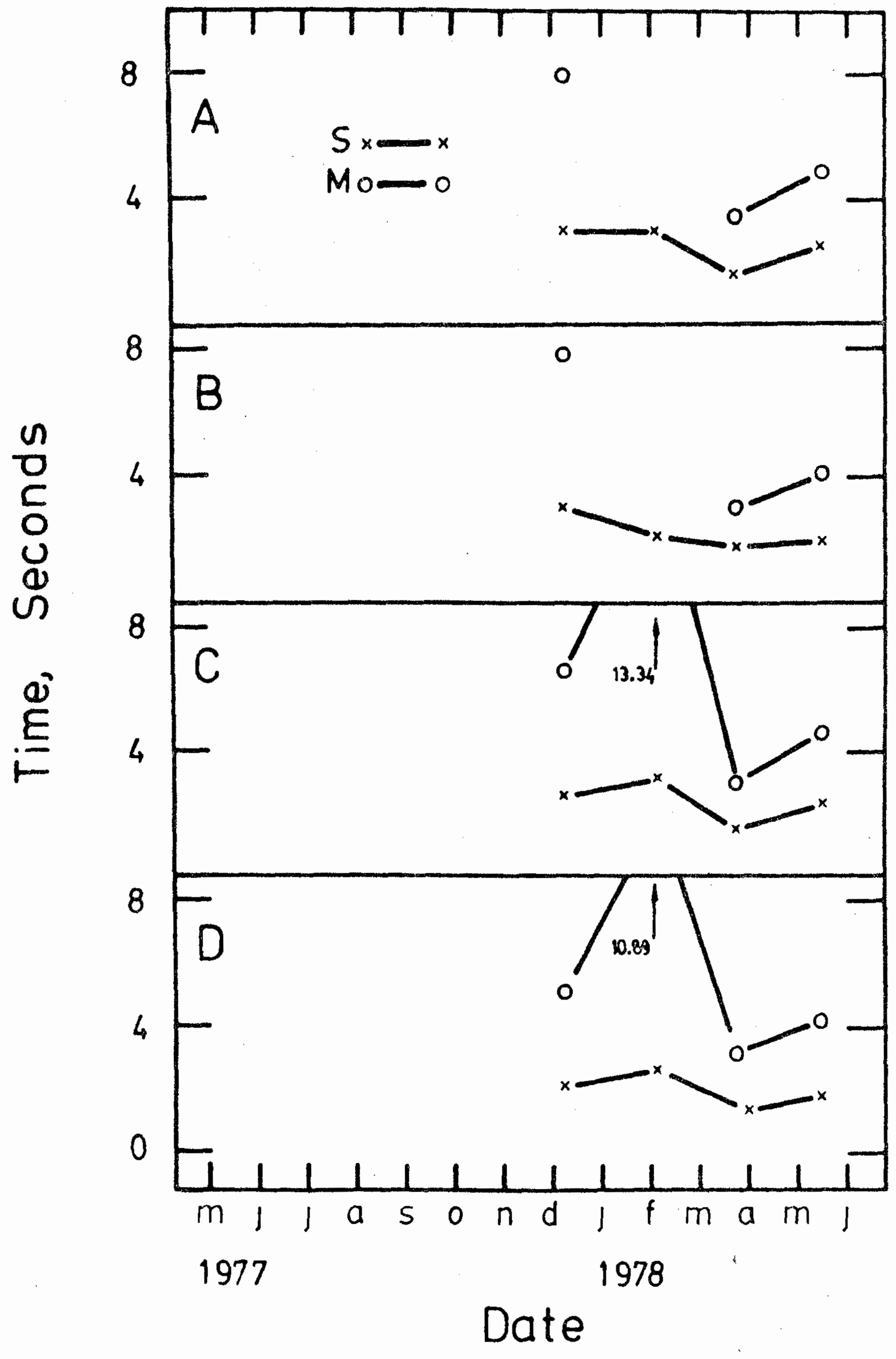

A
B
C
D
S
M
8
4
0
13.34
10.89
Time, Seconds
m
j
j
a
s
o
n
d
j
f
m
a
m
j
1977
1978
Date

Figure V - 5

Mean corrected heights (see Figure V - 2) of selected F_V features in 1978 new needles at SRS. Mean is of all five populations under each light regime.

A, Open; B, 30 (60) %; C, UVT; and D, UVO light regimes.

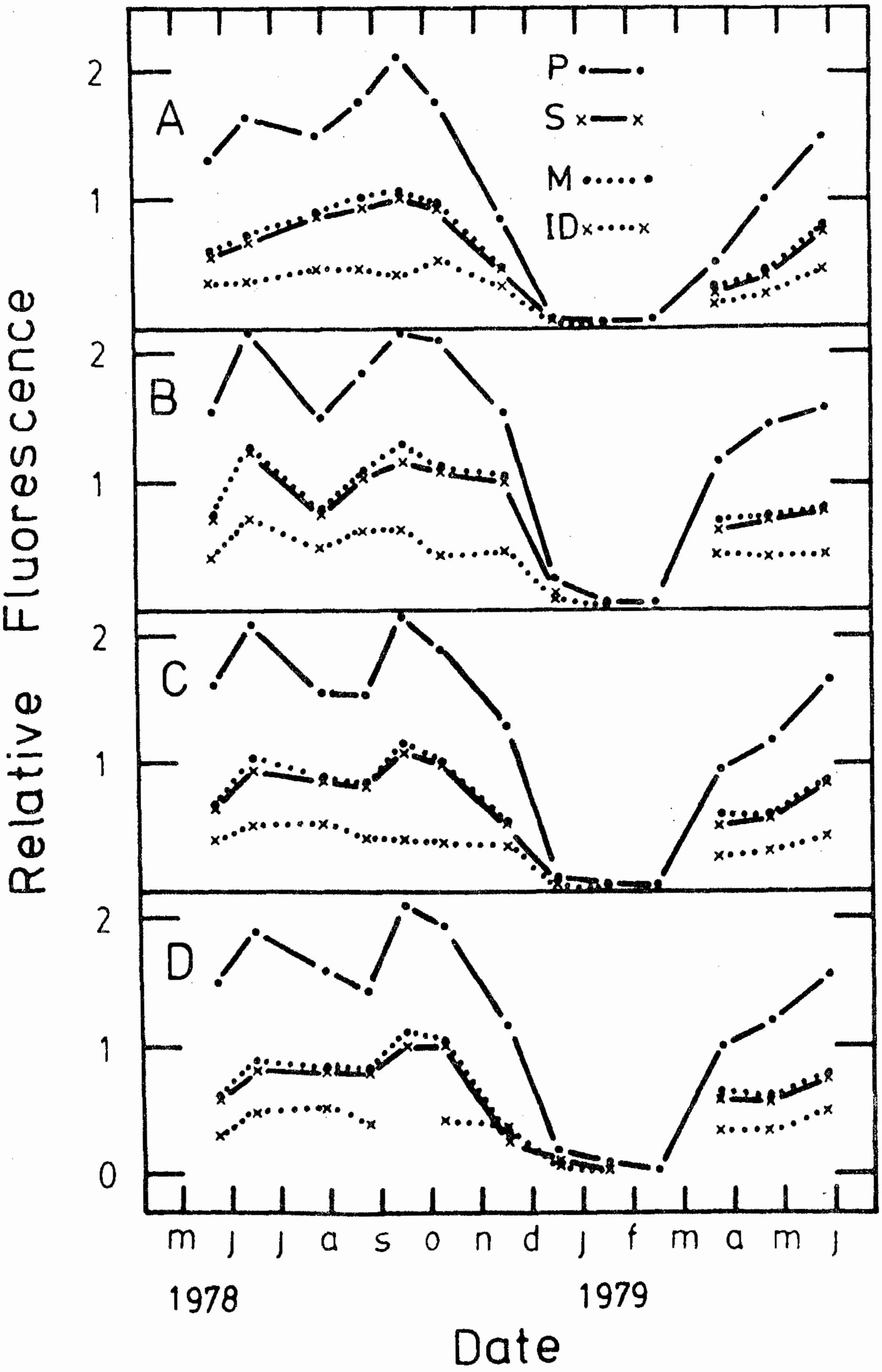

2
1
2
1
2
1
2
1
0
A
B
C
D
P
S
M
ID
Relative Fluorescence
m
j
j
a
s
o
n
d
j
f
m
a
m
j
1978
1979
Date

Figure V - 6

Mean time to P and time to and duration of ID in 1978 new needles at SRS. Mean is of all five populations under each light regime.

A, Open; B, 30 (60) %; C, UVT; and D, UVO light regimes.

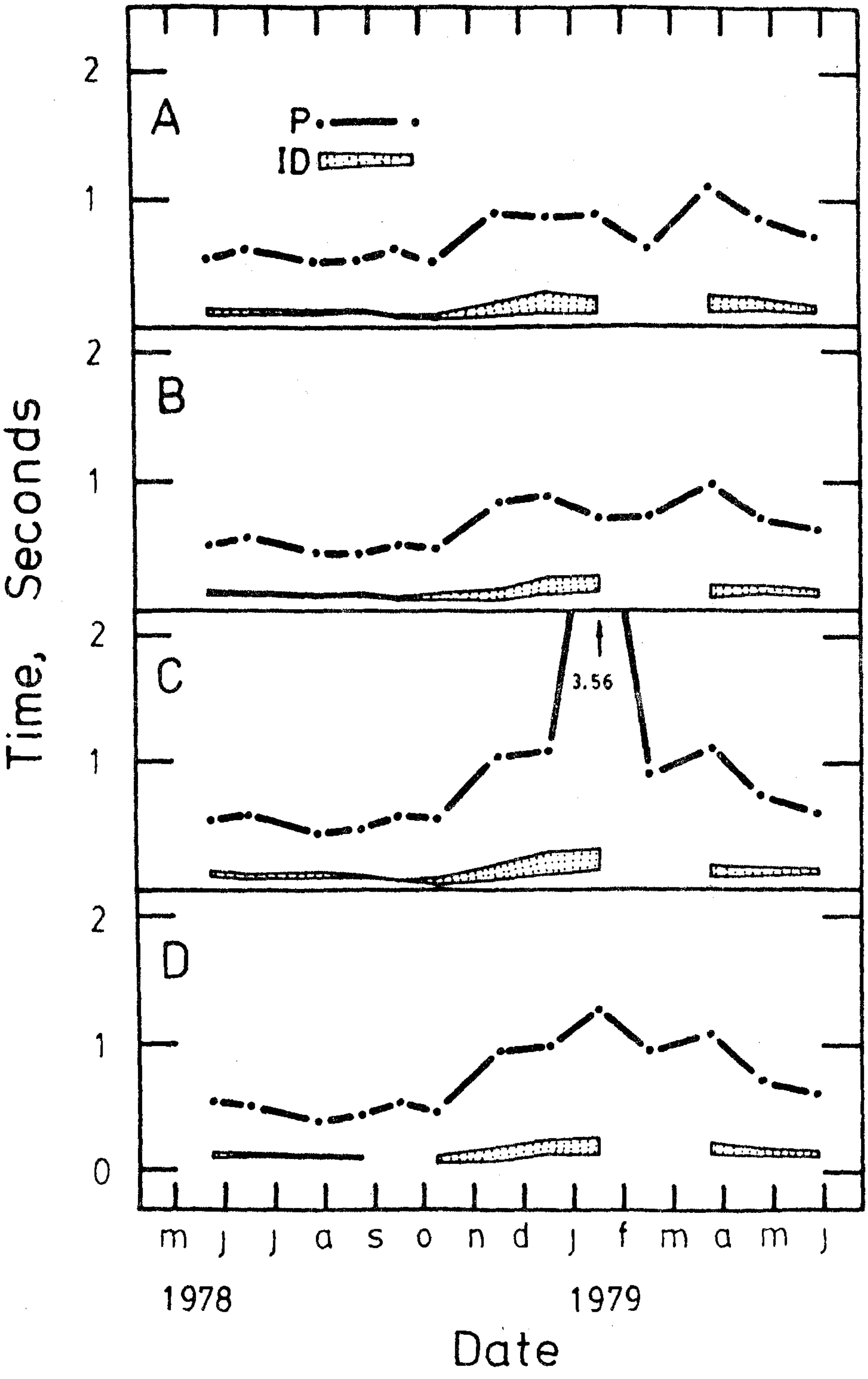
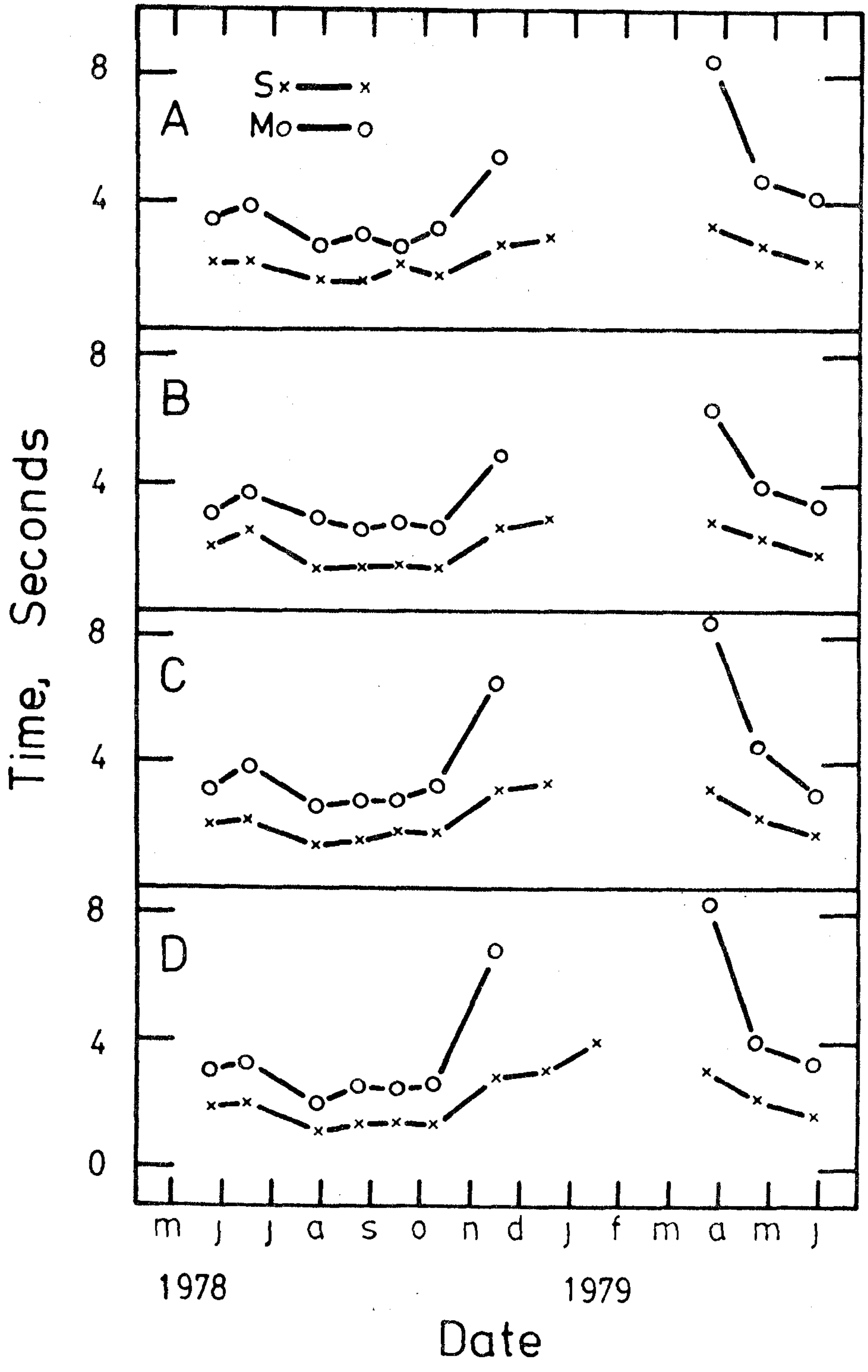

A
B
C
D
P
ID
3.56
2
1
0
Time, Seconds
m
j
j
a
s
o
n
d
j
f
m
a
m
j
1978
1979
Date

Figure V - 7

Mean time to S and M in 1978 new needles at SRS. Mean is of all five populations under each light regime.

A, Open; B, 30 (60) %; C, UVT; and D, UVO light regimes.


S
Mo
A
B
C
D
8
4
0
Time, Seconds
m
j
j
a
s
o
n
d
j
f
m
a
m
j
1978
1979
Date

damage to intersystem electron transport was being witnessed (Schreiber et al. 1978). This period also corresponds to a drop in % WC (Figures III - 6 & 8) and to the frost hardening induction process which is known to involve some dehydration (Blake et al. 1979; Parsons and Li, 1979). The electron donors to PS II and intersystem electron transport have been shown to be sensitive to dehydration (Govindjee et al. 1981; Wiltens et al. 1978). Finally, the photosynthetic apparatus was completely inactivated, indicated by P levels near zero (Figures V - 2 & 5) and a P/O ratio (data not shown) near unity, showing there was no variable fluorescence (Klosson and Krause, 1981a). This is also the time of year when winter inactivation has been observed in temperate boreal conifers (Bamberg et al. 1967; Senser and Beck, 1978). An increase in Chl a/b ratios (Figures IV - 10 & 11) corresponds to the apparent period of photosynthetic inactivation for both years needles. This could indicate that the LHCP is being removed instead of the antennae Chl a (Öquist et al. 1978a). A decrease in Chl a/b ratios paralleling a decrease in P levels could indicate that the antennae Chl a was being destroyed because all of the Chl b is found in the LHCP (Thornber, 1975).

After a period of winter inactivation, P gradually starts to rise and ID returns to values observed in the preceeding growing season (Figure V - 5). ID was constant while P increased, indicating that intersystem electron transport was restored before the PS II electron donors. By May, the photosynthetic apparatus appeared to be fully functional again (Figures V - 2 & 5).

There also was a decline of P, P/O ratio, and ID in some cases, in July-August 1978 (Figure V - 5). This corresponded to a hot dry period at SRS (Tables III - 1 to 3) where water, temperature, and irradiance stresses may have been a problem. In those cases where P and ID declined together, damage was occurring to to the donor side of PS II (Klosson and Krause, 1981b). Where P declined and ID did not, damage was occurring to the donor side of PS II and to intersystem electron transport (Schreiber et al. 1978). A corresponding increase in the Chl _a_/_b_ ratio (Figure IV - 11) could indicate that the LHCP is being destroyed instead of the antennae Chl _a_, which would result in a ratio decrease (Öquist et al. 1978a). This supports the hypothesis of Alberte et al. (1976) that the LHCP could be an important source of amino nitrogen during times of stress. The system recovered once there had been a period of adequate moisture. A similar response for water stress has been reported by Govindjee et al. (1981), while like responses have been observed in plants undergoing heat stress (Schreiber and Armond, 1978), by plants receiving high ozone concentrations (Schreiber et al. 1978) and in plants undergoing high pressure oxygen quenching of fluorescence (Vidaver et al. 1981). These data possibly indicate that most if not all deleterious affects to the photosynthetic apparatus may be initiated in the same manner and at the same location in the system.

The decline of O level during the winter (data not shown) and its return to 'normal' values after the stress period indicate that large changes are occurring to the pigment systems and the PS II reaction center. If O is constant only marginal effects are happening to the pigment systems and PS II reaction centers when P declines (Schreiber et al.

1978). S and M heights followed the same winter trends as P and ID heights. M disappeared under the Open and 60 (30) % light regimes in 1977 needles and under all light regimes for 1978 new needles (Figures V - 2 & 5). This was attributed to the winter of 1978-1979 being more severe (Tables III - 1 to 3) and causing a higher degree of perturbation to the photosynthetic membrane system.

The increased time (Figures V - 3 & 6) to and duration of ID with the onset of cold weather indicated that the reduction of Q was taking longer. Increased time to P could indicate that it takes longer to reduce the electron transport carriers. Both of these phenomena would occur together if:

(1) the water splitting reaction was being impaired and the number of electrons reaching the PS II reaction center was much reduced, as Klosson and Krause (1981b) suggested; and

(2) the excitation energy being received by the LHCP was not delivered to the PS II reaction center, either by uncoupling or destruction of the LHCP from the reaction center in response to sub-zero temperature or by the excitation being passed directly to PS I. This is called indirect quenching (Schreiber and Vidaver, 1976).

The decrease in times to P and ID after the winter was probably the occurrance of the reverse process to inactivation.

The sharp increase in S and M times before inactivation (Figures V - 4 & 7) was probably associated with the winter inactivation of CO_2 fixation (Bamberg et al. 1967; Senser and Beck, 1977). Even cellular respiration ceases at temperatures below -18° C in conifers grown at 69.45 $^{\circ}$ north latitude (Ungerson and Scherdin, 1968) and probably at slightly warmer temperatures at this latitude. The decreasing times to S and M in the spring was probably the reverse of the winter inactivation process, the spring activation process.

Ranking of population P heights was generally the same for both years. P decreased with decreased elevation of the seed source (Tables V - 1 & 2), as pigment contents had. Light regime rankings indicate that P heights decreased with increased light intensity (Tables V - 1 & 2). This is consistent with Schreiber et al. (1977) observation that shade plants had higher P levels than sun plants when tested at the same light intensity. The time to P was shortest in shade grown populations (Figures V - 3B & 6B). This probably occurred because there was a larger LHCP, resulting in a larger PSU, and indicated by a smaller Chl _a/b_ ratio, allowing more photons to be collected and passed on to PS II reaction centers.

The first indication of any stress on the system is indicated by a drop in P level in relation to ID. This demonstrates that electrons are not reaching the PS II reaction center, rather than an increase in PS II fluorescence quenching by PS I (Klosson and Krause 1981a). The generally accepted theory which these data support is that water splitting is damaged or inhibited, therefore, fewer electrons arrive at reaction center II (Govindjee et al. 1981; Klosson and Krause, 1981a,b). However, it has also been suggested (Öquist et al. 1978a,b) that in conifers less excitation energy is delivered to the reaction center of PS II because the antennae Chl _a_ are destroyed, the LHCP and PS II separate, the LHCP is destroyed or

Table V - 1.

Ranking of light regimes and populations for the seasonally corrected height of P (P corrected = P - O) on fluorescence induction transients in 1977 new needles at SRS. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

Population	Light Regimes						
IH =	60 %	=	UVT	=	UVO		Open
IL	UVO	=	60 %		UVT		Open
IM	UVO		60 %	=	UVT		Open
CL	60 %		UVO		Open	=	UVT
CH	60 %		UVT		UVO	=	Open
Mean	60 %		UVO		UVT		Open

Table V - 2.

Ranking of light regimes and populations for the seasonally corrected height of P (Pcorrected = P - O) on fluorescence induction transients in 1978 new needles at SRS. Populations and light regimes are listed in descending order of ranking unless indicated as being equal by an = sign. Populations are ranked vertically and light regimes horizontally. Abbreviations as in text.

Population	Light Regimes			
IL =	UVO	UVT	30 %	Open
IH	30 %	UVT	UVO	Open
CL	UVO	30 %	UVT	Open
IM =	30 %	UVO	Open =	UVT
CH	30 %	UVT	UVO	Open
Mean	30 %	UVO	UVT	Open

the PS II reaction center Chl is destroyed (Fink, 1978). The data support these hypotheses too. Apparently, after the water splitting system has been inhibited or damaged, the intersystem electron transport system is also inhibited (Klosson and Krause, 1981a,b).

Possibly in conifers where the leaves are long lived, winter photosynthetic inactivation occurrs in a systematic stepwise fashion:

(1) if temperatures are not too severe for too long a period of time, then water splitting is inhibited and P levels decrease. This probably occurs when the P level drops in summer;

(2) if temperatures are colder and of longer duration than in (1), electron transport would be slowed, indicated by a rise in ID relative to P, and finally stopped;

(3) if temperatures are much colder and of even longer duration than in (2), destruction or separation of the LHCP from PS II could occur;

(4) if temperatures are colder and of even longer duration than in (3), Chl molecules would be destroyed by photo-destruction because the normal means of excess energy dissipation would not be operating (Ridley, 1977);

(5) as increased irradiance appears to speed up the inactivation process (Öquist et al. 1978a,b), low temperatures in conjunction with bright sunshine would increase the damage done to the photosystem, LHCP, electron transport, or the photosynthetic membrane in general. This could speed up the stepwise inactivation process leading to a more rapid attainment of a

higher level of inactivation.
It is important to keep in mind that all of the thylakoid membrane constituents, pigments, lipids, proteins and enzymes, are involved in the inactivation process, in the prevention of Chl destruction, and in the normal function of the photosynthetic process (Krause et al. 1978).

The greater degree of inactivation in the winter of 1978-1979 probably occurred because temperatures were lower for a longer period of time, and there was an increase in bright sunshine hours (Tables III - 1 & 3). These observations lend some support to the stepwise inactivation process hypothesis (SIP) as do seasonal morphological and ultrastructural studies by Martin et al. (1978a,b), Öquist et al. (1978a,b) and Senser and co-workers (1975, 1977, 1978).

Section 2: CO_2 Gas Exchange

Rates of CO_2 uptake ranged from 0.85 to 2.63 for high light with 21 % O_2, -0.19 to 1.16 for high light with 2% O_2, 0.89 to 2.63 for moderate light and 0.61 to 1.72 [mg CO_2 (μmol pigment)$^{-1}$ (gm ODW tissue)$^{-1}$ hr^{-1}] for low light tested plants at SRS. All plants displayed decreasing rates of CO_2 uptake with decreasing light intensity (Figure V - 8).

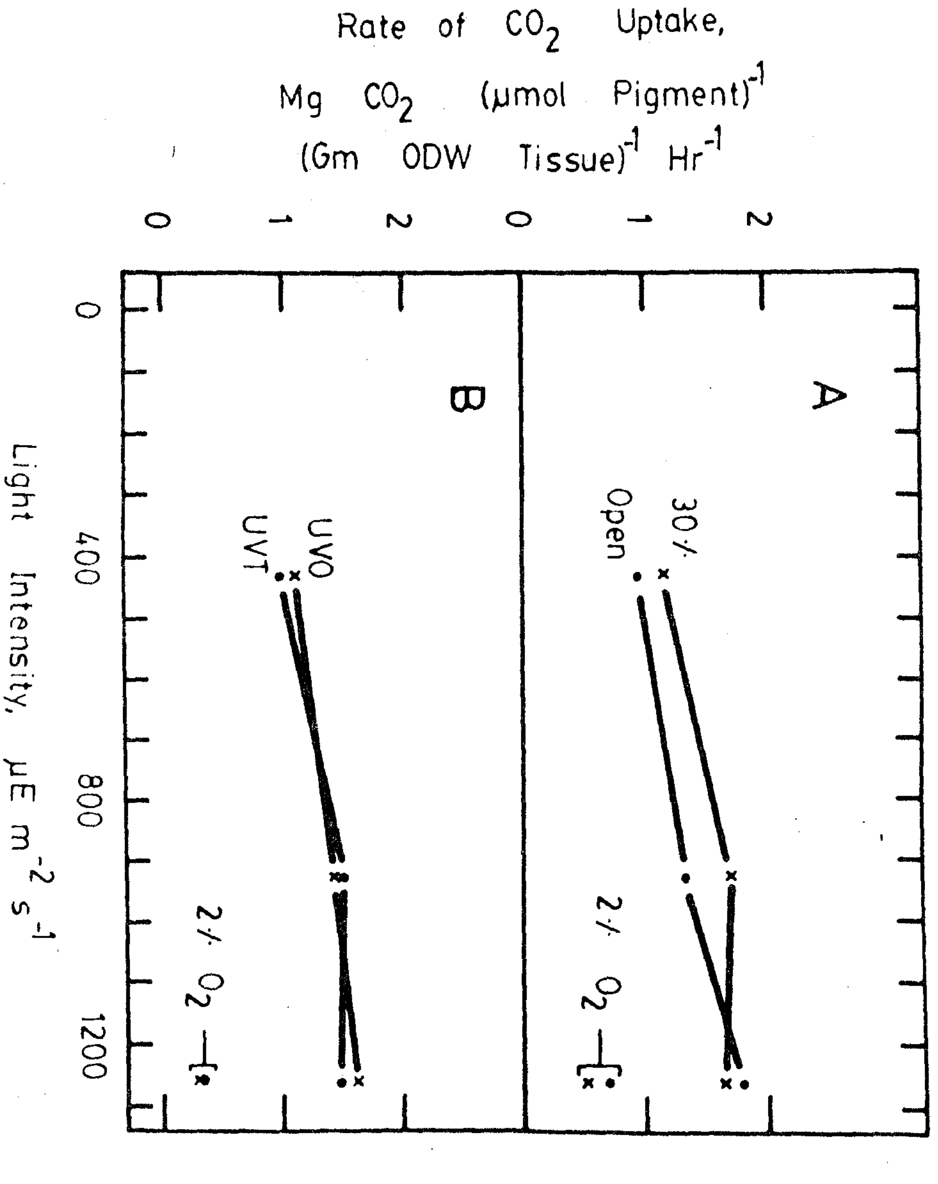
CO_2 gas exchange measurements were conducted initially in early August 1978 at SFU but these yielded large percentage decreases in CO_2 uptake under 2 % O_2, similar to the SRS results. Following a complete system check, gas mixture analysis, and relocation to a different laboratory a complete series

Figure V - 8

Mean rates of CO_2 uptake at 21 % O_2 by 1978 new needles from all five populations under each light regime at SRS. Isolated symbols are the rates of CO_2 uptake at 2 % O_2 by all five populations under each light regime.

A, Open and 30 (60) % light regimes.

B, UVO and UVT light regimes.


Rate of CO2 Uptake,
Mg CO2 (µmol Pigment)-1
(Gm ODW Tissue)-1 Hr-1
A
B
30%
Open
UVO
UVT
2% O2
0
1
2
0
400
800
1200
Light Intensity, µE m-2 s-1

of CO_2 measurements were conducted at SFU. Rates of CO_2 uptake [mg CO_2 (μmol pigment)$^{-1}$ (gm ODW tissue)$^{-1}$ hr^{-1}] were found to range from 0.72 to 3.67 for high light with 21% O_2, 0.85 to 5.66 for high light with 2% O_2, 0.69 to 3.27 for moderate and 0.54 to 2.19 for low light tested plots. All plants tested had decreasing rates of CO_2 uptake with decreasing light intensity (Figure V - 9).

Generally, interior origin populations had the greatest rates of Ap/s under all experimental conditions at both sites (data not shown). This result is contrary to that reported by Krueger and Ferrell (1965) and Sorensen and Ferrell (1973) for the two Douglas-fir varieties. Low light grown plants having higher rates of Ap/s at lower light intensities than high light grown ones, has been reported previously (Lewandowska et al. 1976, 1977, 1978). Tsel'niker's (1979) report of lower Ap/s rates for plants grown at lower habitat irradiances but tested at high light intensities is supported by this data, except for the SFU 30 (60) % light regime populations (Figures V - 8 & 9). This deviation cannot be explained at this time. The higher rates of Ap/s observed at the coastal site compared to the interior site supports the findings of Sorensen and Ferrell (1973). Increased rates of Ap/s could be due to the higher pigment levels found in SFU populations.

The amount of p/r observed at SFU (Figure V - 9, 2 % O_2) was in the region of previous and later determinations done on Douglas-fir (data not shown). However, the p/r data obtained at SRS was completely baffling (Figure V - 8, 2 % O_2). Instead of Ap/s increasing when 2 % O_2 was

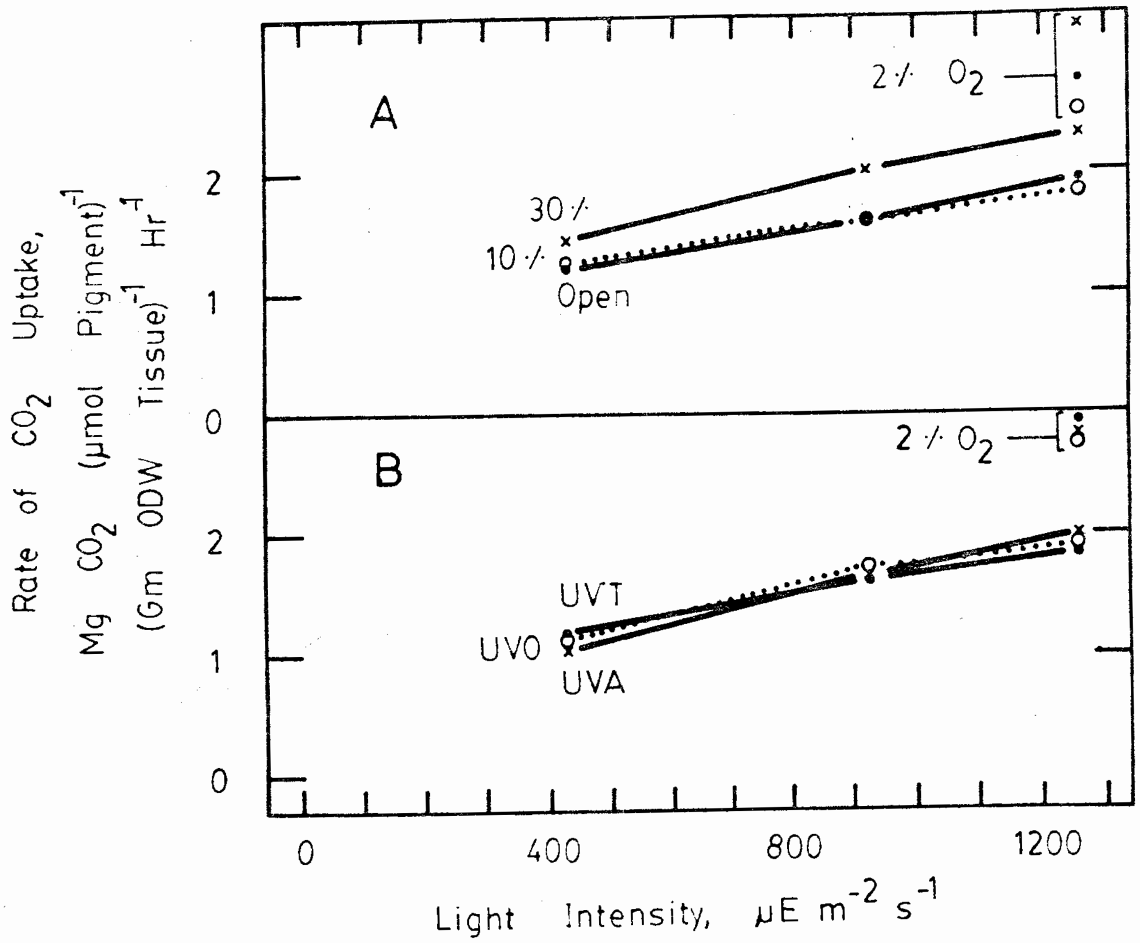
Figure V - 9

Mean rates of CO_2 uptake at 21 % O_2 by 1978 new needles from all five populations under each light regime at SFU.

Isolated symbols are the rates of CO_2 uptake at 2 % O_2 by all five populations under each light regime.

A, Open, 30 (60) %, and 10 (30) % light regimes.

B, UVO, UVA and UVT light regimes.


A
B
Rate of CO_2 Uptake,
Mg CO_2 (μmol Pigment)$^{-1}$
(Gm ODW Tissue)$^{-1}$ Hr^{-1}
0
1
2
0
1
2
0
400
800
1200
Light Intensity, μE m^{-2} s^{-1}
30 %
10 %
Open
2 % O_2
UVT
UVO
UVA
2 % O_2

introduced, it decreased, which indicates that decreased O_2 levels promote p/r but the opposite view is held (Berlyn, 1978). Increased rates of p/r with the increased temperatures experienced during these tests were considered but even if p/r increased with increased temperature, the rate of Ap/s with 2 % O_2 should increase not decrease.

The clue came when the meaning of the negative rate of fixation with 2 % O_2 at high light intensity was comprehended. The tree was giving off CO_2 in the presence of low O_2 levels and high light intensities. There was an obvious procedural difference between determining the rates of Ap/s at 2 and 21 % O_2:

(a) for the 21 % O_2 determinations ambient air was used to flush and saturate the system, it had an O_2 concentration of about 21 % and a CO_2 concentration form 380 to 410 ul/liter;

(b) for the 2 % O_2 determinations a prepared gas mixture was used to flush and saturate the system, it had an O_2 concentration of near 2 % and a CO_2 concentration of 330 ul/liter.

The question then arose of whether Γ could be raised considerably from its usual level, about 75 ul/liter (Clark and Lister, 1975), to a value greater than 330 ul/liter, at least on one occassion when the negative Ap/s occurred. It would mean that the Ap/s determinations with 2 % O_2 were being done on the shallowest part of the rate determination CO_2 compensation point curve, while the Ap/s determinations at 21 % were being done on a much steeper, higher rate, part of the curve. In the lower regions of the curve, a small decrease in the ambient CO_2 level can bring about a large decrease in the rate of Ap/s. Because, here, the rate is rapidly changing from being extremely positive, to being zero at Γ, to being negative when the lights are turned off.

Brix (1968) reported Γ values for Douglas-fir seedlings of 380 ul/liter at 28° C but at very low light intensities, while other workers (Bauer 1978, Bauer and Senser, 1979) have reported increased Γ with prolonged increased temperatures of growth. Smith et al. (1976) reported that Γ increased with temperature but was not affected by light intensity and Beadle et al. (1981) observed increases in it with low xylem water potentials. Could the apparent increase in Γ be due to increased p/r caused by increased temperatures, probably not, because:

(1) if the increased Γ had been due to increased rates of p/r, when tested with 2 % O_2, the rate of Ap/s would have increased not decreased;

(2) Bauer (1978) found that the increase in Γ with temperature was not due to a stimulation of p/r but that the photosynthetic process itself was impaired;

(3) Bauer and Senser (1979) found that when Γ was elevated the Hill reaction and membrane ultrastructure were reversibly heat sensitive, while the enzyme RuBP carboxylase was extremely heat stable;

(4) it was observed in late July and early August of 1978 utilizing F_V analysis that there was a reduction in water splitting capacity and a reduction in or a destruction of the LHCP. This lends support to Bauer and Senser's (1979) observations.

The increased Γ was probably not due to increased rates of p/r but may be due to decreased O_2 concentrations and membrane structural changes which decrease the amount of reducing power beyond PS I. This impairs CO_2 fixation because the enzyme responsible for CO_2 fixation is very heat stable. These factors then combine to raise the rate of apparent cellular respiration resulting in high Γ values.

CO_2 gas exchange measurements showed that interior variety populations had higher rates of Ap/s at both sites, contrary to the literature (Krueger and Ferrell, 1965; Sorensen and Ferrell, 1973) and to the 1978 mean leader shoot elongation. However, the decreased rates of Ap/s at SRS with 2 % O_2 did illustrate how the entire photosynthetic process, photochemical reactions, biochemical reactions, and membrane ultrastructure is interrelated. One should attempt to view the photosynthetic reactions as the sum of all their parts, not as individual parts, for these reasons.

CHAPTER VI

SUMMARY

DISCUSSION

The seasonal trends for individual pigments and ratios (Figures IV - 1 to 13) were influenced by the % WC of the needles (Figure III - 6 to 9) because all pigment values were calculated /gm ODW. However, the seasonal trends were due to natural internal rhythms of the leaves and not to the annual decline in % WC, because seldom did a pigment or ratio maximum or minimum correspond to a % WC maximum or minimum. Often the pigment minimum corresponded to a % WC maximum or vice versa. If anything, the effect of % WC on the seasonal trends was to moderate them.

Generally, two year old needles had higher pigment contents and ratios than new needles. This was due to there actually being more pigment in the two year old needles because % WC was about the same between new and two year old needles.

For all of the parameters that were examined which involved comparisons between SRS and SFU, SFU grown populations always had the larger value, except for 1978 mean leader elongation. The better performance by the SFU populations has been attributed to the coastal climate being more moderate than the interior.

Of the 32 broad needle age groups of data responses examined for growth, % WC, pigments, ratios, F_V curves, and rates of p/s, populations of interior origin had the largest values 23 times. Because interior variety populations originate at much higher altitudes, the above can be generalized to; 72 % of the time the response being examined increases with increased altitude of the seed source. This is complementary to the observations of Garrett (1969) for Chl and Car pigments, and contrary to the reports of Baldwin (1955) and Linder (1972) for Chl and Car pigments, Griffin and Ching (1977) for leader growth, and Sorensen and Ferrell (1973) for rates of p/s.

Only growth, in both years new needles, and Chl a content, in 1977 new needles, showed a latitudinal relationship. The response decreased with decreased latitude of the seed source. This has been reported for growth rates, biomass increases, and some pigment contents (Zavitkovski et al. 1981). Because the populations being examined only covered 2.9° of latitude, this may be too small a range to observe a general latitudinal effect; the altitudinal variations may have been more pronounced than the latitudinal ones; or both phenomena may have been occurring simultaneously. It is generally accepted that species with long north-south distributions have latitudinal ecotypes. Therefore, it cannot be stated categorically from this data that there was no relationship between response and latitude of origin, even if 81 % of the responses were negative.

Chl a/b ratios, Car content, and p/s rates all increased with increased light intensity. The other responses all decreased with increased light intensity. A generalized statement cannot be made concerning plant responses to ambient light intensity because some increase, others decrease, and some do both with increased light intensity. However, plants do respond to changes in light intensity in a very characteristic way for each response, and the response ranking appears to be maintained between the five populations growing under each light regime.

Changes in F_V curves with season can be correlated to the seasonal changes of the photosynthetic pigments. From these data inferences about the status of the photosynthetic system can be made. Therefore, F_V curve analyses in conjunction with photosynthetic pigment determinations can be a very powerful tool when examining the effects of just about any condition or situation on the photosynthetic process. This is because photosynthesis is directly related to the plants well being.

It appears to have taken at least one year for the seedlings to re-establish themselves because:

(a) 1978 growth was much greater than 1977 growth;

(b) most of the responses examined had more variability in the 1978-1979 needle year, indicating that the plants had overcome the initial stresses and become re-established.

Once the plants are re-established their response to various environmental parameters appears to be maintained within certain limits. Even though light regime rankings can change markedly for a given response, the ranking of the populations in relation to each other often did not change at all. From the population rankings, the IM population appeared to be intermediate in response characteristics between coastal, CL and CH, and interior, IL and IH, populations. Possibly because the annual precipitation at the IM seed source was much greater than at the other interior sites (Anon. 1977 to 1979). This locale is characteristic of the coastal region, except for temperature extremes. IM would possess many coastal like adaptations to accomodate the increased precipitation. Von Rudloff (1973) utilizing leaf terpene oils as the method of classifying Douglas-fir populations, found that populations from the IM area were interior intermediate to coastal variety, and that the other two interior areas were true interior varieties.

The good growth by the coastal varieties at the interior site may warrant more investigations over an extended period of time. If coastal variety populations could be found that grew well in the interior, then productivity of the interior forests could be increased. Conversely, interior variety populations could be established in the more xeric coastal regions to increase productivity there. However, more intensive studies of this sort would have to be conducted over many years to yield this potentially valuable information.

The data indicates that at least for these populations:

(1) their response to a given environmental parameter is relatively small, not very plastic; and

(2) their genotype is most important in determining the characteristic responses under these experimental conditions.

This illustrates why studies of populational ecological adaptations are basic to successful practical programs of tree improvement and reforestation.

APPENDIX I

The order and protocol of the CO_2 gas exchange measurements at SRS and SFU, read across then down.

SRS

Open	Y	G	B	O	R
30 %	R	O	B	G	Y
UVT	Y	G	B	O	R
UVO	R	O	B	G	Y
UVO	Y	G	B	O	R
UVT	R	O	B	G	Y
30 %	Y	G	B	O	R
Open	R	O	B	G	Y

SFU

Open	Y	G	B	O	R
30 %	R	O	B	G	Y
10 %	Y	G	B	O	R
UVT	R	O	B	G	Y
UVA	Y	G	B	O	R
UVO	R	O	B	G	Y
UVO	Y	G	B	O	R
UVA	R	O	B	G	Y
UVT	Y	G	B	O	R
10 %	R	O	B	G	Y
30 %	Y	G	B	O	R
Open	R	O	B	G	Y

Each of these protocols was repeated once to give the total of four experimental trees for each population under each light regime.

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