

AN ABSTRACT OF THE THESIS OF

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Abstract approved: _____
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During the past 20 years, repeated thinning of a Douglas-fir forest, now 65 years old, has allowed desired limits of basal area to be maintained. In the process, the understory environment has altered sufficiently to allow Douglas-fir reproduction to establish in abundance. The forest is located on the east side of the Coast Range, north of Corvallis, Oregon.

A study was undertaken to examine growth patterns of understory trees in relation to microenvironment, physical attributes of the tree and time. This information would help determine how long a tree can be maintained at a given level of shade and still function properly. This information also would add to the understanding of modification of growth strategies for survival.

To characterize the understory environments of the three thinning intensities (23 to 30, 30 to 37 and 37 to 44 m²/ha basal area), measurements were made of plant moisture stress, evaporative demand, air and soil temperature, light and vegetative cover. Light measured at seedling crown best separated the environments; light was found

to increase with a decrease in stand basal area, averaging 5, 8 and 12 percent of daily sun for the three thinning levels.

Trees, randomly selected, ranged in height from 10 cm to 1.5 m and in age from 4 to 15 years. Parameters measured included leader growth for the past two seasons, diameter growth, above-ground biomass, height and age. Bud phenology and beginning of cambial activity were also observed.

Development of buds in the spring was inversely related to light while renewed cambial activity was directly related to tree size and light. Increments of height and diameter growth were found to increase with light and tree height. Linear differences in average leader and diameter growth and above-ground biomass production were found between the three intensities of thinning, with trees under the heaviest thinning growing most. Average growth is predictable for at least two years. However, rates of leader growth and biomass production, in relation to growth of the previous year and leaf biomass, were not different for individual trees from the three understory environments. A balance of foliar to stem biomass was maintained by understory trees. Physical characteristics of the tree accounted for most of the variation in growth.

As thinning of young Douglas-fir becomes a widespread management practice, it can be expected that, in similar vegetation types, Douglas-fir seedlings will establish naturally in the understory. If the new forest is established at final harvest several years in lag time may be saved; regeneration problems often associated with clear-

cutting will be alleviated, planting costs reduced or eliminated, and the forest gene pool maintained.

Growth Behavior of Douglas-fir Reproduction
in the Shade of a Managed Forest
in the Interior Coast Range of Oregon

by

Ernest Del Rio

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Growth Behavior of Douglas-fir Reproduction
in the Shade of a Managed Forest
in the Interior Coast Range of Oregon

Chapter 1. Establishment and Mean Growth

Abstract

Thinning Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) on the east side of the Oregon Coast Range has allowed Douglas-fir seedlings to establish naturally in the understory. The degree of reproduction appears related to the level of thinning. This study examined the vigor of the reproduction and described the understory environments of three thinning intensities.

Differences in environments were best separated by the amount of daily sunlight reaching the understory. Douglas-fir can grow for at least 15 years at an average of 5 to 12 percent of daily sun. Increment of growth increases with light and tree height. Linear differences in average growth were found between the three thinning levels, with trees under the heaviest thinning growing most; average growth is predictable for at least two years.

Introduction

There is agreement as to the benefit of shade for survival of Douglas-fir during the early stages of reproduction, especially on more severe sites (Isaac 1943, Minore 1971, Williamson 1973, McDonald 1976, Lindquist 1977). Several studies have shown that Douglas-fir has the ability to establish and function properly at low light. Atzet and Waring (1970) determined the lower light requirement for survival and growth of Douglas-fir to be less than two percent of full sun when moisture is not limiting. Emmingham and Waring (1973) found that Douglas-fir 1 to 2 meters tall could grow 5 to 10 cm in height per year at 7 to 35 percent of full sun. Hodges and Scott (1968) found in Douglas-fir that shade foliage was more efficient in assimilating carbon dioxide than was sun foliage. The capacity of Douglas-fir to grow at low levels of light over prolonged periods of time has not been established.

Thinning will play a major role in management of young Douglas-fir (Berg 1976). At the Gerlinger State Experimental Forest, near Falls City, Oregon, this practice has allowed Douglas-fir to establish naturally in the understory. A study was undertaken to assess vigor, in terms of growth, of Douglas-fir reproduction beneath different levels of overstory thinning. In addition, thinning levels were examined for differences in understory environments. This information would give a better understanding of how long Douglas-fir reproduction can remain in heavy shade and still function properly, rendering it usable for regeneration of the forest.

Study Area

The study was conducted within the Black Rock Unit of the George T. Gerlinger State Experimental Forest located on the east side of the Coast Range, 40 miles northwest of Corvallis, Oregon.

The climate is wet but mild, with an average annual precipitation of about 200 cm, falling mostly as rain in the winter, and a frost-free growing season of more than 200 days. The soils have developed in residuum and colluvium from Eocene sandstones, shales and siltstones and from Miocene coarse-grained gabbro and diorite, both basic igneous intrusive rocks (Youngberg 1964). A large portion of the sedimentary formation, where the study plots were located, occurs as a large, south-facing, gentle, uneven slope. The soils have strong granular structure in the surface and moderate subangular blocky structure in the subsoil. They are moderately acid in the surface and become strongly acid in the subsoil.

The area supports a naturally regenerated stand of Douglas-fir, 65 years old. Dominant trees are about 40 m tall. Some western hemlock (Tsuga heterophylla (Raf.) Sarg.), grand fir (Abies grandis (Dougl.) Lindl.), and western redcedar (Thuja plicata Donn.) are scattered throughout the forest. The most common hardwoods are red alder (Alnus rubra Bong.), bigleaf maple (Acer macrophyllum Pursh), and Pacific dogwood (Cornus nuttallii Aud.). Shrub species include Acer circinatum Pursh, Berberis nervosa Pursh, Gaultheria shallon Pursh and Holodiscus discolor (Pursh) Maxim.

The plots selected for this study have been maintained between 23 to 30, 30 to 37, and 37 to 44 m²/ha of basal area for the last 20 years. There are four replications of the three thinning treatments. All plots are 0.4 ha in size. Aspect on the plots ranges from S45°W to S45°E, with slopes from 5 to 40 percent. Elevation of plot centers ranges from 332 to 579 m. All yarding on these plots is done by horse so that logging damage will be minimized. Advance reproduction of Douglas-fir is abundant on most of the thinned plots.

Materials and Methods

A survey was conducted in the fall of 1976 to determine density and age of Douglas-fir reproduction beneath the three thinning intensities (Berg and others, unpublished manuscript). Table 1-1 summarizes information from that survey. In this study all four replications of the thinned plots described in the previous section were used. An open area supporting young Douglas-fir reproduction was used as a reference plot.

To characterize the understory environments of the three thinning levels and that of the open plot, the following measurements were made:

1. Relative light energy received at the crown of each sample tree was measured over an entire day in mid-July by the ozalid paper technique (Friend 1961, Emmingham and Waring 1973); the paper was calibrated against a solarimeter. The maximum light energy recorded in the open was assigned a value of 100 percent, and all other light readings were expressed as a percentage of this.
2. Plant moisture stress (Waring and Cleary 1967) was recorded at three week intervals from June 25 to Sept. 8, 1977 on three reference trees per plot. PMS was recorded during predawn hours and between 12 and 2 p.m. on the day of measurement.

Table 1-1. Summary of Distribution of Douglas-fir in the Understory at Black Rock a.

<u>Plot</u> ^{b.}	<u>Overstory</u> ^{c.} <u>Thinning</u> <u>Treatment</u>	<u>Trees/HA</u>	<u>Age</u> <u>Range</u>	<u>Mean Age of Trees</u> <u>Used in This Study</u>
22	Heavy	1,608	2-13	9
24	Medium	865	2-15	9
25	Light	380	2-14	8
30	Heavy	3,038	2-11	7
28	Medium	793	2-10	8
29	Light	673	2-10	7
36	Heavy	5,400	2-11	8
35	Medium	12,153	2-10	7
34	Light	5,400	2-10	7
41	Heavy	10,353	2-14	9
38	Medium	6,055	2-14	9
40	Light	4,848	2-13	8

- a. Douglas-fir standing $\bar{<}$ 1.7 m
b. Plot size = 0.4 ha
c. Heavy = 23-30 m²/ha Basal Area
Medium = 30-37 m²/ha Basal Area
Light = 37-44 m²/ha Basal Area

3. Dry and wet bulb temperatures were read on a sling psychrometer during PMS readings. This information was later converted to estimates of evaporative demand as a function of vapor pressure deficit.
4. Air and soil temperatures were monitored continuously from May 15 to Sept. 8, 1977 on four 30-day recording thermographs; one thermograph was placed in the open and one each at the center of a representative plot of the light, medium and heavy overstory thinnings. Thermographs were housed in ventilated wooden shelters. Air temperature was measured at a height of 1.5 m; soil temperature was measured at a depth of 20 cm. Thermographs had been calibrated against laboratory instruments.
5. Vegetative cover around each of the trees selected for growth analyses was estimated visually by laying a metal ring of 30 cm radius on the ground, with the sample tree as center, and estimating the area of the circle occupied by vegetation. Cover was separated into woody and herbaceous species.

Twenty Douglas-fir trees per plot were randomly selected. To ensure adequate representation of a plot, 20 evenly distributed points were located on the plot. From each of these points, a random distance (0.3 to 2 m) and direction was offset. At the offset point, the nearest Douglas-fir tree with four or more terminal bud scars or standing between 10 cm and 1.5 m was selected as a sample tree. A

total of 260 young Douglas-fir was selected and tagged during April, 1977, before the start of active growth. (By the end of active growth, 14 trees had died, reducing the total sample size to 246 trees.)

During selection of sample trees, the average diameter of each tree was measured to the nearest 0.1 mm with a caliper rule at a point on the stem 1.0 to 1.5 cm above the ground. The point of measurement was marked for later reference.

Development of lateral and terminal buds was observed during the periods April 10 to April 17 and April 30 to May 1, 1977. Observations began on the replications at the lower elevations, proceeded to the replications at the upper elevations, and ended at the open plot. At each of the two periods of observation, an insect mounting pin (size 00) was inserted into the main stem of each of the sample trees; the pin, by damaging a few cells, created a marker whereby beginning of cambial activity could later be determined (Wolter 1968). The two pins were inserted directly below the point where diameter had been measured.

During the third week of Sept. 1977, the following measurements were made on sample trees:

1. leader growth 1977 (cm)
2. leader growth 1976 (cm)
3. tree height 1976 (cm)
4. final diameter (mm)

Trees were then harvested by clipping at ground level. Current season needles and stems were clipped and sealed in a bag; the remainder of the above-ground portion of the tree was sealed in another bag. Each

bag was labeled "current" or "old," numbered and transferred to the laboratory. This process was repeated for each of the sample trees.

After drying for 48 hrs. at 70°C, needles were carefully stripped from stems. Each component was then weighed to the nearest 0.1 g. In this fashion, dry weight of current needles and stems (new biomass), as well as dry weight for older (>1 year) needles and stems (old biomass), was determined for each tree.

Prior to drying, a small segment of the main stem of each tree, where the two pins had been inserted, was removed and preserved in 20 percent ethanol. Tree age was determined by air drying the segment, sanding the crosssection, staining it with rhodamine dye, then counting the annual rings. Trees were found to range in age from 4 to 15 years.

From a random subsample of 39 of these stem segments (represented by three trees from each of the 12 thinned plots plus three open grown trees), thin sections of the wound area were prepared and permanent microscopic slides made. Xylem expansion for the last three years was measured by a micrometer inserted into the eyepiece of a light microscope. Thin sections were also viewed for signs of an active cambium at the two periods of pinning. Each segment was eventually dried, weighed, then that weight added to the old biomass of the tree. (Bud development and the beginning of cambial activity, in relation to light and physical condition of the tree, will be discussed in the following chapter.)

Analysis of variance and least squares regression techniques were used to detect differences between the different thinning intensities in understory environments and average growth of trees; those

parameters contributing most to explain the variation in growth of trees were isolated.

In addition to those trees randomly selected, six larger trees on each of three heavily thinned plots and one medium thinning were subjectively chosen as a means of emphasizing potential growth of Douglas-fir under lower levels of light. Total height and leader growth for 1977 were measured.

Results

I. Understory Environments

Average daily sunlight reaching the crown of understory trees was found to decrease linearly with increasing basal area (Figure 1-1). Daily sunlight averaged 4.8, 7.8 and 11.5 percent for the light, medium and heavy thinning treatments, respectively (maximum light energy in the open on the day of measurement was 528 ly). However, light varied greatly from one tree to the next on all thinned plots. Coefficient of variation for average light measured at the crown ranged from 40 to 76 percent and was highest on the plots thinned most heavily.

No differences in plant moisture stress were found among the thinning treatments so the data for all understory trees were combined (Figure 1-2). Average maximum stress in the understory during predawn hours was 13.2×10^5 Pa; between 12 and 2 p.m. the average maximum stress recorded was 19.6×10^5 Pa.

Curves for evaporative demand (Figure 1-3), as a function of vapor pressure deficit, followed closely the curves for plant moisture stress. No treatment differences in evaporative demand were found.

Although temperature at 1.5 m did not differ among the thinning levels, soil temperature at a depth of 20 cm did, except for the month of August (Table 1-2). Generally, soil temperature increased with thinning intensity (Berg 1970).

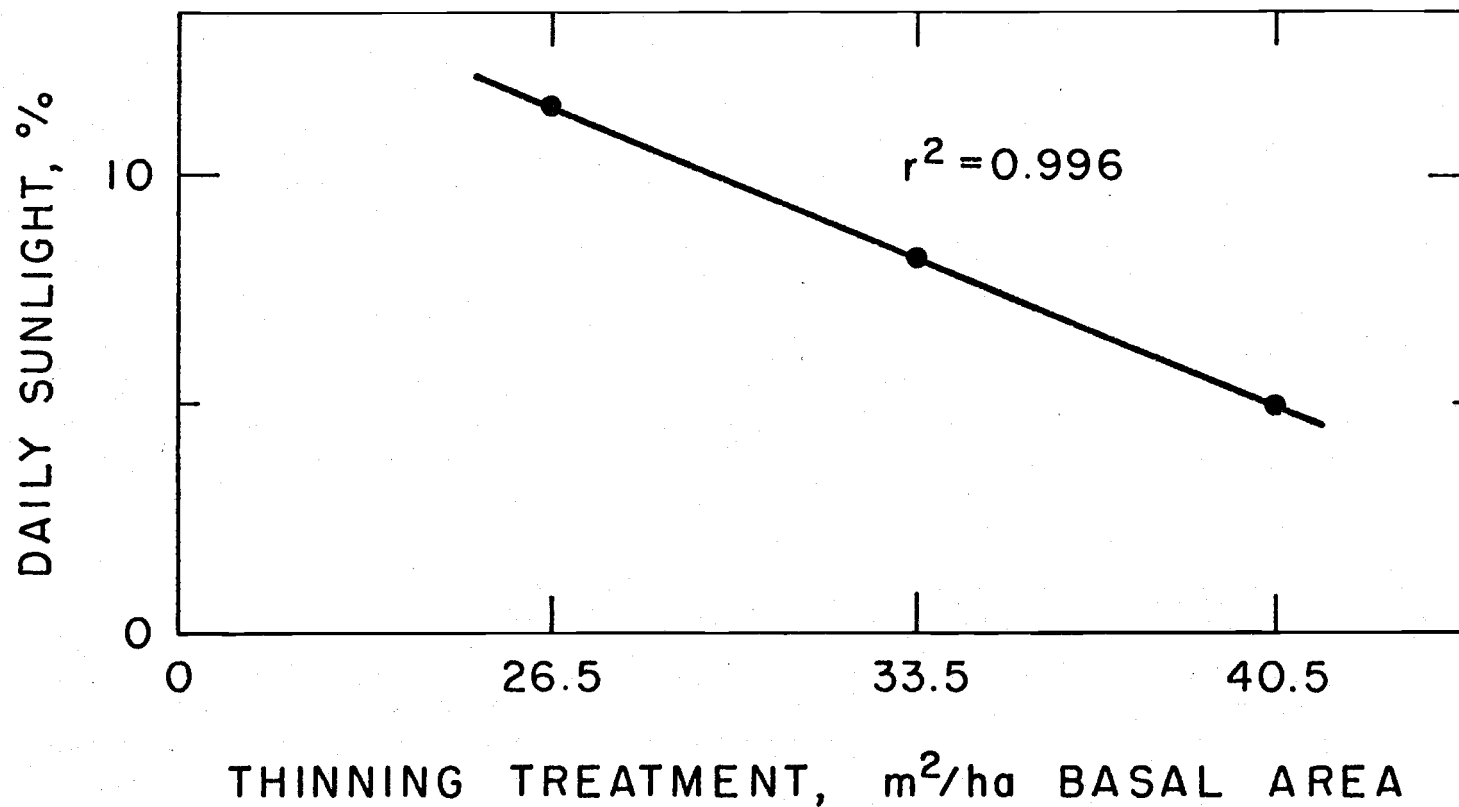


Figure 1-1. Relationship Between Average Percent of Full Sunlight Received at Seedling Crown Over an Entire Summer Day and Thinning Level of Overstory (65 Year Old Douglas-fir). Each Point Represents the Average of 80 Understory Trees.

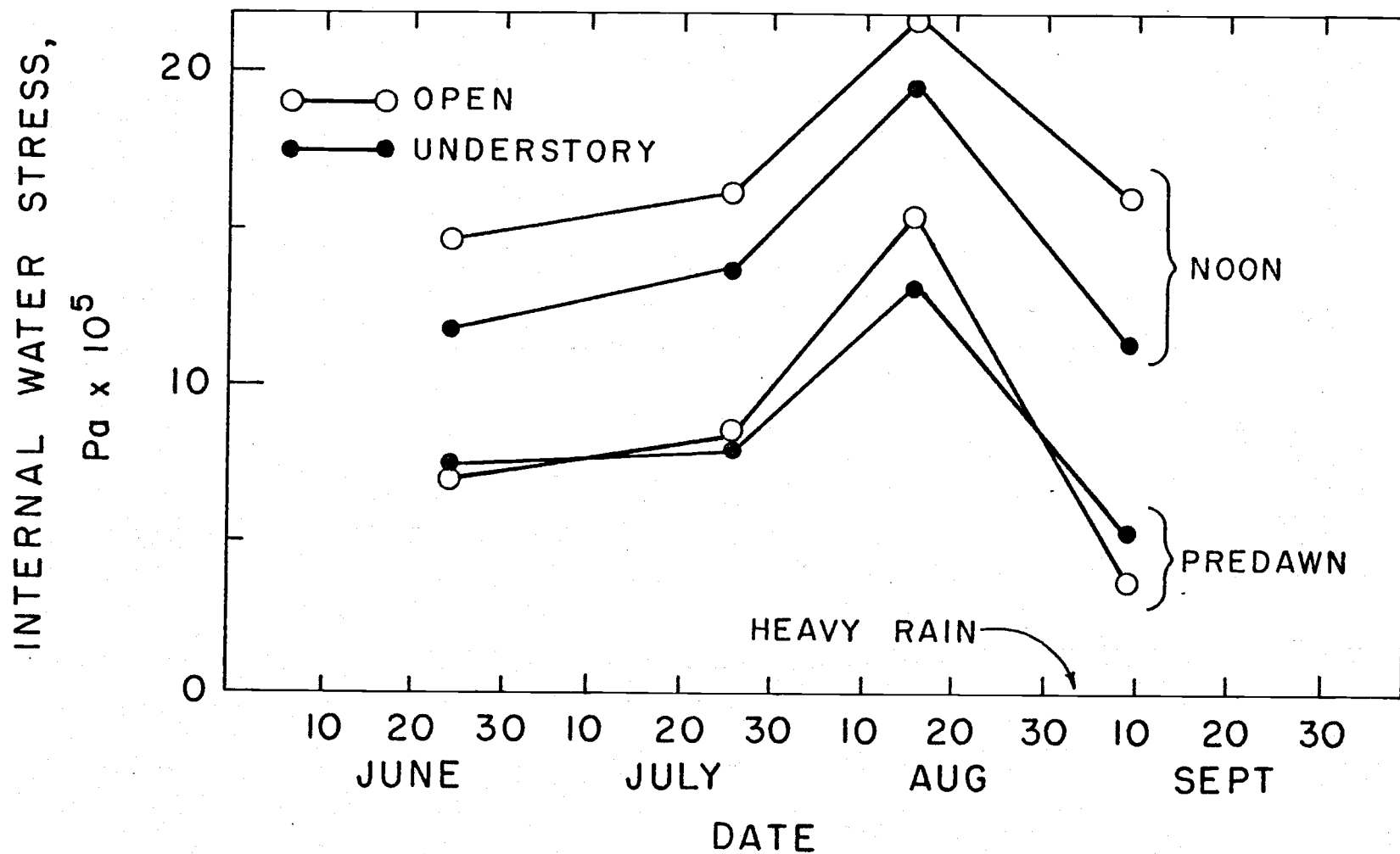


Figure 1-2. Water Stress Patterns Recorded During Summer 1977 in Young Douglas-fir Growing in the Understory and in the Open.

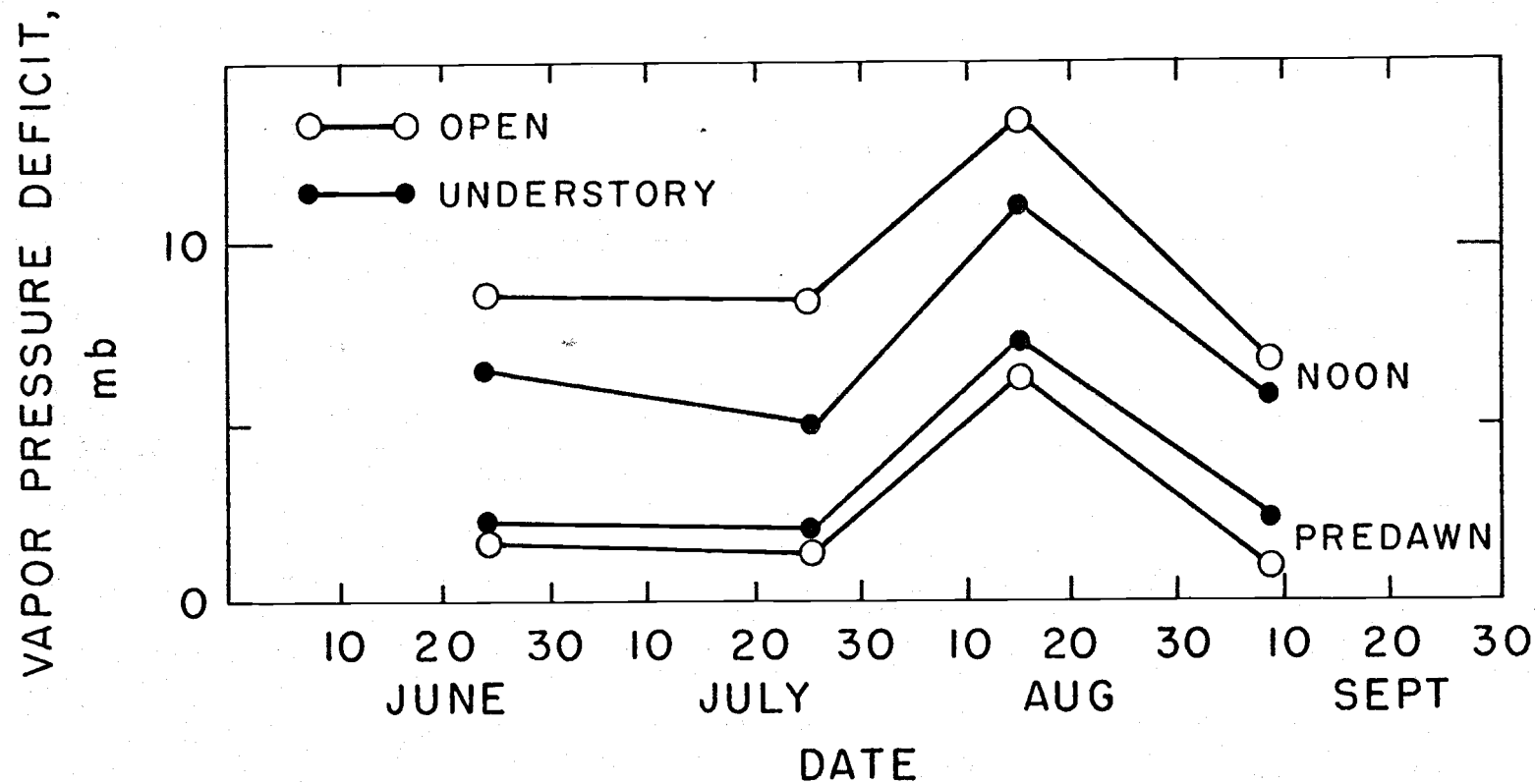


Figure 1-3. Evaporative Demand in the Shade of a Thinned Stand of Douglas-fir and at an Open Site.

Table 1-2. Summary of Temperature Data Collected at Black Rock (May 15 - Sept. 8, 1977) Beneath Light, Medium and Heavy Overstory Thinnings and at an Open Site. ¹.

	<u>Light</u>		<u>Medium</u>		<u>Heavy</u>		<u>Open</u>	
	Diurnal Monthly Mean	Range ^{2.}	Diurnal Monthly Mean	Range	Diurnal Monthly Mean	Range	Diurnal Monthly Mean	Range
<u>Air (°C)</u>								
May	8.6 ^a ^{3.}	10.9-6.3	7.3 ^a	9.9-4.7	7.5 ^a	9.7-5.2	11.3 ^b	15.5-7.1
June	16.6 ^a	20.3-12.9	16.5 ^a	20.8-12.4	17.7 ^a	21.7-13.7	16.2 ^a	22.7-9.6
July	16.3 ^a	20.3-12.4	N/A ⁴		15.3 ^{a,b}	19.9-10.6	17.9 ^{a,c}	24.9-10.8
August	20.5 ^a	24.5-16.5	20.2 ^a	24.8-15.5	19.5 ^a	24.2-14.9	22.3 ^a	29.7-14.9
September	15.4 ^a	17.9-12.8	15.2 ^a	18.3-12.1	14.5 ^a	17.2-11.7	16.6 ^b	22.2-10.9
<u>Soil (°C)</u>								
May	7.4 ^a		N/A		6.3 ^b		9.1 ^c	
June	10.3 ^a		N/A		10.9 ^b		13.0 ^c	
July	12.55 ^a		N/A		13.6 ^b		14.4 ^c	
August	16.5 ^a		N/A		16.4 ^a		16.6 ^a	
September	14.1 ^a		N/A		14.6 ^b		14.4 ^b	

1. 30-day recording thermographs were used. Air temperature measured at 1.5 m; soil temperature at -20 cm.

2. Range extends from mean of monthly high to mean of monthly low.

3. Any two means with different letters are significantly different at the .05 level.

4. N/A means not available.

Average total vegetative cover around sample trees was not different between the thinning levels (Table 1-3). Although differences in cover of woody species, as well as cover of herbaceous species, appear great, within plot variation has negated any significance (Witler 1975, Temmes 1978). The proportion of herbaceous cover increases with thinning.

II. Tree Growth in the Understory

Table 1-4 shows average leader growth, diameter growth and tree height for understory trees from each of the replicated plots within each thinning treatment; open-grown trees are also shown.

Average heights of understory trees for the past three years are represented by Figure 1-4. The slopes of the lines increase with thinning, especially between the heavy and light, and medium and light treatments.

Figure 1-5 shows average xylem expansion over the last three years. Rate of growth is increasing, especially for trees from the heavily thinned plots.

The interaction of light and tree height on growth is summarized in Table 1-5. Both leader and diameter growth increase with light; and within any light class the increment of growth increases with height of tree.

The relationship between each of the following pairs of variables was tested. Simple correlation coefficients are for understory

Table 1-3. Average Vegetative Cover (%) Measured Around Sample Trees at Each Plot

<u>TMT</u> ^{1.}	<u>REP.</u>	<u>N</u>	<u>MEAN</u> ^{2.} <u>TOTAL</u>	<u>MEAN</u> <u>WOODY</u>	<u>MEAN</u> <u>HERBACEOUS</u>
L	1	18	63	58	5
	2	17	24	19	5
	3	17	25	14	11
	4	18	15	8	7
\bar{X}			32	25	7
M	1	20	51	46	5
	2	20	44	36	8
	3	19	21	14	7
	4	20	33	19	14
\bar{X}			37	29	8
H	1	19	26	19	7
	2	19	40	17	23
	3	20	46	9	37
	4	20	27	17	10
\bar{X}			35	15	20
0	-	19	78	15	63

1. TMT: L, M, H = Light, Medium, Heavy Overstory Thinnings;
0 = open plot.

2. Mean Total = Mean Woody Component + Mean Herbaceous Component

Table 1-4. Average Height, Leader and Diameter Growth for 1977 of Understory and Open Grown Douglas-fir

<u>Level of Overstory Thinning</u>	<u>Replication</u>	<u>Leader Growth (cm)</u>	<u>Height (cm)</u>	<u>Diameter Growth (mm)</u>	<u>n</u>
Light	1	4.6	28.5	0.9	18
	2	4.2	33.2	0.7	17
	3	3.3	32.5	0.7	17
	4	3.9	30.3	0.8	18
Medium	1	3.9	27.0	0.9	20
	2	5.9	37.8	1.0	20
	3	4.2	32.7	0.6	19
	4	9.7	59.7	1.6	20
Heavy	1	6.8	38.3	1.2	19
	2	6.5	40.4	1.3	19
	3	8.0	55.6	1.1	20
	4	8.2	49.4	1.4	20
Open Grown	-	20.1	76.1	3.1	19

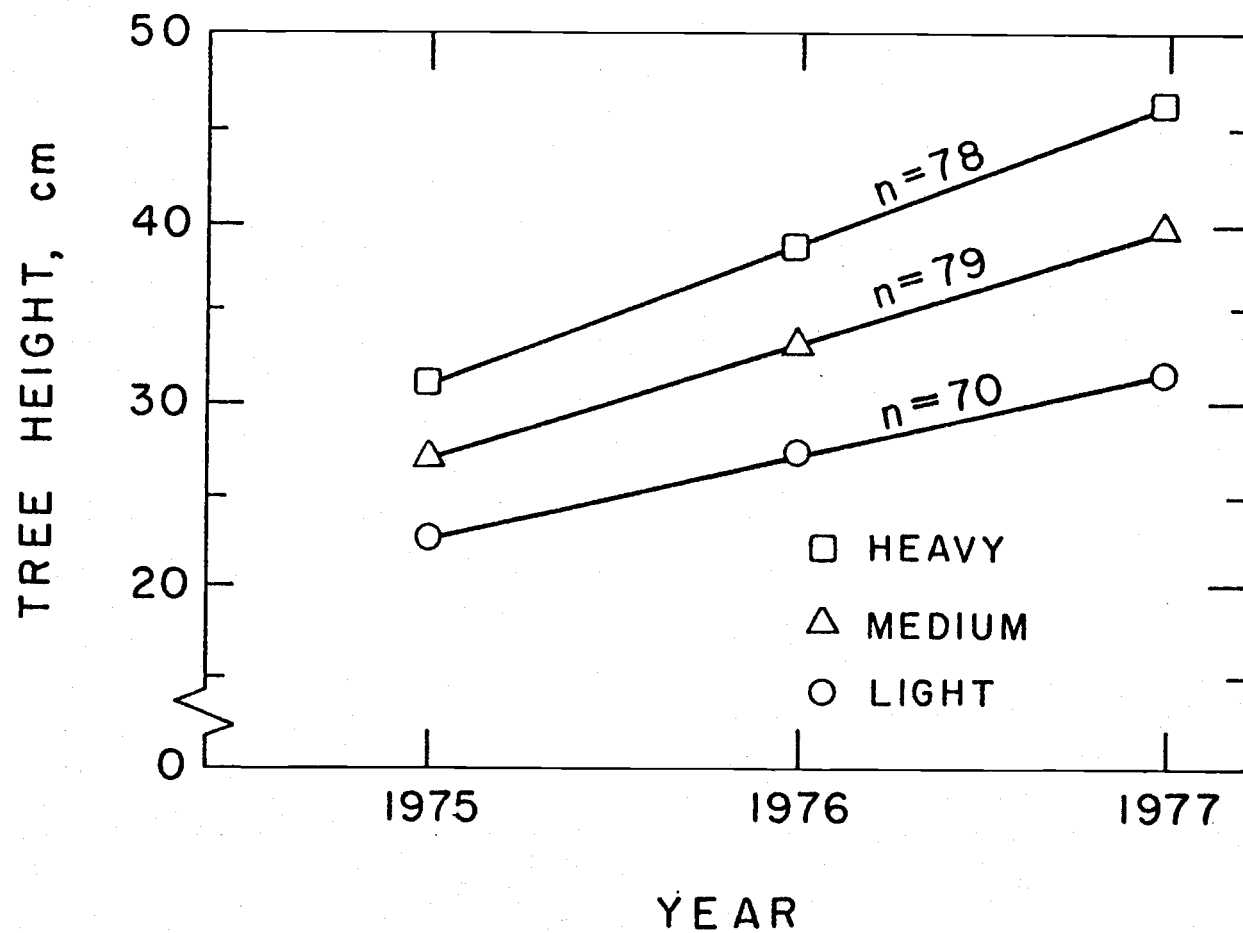


Figure 1-4. Average Heights for the Last Three Years of Young Douglas-fir Growing Beneath Three Levels of Overstory Thinning.

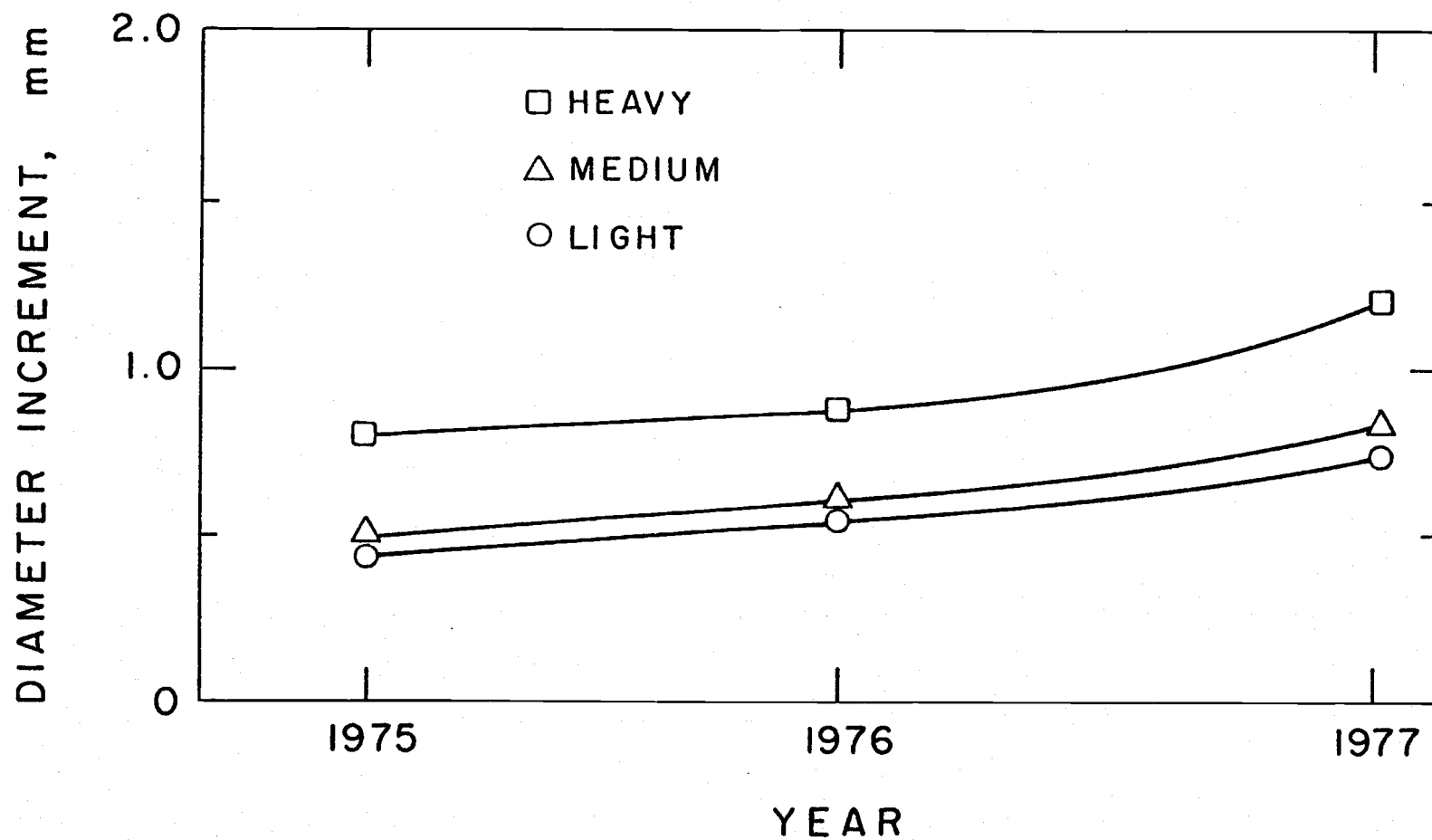


Figure 1-5. Diameter Increment (Inside the Bark) for the Past Three Years of Young Douglas-fir Beneath Three Levels of Overstory Thinning. Each Point is the Average of 12 Measurements.

Table 1-5. Mean Leader (cm) and Diameter (mm) Increment
in Relation to Daily Sunlight and Tree Height.

A. Leader Growth 1977

HGT (cm)	% Daily Sun								\bar{X}
1976	0-5	5-10	10-15	15-20	20-25	40-45	45-75	75-100	
0-15	1.2 ^a (2)	2.1 (4)	N/A	N/A	N/A	N/A	N/A	N/A	1.78
15-30	3.3 (44)	4.1 (63)	3.3 (7)	4.5 (16)	N/A	11.2 (2)	8.8 (1)	4.7 (3)	3.97
30-45	6.3 (15)	6.9 (27)	2.2 (1)	7.7 (8)	N/A	N/A	10.9 (1)	12.3 (3)	7.11
45-60	8.6 (4)	9.1 (14)	N/A	11.9 (6)	17.0 (1)	8.7 (1)	16.2 (2)	15.1 (1)	10.56
60-75	6.7 (1)	12.9 (1)	N/A	18.2 (2)	N/A	N/A	N/A	31.3 (2)	19.77
75-90	N/A ^b	15.1 (3)	N/A	12.8 (2)	N/A	N/A	N/A	55.0 (1)	20.97
90-105	N/A	23.8 (2)	12.0 (1)	18.2 (1)	N/A	N/A	N/A	48.8 (1)	25.30
105-150	11.4 (1)	N/A	N/A	N/A	N/A	N/A	N/A	37.2 (2)	28.57
\bar{X}	4.36	5.99	4.13	8.16	17.00	10.37	13.03	23.61	

a. The mean value for each category is based on the number of observations shown in parenthesis.

b. N/A mean not available.

B. Diameter Growth 1977

HGT (cm)	% Daily Sun								\bar{X}
1976	0-5	5-10	10-15	15-20	20-25	40-45	45-75	75-100	
0-15	0.3	0.6	N/A	N/A	N/A	N/A	N/A	N/A	0.52
15-30	0.7	0.9	0.7	1.2	N/A	1.5	1.4	1.2	0.84
30-45	0.9	1.2	1.3	1.4	N/A	N/A	1.6	2.5	1.24
45-60	1.5	1.2	N/A	1.5	2.2	1.9	3.0	2.5	1.54
60-75	1.3	1.4	N/A	2.2	N/A	N/A	N/A	4.8	2.78
75-90	N/A	2.2	N/A	1.6	N/A	N/A	N/A	7.6	2.90
90-105	N/A	2.3	3.0	2.4	N/A	N/A	N/A	6.7	3.32
105-150	1.8	N/A	N/A	N/A	N/A	N/A	N/A	4.4	3.50
\bar{X}	0.81	1.03	1.00	1.41	2.20	1.60	2.25	3.55	

trees and each is significant at the .01 level.

Leader growth 1977 with leader growth 1976	$r = .87$
Leader growth 1977 with tree height 1976	$r = .79$
Leader growth 1977 with tree height 1975	$r = .72$
Diameter growth 1977 with diameter 1976	$r = .68$
Diameter growth 1977 with tree height 1976	$r = .69$
New biomass (new needles + new stems) with tree height 1976	$r = .88$
New biomass with tree height 1975	$r = .84$

Simple correlation coefficients between leader and diameter growth and new biomass vs. light are .29, .36 and .36, respectively. These relationships were examined graphically (not presented) for each of the thinning treatments and for replications within the treatments to ensure that patterns were essentially the same.

Analysis of variance of the following form was conducted to test differences in average growth of understory trees between the three intensities of overstory thinning:

<u>Source</u>	<u>df</u>
Replication	3
Treatment	2
Linear	1
Quadratic	1
Replication X Treatment	6
Residual	215

The orthogonal contrasts for the linear and quadratic components were based on the idea that midpoints of overstory thinning levels (26.5, 33.5 and 40.5 m²/ha BA) were equally spaced. Significant (.05 level) linear differences were found among the treatments in leader and diameter growth and new biomass production.

Analysis of variance revealed a significant linear effect, while simple correlation of those variables previously mentioned was strong. Knowing this, regression functions were developed whereby average response of leader and diameter growth and new biomass could be estimated at each of the thinning levels (Table 1-6). From these regression functions, mean leader growth, estimated at each of the three levels of thinning, agreed within ± 0.1 cm, diameter growth within ± 0.02 mm and new biomass within ± 0.2 g.

Because of linear differences in growth, estimation of average responses between thinning levels is possible. However, within any one level variation in growth between trees is high; especially under the heaviest thinning. Microsite differences are great, particularly in regard to light. Trees must adjust growth strategies to make most efficient use of resources available. Such adjustments in growth patterns will be examined in the following chapter.

On the heavily thinned plots, those understory Douglas-fir chosen subjectively for their larger size average 28.6 cm in leader growth and 186 cm in height at nine years of age; larger trees beneath the medium thinning averaged 26.9 cm in leader growth and 155 cm in height at seven years.

Table 1-6. Parameter Means and Linear Functions, Developed From These Means, for Estimating Mean Response of Understory Douglas-fir at Three Levels of Overstory Thinning.

Level	a.	<u>Means</u>						
		(cm) Leader Growth 1976	(cm) Leader Growth 1977	(cm) Tree Height 1975	(cm) Tree Height 1976	(mm) Stem Diameter 1976	(mm) Diameter Growth 1977	(g) New Biomass
L		4.509	3.984	22.577	27.086	3.166	0.787	0.841
M		6.423	5.946	27.020	33.443	4.066	1.025	1.797
H		7.587	7.381	31.105	38.692	5.289	1.253	3.334

Linear Functions

Dependent	Concomitant	b_0	b_1	r^2
Leader Growth 1977	Leader Growth 1976	-0.996	1.097	.998
Leader Growth 1977	Tree Height 1976	-3.928	0.293	.999
Leader Growth 1977	Tree Height 1975	-4.962	0.399	.996
Diameter Growth 1977	Diameter 1976	0.114	0.218	.990
Diameter Growth 1977	Tree Height 1976	-0.303	0.040	.998
New Biomass	Tree Height 1976	-5.040	0.213	.965
New Biomass	Tree Height 1975	-5.843	0.291	.975

a. L, M, H = Light, Medium, Heavy Overstory Thinning; N = 70, 79, 78 for L, M, H, respectively.

Discussion

Of those variables measured to describe the understory environments, light separated the thinning levels best. Variation in light reaching the understory, from one point to the next, increased with degree of thinning. Growth of understory trees follows this pattern. All growth measurements varied least under the lightly thinned plots and greatest under those plots thinned most heavily. The light thinning approaches the open plot in producing a more uniform light environment near the ground.

The strong relationship found between current year leader growth and leader growth or tree height of previous years agrees with the data of Emmingham and Waring (1973) and indicates that the individual tree depicts well the influence of light and other factors on productivity.

Simple correlation between tree height 1977 and age is much lower for understory trees ($r = .40$) than for open grown trees ($r = .73$), though both correlation coefficients are highly significant ($p < .01$). The lower correlation between height and age for the understory trees undoubtedly is because of a more varied environment. Blum (1973) attributed the relatively low correlation between height and age in Abies balsamea (L) Mill. to a high degree of tolerance for shade.

Differences in mean height and diameter growth of trees under the three thinning levels show the sensitivity of Douglas-fir to a change of only a few percentage points of light (Brix 1970). Growth increment

increases not only with light but also with size of the tree and indicates that understory trees are following the same pattern of growth as Douglas-fir on an exposed mesic coastal site (Newton 1964), but at relatively reduced rates. Further, regression analysis showed average leader growth and biomass production beneath each thinning level may be estimated from mean tree height at least two years previous, evidence that these growth patterns are well established.

There are two advantages to these slower rates of growth. First, the advanced reproduction competes little or none with crop trees in the overstory. Second, a small tree is more flexible, therefore, mechanical damage during overstory removal is reduced (Williamson 1973).

Root systems were not examined. Other work has shown that shoot to root ratios of Douglas-fir increase as light decreases, when moisture is adequate and temperatures are moderate (Drew and Ferrell 1977, Lavender and others 1968, Brix 1967). This may be an adaptive type of behavior or it may be a modification of development due to a proportional increase of far-red light beneath the coniferous canopy (Holmes and Smith 1977, Atzet and Waring 1970).

Trappe (personal communication)¹ believes that understory trees have formed mycorrhizal associations. Also, the bonding of an understory tree to an overstory tree through a fungal hyphoconnection

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(Trappe and Fogel 1977) is possible. Root grafting between understory and dominant trees may occur also (McMinn 1963).

It must be emphasized that thinning, in contrast to a shelter-wood, has allowed Douglas-fir to reproduce naturally under the canopy. Although the primary objective in thinning has been to increase yield, the future stand of Douglas-fir has established in the process. Such results may be expected when similar vegetation types are thinned elsewhere (Williamson 1973). The number of trees established may be related to light, moisture, temperature and seed fall, as well as to a proper seed bed.

This study has shown that Douglas-fir can establish itself and grow for at least 15 years at an average of 5 to 12 percent of daily sun. These trees are far from static; indeed, patterns of growth are similar to those of Douglas-fir growing in the open: increasing increment of growth with size of tree. Growth measurements made on larger understory trees emphasize the potential of Douglas-fir at low levels of light.

These results suggest that a young forest could be established at the time of final harvest, saving several years in regeneration lag time (Starker 1970). Also, planting costs and planting failures would be avoided and the forest gene pool maintained (Silen 1976).

It is recommended that studies be made of the potential problem of brush encroachment resulting from opening of the stand through thinning, and the effect brush would have on establishment and growth of understory trees. Mechanical damage to trees in the understory,

as a result of overstory removal, must also be quantified. Morphological and physiological response to sudden exposure should also be investigated in understory Douglas-fir.

Growth Behavior of Douglas-fir Reproduction
in the Shade of a Managed Forest
in the Interior Coast Range of Oregon

Chapter 2: Growth Strategies and Light

Abstract

Growth patterns of young Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) occurring naturally in the shade of a managed forest were examined. Bud phenology in the spring was inversely related to light while renewed cambial activity was directly related to tree size and light. Rates of leader growth and biomass production, in relation to growth of the previous year and leaf biomass, were not significantly different for trees from three understory environments. A balance of foliar to stem biomass was maintained by understory trees. Physical characteristics of the tree accounted for most of the variation in growth.

Introduction

Adjustment to microenvironment is necessary if a plant is to function as efficiently as possible; this is especially true if growing conditions are less than optimum. Adjustment may be morphological (Tucker and Emmingham 1977), chemical (Gholz 1978, Koch 1976) or physiological (Bjorkman and others 1971, Fryer and Ledig 1972). Douglas-fir uses each of these approaches when adjusting to a particular environment (Del Rio and Berg 1978, Drew and Ferrell 1977, Aussenac 1973, Sorensen and Ferrell 1973).

The objective of this study was to examine growth strategies of young Douglas-fir occurring naturally under low levels of light.

Materials and Methods

The study site and materials and methods used were described thoroughly in the previous chapter. In review, the light, medium and heavy overstory thinnings averaged 5, 8 and 12 percent, respectively, of daily sun near the ground. No significant differences were found between the three understory environments in plant moisture stress, evaporative demand or vegetative cover.

The beginning of bud and cambial activity in relation to micro-environment and tree size was examined.

Regression techniques were applied to the following relationships to determine the degree of influence of concomitant (independent) variables on growth parameters (dependent variables):

Leader Growth 1977 (cm) with Leader Growth 1976 (cm)

\log_{10} New Biomass (g) with \log_{10} Old Needles (g)

New Needles (g) with New Stems (g)

Old Needles (g) with Old Stems (g)

Relationships were examined for understory trees from each thinning treatment and with the treatments combined to determine if the degree of influence among thinning treatments was different; the following method was applied.

For each treatment:

<u>Source</u>	<u>df</u>	
Replication	3	
Regression	X	
Residual	66-X=L	Light Thinning
	75-X=M	Medium Thinning
	74-X=H	Heavy Thinning

For treatments combined:

<u>Source</u>	<u>df</u>	
Replication	3	
Treatment	2	Used to test dif-
Linear	1	ferences among
Quadratic	1	treatments in
Replication X Treatment	6	average growth
"Common" Regression	X	
Residual	215-X=D	

To test for differences in the regression among treatments, the lower half of the analysis of variance table for treatments combined was modified to:

<u>Source</u>	<u>df</u>
"Common" Regression	X
Differences in Regression	D-L-M-H
Among Treatments	
Residual	L+M+H

Open grown trees were examined separately using simple regression:

<u>Source</u>	<u>df</u>
Regression	X
Residual	18-X

Results

Table 2-1 summarizes observations of bud phenology made during two periods in spring, 1977. Buds were active earliest under the least amount of light. These observations agree with those of Drew and Ferrell (1977).

The lag of terminal behind lateral buds reported by Sweet (1965) is also apparent in Table 2-1. To quantify this lag, the relative fraction of terminal to lateral bud activity (T/L) was developed. This fraction is not constant; it decreases with time and with light. And, of course, a decrease in the fraction means an increase in the lag of terminal behind lateral buds. The greatest lag was in the open. At the second time period of observation, not one tree in the open had yet burst a terminal bud.

Microscopic examination of 39 stem cross-sections showed 14 to have an active cambium at the second pinning period of April 30 to May 1, 1977 (refer to methods, Chapter 1). Of those 14, seven were from the heavily thinned stands (Table 2-2). All three of the open grown trees examined showed an active cambium, although none of those three had displayed bud activity three weeks previous.

No difference was found in the pattern of leader growth relative to growth of the previous year for individual trees growing under the three thinning levels (Figure 2-1).

Individual trees from the three understory environments added new biomass (new needles + new stems) in relation to old needle biomass at

Table 2-1. Observed Activity of Lateral and Terminal Buds on Understory and Open Grown Douglas-fir

TMT ^{1.}	n	<u>4/10 - 4/17 1977</u>			<u>4/30 - 5/1 1977</u>		
		<u>% Budswell</u>			<u>% Budbreak ^{2.}</u>		
		LAT	TERM	T/L ^{3.}	LAT	TERM	T/L
L (5%)	80	79	45	57	76	31	41
M (8%)	80	69	43	60	79	28	33
H (12%)	80	61	31	50	70	18	22
O (80%)	20	40	15	38	50	0	0

1. TMT: L, M, H = Light, Medium, Heavy Overstory Thinning;
O = open plot.
Parenthetical value is average daily sunlight at seedling crown.
2. Budbreak is any green showing.
3. T/L is the relative fraction of terminal bud activity to lateral bud activity.

Table 2-2. Beginning of Cambial Activity Relative to Bud Activity at Different Light Environments

TMT ^{1.}	n	No. of Trees Showing Active Buds on 4/10 - 4/17/77	No. of Trees Showing Active Cambium on 4/30 - 5/1/77
L (5%)	12	9	2
M (8%)	12	8	2
H (12%)	12	8	7
0 (80%)	3	0	3

1. TMT: L, M, H = Light, Medium, Heavy Overstory Thinning;
 0 = open plot
 Parenthetical value is average daily sunlight at seedling crown.

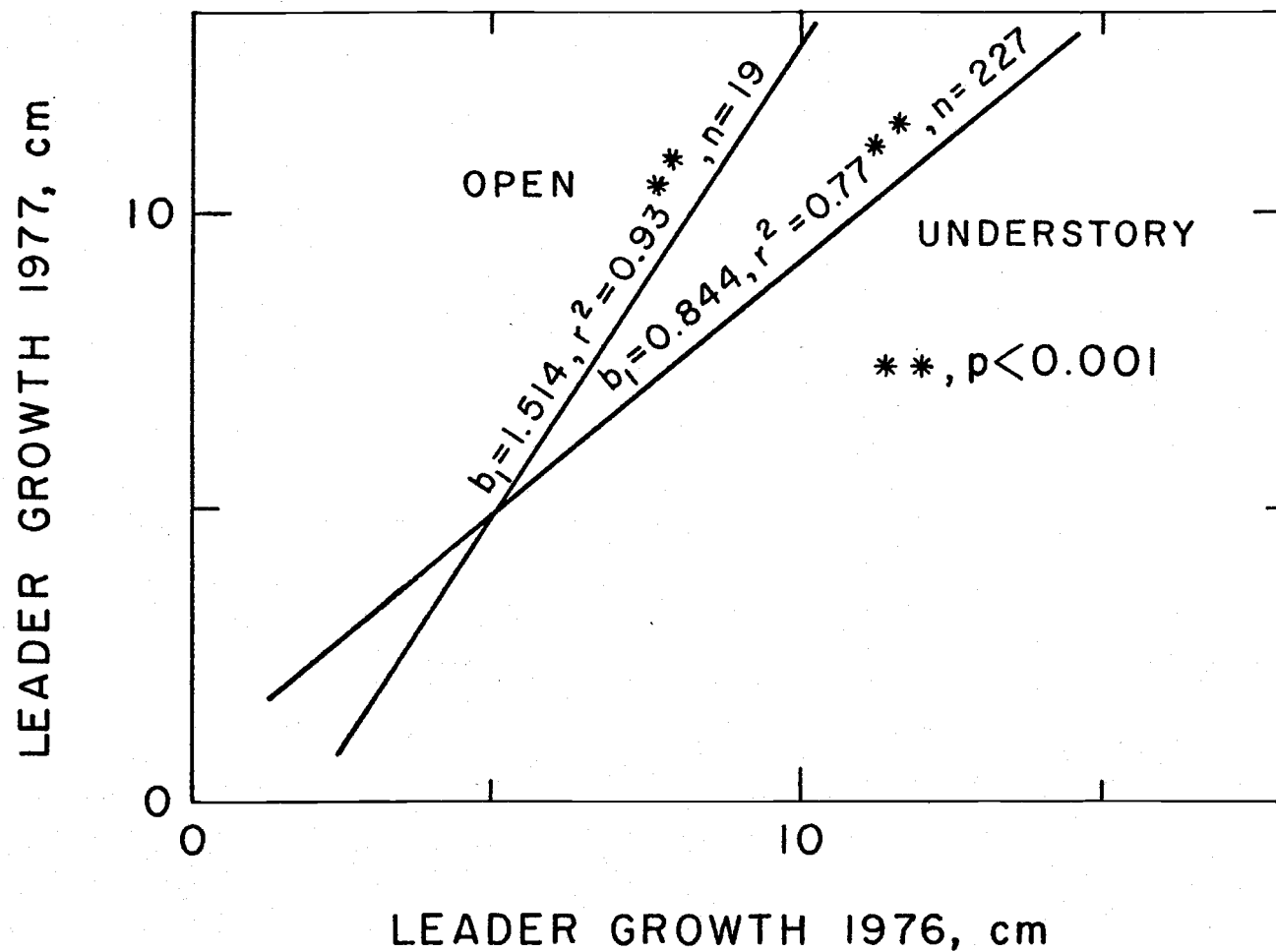


Figure 2-1. Current Year Leader Growth Relative to Leader Growth of the Previous Year for Understory and Open Grown Douglas-fir.

rates that were not significantly different from each other (Figure 2-2). Further, Figure 2-2 shows that understory trees were following patterns of growth similar to open grown Douglas-fir. Satoo (1971) reported a similar finding in Japanese larch.

Production of new needles in relation to new stems increased with level of overstory thinning (Figure 2-3). Regression coefficients of the light, medium and heavy thinnings were compared with a "t-test" and the slopes were found to be significantly different ($p < .05$) from one another. No differences among treatments were found in the ratios between needles and stems one year or older (Figure 2-4).

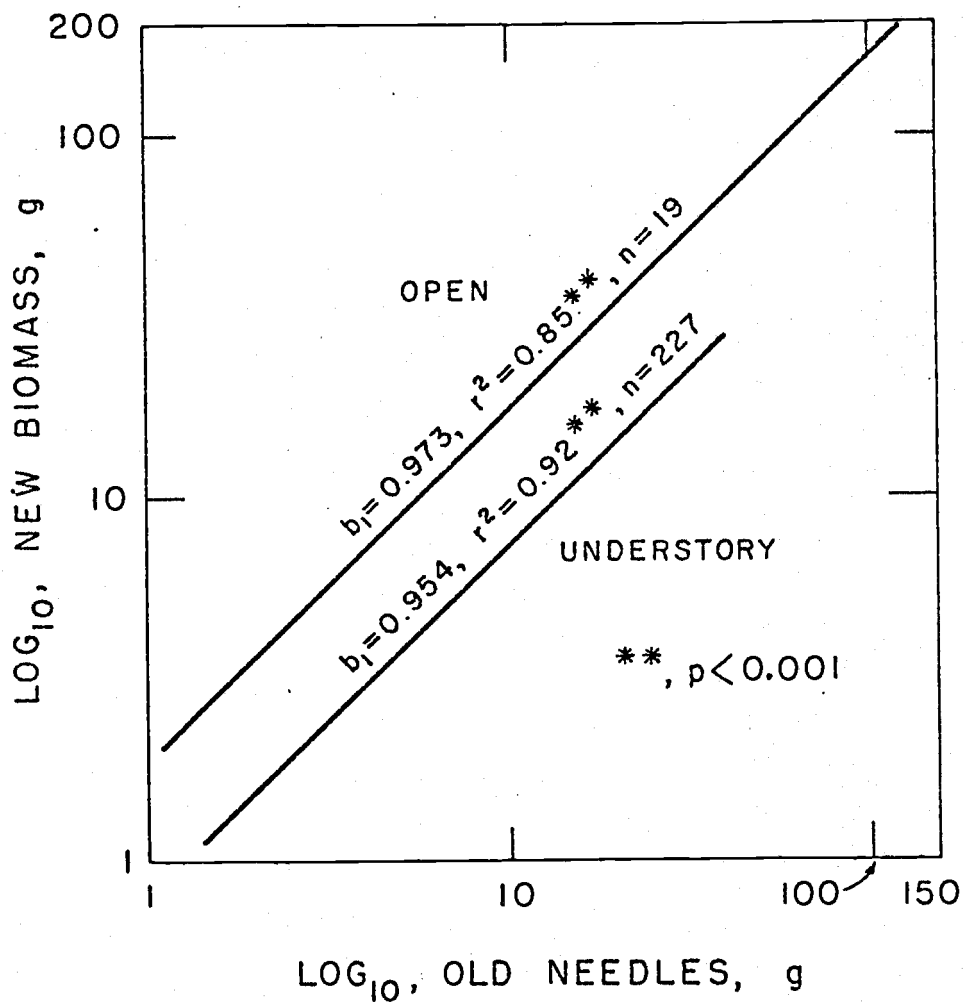


Figure 2-2. Production of New Biomass (Needles + Stems) in Relation to Biomass of Old Needles (> 1 Year) for Understory and Open Grown Douglas-fir.

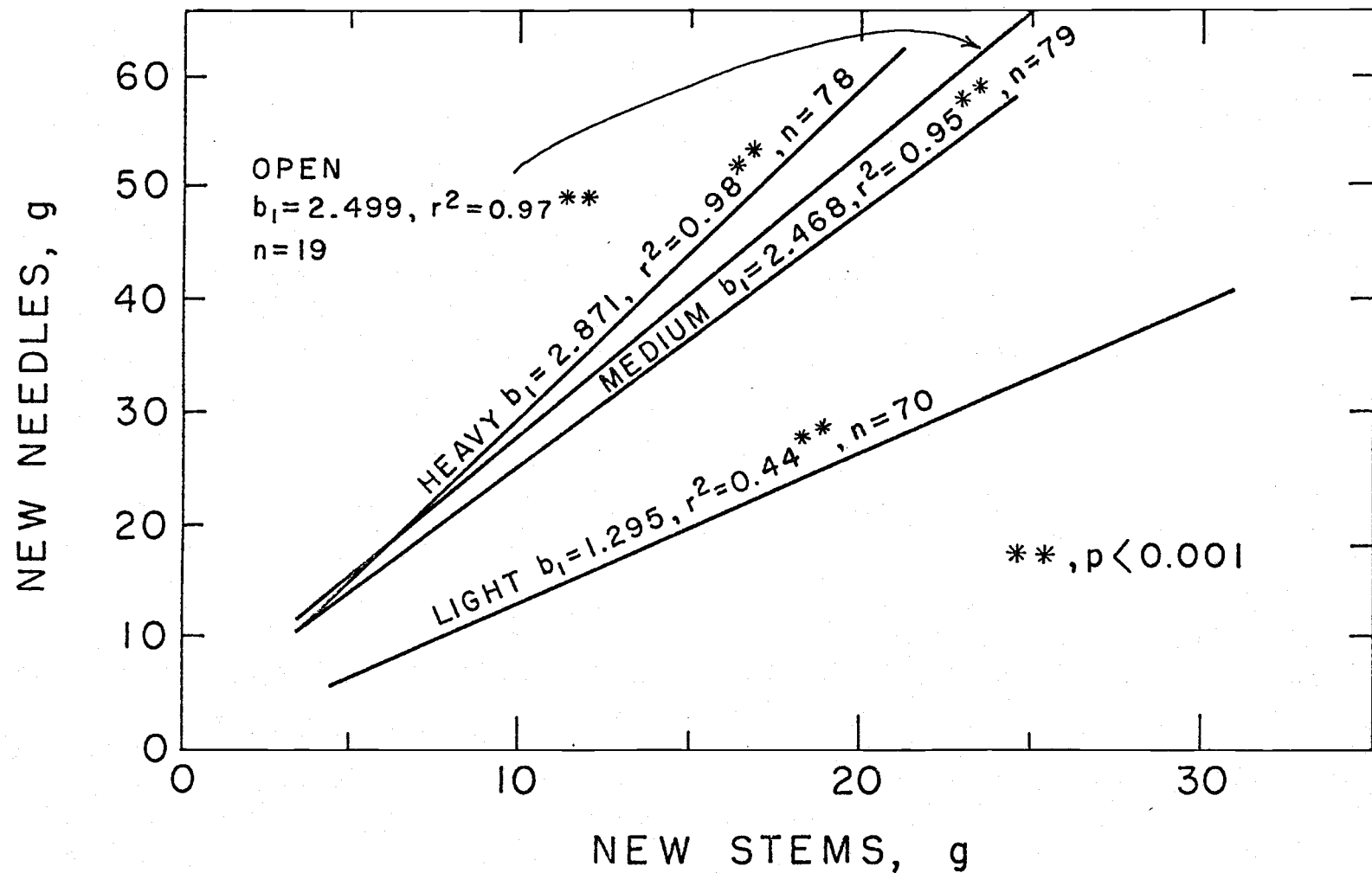


Figure 2-3. Mass of New Needles in Relation to New Stems for Douglas-fir Beneath Three Levels of Overstory Thinning and in the Open.

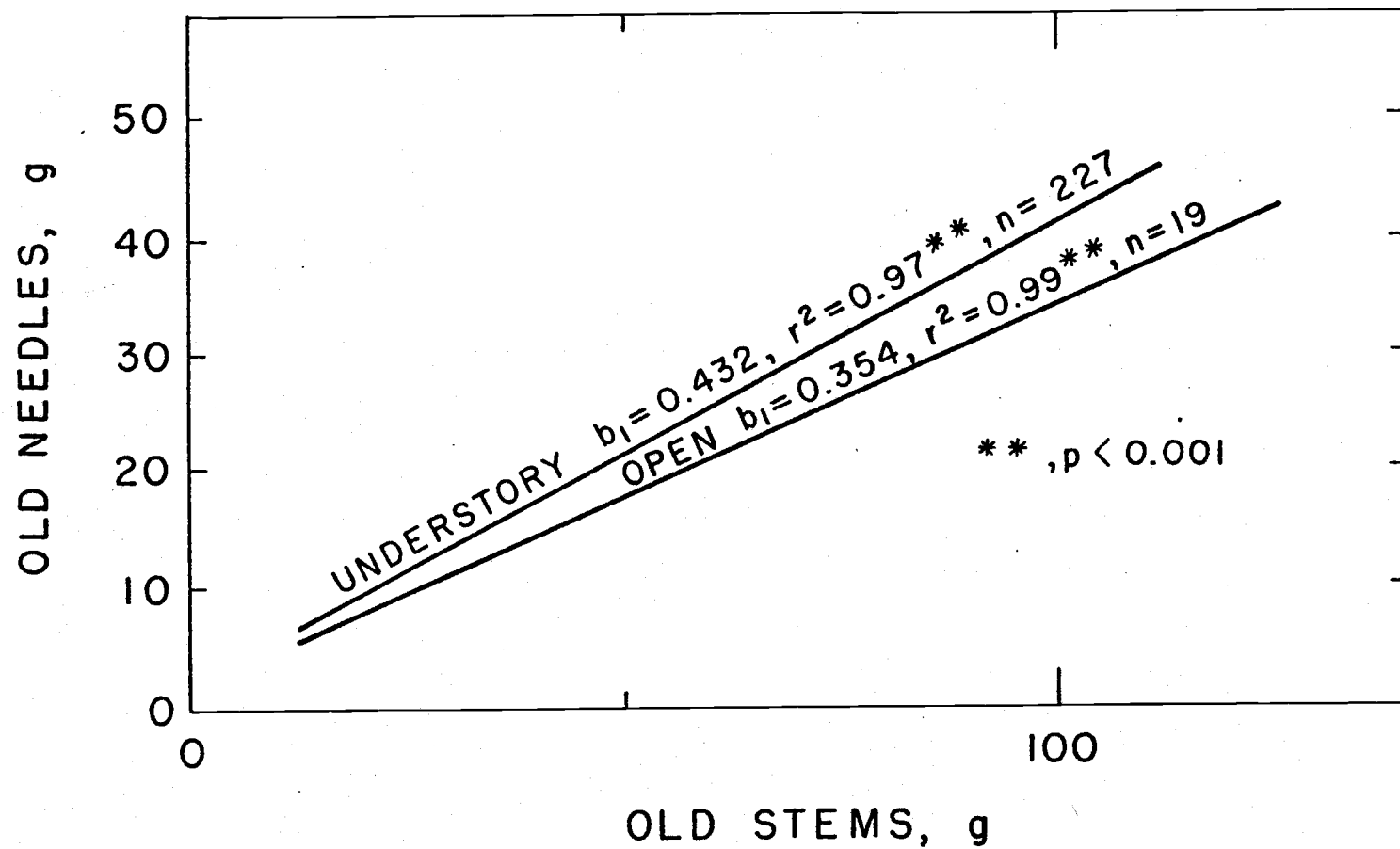


Figure 2-4. Mass of Old Needles in Relation to Old Stems for Understory and Open Grown Douglas-fir. Old > 1 year.

Discussion

Flushing of buds in the spring occurs as an interaction of photoperiod and temperature for some species of plants while others are independent of one or the other (Wareing 1956). This study showed an inverse relationship between beginning of bud activity and level of overstory thinning. This could be in response to warmer mean diurnal temperatures normally found beneath vegetative canopies (although air temperature data collected by Berg (unpublished) showed a nonsignificant difference of less than 2°C in diurnal mean beneath a lightly thinned stand and a fully exposed area during the month of April, 1977). However the influence of light cannot be discounted (Drew and Ferrell 1977). It would certainly be of adaptive value for a tree growing under a low level of light to expand new foliage as early as possible in the spring; the added photosynthetic tissue could capture that much more light for production of carbohydrate.

Renewed cambial activity in the spring is initiated by transport of auxin, indoleacetic acid, from the apical meristems of the tree (Wareing 1951). The renewed transport of auxin apparently is linked closely with the beginning of bud activity. Therefore, one might expect trees that begin bud activity earliest would begin cambial activity earliest as well. However, that was not the case here. Although buds began developing sooner in heavier shade, the start of cambial activity was more closely related to larger trees and

higher levels of light. Larger tree size implies greater physiological health; higher light suggests more carbon assimilation during the winter months (Emmingham and Waring 1977), resulting in a ready reserve of food at the onset of spring.

This work has shown that Douglas-fir can be very efficient in use of available light. Average leader growth and biomass production of understory trees were significantly different ($p < .05$) at 5, 8 and 12 percent average daily sunlight (Chapter 1); however, rates of growth of individual trees, in relation to growth of the previous year and leaf biomass, were not. Further, rate of biomass production for understory trees parallels that of open grown Douglas-fir. This points clearly to the very fine adjustment to a particular growing situation an individual tree makes. This hypothesis is supported by the fine balance of foliar biomass to stem biomass eventually attained by trees from the three understory environments, and by the sensitivity of specific leaf area of Douglas-fir to light (Del Rio and Berg 1978).

Those physical attributes of the tree selected as concomitant variables to account for variation in growth summarize the physiological condition of the tree with respect to its microenvironment. The addition to the regression model of variables such as light measured at the crown and vegetative cover around the tree added little to the explanation of variation in growth, indicating such information was incorporated in the tree. The plant is a product of its environment; interpreting the plant allows one to perceive the conditions of growth (Waring and others 1978).

The fine attunement of a plant to its environment explains the crisis suffered by understory plants that are suddenly exposed to increased light through clearcutting (Aussenac 1973). A gradual opening of the stand by commercial thinning may allow understory trees time to make the morphological and physiological changes needed to cope with more exposed conditions (Drew and Ferrell 1977, Hodges and Scott 1968).

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APPENDIX

Appendix I

Literature Review

Establishment and growth of natural tree seedlings, in conjunction with management practices such as thinning, involve a number of considerations; several will be discussed here.

Overstory thinning can alter patterns of light, moisture and temperature in the understory (Berg 1970, Strand 1968). Understory vegetation responds to changes in the physical environment, but the response varies. Anderson and others (1969) found that the herb layer under a forest in northern Wisconsin was more responsive to differences in throughfall precipitation determined by canopy opening than to differences in light. Emmingham (1971) believed that plant composition under mixed conifer stands in southwestern Oregon depended more on level of light since moisture was marginal on most sites while light varied greatly. Wiltner (1975), working with Douglas-fir on the Coast Range of Oregon, found that cover frequency of herbaceous plant species increased with overstory thinning. However, there was no consistent relationship between cover frequency of woody species and thinning but Douglas-fir in the understory increased significantly to about the same average level for all three thinning treatments. These changes in understory vegetation were primarily in response to increased light, though the greater number of Douglas-fir in the understory was, undoubtedly, influenced by the heavier seed crops resulting from thinning (Berg 1970, Reukema 1961).

The establishment of tree seedlings is a function of the physical environment (Hermann and Chilcote 1965). A number of studies have shown the benefit of shade for establishing seedlings on severe sites (Lindquist 1977, Williamson 1973, Coffman 1975). However, a seedling in a sheltered position must compete not only for moisture and nutrients, but for light as well (Newton 1964). Atzet and Waring (1970) found the lower limit of light energy for survival to be 1.85 ly per day for white fir and Douglas-fir and 36.8 ly per day for ponderosa pine; but as moisture became limiting, the lower limit was driven upward. Working with red pine seedlings, Strothmann (1967) reported that the removal of competition for light invariably produced a larger growth response than did the removal of competition for moisture. Kozlowski (1949) concluded that the interaction of light and moisture is difficult to separate. It is possible that over compensation by one may improve the situation caused by a deficiency of the other.

To survive at low light, a plant must photosynthesize efficiently, it must be able to translocate photosynthate to all functional organs, and it must have an inherent vigor which allows it to remain healthy at low rates of metabolism (Bordeau and Laverick 1958). Variation in photosynthetic efficiency varies among and within species of forest trees (Ferrell 1970). For example, photosynthesis at low light was greater in sugar maple than in black oak (Wuenschel and Kozlowski 1970). The photosynthetic apparatus of yellow birch was found to adapt poorly to shaded conditions (Logan 1970). In saturating light, the rate of apparent photosynthesis of young leaves of shade-grown

seedlings was only half that of sun-grown seedlings; for old leaves the reduction was even greater. On the other hand, Hodges and Scott (1968) found that shade foliage of six conifer species (including Douglas-fir) was more efficient in assimilating carbon dioxide than was foliage from sun grown plants. Wuenscher and Kozlowski (1970) speculated that differences in photosynthetic rates at low light between tolerant and intolerant species were partially explained by transfer resistance of carbon dioxide; at low light greater stomatal resistance limited CO_2 intake of intolerant species. Hodges and Scott (1968) speculated that within a species sun grown foliage decreased membrane permeability to resist water loss and thereby increased resistance to CO_2 diffusion. Helms (1972) concluded that establishing strong relationships between net photosynthesis and environmental factors was difficult because of the interdependence of variables.

Patterns of growth and distribution of growth are influenced by the environment. Hellmers and others (1970) concluded that night temperatures had the greatest influence on height growth and seedling development in Engelmann spruce, while day temperatures affected bud development and seedling survival. Brix (1967) found that increasing light intensity affected dry matter production of Douglas-fir in two opposing ways: it increased the rate of photosynthesis per unit leaf area, and it decreased the leaf area added per unit of dry matter produced. Red pine seedlings grown under abundant light had a significantly higher proportion of their total dry weight in the needles than did shade-grown seedlings (Strothmann 1967). The

uptake of carbon dioxide by Douglas-fir seedlings and the allocation of photoassimilated carbon were closely related to seedling phenology (Webb 1977). Newly flushing needles had the largest requirement for photoassimilated carbon; as these needles matured, this carbon requirement declined. Drew and Ferrell (1977) noted that under adequate moisture and moderate temperatures Douglas-fir seedlings progressively allocated more dry matter production to shoots than to roots as light decreased; as temperature increased and moisture became limiting root growth was favored over shoot growth.

Development of the root system is affected by conditions of growth. McMinn (1963) found that intermediate and suppressed Douglas-fir had a tap root habit with very little branching. He believed that little branching may be advantageous in young trees in that it allows pioneer roots to extend over more area while establishing the main structural elements of the root system. McMinn also observed that the roots of small trees were grafted to the main lateral roots of larger trees. Eis (1972) examined the root systems of Douglas-fir, western hemlock and western redcedar and determined that dominant trees usually supported the growth of the root system and lower boles of grafted suppressed trees. Also, bonding of an understory tree to a larger tree is possible through a fungal hyphoconnection (Trappe and Fogel 1977).

A plant adjusts to a particular environment both physiologically and morphologically. If that environment is altered, readjustment becomes necessary. Bjorkman (1968) studied the photosynthetic properties in sun and shade ecotypes of Solidago virgaurea to

determine the cause of the drop in photosynthetic efficiency of the shade type when grown in strong light after weak light. The shade type had less carboxydismutase than the sun type; there was a high degree of correlation between enzyme concentration and rate of light saturation. Sorensen and Ferrell (1973) found that when Douglas-fir plants from two growth environments were interchanged, the photosynthetic rates of the seedlings changed to those of the new environment within 10 days. Tucker and Emmingham (1977) noted marked effects on the leaves of residual western hemlock after clear and shelterwood cutting. Leaves that had developed in the shade and were later exposed showed changes in leaf area and structure toward a configuration which was more efficient in the utilization of light and water. Several recent studies have reported changes in pigment and nutrient concentrations in leaves in relation to light (Gholz 1978, Lewandowska and Jarvis 1977, Koch 1976).

This paper has discussed the factors that allow tree seedlings to become established, tree growth in relation to environment, and the inherent ability of many plant species to readjust as the environment is modified. Two very important questions remain unanswered regarding Douglas-fir in the understory:

1. How long will growth continue at levels of light far below optimum?
2. How will response to release vary with time of understory existence?