

AN ABSTRACT OF THE THESIS OF

Eva Karin Marianna Temmes for the degree of Master of Science
in Forest Science presented on November 18, 1977
Title: The Quantity and Composition of Ground Vegetation in Different
Light Environments under a Douglas-fir *Pseudotsuga menziesii* (Mirb)
Franco, Stand in the Oregon Cost Range
Abstract approved: _____

Alan B. Berg

The relationship between ground vegetation and light intensity under a 60 to 65-year-old Douglas-fir forest was investigated. Biomass and height of ground vegetation were measured and cover was estimated on small sample units (30 centimeters in diameter) on permanent research plots, one-acre in size, on the George T. Gerlinger Experimental Forest at Black Rock, Oregon. Three thinning intensities, from light to heavy, have been maintained on the research plots over approximately 20 years. Light intensity was measured with photosensitive paper as a light integrator for one day in the summer.

Also basal area of the trees and taller shrubs surrounding the sample units of ground vegetation were measured. These variables were assumed to represent root competition between ground and overstory vegetation.

The results show that with increased thinning intensity the average light intensity near the ground, the average cover and height of ground vegetation all increased. But no significant differences were found in the

biomass of ground vegetation between different thinning intensities, because of the great variation in biomass within each research plot.

However, no meaningful correlation was found between either biomass, cover, or height of ground vegetation and light intensity on the small sample units. A multiple linear regression analysis with the additional variables of the basal areas of the surrounding trees and shrubs also revealed no meaningful correlation.

The most important species on the research plots were Oregon grape (Berberis nervosa), bracken fern (Pteridium aquilinum), and a few herbaceous species such as Trientalis latifolia. There was too much inexplicable variation in the data also when examining the response of the most important species to light separately, although the variation was smaller. The regime of light intensity measured (1 to 30 percent of full sunlight) seemed to be sufficient for growth of these shade tolerant species of ground vegetation.

The results show clearly that, under the conditions of the Douglas-fir stand studied, the light intensity as measured on the sample units does not relate to the amount and composition of ground vegetation on these sites. Other unknown factors seem to have more influence on the distribution and quantity of ground vegetation in this Douglas-fir stand.

The Quantity and Composition of Ground Vegetation in
Different Light Environments under a Douglas-fir,
Pseudotsuga menziesii (Mirb) Franco, Stand
in the Oregon Coast Range

by

Eeva Karin Mariana Temmes

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed December 5, 1977

Commencement June 1978

APPROVED:

Professor of Forest Science

Head of Forest Science Department

Dean of Graduate School

Date thesis is presented December 18, 1977

Typed by Susan Ellinwood for Eeva Temmes

ACKNOWLEDGEMENTS

There are many people who have contributed to this project and to all who have supported me, I am sincerely grateful.

I wish to thank my major professor, Dr. Alan B. Berg for his guidance and encouragement throughout my degree program. He and my other instructors made my studies at Oregon State University most interesting and valuable for the development of my professional views.

Also, I especially wish to thank Ernie Del Rio who patiently shared an office with me, helped and encouraged me during all stages of my studies.

My stay at OSU was made financially possible by the generous ASIA-Fulbright and Oregon State Foreign Student Scholarships.

I thank all my international friends in Oregon who have made my stay in the U.S.A. most pleasant and valuable. I will take home to Finland many warm memories and rich experiences.

Thank you.

Eeva

TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION.	1
LITERATURE REVIEW	3
METHODS	9
Description of the Study Area.	9
Approach	12
Estimation of the Variables.	13
Cover and biomass of ground vegetation.	13
Light intensity reaching the ground	14
Basal area of the surrounding trees and taller shrubs.	17
Sampling Procedure	18
Analysis of the Data	19
LIMITATIONS	20
RESULTS	22
General Description of the Vegetation.	22
Cover.	22
Biomass.	24
Light.	26
Other Variables.	30
Correlations of the Variables.	31
CONCLUSIONS AND DISCUSSION.	33
LITERATURE CITED.	40

	<u>Page</u>
APPENDICES	
Appendix I Sampling Procedure.	44
Appendix II The Model of Multiple Linear Regression Analysis Used	45
Appendix III List of the Species Found on the Study Plots. .	46
Appendix IV Statistical Comparison of the Study Plots for Biomass and Cover of Ground Vegetation and Light Intensities Reaching the Ground . .	48
Appendix V Location of the Study Area and Plots.	49

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	The Basic Data of the Study Plots.	11
2	The Braun-Blanquet Classes for Estimating Cover of Ground Vegetation	14
3	Cover of Ground Vegetation by Plot	23
4	Biomass of the Ground Vegetation and Light Intensity on the Sample Units by Plot.	25
5	Maximum Cover of Common Plant Species in a Sample Unit by Classes of Percentage of Full Sunlight.	30

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Calibration Curve of the Ozalid Paper	16
2	Frequency Histogram of the Biomass Data	27
3	Frequency Histogram of the Light Data	27
4	Frequency Histograms of the Biomass Data on Each Plot	28
5	Frequency Histograms of the Light Data on Each Plot	29

THE QUANTITY AND COMPOSITION OF GROUND VEGETATION IN
DIFFERENT LIGHT ENVIRONMENTS UNDER A DOUGLAS-FIR,
PSEUDOTSUGA MENZIESII (Mirb) Franco, STAND
IN THE OREGON COAST RANGE

INTRODUCTION

For decades plant ecologists have been interested in the composition and structure of plant communities. What is the nature of a plant community? What are the environmental factors that form different patterns of vegetation in an ecosystem and how do these patterns change in time?

Forest ecosystems have generated much interest because of their diversity and complexity, but generally uniform structure. Forest ecosystems have described and classified for a long time and this has proved a useful tool for forest management. However, many theoretical and practical problems must be solved before the structure and function of forest communities can be understood.

In a forest ecosystem the amount and composition of understory and ground vegetation vary with site class and from stand to stand, and even within a stand. Even under a uniform stand there may be great variation in the structure of ground vegetation. It is known that there are many abiotic and biotic factors involved in every ecosystem but what causes the distinct microvariation of ground vegetation under a forest stand.

Beneath a tree canopy, differences in light intensity are very apparent to the eye. Does light direct the development of vegetational

patterns? Light conditions beneath a forest canopy have been investigated frequently. Scientists especially have studied the light environment of tree seedlings. Little concern has been given to the response of other understory plants. The response of ground vegetation to light usually is given as an average.

Witler (1975) studied the response of understory vegetation to different thinning intensities in a Pseudotsuga menziesii stand. To further clarify light and vegetational relationships, this study was undertaken to examine the quantity and composition of ground vegetation on microsites with different light environments. A secondary objective was to study the specific light requirements of certain species of ground vegetation.

Understanding the development and succession of ground vegetation is very important in regeneration of a stand. Ground vegetation often competes with tree seedlings suppressing them. This competition can lead to unsatisfactory regeneration. Understanding light relationships, and mineral and water cycles, to ground vegetation could help overcome some present problems especially in natural regeneration.

LITERATURE REVIEW

When studying forest ecosystems and the factors modifying those plant communities one has to deal with the basic theoretical concepts of plant communities. In modern ecological studies of complex biological systems, such as plant communities, simple observations and descriptions of particular instances are not enough. Many diverse approaches must be used to abstract from many observations the patterns which are realized in nature. However, appropriate observations may suggest avenues, and perhaps limits, for theoretical and experimental procedures. In any event, community properties must be studied by examining communities as well as by extrapolating from experimental-inductive studies and theoretical models (McIntosh, 1970).

Plant ecologists have stressed the importance of competition in community organization. The concept of competition is defined by Clements et al. (1929):

"When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition begins. ... As a function, it is necessarily a dynamic process, which may lead to equilibrium, suppression, subordination, or extinction."

A striking attribute of most temperate communities is that a few species gain a disproportionate amount of the resources of a site (dominance), but not to the complete exclusion of other species (McIntosh, 1970). This is the case with conifer forests where one single conifer species gains dominance and the main competition occurs within this species (intra-specific competition). Understory vegetation usually remains on the site forming one component in the competition. Since the great majority of plant species in nature are clumped in varying degrees, the effect of this pattern on competitive ability in a community is particularly important.

Most investigators studying the patterns of vegetation have concluded that plants rarely are distributed randomly even within a small homogeneous area. For example, Smith and Cottam (1967) found that in ten similar, old-growth stands of maple-basswood forest in Wisconsin the average number of species per square foot varied from 1.9 to 5.0 and that herbaceous composition and distribution was highly non-randomly variable.

Although it is generally known that species tend to be aggregated, little work has been done to discover the causes of aggregation. Greig-Smith (1964) and Kershaw (1964) discuss the problem and causes of aggregation. Many hypotheses in the literature present reasons for spatial patterns, such as preconditioning of an area by species previously occupying the site, vegetative reproduction, heavy seed, allelopathy, moisture, light, soil characteristic, microtopography, life history of the species, burning, and so on. The interaction of many factors probably determines the kind of species aggregation found on an area.

If one or a few factors have a disproportionately great effect on a performance or survival of a species, then the distribution of that species will tend to be determined by that particular factor or factors. If the values of the factor are themselves randomly distributed, then the distribution of the species will also be random. Thus, there is a hypothesis that departure from randomness of species distribution indicates that one or a few factors are determining the performance or survival of the species (Greig-Smith, 1964).

Light beneath a forest canopy varies diurnally in space and time from sunflecks, small patches of high intensity light moving slowly across the forest floor, to heavy shade. Light conditions in forests have been

investigated frequently. The studies have been concerned with scattered distribution of high light intensity in the understory. Many scientists emphasize the importance of sunflecks, but little is known about the effect of sunflecks and overall diffuse light on photosynthesis in ground vegetation. Allard (1947) believes that sunflecks are very important to the few green plants which are able to tolerate the low light intensities prevailing in a very dense forest. Toumey and Korstian (1947) conclude, however, that it is doubtful whether the fluctuations of light under a forest canopy are sufficiently rapid to cause much increase in the rate of photosynthesis above that occurring at the mean light intensity. The conclusions about the effect of sunflecks in these two sources seem to be merely speculative. The importance of sunflecks on plant growth probably depends on the relationship between size of fleck and size of plant, the intensity of light in fleck and shadow, and the duration of time that the plant is bathed in light from the fleck (Logan and Petersen, 1964).

As an extreme example of variation in light with time, readings at one point under a pine stand varied from 2 to 100 percent of full light during the period from 8:00 A.M. to 2:30 P.M. (Logan and Petersen, 1964). Reifsnnyder et al. (1971) found that under a pine stand coefficient of variation for diffuse light was 9 percent and for direct sunlight varied from 121 percent for individual five-minute observations to 56 percent for data averaged over two hours. Witler (1975) measured the light under the same Pseudotsuga menziesii stand in which this study was conducted and found that in stands heavily thinned the range of light under the canopy (integrated light) was from 2 to 31 percent of full sunlight.

Toumey and Korstian (1947) write that the weight of experimental evidence clearly shows that the minimum light intensity required for photosynthesis to balance respiration is very low as compared with full light in the open, occasionally less than 1 percent.

Most studies on ground vegetation in different light environments deal with tree seedlings in natural regeneration. The relationship of minimum light energy requirements and seedling survival and growth have been studied (Isaac, 1938). Atzet and Waring (1970) found an important interaction between light and moisture. The minimum requirements of light for survival of Douglas-fir increase more than three times on environments where moisture stress reaches critical levels.

In the Pacific Northwest and elsewhere, many studies have measured the response of tree seedlings and ground vegetation to thinning and light intensities beneath a forest canopy. The results show the heavier the thinning, the more light penetrates through a canopy, and as crown cover decreases, the amount of ground vegetation increases (Agee and Biswell, 1970; Emmingham, 1972; Witler, 1975). The correlation between vegetation and light intensities is usually estimated with mean values and the causes of this general trend have not been analyzed further.

Krueger (1960) studied ground vegetation under two Pseudotsuga menziesii stands which were lightly and moderately thinned. During the six years after thinning there was no significant change in cover of ground vegetation under the two stands. However, light and moderate thinning were not defined.

Emmingham (1972) studied plant distribution under different light environments in the Siskiyou mountains, Oregon. He found that most plants

can occur under a wide range of light conditions, but a plant-light-water interaction is most commonly operative. With a marginal water supply, light becomes a limiting factor. Plant cover and floristic richness do not appear sensitive to light except at extremely low levels. Still, Emmingham found a general increase in cover with increase in light, but cover and number of species seemed more strongly influenced by available moisture.

Witler (1975) when studying the response of understory vegetation to different thinning intensities found that despite the large within-treatment variation, several trends in cover and frequency were noted. Total cover was highest on heavily and moderately thinned plots. Herbaceous cover increased with thinning intensity, but the cover and frequency of woody species showed no consistent relationship with thinning. The results for understory biomass roughly paralleled those for cover. Due to the great variability in the biomass samples, the differences in total biomass between thinning intensities were not significant. Average biomass varied from 7488 kilograms per hectare for heavily thinned plots to 960 kilograms per hectare for unthinned. The amount of canopy opening and of light reaching the understory varied with thinning treatment. Light levels in the understory differed significantly between treatments, except between light and moderate thinning.

A study conducted in natural pine forest in Wisconsin examined herbaceous response to canopy cover, light intensity, and throughfall precipitation (Anderson et al., 1969). They found that the leaf surface area of the understory was influenced strongly by the overstory canopy. However, the correlation between the leaf surface area and light intensities

was weak. The study also indicated that the character of the understory herbaceous layer depended on throughfall and random drip precipitation. Although insufficient light may limit shade-adapted species at very low light intensities, it was concluded that the range in light sampled in the study, 8 to 17 percent of full sunlight, was well above the threshold level, and little further response with increased light should be expected.

In an earlier study (Toumey, 1929) light and moisture relationships of vegetation on the forest floor were examined. The experiments indicated that light intensity did not control the establishment of natural vegetation under a canopy of the pine stand studied. The two controlling factors seemed to be soil moisture and leaf litter. Poor regeneration of white pine was due to inadequate soil moisture at critical periods during the growing season and effect of leaf litter.

In ecological research micro- and macroclimate and soil characteristics play an essential role. Thus, broad generalizations about the main environmental factors involved cannot be drawn from the studies cited above.

METHODS

Description of the Study Area

The study area is located at Black Rock on the George T. Gerlinger Experimental Forest, three miles west of Falls City, and 40 miles northwest of Corvallis, Oregon. Research is conducted on the area by the Oregon State University Forest Research Laboratory in cooperation with the Oregon State Forestry Department. The permanent study plots were established between 1952 and 1956, and data collecting has continued over 25 years.

Geographically the forest lies on the east side of the Coast Range where the climate is wet and mild. Average annual precipitation is about 200 centimeters. The rain falls mostly during the winter, while summer months get only light showers. Active frost-free growing season is more than 200 days. Topography of the area varies from gentle to very steep, elevation from 300 to 600 meters.

The area supports a stand of 60- to 65-year-old naturally regenerated young-growth Pseudotsuga menziesii. Site classes range from IV to II with most of the area in site class III. Some Tsuga heterophylla and Abies grandis can also be found throughout the forest. The most common hardwoods are Alnus rubra, Acer macrophyllum, and Cornus nutallii.

The area was logged between 1909 and 1913, after which the slash probably was burned. Before the 1940's some natural fires went partially through the area, but for about 30 years fires have been excluded from the forest.

At Black Rock several methods, intensities, and frequencies of intermediate cuttings have been applied. All logging is conducted on a

small scale using horses to minimize damage to the stand. The basic experimental unit is one-quarter acre (0.10 ha) in size. Density in terms of basal area or number of trees is controlled according to the particular experimental design. Four one-quarter acre units are combined to form a one acre experimental plot. A buffer strip to minimize edge effect is maintained around each plot.

The plots used in this study are thinned according to three regimes based on density in terms of basal area. For the heavy thinning the basal area of young-growth Pseudotsuga menziesii is maintained between 100 and 130 square feet per acre (23 to 30 m²/ha), in medium thinning between 130 and 160 square feet per acre (30 to 37 m²/ha), and in light thinning between 160 and 190 square feet per acre (37 to 44 m²/ha). This basal area includes only the young-growth Pseudotsuga menziesii with a diameter at breast height of 7.6 inches (19.3 cm) or over. Hardwood species and an occasional old-growth Pseudotsuga menziesii which do not interfere with spacing of the active growing stock are retained on the plots.

For this study two of the four replications were selected subjectively according to the most uniform general characteristics in topography and vegetation within each replication. Table 1 is a list of the basic data of the selected study plots, and Appendix V shows a map of the study area at Black Rock. All the study plots are located on a southfacing slope, the aspects from SSW to SSE. The elevation of the lower replication is between 320 and 360 meters (plot 22, 24, and 25) and the upper (plot 38, 40, 41) between 500 and 570 meters.

Because the stand of Pseudotsuga menziesii is young (lower replication 68 years, upper 59 years) understory vegetation is in a successional

TABLE 1

The Basic Data of the Study Plots

Plot No.	Thinning Intensity	Basal Area of Douglas-fir, 19.3 cm DBH and Larger (m ² /ha)	Total Basal Area, All Trees 1976 (m ² /ha)	Elevation (meters) and Aspect	Average Stand Age	Thinning Years
<u>Lower Replication</u>						
22	Heavy	23-30	32.7	360 SSW	68	1959, 1960 1965, 1971
24	Medium	30-37	36.8	329 S	68	
25	Light	37-44	45.7	357 S	68	
<u>Upper Replication</u>						
41	Heavy	23-30	35.3	579 S	58	1957, 1960 1962, 1966
38	Medium	30-37	40.1	497 SSE	59	1969
40	Light	37-44	47.4	549 S	59	

stage. However, Witley (1975) suggests that the species composition on undisturbed areas is similar to that of Becking's lowland salal-Douglas-fir type (Becking, 1954). It is also similar to the ocean spray-salal and the vine maple-salal communities described by Corliss and Dyrness (1961). All of these communities are generally characterized by a greater coverage of Gaultheria shallon than is found on the study plots.

However, the thinning intensities and the many repeated thinnings (4 to 5 on each plot) have changed the pattern of succession and created a more suitable environment for understory vegetation than in a natural unthinned young-growth stand.

Approach

In ecological research, identifying the many factors interacting in essential processes within an ecosystem is difficult. That is why selecting the main variables and planning the data collecting are the most important stages. Selecting the right variables for hypothesis testing is especially important when studying natural ecosystems where variation is great and many unknown factors are involved.

In this study I chose cover and biomass of ground vegetation as dependent variables. I assumed that the biomass of ground vegetation describes the productivity and growth of plants, and their competitive ability also. The amount of biomass of vegetation reflects the sum of all biotic and abiotic factors affecting its total photosynthesis.

I measured light microenvironment as an environmental factor and related its effect to the biomass of ground vegetation. To reduce the variation, which, as mentioned, is known to be great in this kind of

ecological study. I formed other independent variables which might explain part of the variation. I assumed that surrounding trees and taller shrubs have competitive effect on the ground vegetation of a microsite. Basal areas of the surrounding trees and taller shrubs represent this competitive factor as independent variables. These two variables are assumed to reflect the root competition for water and nutrients on ground vegetation.

Estimation of the Variables

Cover and biomass of the ground vegetation

At each sample point the biomass of ground vegetation was estimated within a circle 30 centimeters in diameter.¹ All the vegetation growing inside this circle was clipped, oven-dried (70°C) and weighed. Green parts (leaves) were separated from woody parts when possible. Samples of biomass included only above-ground parts, roots were excluded because of a lack of time. Witler (1975) in his study on the same plots found that Berberis nervosa, Pteridium aquilinum, and Gaultheria shallon were the important species of ground vegetation. The samples of biomass were divided into these species, and a fourth group of all other species. This division made it possible to examine responses of the most important species separately.

Witler (1975) found no consistent relationship between moss cover and thinning intensity. The light environment of mosses under other ground vegetation is so different from the one of herbs and shrubs that I did not include moss biomass into the dependent variable.

¹Circles are the most suitable sampling units to use when focussing attention on the spread of vegetation around a point (Brown, 1954).

The cover of ground vegetation also was estimated within the same sample units. The maximum height of ground vegetation also was measured. All species were listed, and cover of each species was estimated separately. Cover, vertical projection of the plants onto the ground, was determined by using the Braun-Blanquet technique (Brown, 1954), Table 2.

TABLE 2

The Braun-Blanquet Classes for Estimating
Cover of Ground Vegetation (Brown, 1954)

<u>Cover</u>	<u>Braun-Blanquet Class</u>
75-100%	5
50- 75%	4
25- 50%	3
5- 25%	2
1- 5%	1
present, but covering less than 1%	x

Light intensity reaching the ground

Light intensity is a measure of the total electromagnetic energy available for plants (Monsi and Oshima, 1955). There are many difficulties in measuring the light which reaches the ground. A convenient measure to relate the light received by a plant community to growth is a comparison of the light in the community as a percentage of the light in the open. Under a canopy, sunflecks, variation in spectral composition and the spatial distribution of light combine to make the relationships complex (Anderson, 1964).

In this study light was measured just above the level of ground vegetation on each sample unit. The ozalid paper technique described by Friend (1961) was used to measure light intensity. Fifteen sheets of photosensitive ozalid paper in a stack were exposed to daylight for one clear day. The light energy received then was estimated by the number of layers of paper penetrated by light, revealed after a dry development with ammonia vapor. Light was measured on every sample unit during one clear day in mid-July. The ozalid paper was set out in the evening and collected the next evening to insure equal exposure time for all light integrators. An estimation of light throughout a clear summer day is a measure of the light available to the plants under the canopy relative to the light in the open for the entire growing season.

Two weeks after the field measurement, the ozalid paper was calibrated using a Kipp solarimeter on a clear day in early August, 1977, at Forest Research Laboratory, OSU, Corvallis. The paper was exposed in the open for 1, 2, 4, 8, 16, and 30 minutes and 1, 2, 4, 8, 16 hours and all day with the midpoint of each measurement at 12:00 noon. The calibration gives the logarithmic response of the paper to light, Figure 1. The Kipp solarimeter provided an estimate of the absolute energy received. The light readings were transferred to relative light intensities as a percentage of full sunlight in the open. A measure of full sunlight for one day in the open was derived from the calibration.

In Chapter IV of this paper there is a short review of the limitations of the ozalid method found for example by Anderson (1964). However, Emmingham (1972) and Emmingham and Waring (1973) have studied the

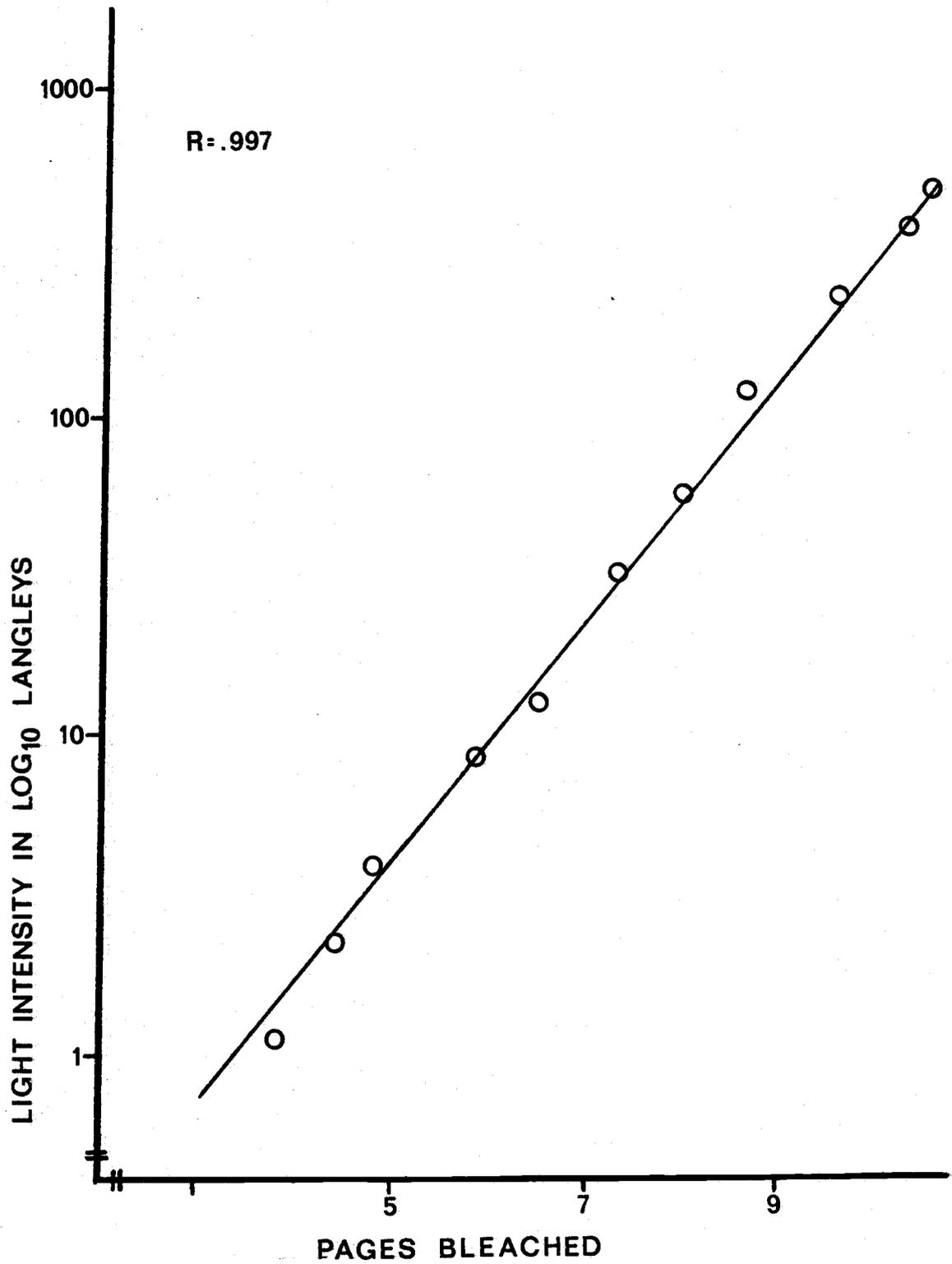


Figure 1. Curve of the Ozalid Paper

ozalid paper method thoroughly and concluded that the method was accurate enough for this kind of ecological study. Because the method is inexpensive and easy to use many simultaneous measurements of light can be made in the field.

Basal area of the surrounding trees and taller shrubs

I assumed that the basal area of actively growing trees in the over-story represents the competitive effect of the trees upon ground vegetation of a stand. Trees and shrubs compete effectively with ground vegetation for all elements needed for growth; for example light, water, and nutrients. The size of trees and shrubs in particular can represent an estimate of root competition assuming the larger the basal area of a tree or a shrub the better its root system is developed and the stronger competitor it is. This competition between ground and higher vegetation is considered an important factor controlling growth and production of dry matter (Kershaw, 1964; Monsi and Oshima, 1955).

The measures of basal area that were used in this study are (1) the basal area of the study plot (1 acre) and (2) the basal area of trees and of higher shrubs, separately, surrounding each sample unit of ground vegetation. The basal area of all living trees over six meters tall surrounding each sample unit was measured within a circle 12 meters in diameter. The basal area of all living shrubs (1 to 6 meters tall) was estimated within a circle five meters in diameter. The basal area of each shrub was measured at the base of the trunk or just above the base if it was noticeably swollen.

Sampling Procedure

The basic sampling unit was a sample of ground vegetation, on a circle 30 centimeters in diameter. On each experimental plot (1 acre) 15 samples of ground vegetation were collected, for a total of 90 samples. These sample units were placed 12 meters from each other on north-south lines through the plots. On each plot three lines were randomly placed starting from either the south or north edge of the plot. The starting point of a line was then determined by randomly choosing a distance from either the east or west corner of that particular edge. However, the lines were placed not less than five meters from the borders of a plot and not less than ten meters from each other.

The first sample unit of ground vegetation on every plot line was randomly placed from five to ten meters from the border. Altogether five sample units were placed on each plot line, 12 meters apart. If a unit fell on a log, stump, or trunk of a tree or taller shrub the location was randomly changed two meters east or west from the spot. If the new location of the sample unit was not suitable for the same reasons one more correction was made by changing the location one meter to a compass direction which was randomly picked.

From the center of every sample unit two circles were drawn, one with a five meter diameter for estimating the basal area of the surrounding taller shrubs, the other a circle 12 meters in diameter for estimating the basal area of the surrounding trees. Appendix I shows the sampling procedure on a plot.

Analysis of the Data

All observations were subjected to a statistical analysis to determine means, variances, ranges, and simple correlations between variables. Multiple linear regression analysis was used to determine the relationship between the dependent and independent variables. Appendix II gives the basic form of multiple linear regression analysis used and a list of the main variables. The analysis of the data was accomplished on the Oregon State University Control Data 3300 computer system.

LIMITATIONS

This study dealt with competition in understory plant communities in which none of the competitive factors involved were manipulated. Because it is impossible to consider all of the factors, either known or unknown, the selection of important and critical variables for the questions studied is important. Too many limitations in a study prevent conclusions. This problem is one of the greatest in ecological studies.

In biomass of ground vegetation, the dependent variable, I included only above-ground vegetation. This may be a serious limitation, because patterns of root development and distribution of roots play an important role in plant competition (Lee, 1960; Scully, 1942).

Basal area of surrounding trees, assumed to reflect the competitive effect of these trees upon ground vegetation, also may have limitations. This variable especially represents the factor of root competition but also of throughfall precipitation which influences soil moisture. Almost nothing is known about the root layer relative to crown development of trees. However, I assume that the basal area of a tree has a positive correlation with the size of both crown and root system.

I assumed that soil characteristics do not vary between microsites. This assumption may not be valid. Also the variation in moisture conditions, an important factor, is unknown.

Many difficulties in measuring relative light intensity, the main independent variable, on microsites are apparent. The light is continuously altering in intensity and composition. The aerial parts of a plant community reflect, absorb, and transmit different wavelengths of light to a varying extent. Because of this variation a compromise between

detailed accuracy and practicality must be made when conducting a field study. The photosensitive paper used in this study is sensitive mainly to short wavelengths. Also, the ozalid paper technique has the added complication that each layer of paper will act as a spectrally selective filter for layers below (Anderson, 1964). When comparing light intensity under a canopy with that in the open using the ozalid paper method one especially should be aware of the possible change in spectral distribution of light that penetrates a canopy. Atzet and Waring (1970) found, however, that in general the 400- to 700-nm range of light is rather uniformly absorbed by a mixed coniferous canopy. Averaged for an entire day, only the far red band showed a significant proportional increase. Egle (1937) and Federer and Tanner (1966) got the same kind of results in a Picea sp. stand.

As mentioned earlier, however, the ozalid paper technique has proven to be accurate enough for these types of studies, as long as shortcomings are kept in mind when interpreting results.

The multiple linear regression analysis used in this study has some limitations. Many scientists have shown that in ecosystems different physiographic combinations can produce equivalent environments. The multiple regression analysis is unable to account for such compensation and interaction of factors, although cause and effect complications are avoided (Major, 1961). For this reason it may be unsatisfactory in studying the relationships between plants and their environments.

RESULTS

General Description of the Vegetation

Appendix III is a list of all the species of the ground and taller understory vegetation that occurred on the sample units and of the tree species growing on the study plots. Altogether, 31 species of ground vegetation were found on the sample units.

Generally, the most important species of ground vegetation on all the plots of the lower replication (plots 22, 24, and 25) was Oregon grape Berberis nervosa. Other frequent species were bracken fern Pteridium aquilinum, and Trientalis latifolia, Galium triflorum and Campanula scoulerii. On the upper replication (plots 38, 40, and 41) the most important species of ground vegetation was Pteridium aquilinum. Another rather frequent species was Campanula scoulerii. The species composition was quite the same on all the plots, but patterns of vegetation, cover, and biomass varied greatly from plot to plot and within each plot.

Cover

The cover of ground vegetation for all samples varied from 0.0 percent (no vegetation) to 152.5 percent. In Table 3 the range and mean of cover for each plot, and the cover value for the most important species on every plot are given. Table 3 shows that on the lower replication the range of cover was greatest on the heavily thinned plot and least on the light thinning. However, the mean cover of the medium thinning is greater than that of the heavy thinning. There was a significant difference in cover between heavy thinning (plot 22) and light thinning (plot 25) and between medium (plot 24) and light thinning.

TABLE 3

Cover of Ground Vegetation by Plot

Plot No	Thinning Intensity	Range of Cover (%)	Mean of Cover (%)	Most Frequent Species	Most Covering Species	Average Cover of the Most Frequent Species
<u>Lower Replication</u>						
22	Heavy	5.0-152.5	44.8	<u>Berberis nervosa</u> ¹ (1/15)	same	35.8
24	Medium	5.0-102.5	51.8	<u>Berberis nervosa</u> (12/15)	same	37.5
25	Light	0.0- 62.5	18.5	<u>Trientalis latifolia</u> (8/15)	<u>Berberis nervosa</u>	5.6
<u>Upper Replication</u>						
41	Heavy	5.0- 90.0	40.5	<u>Pteridium aquilinum</u> ² (12/15)	same	35.4
38	Medium	0.0- 62.5	10.2	<u>Pteridium aquilinum</u> ³ (4/15)	same	12.5
40	Light	0.0-115.0	24.3	<u>Pteridium aquilinum</u> ⁴ (6/15)	same	18.3

¹ The number in parentheses shows on how many sample units out of total 15 in the species occurred.

² Campanula scoulerii as frequent.

³ Trientalis latifolia and Campanula scoulerii as frequent.

⁴ Symphoricarpus mollis as frequent.

On the upper replication the trend of the range of cover was not clear, probably because under light thinning (plot 40) the range and mean of cover is affected by a few dense clumps of vegetation. However, there is a highly significant difference between heavy (plot 41) and medium (plot 38) thinning, see Appendix IV.

Berberis nervosa on the lower plots dominated the site strongly so that on plot 22 (heavy) and 24 (medium) it was distinctly the most important species in both cover and frequency. On the upper plots Pteridium aquilinum had the greatest cover but both Campanula scoulerii and Trientalis latifolia associated with it had the same frequency. These herbs are small in size and grow under Pteridium aquilinum and do not cover but a small part of the site.

Biomass

The most striking characteristic of the biomass of ground vegetation growing on the sample units was that it varied greatly. The range of the biomass on all sample units was from 0.00 to 104.47 grams. Table 4 gives the range, mean, and median of the biomass samples on each plot.

The heavy biomass samples consisted of shrub species, mainly Berberis nervosa, and Rosa gymnocarpa, and herbaceous species such as Pteridium aquilinum and Polystichum munitum. The different lifeforms of the species made the variation in the biomass so great that it was not reasonable to analyze the data without dividing it into different species or lifeforms. In the most important species, the variation in the biomass was less. For example the biomass of Berberis nervosa varied from 1.28 grams to 85.39 grams on the sample units and of Pteridium aquilinum from 3.02 grams to 21.02 grams.

TABLE 4

Biomass of the Ground Vegetation and Light Intensity
on the Same Units by Plot

Plot No.	Thinning Intensity	BIOMASSS (grams)			LIGHT INTENSITY (% of full light)		
		Range	Mean	Median	Range	Mean	Median
<u>Lower Replication</u>							
22	Heavy	0.00- 85.49	14.83	6.47	0.77-18.22	11.94	11.91
24	Medium	0.18-104.47	18.67	7.22	0.77-14.98	6.49	7.55
25	Light	0.00- 38.25	5.18	0.55	1.22-11.91	5.18	3.03
<u>Upper Replication</u>							
41	Heavy	0.01- 21.28	6.03	4.11	7.55-29.70	16.76	18.82
38	Medium	0.00- 26.39	2.79	0.13	3.81-18.82	8.12	7.55
40	Light	0.00- 33.65	2.89	0.14	1.92-18.82	7.52	7.55

The range of biomass samples on each plot is great and statistically there is no difference between different thinning intensities. The means of biomass samples show a general, weakly decreasing trend from heavy to light thinning. The variation was so great within each plot that there was no significant differences between the mean biomass sampled on the different plots; that is, between the mean biomass of ground vegetation under different thinning treatments.

The median in Table 4 being so different from the mean indicates that few heavy samples of biomass affected the mean so that it does not give a clear picture of the distribution of the data. Figures 2 and 4 show the histograms of the biomass data.

Light

The range of the estimates of light intensity under the canopy compared to that in the open varied from 0.77 percent to 29.70 percent. Figures 3 and 5 are histograms depicting the light intensity data. In Table 4 range, mean, and median of light intensity on each plot are given. A general trend of light intensity increasing with the intensity of thinning is evident. Light intensity is highest on the plots of heavy thinning. Statistically there is a highly significant difference between the plots of heavy and medium thinning on both replications, see Appendix IV. The mean light intensity on the plots of medium and light thinning was almost the same on both replications. The plot with heavy thinning of the upper replication (plot 41) received the most light.

In examining the light environment of several important species, maximum cover of the species under different classes of light intensity was used. Table 5 is a list of some of the most common plant species with

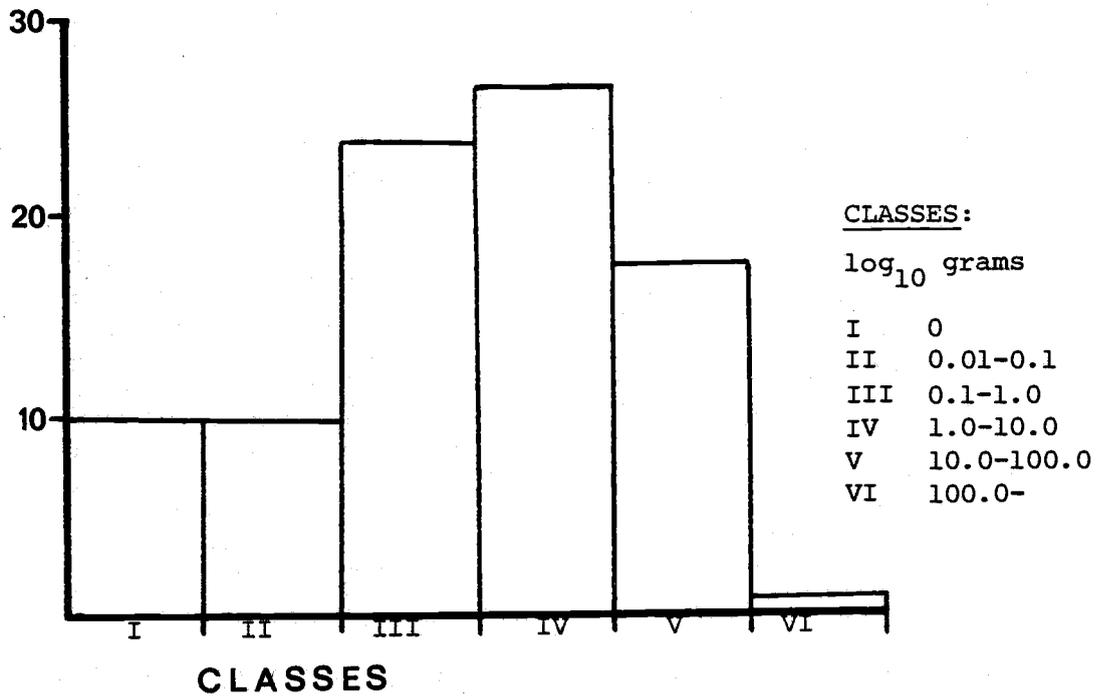


Figure 2. Frequency Histogram of the Biomass Data

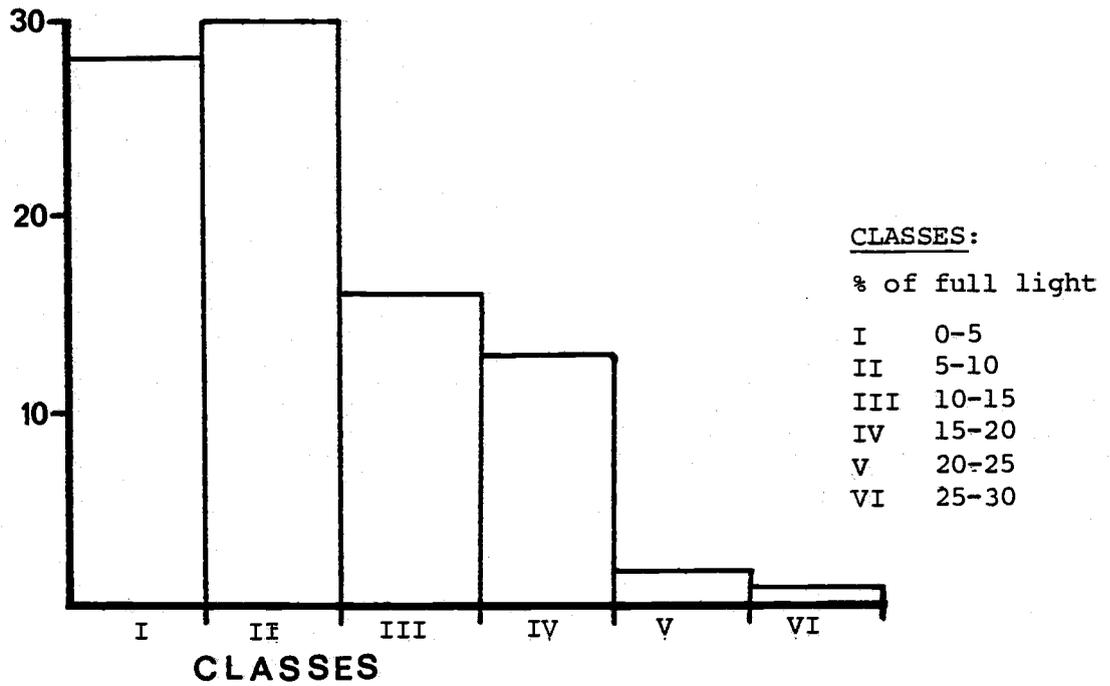


Figure 3. Frequency Histogram of the Light Data

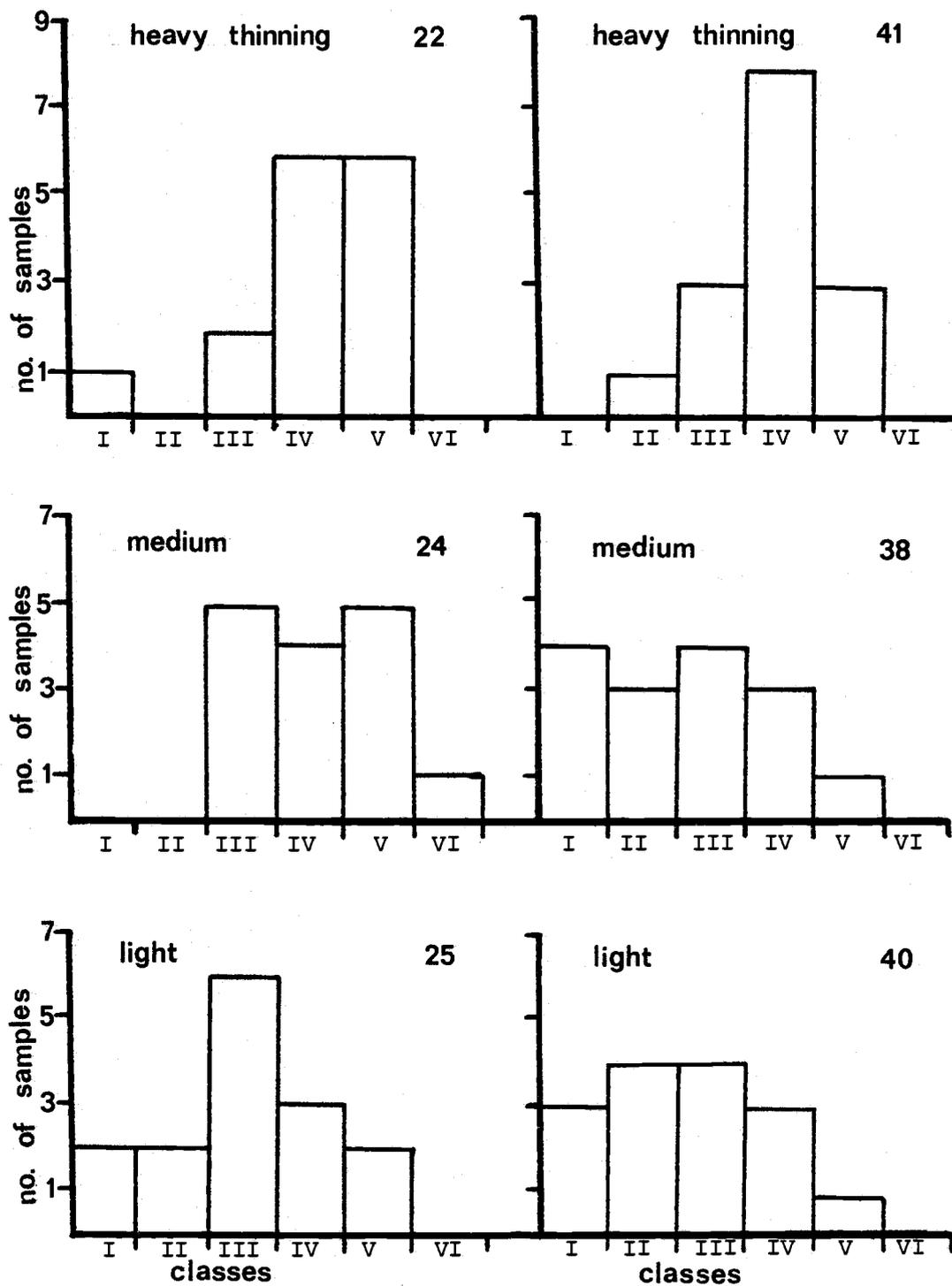


Figure 4. Frequency Histograms of the Biomass Data on Each Plot. Classes Listed in Figure 2.

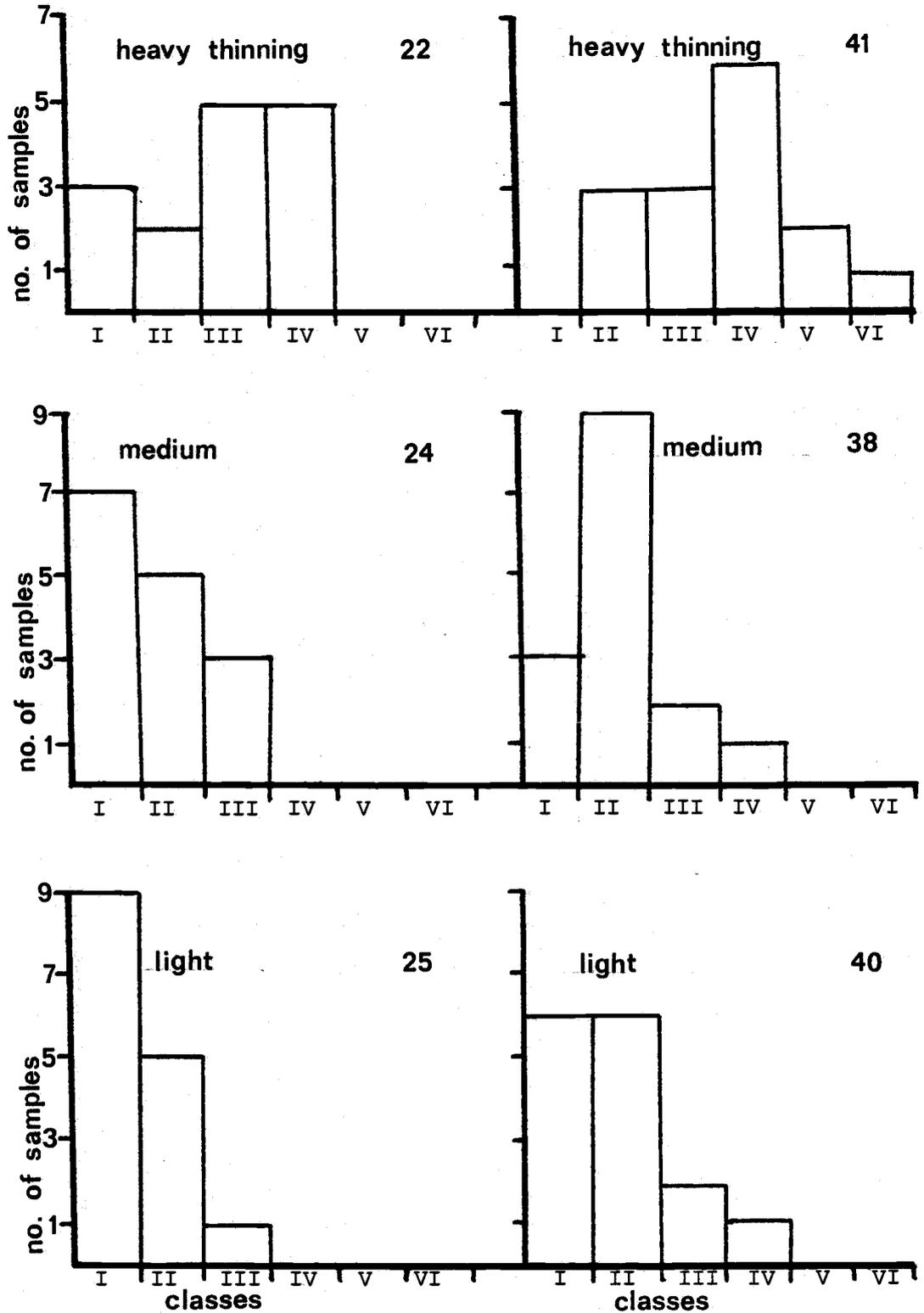


Figure 5. Frequency Histograms of the Light Data on Each Plot. Classes Listed in Figure 3.

maximum cover by classes of percentage of full sunlight. The table shows that these species generally can occur in a wide range of light intensity and under very low light intensities. The maximum cover, for example of Berberis nervosa and Pteridium aquilinum, can reach from 50-100 percent even under very low light intensities. On the other hand, there are species which cover only 1-25 percent regardless of the light intensity, for example Trientalis latifolia, and Galium triflorum.

TABLE 5

Maximum Cover of Common Plant Species
in a Sample Unit

<u>Species</u>	<u>Classes of Percentage of Full Sunlight</u>				
	<u>0-3</u>	<u>3-6</u>	<u>6-12</u>	<u>12-20</u>	<u>20-30</u>
<u>Berberis nervosa</u>	100	75	100	50	--
<u>Pteridium aquilinum</u>	50**	50	75	75	50**
<u>Trientalis latifolia</u>	5	25	25	5	---
<u>Campanula scoulerii</u>	1*	5	5	50	25**
<u>Galium triflorum</u>	5	5	5	1*	--
<u>Symphoricarpus mollis</u>	1*	25	75	50*	--

* one observation in the class

** two observations in the class

Other Variables

The maximum height of the ground vegetation ranged from 1 centimeter to 100 centimeters, the mean being 32.6 centimeters. There was a significant difference in the height of the ground vegetation between heavy and

medium thinning on both replications but not between medium and light thinning.

The basal area of the trees surrounding the sample units of ground vegetation varied from 0.025 square meter to 0.966 square meter. The mean basal area of the surrounding trees on different plots was as follows:

	<u>Lower Replication</u>	<u>Upper Replication</u>
Heavy Thinning	0.346 m ²	0.357 m ²
Medium Thinning	0.427 m ²	0.547 m ²
Light Thinning	0.527 m ²	0.511 m ²

The basal area of taller shrubs around the sample units of ground vegetation varied from 0.0 square centimeter to 192.92 square centimeters. Taller shrubs were so unevenly distributed that no clear pattern of distribution could be found.

Correlation of the Variables

The data was subjected to statistical analysis in order to find simple correlations between the different variables and finally multiple regression analysis was used, Appendix II. The correlation between light intensity and biomass of ground vegetation was tested, first with all species, and then with Berberis nervosa and Pteridium aquilinum separately. No meaningful correlations were found between the light intensity and the amount of biomass of ground vegetation on the sample units. As an example of the variation in the data there were samples of biomass from 0.01 gram to 104.7 grams under 3.03 percent of full sunlight, and from 0.01 gram to 22.29 grams under 18.82 percent of full sunlight. No patterns of distribution could be found. The cover of the

sample units as the dependent variable, showed no better correlation with light intensity.

Other correlations tested were light intensity and basal area of the trees surrounding the sample units of ground vegetation, light intensity and the maximum height of ground vegetation, biomass of ground vegetation and basal area of the surrounding trees. No meaningful correlations were found.

Because of weak simple correlations between the different variables a multiple regression analysis was tried, but as was expected, this gave no better results. There was so much inexplicable variation in all the variables measured that no meaningful correlations could be found.

CONCLUSIONS AND DISCUSSION

The results show clearly that under the experimental conditions of the Douglas-fir stand studied the light intensity as measured on the microsites does not determine the amount and composition of ground vegetation. In other words, the light intensity is not the main environmental factor effecting the patterns of development of species composition and limiting the growth of ground vegetation on the microsites under this Douglas-fir stand.

However, there are some general trends to be seen in the development of ground vegetation. The basal area of the trees increases, canopy cover increases, (thinning is lighter), the cover and height of ground vegetation decreases at the same time as light intensity decreases. This is the same trend as Witley (1975) found when studying the same Douglas-fir stand. Also Emmingham (1972) found this kind of general trend in his study. However, on small microsites within treatment this trend disappears and great variation in biomass and cover occurs which cannot be explained by differences in light intensity or in basal area of the surrounding trees.

The lowest light intensity measure (1 to 5 percent of full sunlight) under the canopy was still high enough to supply the necessary light energy for photosynthesis in the most common species. Even with the minimum light the rate of photosynthesis exceeds the compensation point, at least enough to keep them alive. Anderson et al. (1969) draw similar conclusions and Emmingham (1972) mentions that when there is abundant water, most plants can occur under a wide range of light conditions. The fact that all the most common species were perennials may

indicate that they are not so sensitive to changes in light conditions and that they are more persistent than annuals. They are able perhaps to survive for a number of years under unfavorable light conditions.

This study indicates that light as an environmental factor does not have a clear and distinct effect on formation of spatial patterns of ground vegetation locally within treatments under this particular Douglas-fir stand. Every forest ecosystem is a dynamic system, continuously changing in space and time. The environment beneath a forest canopy is in a stage of slow change normally with closure or opening of the canopy. This change in environmental influences the species composition and spatial patterns of ground vegetation. The microenvironmental changes are slow and the response of vegetation to these changes may be even slower. Vegetation may reflect the environmental conditions of previous years, as well as those prevailing at present.

The Douglas-fir stand at Black Rock does not follow natural successional pattern. For more than two decades many man-made changes have occurred due to frequent thinnings. At every thinning the canopy cover decreased and small openings were created. The residual trees have occupied the free space quite rapidly, and the canopy closed again in from three to five years. The opening and closing of the canopy creates a fluctuating change in light environments for ground vegetation. Throughfall precipitation measured on the plots for several years indicated that precipitation immediately after thinning varied according to treatment; the more open the canopy the higher the throughfall precipitation. However, a few years after thinning throughfall reached a common level on all treatments (Berg, 1968). This may indicate that, although the basal

area of the plots varies according to the treatment, the canopy cover may be very similar. Thus the light and moisture environment may be more uniform than the different regimes of basal area would suggest. This may be one reason for the fact that there were no significant differences between the mean biomass of ground vegetation on different plots, and that differences in cover were only partly significant. This does not explain the whole question, however, because some significant differences in light intensity were found between different plots.

A parallel to the opening and closing of the canopy may exist in the root layer. After thinning, the residual trees probably begin to occupy the free space in the ground provided by the removal of the thinned trees. What are the patterns of this change and how strong is root competition between the dominant trees and ground vegetation? These questions may be very important in explaining the spatial patterns of ground vegetation. Scully (1942) claims that the actual root distribution is conditioned by the type of root system of the dominant and subdominant species. Anderson et al. (1969) mention that the northern herbaceous species root in the surface layers and can therefore be expected to be more closely coupled to the moisture recharge influenced by canopy opening. How strongly do the shrub species with deeper root systems compete with trees and herbaceous species? For example, differences in shoot/root ratio probably reflect this competition. Thus, the root layer of ground vegetation should be studied to answer these questions.

A very important factor, related to root competition, is available soil moisture. Many studies, especially those involved with the problems of natural regeneration under a forest canopy, consider soil moisture,

as well as light, as a possible limiting factor. Moreover, in many studies, soil moisture has been found to be the main limiting factor (Roeser, 1924; Toumey, 1947). The results of these studies cannot be generalized, because so many local environmental factors have an influence on the ability of plants to pull water from the soil. Anderson, et al. (1969) found that throughfall precipitation explained more of the variation in herbaceous ground vegetation under a pine forest than light intensity.

The variation in moisture availability for ground vegetation under the Douglas-fir stand studied is not known. During the summer of 1977 moisture stress measurements on natural Douglas-fir seedlings were carried out on the same plots (Del Rio, unpublished data). No significant differences in moisture stress of Douglas-fir seedlings on plots with different basal areas were found. Neither was there a significant difference in moisture stress between seedlings on each plot. This does not, however, indicate that moisture can't be an important factor involved in development of spatial patterns of ground vegetation. Much more investigation on local variation in moisture stress of different species of ground vegetation and on soil moisture content is needed before conclusions can be drawn.

Kershaw (1964) outlines three main categories of patterns of vegetation: morphological, environmental, and sociological. Environmental factors generally cause a large-scale pattern whereas the morphological pattern is usually small-scale. The sociological category includes medium-scale types of patterns which are tied to competition between species and

microenvironmental factors. My study was concerned mostly with the sociological category. In patterns of ground vegetation both morphological and environmental, but especially the morphological aspect, should be considered. Therefore it is very important to know the history of the stand and of the ground vegetation so that the variations in ground vegetation can be understood. It is important to know the species that were on the area previously, what kind of distributional pattern existed, and how the soil has been modified.

Morphological characteristics of individual species may have an influence on spatial distribution. Methods of reproduction influence vegetational patterns of species tremendously. For example, heavy seed of vegetational reproduction may lead to clumping of a species. Watt (1955) who has studied thoroughly bracken and heather associations in England, stresses the importance of different ways of dispersion in competition. Bracken shows the marginal vigour of a rhizomatous species with large plots lying side-by-side "making a massed attack along a continuous front." Competitive power varies not only with density but with morphological age and the way plants and shoot are arranged. Bracken and heather have many morphological phases over time which cause the structure of this association to fluctuate. Therefore, the knowledge of the life history of the plants and the structure of the communities they form is important in understanding the patterns of vegetation.

Pure chance also can play an important role in the distribution of plants. The species may have become established during a favorable period in its development. Wind, birds and animals can carry seeds with them and thereby establish new species on an area.

In a forest ecosystem logs have an influence on the development of plant communities. Deteriorating logs change litter and soil characteristics that drastically modify microsites probably for centuries. Although a log may have disappeared many years ago the soil may still possess properties that are favorable for certain species. For example, water holding capacity and mineral content of a site can be improved by the deterioration of logs.

Development of ground vegetation is influenced by so many factors and their interactions that the examination of only a few factors, even though they are important, may not give general or even specific answers to the questions asked. The factors and the interactions affecting the plants in nature seem to be so complicated that multiple linear regression analysis statistically is not sufficient to interpret the data. Taking more and more variables into account may lead only to more difficulties.

To study further uneven distribution of ground vegetation beneath a canopy may require a quite different approach than the one used in this study. A history of the ground vegetation determined by the examination of associations of species coupled with a survey of the development of the associations for several years may be valuable. The life history of perennial herbs and shrubs especially may reveal the formation and structure of spatial patterns in vegetation. A comparison of growth rates and root distribution of species along with the management history of the stand and the climatic factors of the area is also important. And finally, the autecology of individual species, their characteristics and life history is needed. The study of both important environmental factors

and this detailed developmental history of ground vegetation on micro-sites may be the answer to how and why the ground vegetation of a forest ecosystem exists and develops.

LITERATURE CITED

- Agee, J.K. and H.H. Biswell. 1970. Some effects of thinning and fertilization on ponderosa pine and understory vegetation. *Journal of Forestry* 68:709-711.
- Allard, H.A. 1947. Light intensity studies in Canaan Valley, West Virginia. *Castanea* 12(3):63-74.
- Anderson, M.C. 1964. Light relations of terrestrial plant communities and their measurement. *Biological Review* 39:425-486.
- Anderson, R.C., O.L. Loucks and A.M. Swain. 1969. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forest. *Ecology* 50:255-263.
- Atzet, T. and R.H. Waring. 1970. Selective filtering of light by coniferous forest and minimum light energy requirements for regeneration. *Canadian Journal of Botany* 48:2163-2167.
- Becking, R.W. 1954. Site indicators and forest types of the Douglas-fir region of western Washington and Oregon. Doctoral dissertation. Seattle, University of Washington. 139 numb. leaves.
- Berg, A.B. 1968. An introduction to sociological and ecological aspects of young-growth management. Management of young-growth Douglas-fir and Western Hemlock. Proceedings of a Symposium held June 10-14, 1968. December 1970. School of Forestry, Oregon State University, Corvallis, Oregon.
- Brown, D. 1954. Methods of surveying and measuring vegetation. Bulletin No. 42. Commonwealth Bureau of Pastures and Field Crops. Hurley, Berks. Commonwealth Agricultural Bureaux. Farnham Royal Bucks. England.
- Clements, F.E., J.E. Weaver and H.C. Hanson. 1929. Plant competition. Carnegie Inst. Wash., Pub. 398. Wash., D.C.
- Corliss, J.F. and C.T. Dyrness. 1961. Alsea Basin area soil and vegetation survey. General and technical information for use in the final review. Unpublished manuscript. Available from Department of Soils Science, Oregon State University, Corvallis.
- Egle, K. 1937. Zur Kenntnis des Lichtfeldes der Pflanze und der Blattfarbstoffe. *Planta* 26:546-583.
- Emmingham, W.H. 1972. Conifer growth and plant distribution under different light environments in the Siskiyou Mountains of Southwestern Oregon. Master's thesis. Corvallis, Oregon State University, 50 numb. leaves.

- Emmingham, W.H. and R.H. Waring. 1973. Conifer growth under different light environments in the Siskiyou Mountains of Southwestern Oregon. *Northwest Science* 47:88-99.
- Federer, C.A. and C.B. Tanner. 1966. Spectral distribution of light in the forest. *Ecology* 47:555-560.
- Friend, D.T.C. 1961. A simple method of measuring integrated light values in the field. *Ecology* 42:577-580.
- Greig-Smith, P. 1964. *Quantitative plant ecology*. Butterworth Scientific Publications. London. 256 p.
- Hitchcock, L.C. and A. Cronquist. 1973. *Flora of the Pacific Northwest. An illustrated manual*. Seattle, University of Washington Press. 730 p.
- Isaac, L.A. 1938. Factors affecting establishment of Douglas-fir seedlings. United States Department of Agriculture, Washington, D.C.
- Kershaw, K.E. 1964. *Quantitative and dynamic ecology*. American Elsevier Publishing Company, Inc. New York. 183 p.
- Krueger, K.W. 1960. Behavior of ground vegetation under a partially cut stand of Douglas-fir. USDA Forest Service Research Note. Pacific Northwest Forest and Range Experiment Station. No. PNW-198.
- Lee, J.A. 1960. A study of plant competition in relation to development. *Evolution* 14:18-28.
- Logan, K.T. and E.B. Petersen. 1964. A method of measuring and describing light patterns beneath the forest canopy. Canada Dep. For. Publ. 1073. 26 p.
- Major J. 1961. Use in plant ecology of causation, physiology, and a definition of vegetation. *Ecology* 42(1):167-169.
- McIntosh, R.P. 1970. Community competition and adaptation. *Quarterly Review of Biology* 45:259-270.
- Monsi, M. and Y. Oshima. 1955. A theoretical analysis of the succession process of the plant community based upon the production of matter. *Jap. J. Bot.* 15:60-82.
- Roeser, J., Jr. 1924. A study of Douglas-fir reproduction under various cutting methods. *Jour. Agr. Research* 28:1233-1242.
- Scully, N.S. 1942. Root distribution and environment in a maple-oak forest. *Botanical Gazette* 103:492-517.

Smith, B.E. and G. Gottam. 1967. Spatial relationship of mesic forest herbs in southern Wisconsin. Ecology 48:546-558.

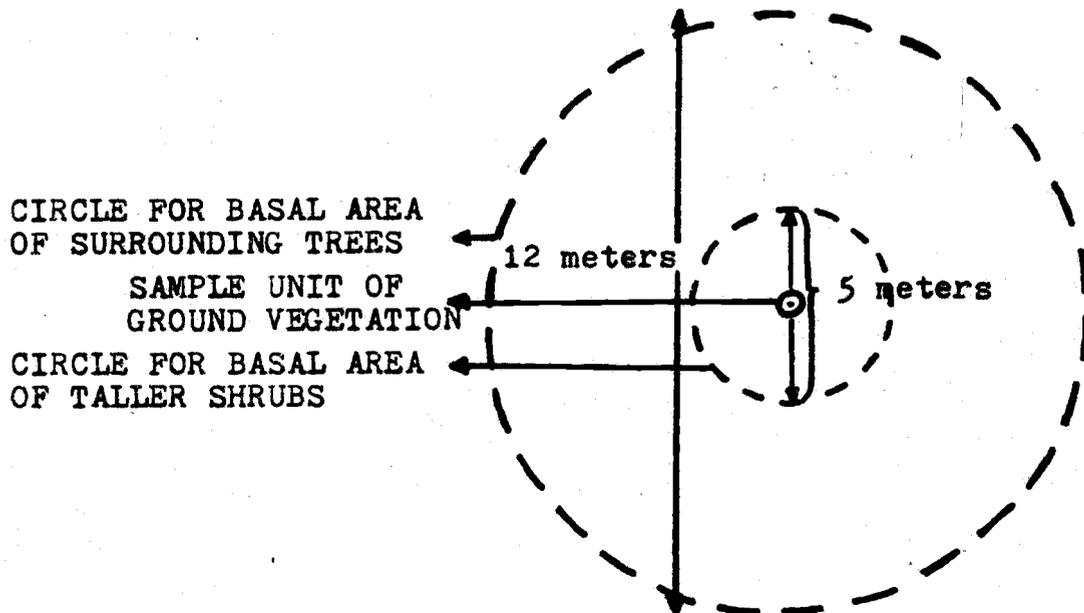
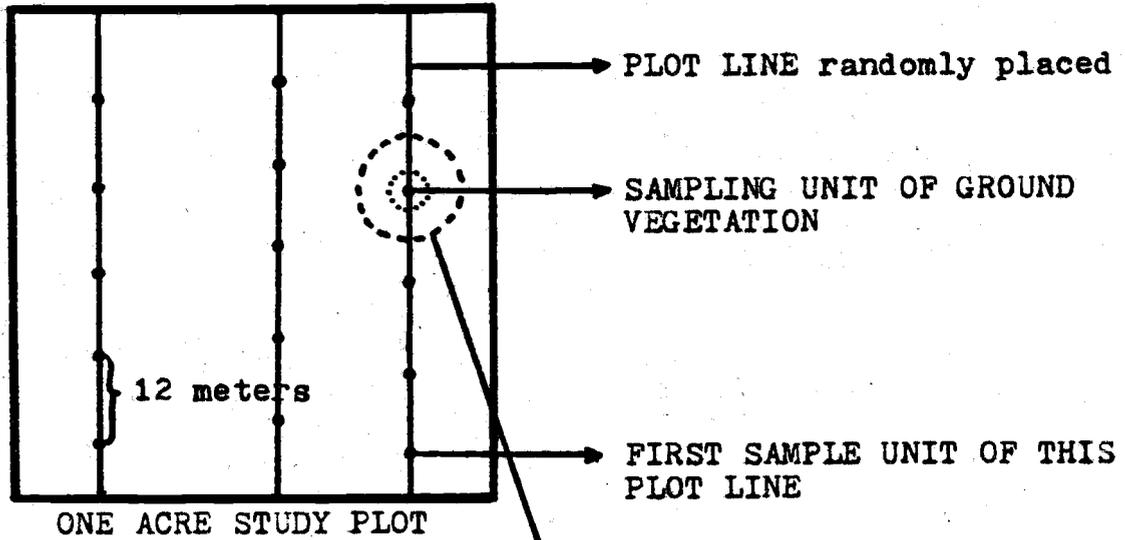
Toumey, J.W. 1929. The vegetation of the forest floor: Light versus soil moisture. Int. Congr. Plnt. Sci. Proc. 1:575-590.

_____ and C.F. Korstian. 1947. Foundation of silviculture upon an ecological basis. John Wiley & Sons, New York. Second edition, revised. 468 p.

Witler, J.W. 1975. The effect of thinning intensity upon understory growth and species composition in an Oregon Coast Range Pseudotsuga menziesii stand. Master's thesis. Corvallis, Oregon State University. 95 numb. leaves.

APPENDICES

APPENDIX I SAMPLING PROCEDURE



APPENDIX II

The Model of Multiple Linear Regression Analysis Used

The model used:

$$Y_i = \beta_0 + \beta_1 X_{i,1} + \beta_2 X_{i,2} + \beta_3 X_{i,3} + \epsilon_i$$

where:

Y_i = Dependent variable, biomass or cover of ground vegetation or a species on a sample unit

$X_{i,1}$ = Light intensity as a percentage of full sunlight on a sample unit

$X_{i,2}$ = Basal area of the trees surrounding a sample unit

$X_{i,3}$ = Basal area of taller shrubs surrounding a sample unit

ϵ_i = Error term

APPENDIX III

List of the Species Found on the Study Plots

Scientific names for the species follow Hitchcock and Cronquist (1973). Common names are derived from a variety of sources.

<u>Tree Species</u>	<u>Common Name</u>
<u>Abies grandis</u> (Dougl.) Forbes	grand fir
<u>Acer macrophyllum</u> Pursh	big-leaf maple
<u>Alnus rubra</u> Nutt.	red alder
<u>Arbutus menziesii</u> Pursh	Pacific madrone
<u>Cornus nutallii</u> Aud.	Pacific dogwood
<u>Pseudotsuga menziesii</u> (Mirb.) Franco	Douglas-fir
<u>Taxus brevifolia</u> Nutt.	Pacific yew
<u>Shrub Species</u>	
<u>Acer circinatum</u> Pursh	vine maple
<u>Berberis nervosa</u> Pursh	long-leaved Oregon grape
<u>Corylus cornutata</u> Marsh var.	
<u>Californica</u> (DC.) Sharp	western hazel
<u>Gaultheria shallon</u> Pursh	salal
<u>Holodiscus discolor</u> (Pursh) Maxim.	ocean-spray
<u>Rosa gymnocarpa</u> Nutt.	baldhip rose
<u>Rubus leucodermis</u> Dougl.	blackcap
<u>Symphoricarpos mollis</u> Nutt.	creeping snowberry
<u>Vaccinium ^opervifolium</u> Smith	red huckleberry

(continued on next page)

Herbaceous SpeciesCommon NameAnemone deltoidea Hook.

Columbia windflower

Campanula scoulerii Hook.

pale bluebell

Collomia heterophylla Hook.

varied-leaf collomia

Dentaria tenella Pursh

spring beauty

Elymus glaucus Buckl.

western rye-grass

Festuca occidentalis Hook.

western fescue

Festuca subuliflora Schribn.

Coast Range fescue

Galium aparine L.

bedstraw

Galium triflorum Michx.

fragrant bedstraw

Hieracium albiflorum Hook.

white hawkweed

Iris tenax Dougl.

purple iris

Lotus crassifolius (Benth.) Greene

big deervetch

Lotus micranthus Benth.

small-flowered deervetch

Luzula campestris (L.) DC.

field woodrush

Nemophila parviflora Dougl.

wood memophila

Osmorhiza chilensis H. & A.

mountain sweet-cicely

Polystichum munitum (Kaulf.) Presl

sword-fern

Pteridium aquilinum (L.) Kuhn var.pubescens Underw.

western bracken

Pyrola picta Smith

white-veined shin-leaf

Senecio jacobaea L.

tansy ragwort

Trientalis labifolia Hook.

western starflower

Viola sempervirens Greene

evergreen violet

APPENDIX IV

Statistical Comparison of the Study Plots for Biomass and Cover
of Ground Vegetation and Light Intensities Reaching the Ground

Comparison of the Study Plots (Thinning Intensities)	Ground Vegetation		Light Intensity Reaching the Ground
	Biomass	Cover	
	<u>Lower Replication</u>		
Heavy vs. Medium	-	-	** ¹
Heavy vs. Light	-	* ²	**
Medium vs. Light	-	**	-
Heavy vs. (Medium+Light)	-	-	**
Light vs. (Heavy+Medium)	-	**	*
	<u>Upper Replication</u>		
Heavy vs. Medium	-	**	**
Heavy vs. Light	-	-	**
Medium vs. Light	-	-	-
Heavy vs. (Medium+Light)	-	**	**
Light vs. (Heavy+Medium)	-	-	**

¹ The difference is significant at the one percent probability level.

² The difference is significant at the five percent probability level.

APPENDIX V

LOCATION OF THE STUDY AREA AND PLOTS

16 inches = 1 mile

