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Title: SELECTIVE FILTERING OF LIGHT BY CONIFEROUS FORESTS AND MINIMUM LIGHT ENERGY REQUIREMENTS FOR REGENERATION

Abstract approved: *Richard H. Waring*
Dr. Richard H. Waring

Spectroradiometric analyses were made to examine the light filtering capacity of coniferous forests and to establish the lower light energy limits for growth of *Pseudotsuga menziesii* (Mirb.) Franco, *Abies concolor* (Gord. and Glend.) Lindl. and *Pinus ponderosa* Dougl. Visible energy (400-750 nm) was recorded at 48 points under four mixed conifer stands and segregated into four spectral bands (blue, 400-450; green, 500-550; red, 650-700; far-red, 700-750). Each energy band was expressed as a proportion of the total visible energy using a linear regression. An analysis of unfiltered solar radiation compared with filtered revealed a significant difference at the 99 percent level for each of the four bands, indicating that a coniferous canopy is a selective filter.

Close linear relationships between the bands and the total energy were established for a range of canopy densities which allowed

penetration of 0.4 to 25 percent of the total energy (400-700 nm) received under the canopy per day. The ratio of blue to total energy (400-700 nm) was 0.1597. Green, red, and far-red had ratios of 0.1919, 0.1240, and 0.1300 respectively.

Terminal growth of 34 seedlings was measured at the light sample points to provide a means of establishing lower light energy limits for survival. The limits for *Abies* and *Pseudotsuga* were 2.0 Clear Day Index (CDI) which is equivalent to 2,000 $\mu W\ cm^{-2}\ day^{-1}$ (400-700 nm). *Pinus* was found only where the light energy exceeded 40.0 CDI.

An interaction with moisture appears to influence the minimum light energy requirements of a species. Where moisture was adequate throughout the growing season, the light limit for *Pseudotsuga* seedling establishment was 2.0 CDI; where moisture became limiting the minimum light requirement increased to 7.0 CDI.

Selective Filtering of Light by Coniferous Forests and Minimum Light Energy Requirements for Regeneration

by

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APPROVED:

____
Professor of Forestry
in charge of major

____
Head of Department of Forestry

____
Dean of Graduate School

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SELECTIVE FILTERING OF LIGHT BY CONIFEROUS FORESTS AND MINIMUM LIGHT ENERGY REQUIREMENTS FOR REGENERATION

INTRODUCTION

It is well known that plants may change the spectral composition of sunlight which filters through their leaves. Coombe (1957), Evans (1966), Federer and Tanner (1966), Robertson (1966), Szeicz (1965), and Vezina and Boulter (1966) have all documented this. Some question exists, however, as to the filtering capacity of a coniferous canopy; usually conifers have been assumed to be fairly neutral (Vezina and Boulter, 1966).

Simple comparisons of light meter reading within and outside a stand have been used extensively, but offer no measure of the total effect during a day and have the built-in assumption of no change in light quality. In 1957, Combe felt that most ecological studies did not require absolute energy measurements. But today, with the development of physiological ecology, absolute energy measurements are seen as desirable (Evans, 1966; Coombe, 1965). Spectroradiometric analysis is becoming one of the more prevalent methods of absolute energy measurement. Both Coombe (1965) and Szeicz (1965) have discussed the necessity for spectroradiometric analysis when considering plant problems. Norris (1968) summarized this point by stating "spectroradiometric analysis appears to offer the only real solution to the problem of evaluating radiation sources." The primary objective of this study, to quantitatively investigate the spectral filtering capacity of a coniferous canopy, was accomplished using spectroradiometric analysis.

The significance of light quality is not in doubt. More than a dozen plant responses can be attributed to specific spectral bands (Table 1). Most plant biologists studying light concentrate their interest in the visible range, 400-700 nm (Federer and Tanner, 1966; McCree, 1966; and Anderson, 1967). Because this range covers most plant responses, and because it is commonly accepted, it was used in this study with an additional band of 50 nm at the red end of the spectrum to include the phytochrome response area.

Many suggestions concerning the segregation of visible light into specific bands have been made. Wassink (1953) suggested three bands: from 400 to 510 nm, from 510 to 610 nm, and from 610 to 700 nm. Robertson (1966) and Vezina and Boulter (1966) each suggested five bands which are in close agreement. Robertson (1966) suggested 336 nm, 440 nm, 532 nm, 640 nm and 740 nm, each with approximately a 40 nm bandwidth, whereas Vezina and Boulter (1966) suggested 338 nm, 444 nm, 531 nm, 646 nm, and 737 nm each with bandwidths of about 20 nm. Actually, as long as continuous data are taken spectroradiometrically, any bandwidth may be segregated and compared with accuracy. I chose the four bandwidths indicated in

Table 1. Effects of light quality upon plants.

Light quality	Influence
Total visible spectrum (400 - 700 nm)	
Influence:	Endogenous rhythms
	Growth
Blue (400 - 450 nm)	
Influence:	Phototropism
	Rhizome polarization
	Photosynthesis
	Chlorophyll synthesis
	Auxin destruction
Green (500 - 550 nm)	
Influence:	Sugar flow
Red (650 - 700 nm)	
Influence:	Photosynthesis
	Photomorphogenic induction
	Chlorophyll synthesis
	Photoperiodic activity
Far-Red (700-750 nm)	
Influence:	Elongation
	Heating
	Photomorphogenic reversal
	Dormancy
	Flowering
	Seedling differentiation
	Anthocyanin formation

Table 1.

To provide some ecological interpretation of light energy data, growth and survival of coniferous seedlings were recorded where spectroradiometric measurements were taken. In particular, minimum light energy requirements were investigated for the establishment of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), ponderosa pine (Pinus ponderosa Dougl.), and white fir (Abies concolor (Gord. and Glend.) Lindl.). The question as to possible shifts in the minimum light energy requirements under favorable and unfavorable moisture stress conditions was also investigated.

METHODS

Instrumentation

Until recently glass and gelatin filters were employed to measure spectral energy. Unfortunately, most such filters have imperfections that affect their transmission properties and produce qualitative and quantitative errors (Van der Veen, 1959). The most recent instruments use an interference grating filter to control the quality of light received and photocells with broad spectral sensitivity to measure energy. Such an instrument was developed by Robertson (1963) for spectroradiometric study of light and its effect upon plants. Recently, spectroradiometers have become commercially available. In this study a portable, (30 x 25 x 18 cm) battery-operated spectroradiometer made by Instrumentation Specialities Company (ISCO) was used. This instrument has a flat cosine-corrected receptor and detects light energy in the 380 nm to 1100 nm band with a resolution of 15 nm. The scale reads in microwatts per square centimeter per nanometer($\mu W\ cm^{-2} nm^{-1}$) within a sensitivity range of 0.01 to 1000 $\mu W\ cm^{-2} nm^{-1}$. According to the instruction manual, it is accurate within seven to ten percent of total energy received.

With normal laboratory use the instrument requires only monthly calibration checks, but when subjected to heavy field use, more frequent calibration is required (Stair, Jackson, and Schnider, 1963).

The question concerning the most appropriate receptor has been widely discussed in the literature. The two most prevalent shapes, flat with cosine correction, and spherical, provide dissimilar information which is not convertible (Reifsnyder and Lull, 1965). Either receptor could have been used, but because the flat cosine corrected receptor yields more constant measurement (Taylor and Kerr, 1941), it was chosen.

Collection of solar energy data, by any means, requires consideration of variation introduced by changes in elevation, weather, and solar angle of incidence. The magnitude of such variation is discussed in the appendix. In this study, sampling was restricted to conditions that permitted direct comparison of radiation data.

Study Area and Stand Descriptions

The study was conducted in the Eastern Siskiyou Mountains (42° N. Lat., 123° W. Long.) upon lands of the Rogue River National Forest in Southwestern Oregon. The region is rough and mountainous with peaks to 2, 300 meters. The climate is influenced by oceanic fronts during the winter and by a system of coastal highs during the summer. Total precipitation varies from 45-125 cm, but less than 5 cm usually fall during the summer growth period.

Geologically, few areas of comparable size are as variable. Granitic, ultrabasic, sedimentary, and metamorphic rocks are represented. The diverse array of soils and local climates which characterize the area provide habitats for more than 600 known species of vascular plants (Waring, 1969).

Within the ecological framework developed by Waring (1969), four mixed conifer stands were selected for investigation. Although temperature patterns and soils differed, the major distinquishing feature was the availability of soil water to plants near the end of the growing season (see Table 2). Moisture stress, as measured with a pressure bomb upon young conifers before dawn in early September, ranged from 8 to 24 atmospheres (Waring and Cleary, 1967). At approximately 18 atmospheres cambial activity ceases. The growing season, defined as the period between bud swell and the 20th of September at which date photoperiod appears to limit further cambial activity, appears to be longer at Stand 3. In reality, growth is prematurely arrested at Stand 3 through the effect of high moisture stress. In a similar manner, the effect of temperature upon the growth of Douglas-fir is overestimated by the Optimum Temperature Day Index (Cleary and Waring, 1969) because interaction with high moisture stress is not taken into account.

Except for Stand 13, the forest canopies were dense and uniform. Under Stand 13, numerous shafts of direct sunlight penetrated,

Table 2. Stand descriptions.

	Stand 1	Stand 3	Stand 13	Stand 14
Topography				
Elev. (m)	1500	800	1340	1250
Slope (%)	25	45	20	35
Aspect	West	North	West	South
Soil				
	Sandy loam from quartz diorite	Sandy loam from quartz diorite	Clay loam from green schist	Clay loam from green schist
Vegetation				
Overstory	PSm-PNp-ABc[1]	PSm-PNp-Qke	PSm-PNp-PNp-ABc	PSm-PNp-ABc
Site Index (ft/100 yrs)	PSm-125 PNp-100	PSm-70 PNp-67	PSm-140 PNp-115	PSm-140 PNp-115
Phenological Growing Season (days)	120	133	119	119
Temperature (°C) (During Growing Season)				
Maximum	39	36	40	41
Minimum	-6	2	-2	-1
Average Day	14	17	19	19
Average Night	12	16	15	15
Average Soil (20 cm)	13	17	13	16
Opt. Temp. Day Index[2]	120	133	119	119
Moisture				
Total Precip. (cm)	80	60	110	110
Snow	60	20	100	100
Drought-Moisture Stress (Atms)[3]	14	24	8	10

[1] PSm-Douglas-fir, PNp-Ponderosa pine, ABc-White fir, Qke-Black oak, PN1-Sugar pine. (After Day, 1967).

[2] Defined for Douglas-fir seedlings under controlled day, night and soil temperatures, expressed for the entire growing season by summing the effectiveness of each day as a fraction of the maximum possible (Cleary and Waring, 1969).

[3] Measured on 2 m tall Douglas-fir before dawn on September 1, 1967(Waring and Cleary, 1967).

permitting an abundant understory vegetation to develop in contrast to that found under the other three stands.

Sampling

To identify minimum light energy requirements for Douglas-fir, white fir and ponderosa pine, samples were taken which were representative of the light energy received near the seedlings. In addition to measuring spectral energy, terminal growth for the last year and for the last five years was measured on each sample seedling. Herbaceous vegetation was also sampled in an area 0.5 m square around each light measurement point. A total of 48 points were sampled, 80 percent of which were located under a dense forest canopy without light gaps. Thirty-four seedlings were measured at these points.

Pilot studies with the spectroradiometer and ozalid paper, a chemical light integrator (Friend, 1961), indicated that sampling variation would be small if sampling was restricted to locations well inside the stand border. No attempt was made to characterize the light environment for the entire stand or to obtain a space average.

Spectroradiometric measurements were taken at intervals of 25 nm over the range from 400 - 750 nm at each point, requiring approximately five minutes. Under dense canopy where light becomes limiting for conifer survival, continuous light energy recording was unnecessary. By not having to sample continuously, it was possible to move the spectroradiometer from point to point within a stand, thereby sampling an average of 12 points per day (from sunrise to sunset). In Stand 13 where sunflecks penetrated the canopy for brief periods of time, the estimate of total daily light energy was less accurate than if sampling had been continuous.

All stands were sampled on completely clear days within the period from June 15th to July 25th. It was essential to sample on clear days for even high level clouds introduce considerable variation (Anderson, 1964). Vezina and Pech (1964) also suggest that the ratio of solar radiation (outside the stand to under the canopy) can best be characterized on a few bright clear days. In addition, it was necessary to sample during a short enough period to exclude variation caused by solar declination. During the stated period, solar declination varied about 5° causing about one percent variation in total energy received.

Analysis

Plotting, correcting, integrating, and summarizing the raw data by computer took less than ten minutes. Integration over quality was performed first, followed by integration over time, then the amount of energy in the four spectral bands (400-450, 500-550, 650-700, 700-750) was computed. Output was summarized by total and by spectral bands as indicated by the example in the appendix.

The spectral quality of the solar beam changes with the thickness of the atmosphere; the greatest changes occur at sunrise and sunset (Robertson, 1966; Johnson et al., 1967). Because such quality changes are most apparent only at low light intensities, they were considered of minor importance in their total daily effect.

In evaluating seedling growth and survival, the integrated light energy recorded on clear days in June and July are best expressed as an index to emphasize that they are not an average for the entire growing season. This Clear Day Index (CDI) is equivalent to 1.0×10^3 μW $cm^{-2} day^{-1}$ over the spectrum from 400-700 nm. The value 2,000 μW $cm^{-2} day^{-1}$ for example, becomes 2.0 CDI.

Over the range of light energy values recorded, the linear regression model

$$Y = bx + \epsilon$$

where

Y = dependent variable or specific color band

b = the slope of the regression line

x = the independent variable or total light received under the stand

ϵ = the error of Y on the regression line

σ^2 = variance about the regression with the assumption

$$E(\epsilon_x^2) = x\sigma^2$$

was found appropriate. This model differs from the standard linear regression equation only in the sense that the variance is assumed to be proportional to the light energy received. A complete statistical treatment is included in the Appendix. This regression model was used to compare the selective filtering capacity of the coniferous forest canopy. Additional graphical analyses were employed to contrast changes in light quality under forest stands with that in the open and to roughly define minimum light energy requirements for establishment of Douglas-fir, white fir, and ponderosa pine regeneration.

RESULTS AND DISCUSSION

The total light energy recorded at the sampling points under the forest stands ranged from 0.4 to 35 percent of full visible sunlight (400-700 nm) with the average point receiving 17.7 CDI, or approximately 4.4 percent of full sunlight. Only four points received more than 50.0 CDI (13 percent of full sunlight) and one of those, in Stand 13, received 149.0 CDI (37 percent of full sunlight). Excluding Stand 13, where numerous sunflecks patterned the forest floor, the plots were almost devoid of sunflecks.

Of the four integrated bands, green showed the highest average energy - 3.4 CDI. Blue, with an average of 2.8 CDI, was greater than red and far-red which averaged 2.2 CDI and 2.3 CDI respectively. Neither red nor far-red exhibited a consistent relationship. When total energy was greater than 10.0 CDI, red was greater than far-red, but the situation reversed itself at energy levels below 8.0 CDI. Similar findings were reported by Vezina and Boulter (1966) who worked primarily with hardwoods. Multiple reflection with little absorption is commonly cited as the cause of green augmentation as opposed to the relative reduction of blue and red by chlorophyll absorption. The low absorption and high transmission and reflection of far-red radiation by the leaves allows them to escape a tremendous potential heat load, and is the cause of the proportional increase in far-red energy under the canopy (Gates, 1965).

Figure 1 illustrates the spectral reapportionment that takes place as sunlight filters through the canopy, and its ordinate, with two different scales, reflects the magnitude of the reduction in energy. The total integrated energy in this case is reduced approximately 140 times.

In Table 3 spectrual changes are compared by calculating the ratios of energy in one color band to that in another.

Table 3. Comparison of spectral ratios under the forest canopy and in the open.

Ratio	Open	Under the Stand
Green/Blue	1. 16	1. 20
Green/Red	1. 79	1. 54
Green/Far-red	2. 30	1. 48
Red/Far-red	1. 29	0. 95

Both Figure 1 and Table 3 show that red is not proportionately decreased as expected; but there is a noticeable drop at 675 nm near the maximum chlorophyll absorption.

A statistical analysis, comparing light for each of the four spectral bands to total visible light, showed a consistent significant filtering at the 99 percent level underneath as compared to above a coniferous canopy. In other words, the coniferous canopy is a

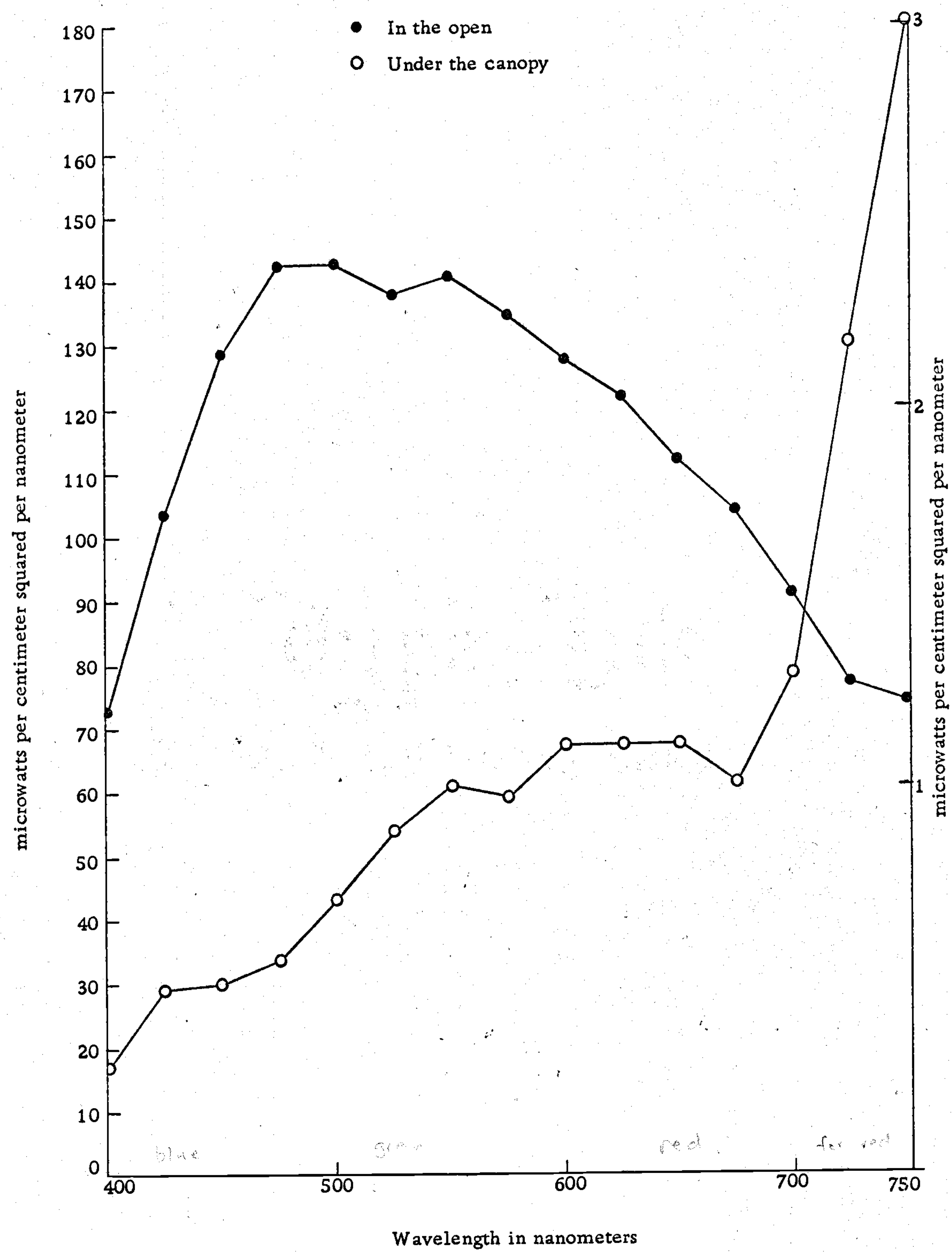

Figure 1. The spectral distribution of light under a coniferous forest canopy and in the open on a clear day.

selective filter that alters the quality as well as the quantity of light received by the understory vegetation (Table 4).

Table 4. Statistical Analysis demonstrating the selective filtering of coniferous foliage.

Color	Band	Open Band/Tot[1]	Under Stand	Limits 99%CL	σ^2	$V(\hat{\beta})$
Blue	400-450 nm	0.1709	0.1597	±0.0103	10.19	1.18×10^{-5}
Green	500-550 nm	0.1989	0.1919	±0.0062	4.06	4.22×10^{-6}
Red	650-700 nm	0.1111	0.1240	±0.0110	9.66	1.35×10^{-5}
Far-red	700-750 nm	0.0864	0.1300	±0.0067	4.20	4.93×10^{-6}

[1] Ratio of energy in a given spectral band to the total visible energy (400-700 nm).

The regression coefficients suggest a higher proportion of green light in the spectrum unfiltered by a canopy. This is an anomaly, as one would expect the reverse to be true. One must keep in mind that although green increases in proportion to blue, it is reduced in proportion to red and far-red (Table 3) and the net result is a decrease in relation to total energy when measured under the canopy. Figure 1 and Table 3 illustrate this point.

The variance of the blue and red bands are twice as large as the variance of the green and far-red bands. This difference may be caused by the sampling of sunflecks under Stand 13. At the time a sunfleck is sampled the blue and red are enhanced disproportionately to the green and far-red light which are reflected and emitted in such a manner as to remain essentially unchanged relatively.

The population tolerance limits (two-thirds of the observed population is expected to fall within these limits) for each light band were generally less than four percent of the energy measured in the visible spectrum (see Appendix Table 1). Thus, the population sampled was very uniform in its transmission properties.

Another result of this uniformity is the narrow regression limits (Appendix Table 2) which allow prediction within $\pm$ 0.5 percent of total visible energy 67 percent of the time. For example, if the total visible energy were 10,000 $\mu W\ cm^{-2} day^{-1}$, the green band would contain 1,597 $\pm$ 34 $\mu W\ cm^{-2} day^{-1}$. This predictive accuracy suggests the possibility of using simple photocells of known spectral sensitivity as light integrators under coniferous forest canopies permitting less than 25 percent of full sunlight to penetrate. Under more open canopies, additional spectroradiometric comparisons are needed. The same linear relationship found in this study at low light intensity is unlikely and more sophisticated statistical analysis will probably be required.

The growth data collected at the sample points showed that no growth was observed on any of the three tree species below the 2.0 CDI level (Figure 2). Species requirements obviously differ, for no

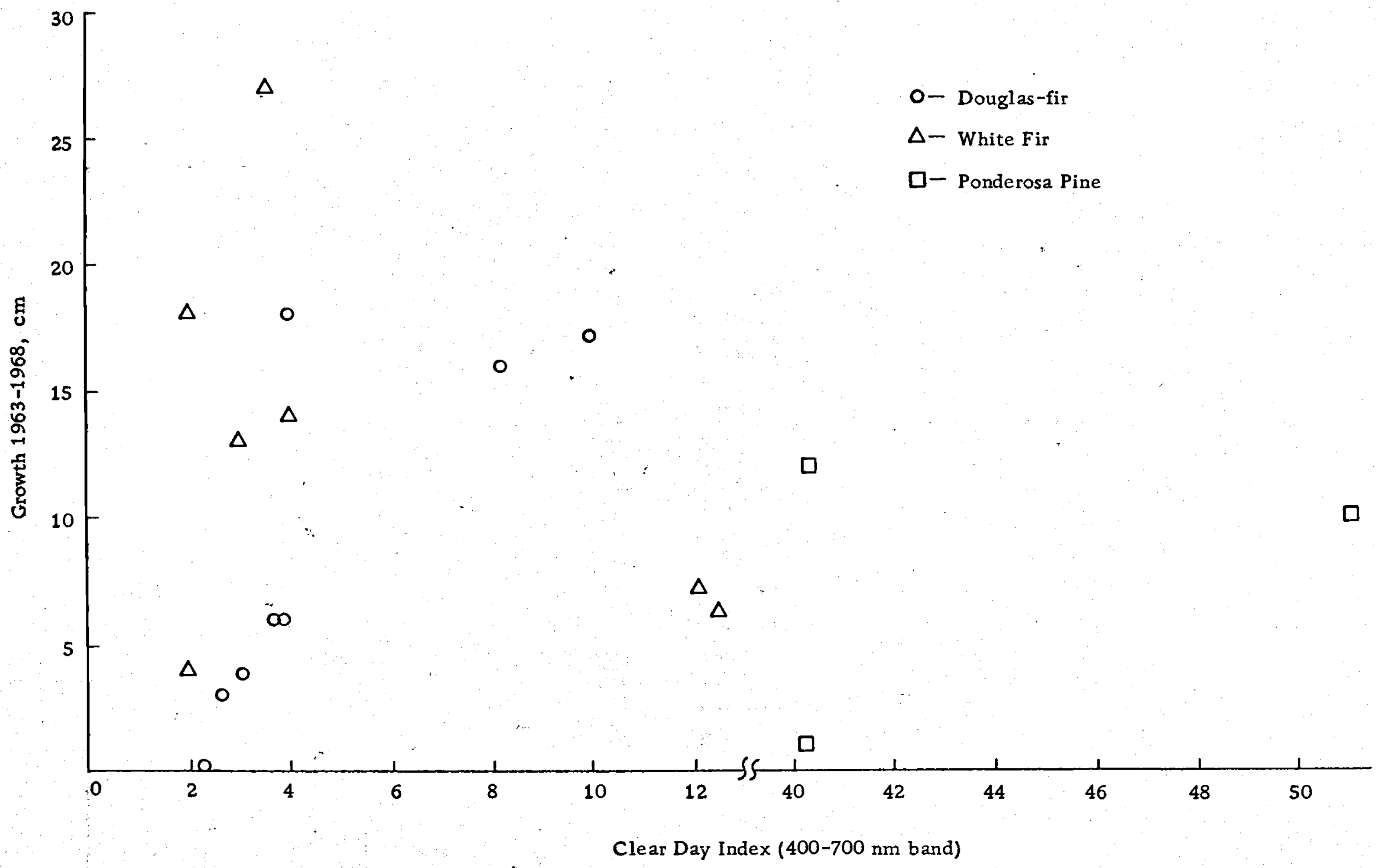

Figure 2. Douglas-fir, white fir, and ponderosa pine terminal growth in relation to total light energy received during the day under the stand.

live pine regeneration was established below 40.0 CDI, whereas Douglas-fir were observed at light energy levels below 3.0 CDI. No regeneration of any kind was found below 2.0 CDI (0.5 percent of full sunlight, 400-700 nm). In fact, only Symphoricarpus mollis Nutt. occurred under such circumstances and its rhizomes may have been attached to plants receiving more light.

Figure 2 indicates that white fir is more responsive to increased light than Douglas-fir. With increased light energy, above 12.0 CDI, two white fir were observed with approximately 6 cm growth, far below that expected by projected trends. Perhaps a disproportionate increase in respiration results from the increased heat load or stomatal closure under increased transpirational stress may reduce photosynthesis. Historical events might also be important--a recent opening in the canopy, wind breakage or deer browsing could all play a part. Any one or any combination of the above explanations could be responsible for an apparent decrease in growth with increasing light. Most certainly light is not the only environmental factor determining a seedling's growth and survival.

The data presented in Figure 3 suggest a basic interaction between light and moisture. Douglas-fir grew at lower light energy levels (2.0 CDI) on environments with only moderate moisture stress (10 to 14 atm) than where moisture stress reached 24 atm in 2 m tall Douglas-fir and minimum light requirements were 7.0 CDI.

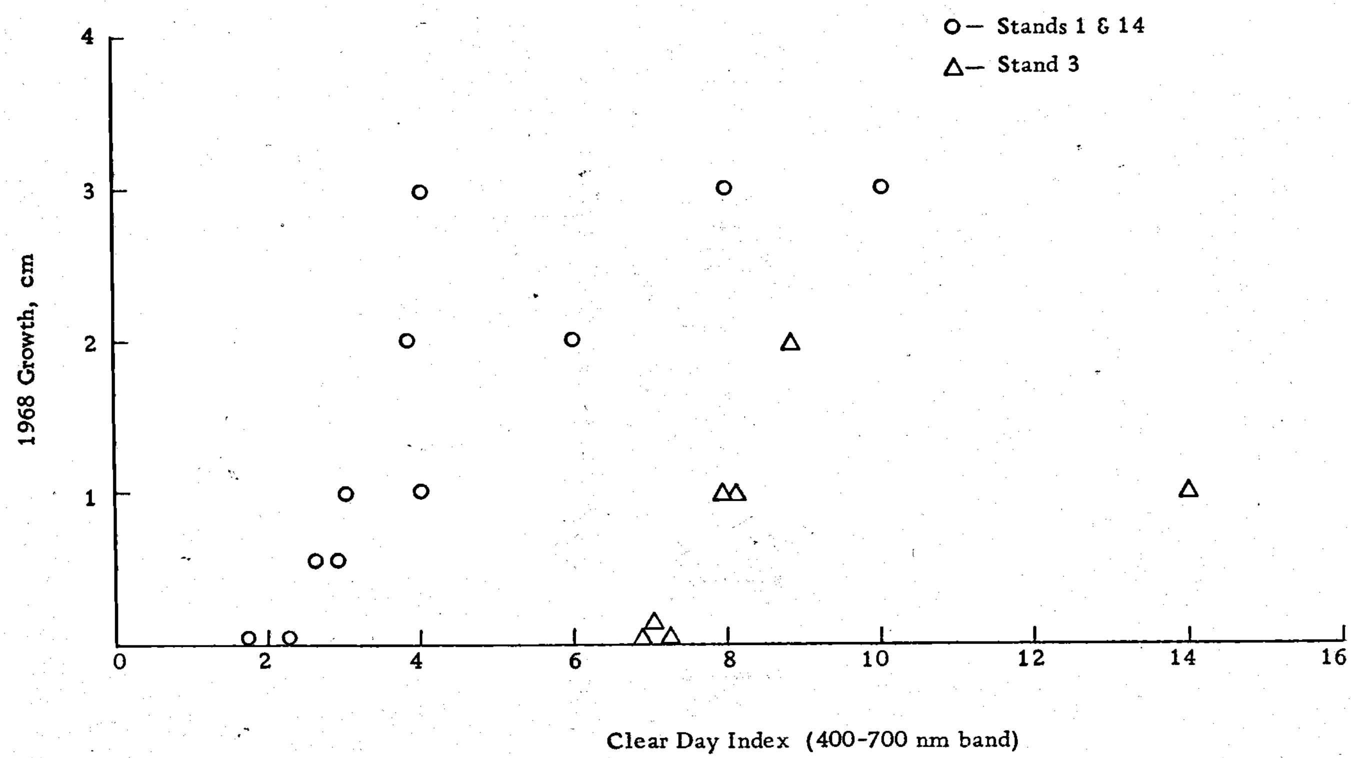

Figure 3. Douglas-fir and white fir terminal growth in relation to total light energy received during the day under the stand.

Partial shading is an advantage for most species, particularly white fir; pine growth appears to still be increasing above 100.0 CDL. Douglas-fir appears to be intermediate in its response and its light compensation point increases as other environmental factors become less favorable. Moisture stress operates to reduce root growth, trigger stomatal closure and decrease net photosynthesis as the summer progresses. Nutritional stress or unfavorable temperatures should act similarly. The demonstration of a moisture-light interaction makes it desirable that ecologists design studies in such a manner that environmental interactions can be evaluated.

CONCLUSIONS

Mixed coniferous forest of Douglas-fir, white fir, and ponderosa pine appear to act as a selective filter of light in the visible spectrum. Integrated spectroradiometric analyses indicated that the proportion of energy in the blue (400-450 nm), green (500-550 nm), red (650-700 nm), and far-red (700-750 nm) were all changed significantly in relation to the total energy recorded in the range from 400-700 nm.

Changes in light quality may have ecological significance for plant survival but the total light energy (400-700 nm) appears more critical in determining coniferous seedling establishment. The total clear day requirements for Douglas-fir and white fir appear to be about 2,000 μW $cm^{-2} day^{-1}$ when other environmental factors are favorable. Ponderosa pine did not occur at light energy levels below 40,000 μW $cm^{-2} day^{-1}$. Where moisture became limiting for the growth of Douglas-fir, seedlings of that species did not occur at levels below 7,000 μW $cm^{-2} day^{-1}$.

Under coniferous forests, permitting less than 25 percent of full sunlight to penetrate one may use a linear regression model to predict the amount of energy in any of the four bands, knowing the total energy (400-700 nm).

A spectroradiometer provides information on light quality and quantity. Biological interpretation requires that an organism's response be investigated in relation to the physical environment which it directly senses.

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APPENDIX

APPENDIX

Elevation

The difference in total visible radiation received at 125 m as compared to 2,140 m on a clear day was found to be two percent greater at the higher elevation, which is within the limits of the instrument's precision. Because the greatest elevational difference in this study was less than 700 m, elevational variation was ignored.

Weather

Clouds, fog, and moisture saturated air layers considerably diminish solar intensity and cause spectral variation primarily in the red bands. Variation caused by clouds and fog was avoided in this study by sampling only on clear days, but the variation caused by moist air masses was unknown. But, Weather Bureau radiometers which record 72 percent of theoretical solar radiation revealed that total solar radiation on clear days (up to ten percent cloud cover) varied 6.6 percent. Considering that no recording was undertaken if any cloud cover whatsoever ammassed and that the variation recorded by the Weather Bureau was largely in the infrared region, which I did not record, the variation caused by moist air masses is also negligible in this study. Similarly, turbidity conditions caused by industry did not influence insolation during the study.

Season

During the average growing season, from mid-June to mid-September, the sun's declination changes 15° causing a three percent decrease in energy received per unit area at the earth's surface. From June to August, a 5° declination change occurs and is reflected in the results. Decreasing declination shortens the daylength, changes the spectral distribution in favor of the red end of the spectrum, and lessens the total amount of energy received, all of which affect growth, but are not sufficiently large to change the results reported here.

Radiation Source

Meteorologists and ecologists have often attempted to separate direct from diffuse radiation. Some ecologists, although recognizing the importance to sunflecks, have disregarded them when recording light energy (Evans, 1956). Anderson (1965) emphasized the importance of accounting for direct sunlight, and discussed at length the problems of sampling sunflecks in *Pinus* stands. In this study time integration lessened the effects of sunflecks by including them in the greater amount of shade light, but their effects were sensed by the plant simultaneously with shade light, and separation would lessen biological meaning.

Statistical Treatment

The linear regression model

$$Y = \beta_1 x + \epsilon$$

was used with the assumption

$$E(\epsilon_x^2) = x\sigma^2.$$

This assumption changed the basic model to:

$$Y' = \frac{Y}{\sqrt{x}} = \frac{\beta_1 x}{\sqrt{x}} + \frac{\epsilon}{\sqrt{x}}$$

where

$$\frac{x}{\sqrt{x}} = x'$$

and

$$\frac{\epsilon}{\sqrt{x}} = \epsilon'$$

and

$$E(\epsilon'^2_x) = \sigma^2.$$

The resulting statistics are as follows:

$$\hat{\beta}_1 = \frac{\Sigma Y}{\Sigma x};$$

$$\hat{Y} = x\hat{\beta};$$

$$\hat{\sigma}^2 = \frac{1}{n-1}\left[\Sigma\left(\frac{Y^2}{x}\right) - 2\hat{\beta}\Sigma Y + \hat{\beta}^2\Sigma x\right];$$

$$\hat{V}(\hat{\beta}) = \frac{\hat{\sigma}^2}{\Sigma x^2} \;;$$

$$\text{Rel Vari}(\hat{\beta}) = \frac{\hat{\sigma}^2}{\hat{\beta}^2 \Sigma x^2} \;;$$

$$68\%\ \text{CL}\hat{Y}_{xy} = x\hat{\beta}(1 \pm \sqrt{RV(\hat{\beta})}\,) \;;$$

$$V(\hat{Y}_{mean})_x = x^2\, V(\hat{\beta}) \;;$$

$$V(\hat{Y}_{predicted})_x = V(x\hat{\beta}) + x\sigma^2 \;;$$

$$99\%\ \text{CL}(\beta') = \hat{\beta} \pm 3\sqrt{V(\hat{\beta})} \;.$$

Integrated Energy Values ($\mu W\ cm^{-2} nm^{-1}$)

Sample Points	Total	Blue	Green	Red	Far-red
			Stand 1		
1- 1	40,295	5,664	8,002	5,366	4,713
1- 2	5,692	817	1,235	640	841
1- 3	29,428	4,454	5,934	3,620	3,286
1- 6	2,527	481	507	272	566
1- 7	14,678	1,901	2,948	2,046	1,923
1- 8	12,085	1,842	2,448	1,407	1,372
1- 9	4,260	797	838	471	671
1-10	3,522	525	710	496	850
1-11	1,799	301	382	176	434
1-12	13,192	2,080	2,674	1,569	1,511
1-13	11,924	1,696	2,406	1,513	1,377
1-14	3,088	488	665	350	614
1-15	2,818	489	587	287	566
1-16	2,164	330	461	266	509
1-17	2,548	463	528	252	444
1-18	3,322	580	668	371	524
1-19	5,962	767	1,104	913	1,012
1-20	2,946	466	604	338	627
1-21	3,994	520	838	531	751
			Stand 3		
3- 1	7,783	1,296	1,389	1,049	1,221
3- 2	50,548	8,903	9,128	6,141	5,538
3- 3	7,350	1,342	1,277	946	1,232
3- 4	27,731	4,486	4,912	3,699	3,688
3- 5	8,696	1,938	1,577	807	1,071
3- 6	6,696	1,301	1,245	693	914
3- 7	46,154	6,851	8,283	6,670	5,938
3- 8	37,317	7,432	7,468	3,153	3,174
3- 9	8,668	1,688	1,586	917	1,018
3-10	14,882	2,626	2,681	1,834	1,962
3-11	49,897	8,321	9,093	6,142	5,444

Sample Points	Total	Blue	Green	Red	Far-red
			Stand 13		
13-1	149,250	22,069	30,320	18,098	14,514
13-2	95,093	15,410	18,497	11,983	10,461
13-3	51,755	8,094	10,193	6,658	7,207
13-4	11,895	1,590	2,334	1,738	2,261
13-5	12,084	1,447	2,259	2,007	2,375
13-6	11,170	1,564	1,928	1,877	2,374
13-7	13,537	2,038	2,707	1,695	2,103
13-8	8,073	1,211	1,442	1,445	2,263
			Stand 14		
14-1	11,473	1,701	2,136	1,485	1,560
14-2	2,732	278	127	256	508
14-3	3,873	332	456	301	508
14-4	1,673	287	324	188	535
14-5	10,105	2,992	1,750	858	818
14-6	8,302	1,646	1,552	831	1,346
14-7	4,091	658	758	522	817
14-8	6,219	926	1,154	947	1,133
14-9	14,602	2,393	2,695	1,744	1,719
14-10	1,954	314	367	243	609

Sample of Computer Printout

Point 14-1

Wavelength	Sum
400-450	1.7008E 03
400-550	2.1357E 03
650-700	1.4847E 03
700-750	1.5596E 03
400-700	1.1473E 04

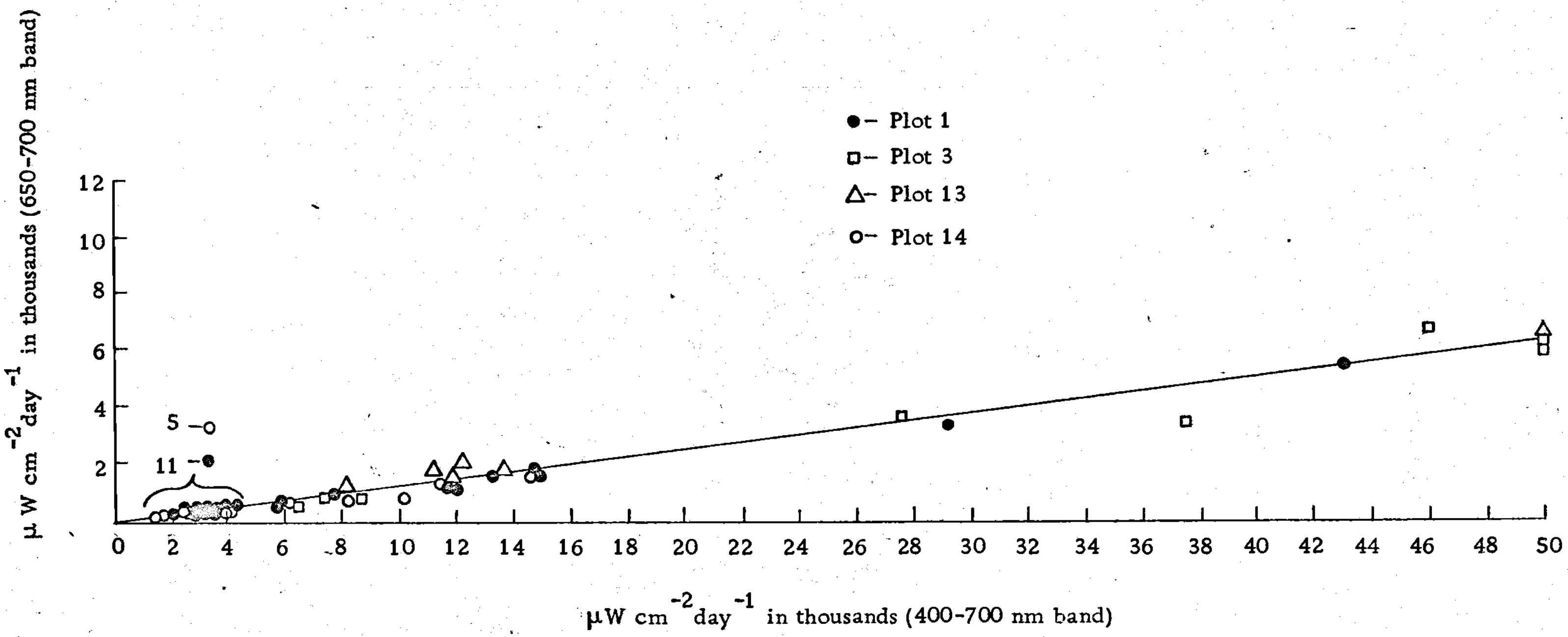
Appendix Table 1. Population tolerance limits for selected total energy values (in μW cm^{-2} day^{-1}).

Total Energy (400-700 nm)	Blue (400-450 nm)	Green (500-550 nm)	Red (650-700 nm)	Far-red (700-750 nm
5,000	±226	±142	±220	±145
10,000	±321	±206	±313	±206
20,000	±456	±288	±446	±293
30,000	±562	±354	±549	±361
40,000	±411	±411	±639	±419

Appendix Table 2. Regression limits with predicted values of selected total energy values (in $\mu W\ cm^{-2} day^{-1}$).

Total Energy (400-700 nm)	Blue		Green	
	Y pred	V(Y)	Y pred	V(Y)
1,000	160	± 3	192	± 2
5,000	798	± 17	960	± 10
10,000	1,597	± 34	1,919	± 21
20,000	3,194	± 69	3,838	± 41
30,000	4,791	±103	5.757	± 62
40,000	6,388	±137	7,676	± 82
50 000	7,985	±172	9,595	±103

x Value	Red		Far-red	
	Y pred	V(Y)	Y pred	V(Y)
1,000	124	± 4	130	± 2
5,000	620	± 18	650	± 11
10,000	1,240	± 37	1,300	± 22
20,000	2,480	± 73	2,600	± 44
30,000	3,720	±110	3,900	± 67
40,000	4,960	±147	5,200	± 89
50,000	6,200	±184	6,500	±111



Appendix Figure 1. Regression line (red vs total energy) with stands identified.