

Selective filtering of light by coniferous forests and minimum light energy requirements for regeneration¹

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Spectroradiometric analyses were made to examine the light-filtering capacity of coniferous forests and to establish the lower limits of light energy for growth of *Pseudotsuga menziesii* (Mirb.) Franco, *Abies concolor* (Gord. and Glend.) Lindl., and *Pinus ponderosa* Dougl. Light energy (400–750 nm) was recorded periodically on clear days in June and July 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 nm). Minor changes in the proportion of light in one band to that in another occur throughout the day, but in general the 400- to 700-nm range appears rather uniformly absorbed by a coniferous forest canopy. Averaged for an entire day, only the far-red band showed a significant proportional increase under a coniferous canopy compared to unfiltered sunlight.

The relation between the energy received in each of the spectral bands and the total recorded in the 400- to 700-nm range was linear. The sampled canopies transmitted up to 25% of full sunlight. Beneath the canopies, the ratio of blue to total energy (400–700 nm) was 0.1540. Green, red, and far-red had ratios of 0.1853, 0.1220, and 0.1207.

Terminal growth of 34 seedlings was measured at the light-sampling points to provide a means of establishing lower limits of light energy for survival. The lower limit for *Abies* and *Pseudotsuga* was 1.85 langley (ly) per day (400–700 nm). *Pinus* grew only where the light energy exceeded 36.8 ly/day.

An interaction with moisture appears to influence the minimum requirements for light energy of a species. Where moisture was adequate throughout the growing season, the lower limit of light for *Pseudotsuga* seedling establishment was 1.85 ly/day; where moisture became limiting, the minimum light requirement increased to 6.64 ly/day.

Introduction

Hardwood canopies are well known to change the spectral composition of sunlight as it filters through their leaves (Coombe 1957; Evans 1966; Gates 1965; Federer and Tanner 1966; Robertson 1966; Szeicz 1965). Conifers, however, have been assumed to be fairly neutral (Vezina and Boulter 1966).

With commercially available spectroradiometers, we evaluated the spectral filtering capacity of mixed coniferous forests, and at the same time established the minimum requirements of light energy for the survival of three species of coniferous seedlings. We also investigated the possibility of a change in a species' minimum requirements for light energy as moisture, another environmental variable, also became limiting.

With a portable spectroradiometer, we periodically measured the energy available in different spectral bands that are important for plant growth and development. Such information is basic for identifying the normal spectrum of light energy available to forest plants and for separating the influences of light quality from light quantity.

Methods

A field study was conducted in the eastern Siskiyou Mountains of southwestern Oregon (42° N lat., 123° W long.), where environmental and vegetational relations have recently been studied by Waring (1969). Within the framework developed by Waring, four mixed conifer stands were selected for investigation. These stands represented different compositions and densities of overstory trees growing in a range of environments differing most notably in the availability of soil water. Soil composition and nutrient availability were considered not significantly different in the stands sampled. Plant-moisture stress, evaluated with the pressure bomb, served as an index to the availability of water to tree roots (Waring and Cleary 1967). In Table I, the overstory composition and drought-moisture stress of the four stands are presented.

The differences in moisture stress reported in Table I have both physiologic and ecologic implications. In stand 2, where drought stress reached 24 atm, cambial growth was prematurely arrested. Stands 3 and 4 remained at relatively low stress because of deep soils with good water storage capacities and some supplemental seepage water. Environments in the Siskiyou with stress values exceeding 16 atm appear too dry for *Abies concolor* to compete. *Quercus kelloggii*, found in stand 2, is unable to compete unless the stress exceeds 20 atm.

In this study, light was measured with a portable (30 × 25 × 18 cm) battery-operated spectroradiometer made by Instrumentation Specialties Company (ISCO). 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

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centimeter per nanometer ($\mu\text{W cm}^{-2} \text{nm}^{-1}$) with eight ranges, from 0.03 to $1000 \mu\text{W cm}^{-2} \text{nm}^{-1}$, full scale. According to the instruction manual, the instrument is accurate within 7 to 10% of "full scale" range. At a given wavelength, repeated measurements agreed within 2% of full scale.

With normal laboratory use, the instrument requires only monthly calibration checks, but more frequent calibration is recommended for use in the field. We maintained our instrument calibration with a National Bureau of Standards Lamp by procedures outlined by Stair *et al.* (1963).

To identify minimum requirements of light energy for Douglas fir, white fir, and ponderosa pine, measurements of spectral light were taken in the vicinity of the seedlings. The terminal growth of each seedling for the last year and for the last 5 years also was measured. A total of 48 points were sampled; 38 of these were located under a dense forest canopy without light gaps. Thirty-four seedlings were measured at these points.

The spectroradiometer was moved from point to point within each stand, to sample an average of 12 points per

day from sunrise to sunset. We spent about 5 min at each point to record the energy over the range from 400 to 750 nm at intervals of 25 nm. Readings were made at about hourly intervals at each point. All measurements were taken on completely clear days between June 15 and July 25 when changes in the solar declination affect the total radiant energy less than 1%. Because direct-beam solar radiation is infrequent but may be important to the survival of seedlings under dense canopies, we did not shield the spectroradiometer to exclude such radiation, as did Federer and Tanner (1966).

Raw data were punched into cards and analyzed by a special program written for a CDC 3300 computer. The program first corrected the raw data based on calibration coefficients for each of the 14 wavelengths measured. Next the amount of energy received over the four, 50-nm-wide, selected bands was obtained. This information was then integrated over time by the trapezoidal rule to obtain daily totals for the four bands. The total daily energy received in the 400- to 700-nm band was also calculated for each of the sample points within each stand.

Results and Discussion

The daily total of light energy recorded at the 48 sampling points under the forest stands ranged from 0.4 to 37% of full sunlight (400–700 nm), and the average point received about 4.4% of full sunlight. Only four points received more than 13% of full sunlight.

Changes in the diurnal transmission of light of different wavelengths through a dense forest canopy are tabulated for one sampling point in Table II. Under a dense canopy, the maximum light energy did not necessarily coincide with true solar noon.

TABLE I
Overstory vegetation and drought-moisture stress for the stands investigated

Stand	Overstory composition	Drought-moisture stress, atm
1	PSm-PNp-ABc*	14†
2	PSm-PNp-Qke	24
3	PSm-PNp-PNl-ABc	8
4	PSm-PNp-ABc	10

*ABc, *Abies concolor* (Gord. & Glend.) Lindl., PNl, *Pinus lambertiana* Dougl., PNp, *Pinus ponderosa* Dougl., PSm, *Pseudotsuga menziesii* (Mirb.) Franco, Qke, *Quercus kelloggii* Newb. (after Day 1967).
†Average stress on five 1- to 2-m Douglas firs measured with pressure bomb before dawn, Sept. 1, 1967 (Waring and Cleary 1967).

TABLE II
Filtering effect of a dense coniferous forest canopy

Band, nm	Time, PST					Total day† %T
	0600 %T*	0900 %T	1200 %T	1500 %T	1800 %T	
400	1.33	0.45	2.82	0.69	2.76	1.25
425	1.36	0.39	2.94	0.69	2.92	1.30
450	1.35	0.49	2.85	0.66	2.80	1.42
475	1.16	0.46	2.93	0.59	2.80	1.44
500	0.83	0.36	2.69	0.56	2.78	1.55
525	1.19	0.38	2.96	0.60	3.12	1.66
550	1.06	0.43	3.19	0.67	3.40	1.69
575	0.97	0.40	3.28	0.59	3.28	1.57
600	0.82	0.36	3.04	0.53	3.06	1.44
625	0.79	0.33	3.02	0.49	2.94	1.38
650	0.67	0.28	3.08	0.43	2.88	1.43
675	0.67	0.33	3.30	0.44	2.75	1.52
700	0.60	0.47	3.70	0.68	3.22	2.50
750	1.38	1.83	8.00	3.26	11.30	

*Expressed as percentages of full sunlight.

†For entire day, this sampling point (stand 1–2) received 1.46% of full sunlight (400–700 nm).

At this particular sampling point, red and blue light apparently were absorbed more than green light rather consistently throughout the day. But this selective transmission was not apparent in more open stands. Because Federer and Tanner (1966) showed a similar relative enrichment under spruce stands when they shielded to exclude direct solar radiation, we believe our data reflect the significant contribution of unfiltered direct solar radiation which penetrates, at least briefly, all but the densest forest canopies. Because we are interested in the total energy available to plants, we designed this study to include both direct solar and diffuse radiation. Within this framework, the selective filtering by coniferous canopies in the 400- to 700-nm range is certainly of minor ecologic significance.

On the other hand, far-red light is consistently enhanced under the canopy in relation to other parts of the spectrum investigated, a finding consistent with the observations of Federer and Tanner (1966). This enhancement may have ecological significance. Dinus (1968) has shown that Douglas fir possesses the reversible phytochrome responses triggered by very low levels of red and far-red light, which in turn affect dormancy and the number and length of leaves, as well as possible sexual development.

To evaluate the data statistically, we chose a weighted linear regression model because the variance appeared proportional to the total visible energy. That is, the model for the observed Y is assumed to be

$$Y = \beta X + E,$$

$$E(\varepsilon^2_X) = X\sigma^2.$$

To apply conventional least square results, Y was transformed to

$$Y' = (Y/X^{\frac{1}{2}}) = [Y/(X)^{\frac{1}{2}}]$$

with the resulting model for Y' ,

$$Y' = (\beta_1 X/X^{\frac{1}{2}}) + (E/X^{\frac{1}{2}}) \text{ and } E(\varepsilon'^2_X) = \hat{\sigma}^2.$$

Then from the usual formulae in Y' and X' we can derive appropriate formulae for the variables Y and X .

$$\hat{\beta}_1 = \frac{\sum Y'X'}{\sum X'^2} = \frac{\sum Y}{(X^{\frac{1}{2}}/\sum X)} \cdot X^{\frac{1}{2}} = \frac{\sum Y}{\sum X}$$

$$\begin{aligned} SS \text{ of } E &= \sum (Y' - \hat{Y}')^2 \\ &= \sum Y^2 - 2\sum Y'\hat{Y}' + \sum \hat{Y}'^2 \\ &= [\sum (Y^2/X) - 2\hat{\beta}_1 \sum Y + \hat{\beta}_1^2 \sum X] \end{aligned}$$

$$\sigma^2 = s^2 = [1/(N-1)] SS \text{ of } E$$

$$V(\hat{\beta}) = (s^2/\sum X^2)$$

$$99\% \text{ C.I. of } \hat{\beta} = \hat{\beta} \pm 3[V(\hat{\beta})]^{\frac{1}{2}}.$$

When we compare slopes of the regression lines for each of the four spectral bands beneath the canopy to similar ratios above the canopy, only the far-red band was consistently enriched throughout the day (Table III). The variances for the blue and red bands were more than twice as large as those for the green and far-red bands. This variation may result from the slight selective absorption of blue and red light under the denser canopies. As mentioned previously, large amounts of unfiltered sunlight would mask the filtering effect suggested from data collected at points receiving less than 2% of full sunlight (Table II).

As a result of the regression analysis, we can predict, within limits, the energy received in any band, based upon the total daily energy received in the 400- to 700-nm range (see Fig. 1). By reversing the dependent and independent variable, we should be able with such regressions to predict the total daily energy under a coniferous forest based on the amount recorded by a simple photocell with a known spectral sensitivity somewhere between 400 and 700 nm.

The data collected on growth at the sample points showed that little was observed on any

TABLE III
Comparison of light energy ratios under full sunlight and under coniferous canopy

Color	Band, nm	Light energy ratios*		99% C.L. of $\hat{\beta}$	s^2 , ly/day	$V(\hat{\beta})$
		Unfiltered sunlight	Under conifers			
Blue	400-450	0.1709	0.1540	± 0.00747	0.0026	6.22×10^{-8}
Green	500-550	0.1989	0.1853	± 0.00777	0.0028	6.70×10^{-8}
Red	650-700	0.1111	0.1220	± 0.000293	0.0004	9.57×10^{-9}
Far-red	700-750	0.0864	0.1207	± 0.00357	0.0006	1.44×10^{-8}

*Ratio of daily energy in a given spectral band to the total daily energy (400-700 nm). Data are for all 48 sampling points.

seedlings of the three tree species below 1.85 ly/day (Fig. 2). The requirements of species obviously differ, for no live pine regeneration was established below 36.8 ly/day, although Douglas-fir seedlings were present at less than 2.58 ly/day. No white fir regeneration was found at less than 1.85 ly/day (0.5% of full sunlight, 400–700 nm). The good growth of a few white fir at low levels of light may appear because of periodic rather than continuous sampling, or may indicate that the canopies have become denser during the last 5 years.

Figure 2 suggests that white fir is more responsive than Douglas fir to increased light. With increased light energy, more than 11.2 ly/day, two white fir were observed with about 6 cm of growth, far below that expected by projected trends. Perhaps stomatal apertures decrease in the needles of the more exposed seedlings, which would reduce photosynthesis. Historical events may also be important: a recent opening in the canopy, wind breakage, or deer browsing could all play a part. Most certainly, light is not the only environmental

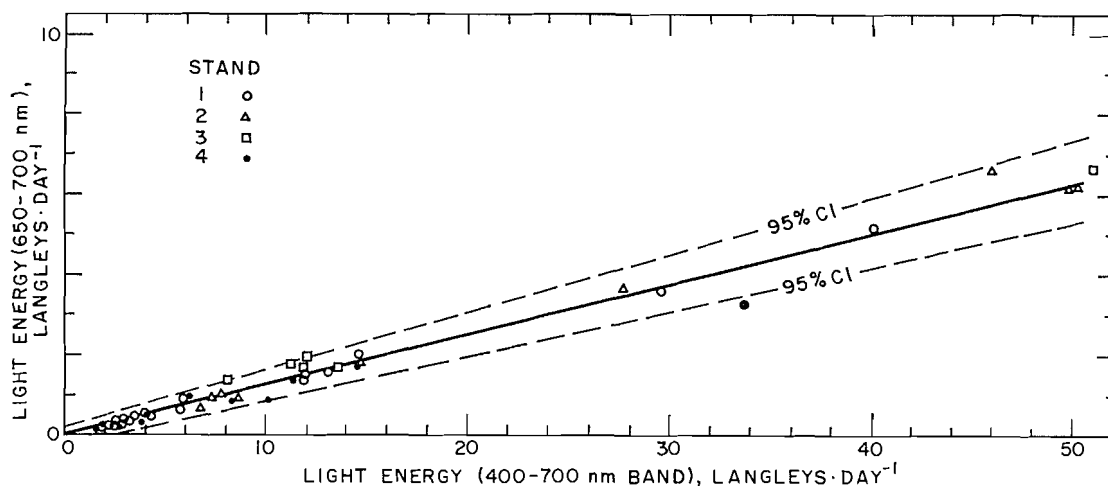


FIG. 1. Total daily energy recorded beneath the canopy in the red band in relation to the entire visible spectrum. Dotted line indicates 95% confidence interval (refer to Table III).

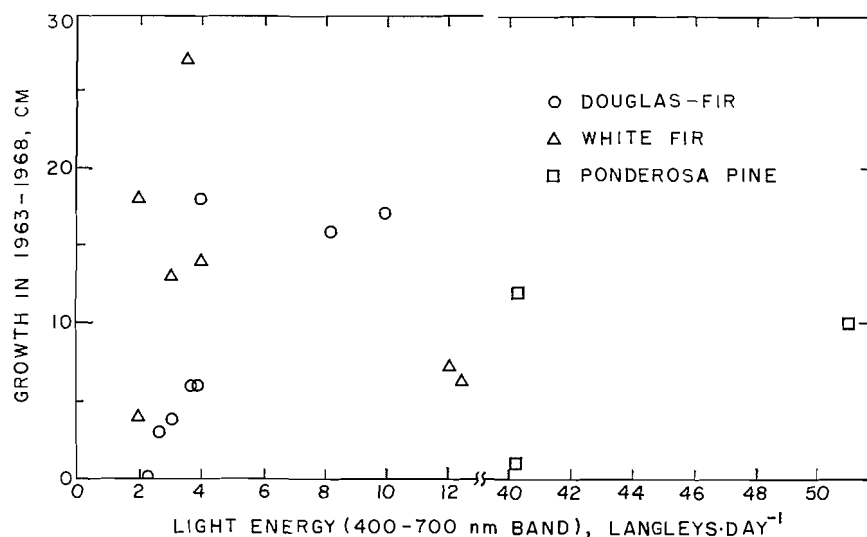


FIG. 2. Lower light limits for terminal growth of Douglas fir, white fir, and ponderosa pine.

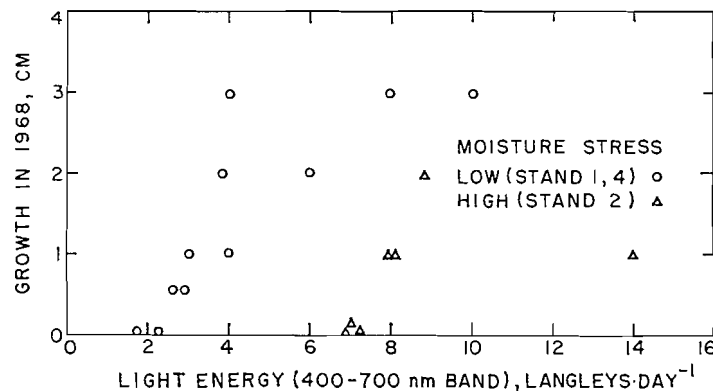


FIG. 3. Change in minimum light requirements for terminal growth of Douglas fir as affected by plant moisture stress.

factor that determines a seedling's growth and survival.

An important interaction between light and moisture is demonstrated in Fig. 3 where the minimum requirements of light for survival of Douglas fir is shown to increase three and one-half times on environments where moisture stress reaches critical levels. Partial shading is an advantage for most species, particularly white fir, but pine growth still appears to be increasing with light energy more than 93.0 ly/day. Douglas fir, intermediate in its light requirements, becomes increasingly demanding as moisture becomes more limiting. Moisture stress may reduce cell elongation, trigger stomatal closure, and decrease net photosynthesis. Nutritional stress or unfavorable temperatures also result in decreased photosynthesis and could increase the light requirement of a plant. The evidence of interaction of moisture and light suggests that additional environmental interactions must also be evaluated.

Acknowledgments

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