

Canopy light transmittance in Douglas-fir–western hemlock stands

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Summary We measured vertical and horizontal variation in canopy transmittance of photosynthetically active radiation in five *Pseudotsuga menziesii* (Mirb.) Franco–*Tsuga heterophylla* (Raf.) Sarg. (Douglas-fir–western hemlock) stands in the central Cascades of southern Washington to determine how stand structure and age affect the forest light environment. The shape of the mean transmittance profile was related to stand height, but height of mean maximum transmittance was progressively lower than maximum tree height in older stands. The vertical rate of attenuation declined with stand age in both the overstory and understory. A classification of vertical light zones based on the mean and variance of transmittance showed a progressive widening of the bright (low variance and high mean) and transition (high variance and rapid vertical change) zones in older stands, whereas the dim zone (low variance and mean) narrowed. The zone of maximum canopy surface area in height profiles, estimated by inversion of transmittance profiles, changed from relatively high in the canopy in most young stands (“top-heavy”) to lower in the canopy in older stands (“bottom-heavy”). In the understory, all stands had similar mean transmittances, but the spatial scale of variation increased with stand age and increasing crown size. The angular distribution of openness was similar in all stands, though the older stands were less open at all angles than the younger stands. Understory openness was generally unrelated to transmittance in the canopy above. Whole-canopy leaf area indices, estimated using three methods of inverting light measurements, showed little correspondence across methods. The observed patterns in light environment are consistent with structural changes occurring during stand development, particularly the diversification of crowns, the creation of openings of various sizes and the elaboration of the outer canopy surface. The ensemble of measurements has potential use in distinguishing forests of differing ages that have similar stature.

Keywords: attenuation, canopy structure, LAI, old-growth, PAR, spatial variation.

Introduction

Forest canopies modify the flux density, spectral quality and spacial distribution of light as tree crowns grow and stands de-

velop. Recent studies suggest that understory light environments change in distinctive ways as canopies develop (e.g., Smith 1991, Brown and Parker 1994). Many aspects of forest structure also change in predictable ways during development (Oliver and Larson 1990, Franklin et al. 2002), but the linkage between these changing variables is poorly understood, particularly in the canopies of tall western conifers.

The net effect of the canopy on light environments has been characterized in the understory of many forests by either direct measurements (Chazdon and Fetcher 1984, Ross et al. 1986, Pierce and Running 1988, Smith 1991, 1993, Sampson and Smith 1993) or all-sky photography (Chazdon and Field 1987, Smith et al. 1992, Martens et al. 1993, Easter and Spies 1994, Roxburgh and Kelly 1995, Clark et al. 1996). Observations have been compared between canopies differing in developmental stage or structure (e.g., Ross et al. 1986, Smith 1991, Brown and Parker 1994). Studies of vertical variation of light within canopies are less numerous (e.g., Sinclair and Knoerr 1982, Baldocchi et al. 1984, Kira and Yoda 1989, Ellsworth and Reich 1993, Maass et al. 1995, Vose et al. 1995, Yang et al. 1999, Weiss 2000), and rarely have the influences of age and structure on the within-canopy pattern been examined (Yang et al. 1999). Furthermore, we know of no studies that have considered the connection between the more commonly measured horizontal variation at the forest floor and the less commonly measured vertical variation in the canopy above.

From observations of structural changes in developing Douglas-fir forests (e.g., Franklin et al. 2002), we postulated that there would be some corresponding changes in light environments. We predicted that mean transmittance near the ground (the bulk effect of the whole stand) decreases with stand age but that variability increases as overstory trees die and larger canopy openings appear. In the upper canopy, the vertical change in transmittance per unit height declines with stand age as crowns differentiate and the canopy surface elaborates. We also predicted that overhead openness seen from the understory would increase at the zenith but decrease toward the horizon with stand age. Young stands have small crowns, tightly packed in one elevated layer, whereas older stands have more openings extending toward the forest floor (more openings at the zenith but less lateral light).

A primary objective of the study was to evaluate whether

key attributes of stand structure can be inferred from measurements of the within-canopy light environment. Specifically, we wanted to determine if stand structure in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests affects canopy light environments, including the flux density and spatial variation in understory global photosynthetically active radiation (PAR), its vertical profile, and the angular distribution of openings in the understory. A second objective was to test a set of three hypotheses about change in light environment in forests of different ages. (1) Estimates of stand leaf area index (LAI) and its vertical distribution derived from the various light measures are related to structural features that change with age. (2) Ground-based observations of light or openness are consistent with measurements made in the canopy above. (3) Generally, measurements of light environments are useful for inferring structural aspects of tall western conifer forests.

Materials and methods

Study sites

Observations of light were made in five stands of different ages at and near the Wind River Canopy Crane Research Facility (WRCCRF) in southern Washington, USA (45°49' 13.76" N 121°57'6.88" W). The stands were chosen to represent common stages of the development of Douglas-fir forests in the central Cascades. The two youngest stands were planted after harvesting, whereas the three older stands were naturally regenerated. The youngest stand (20 years old) has a high density of Douglas-fir, with some *Abies amabilis* Dougl. ex J. Forbes and *Tsuga heterophylla* (Raf.) Sarg.; the 40-year-old forest has an understory of *Acer circinatum* Pursh and some mid-canopy *Alnus rubra* Bong.; the 98-year-old stand, regenerating following the 1902 Yacholt burn (J. Franklin, University of Washington, Seattle, WA, personal communication) has an understory of *Acer circinatum*; the 155-year-old stand, dating from a fire in 1845 (J. Franklin, personal communication), has *Tsuga heterophylla* in the mid-canopy and *Acer circinatum* in the understory. The old-growth stand (500 years old) has a variety of overstory and understory species (described by Franklin 1972, DeBell and Franklin 1987, Franklin and DeBell 1988). Though the regional topography is variable, the plots studied were on locally flat areas; elevations ranged from 305 to 561 m. Table 1 summarizes the stem characteristics of these stands.

Light measurements

Global PAR (400–700 nm) was measured with a cosine-corrected quantum sensor (Model LI-190SB, Li-Cor, Lincoln, NE) in vertical profiles and along horizontal transects, about 1 m above ground. The measurements were taken under clear skies within 3 h of solar noon near midsummer; observations in the oldest stand were taken in 1995, and the other stands were measured in 1999 and 2000. In 1999, profile measurements were taken during overcast conditions in the 20- and 155-year-old stands at the same locations used in 2000. Each radiation measurement was converted to a fractional transmit-

Table 1. Stand characteristics from live trees with diameter at breast height (dbh) ≥ 5 cm in the five forests studied.

Stand age (years)	Density (ha ⁻¹)	Basal area (m ² ha ⁻¹)	Quadratic mean dbh (cm)
20	1525	20.6	12.5
40	1360	66.9	25.0
98	595	55.7	17.8
155	617	69.4	37.9
500	441.3	82.7	48.8

tance, the ratio of the in-canopy value to the corresponding time-matched external value. The mean vertical profile of transmittance, $T(h)$, is referenced to height above ground level. Details about the methods used in vertical sampling are summarized in Table 2.

Vertical profile

The vertical pattern of PAR attenuation was measured by means of several access systems. In the 20-year-old stand, the sensor was mounted atop a telescopic pole that could be raised to 15 m (Tel-o-pole, Hastings Fiber Glass Products, Hastings, MI). Balloons of different sizes (Parker et al. 1996) were used in the 40-, 98- (lift capacity of 1.3 kg) and 155-year-old stands (lift capacity of 1.5 kg). In the 500-year-old stand, within the circle reached by the crane jib, the sensor was mounted on a platform suspended from the gondola of a tower crane (Parker et al. 1992). At each sampling location in each stand, we made measurements of PAR along vertical transects within the canopy. In the balloon and pole transects, ten 0.4-s measurements of PAR were taken at each vertical position and the average recorded by a Campbell CR21X data logger (Campbell Scientific, Logan, UT). In the crane transects, single sensor readings were recorded every 10 s as the gondola rose and vertical position was calculated from the lifting rate. The topmost light readings in each transect were used to calculate within-canopy transmittances in that transect.

In the balloon transects, no measurements were taken below 2 m, the height of the balloon. Transects taken from the telescopic pole (40-year-old stand) began at 1 m above ground, and those from the crane gondola (500-year-old stand) began at the forest floor. The vertical resolution was 1 m in all stands except the 500-year-old stand, where it was 2 m. Values recorded when the balloon or pole moved or tilted during data acquisition were deleted and new measurements taken when the platform stabilized. All transects passed through the entire canopy, with the topmost measurement taken above the local treetop height.

Transmittance profiles and derived measures

For each stand, we grouped and calculated statistics on the transmittance values by height. We defined three measures derived from the mean transmittance profiles: (1) the vertical change in transmittance per unit height (attenuation rate) in both the outer canopy and in the understory (typically to 5 m

Table 2. Details of vertical sampling and methodology.

	Stand age (years)				
	20	40	98	155	500
Access method	Pole	Balloon	Balloon	Balloon	Crane
Vertical spacing (m)	1	1	1	1	2
Minimum height (m)	1	2	2	2 (some 3)	0
Sampling scheme	3 × 6 grid	3 × 5 grid	2 × 7 grid	2 × 7 grid	polar
Transect spacing (m)	5 × 5	10 × 10	10 × 20	10 × 20	ca. 20
Overcast sky during measurements	18	0	0	11	0
Clear sky during measurements	18	15	14	14	16

above the lowest measurement); (2) the height where mean $T(h) = 1.0$ (mean canopy top) and mean $T(h) = 0.5$ (lumicline); and (3) for each profile, the height where $T(h) = 1.0$ (local tree-top height). In each stand, we defined three vertical zones based on the pattern of the mean and variance of transmittance (Parker 1997): (1) the region where mean transmittance is high with low variability (“bright” zone); (2) where transmittance is most variable and the mean changes rapidly with height (“transition” zone); and (3) where both the mean and variability are low (“dim” zone).

Canopy surface profile

To obtain the relative vertical distribution of canopy surfaces ($L_r(h)$) in each stand, we inverted the mean transmittance profile using the Beer-Lambert rule (Parker 1997). All the profiles of mean transmittance were smoothed because they were non-monotonic, often with reverses due to flaring light or sunflecks. A monotonic profile is needed because an increase in transmittance with depth (i.e., a negative absorption) implies a negative canopy surface area. We used a five-point moving boxcar average.

Whole-canopy transmittance observed in the understory

To assess variation in understory PAR, we took numerous measurements with a TRAC system (“Tracing Radiation and Architecture of Canopies,” from 3rd Wave Engineering, Nepean, ON, Canada) in all stands. This hand-held instrument records PAR from quantum sensors at a high rate (32 Hz) as the operator walks along the ground. The sensor was held about 0.7 m above ground and kept level with reference to a bulls-eye level. Transects ranged from 2 to 5 in number and from 25 to 200 m in length; the number of light readings ranged from 6300 to 16700, with a spatial resolution from 1.4 to 2.5 cm. In the oldest stand we used the same transects as those used by Song (1988). The location of each reading was estimated assuming a constant walking pace along each transect. The understory readings of PAR were converted to transmittances (T_{bulk}) based on supplementary observations taken with the TRAC in nearby open areas before and after the understory measurements. For each transect, we calculated the distance at which the autocorrelation of transmittance fell to zero (called the integral scale by Tennekes and Lumley (1992), but termed the correlation distance (CD) here).

Hemispherical canopy images from the understory

Hemispheric images of the overhead canopy were acquired in all stands, except the 98-year-old stand, from each vertical transect location at 1 m above ground, using a digital imaging system with a gimbaled 180° lens (CID-110 with LLP Lens, CID, Vancouver, WA). All images were taken at low sun elevations in early morning or late evening. Each image was analyzed for the fraction of open pixels (gap frequency) in each 10°-wide annular band.

Estimation of stand LAI from radiation measurements

We estimated stand LAI from radiation measurements by three methods. One method employed the Beer-Lambert law (e.g., Pierce and Running 1988), using the mean understory transmittance and an extinction coefficient of 0.40 reported for Douglas-fir by Marshall and Waring (1986). We used the method of gap frequency (gap-fraction) inversion (Rich 1990, Martens et al. 1993, Chen 1996) for data on angular distribution of openness from the hemispherical images to estimate LAI using manufacturer-supplied software (CID-110, Version 3.0.0). For the data from the understory transects, we used the method of inverting the sunfleck-size distribution (Miller and Norman 1971, Chen and Cihlar 1995, Chen 1996), a “characteristic element length” parameter reported for Douglas-fir by Chen and Black (1992), and software supplied by the manufacturer (TRAC_WIN, Version 1.3.5).

Results

In general, the frequency distributions of transmittance were non-normal according to a Shapiro-Wilks test in all the ground transects and at each height in vertical transects. Even when log-transformed, the frequency distributions of transmittance often remained markedly skewed. Therefore, we report non-parametric statistics such as the median, percentiles of the distributions and the inter-quartile range (e.g., Siegel 1956, Tukey 1971). For comparison with literature reports, however, we also present parametric measures based on the normal distribution.

Vertical patterns in five canopies

In each stand, the mean and median transmittance coincided at the height where both equaled 0.5 (the height of the lumicline).

The vertical gradient was always steeper for the median than for the mean: mean transmittance was less than median transmittance above the lumicline, whereas the reverse was true below the lumicline. The distribution of transmittance values was rarely symmetrical at any height and ranged from positively skewed in the understory (mostly dark with rare bright patches) to negatively skewed in the upper canopy (mostly bright, with rare dark patches). The skewness coefficient declined regularly from strongly positive in the understory to very negative in the upper canopy—it was usually zero at the lumicline height (Figure 1). At heights where skewness was about zero, the distributions were not centrally grouped but rather bathtub-shaped. That is, although symmetrical, transmittance observations at the lumicline height were not clustered near the mean but in two groups, both removed from the mean.

Light environment zones

The shape of the mean transmittance profile changed with stand age. The mean height of full incident light increased with stand age and the zone of greatest variation broadened from 10 m in the youngest stand to 28 m in the oldest stand. Vertical light environment zones based on patterns of mean transmittance differed between stands (Figure 2). All zones increased absolutely in depth with stand age, and the zones ranked in decreasing size as transition, dim and bright zones. The bright zone was widest, both absolutely and relatively, in the oldest stand. Note that if the median and inter-quartile range (Figure 3) were used to define zone boundaries, the transition zone would be narrower, with a higher lower boundary and a lower upper boundary, than if based on the mean and standard deviation.

The vertical gradients in PAR attenuation in both the overstory and understory declined as stands aged (Figure 4). A strong vertical change in mean light in young stands at the outer canopy interface and in the understory became progressively relaxed in the older stands. The gradients in the 98-

year-old stand were higher than expected from this pattern. The attenuation rate was greater by a factor of at least three in the overstory than in the understory.

Bulk transmittance in five understories

Frequency distributions of horizontal understory transmittance measured with TRAC were positively skewed, with many dark values and few bright ones: the means always exceeded the medians (Figure 5, lower panel). Because of high variability, there was little difference between stands, but there was a slight increase with stand age. The darkest understory was in the 40-year-old stand (mean transmittance of 0.032) and the brightest understory was in the 500-year-old stand (mean transmittance 0.081). However, the scale of the spatial covariance, given by the correlation distance (upper panel of Figure 5), was related to stand age. The young stands had low correlation distances, whereas the largest correlation distance was in the oldest stand.

Sky conditions

Mean profiles taken at the same sites with the same platforms in two stands in 1999 (overcast skies) and 2000 (clear skies) differed little (Figure 6). In both stands, light penetrated somewhat more deeply into the upper canopy when the sky was overcast than when clear. However, the shapes of the transmittance profiles were similar, and the clear sky lumicline was about 1 m above that for overcast conditions in both cases. Variation within a profile was also greater for profiles obtained under clear skies than under overcast skies. The profiles obtained under clear skies appeared to be both more spatially variable and jagged in shape than the profiles obtained under overcast skies, which were smoother in shape.

Overhead gap fraction

Canopy openness was greatest (range 0.52–0.68) directly overhead and declined rapidly toward the horizon (range 0.04–0.14) in all stands (Figure 7). The patterns were similar

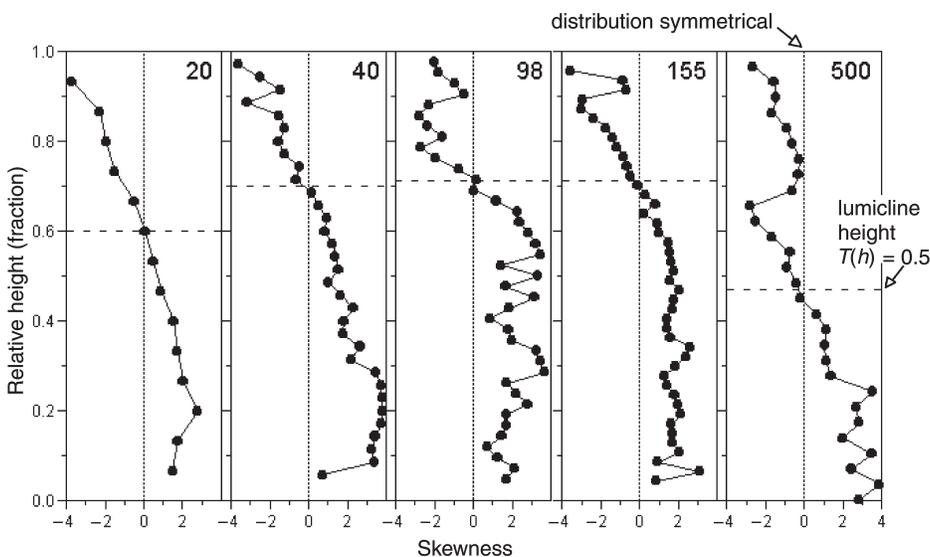


Figure 1. Vertical change in the skewness coefficient of transmittance distribution relative to maximum height in five Douglas-fir stands. In each panel, the dotted vertical line denotes zero skewness and the dashed horizontal line denotes the height of the lumicline.

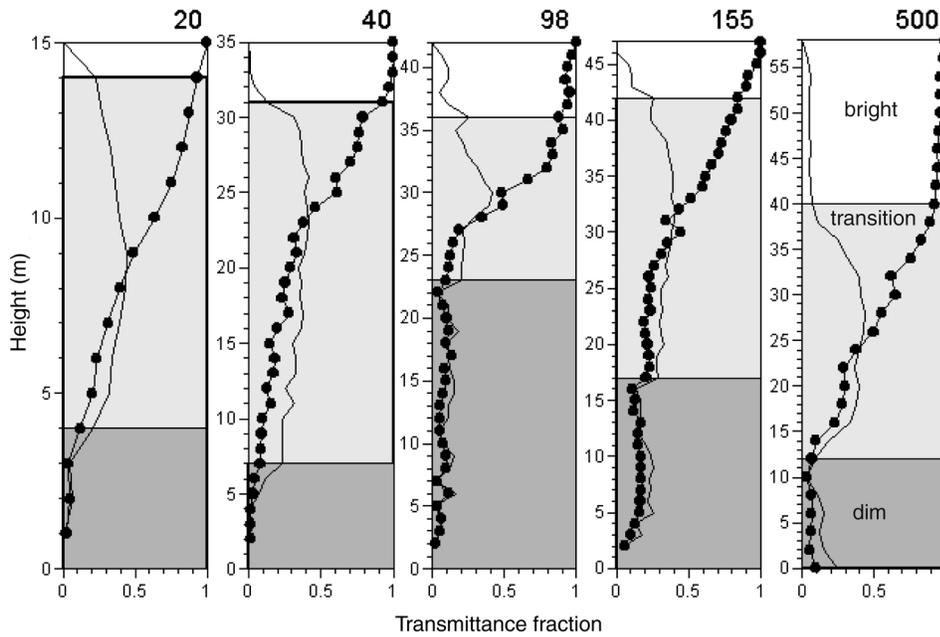


Figure 2. Vertical light environment zones in the canopies of five stands using a classification of low variability/high mean (bright), high variability and changing mean (transition) and low variability/low mean (dim) based on the vertical change in mean transmittance (●) and the standard deviation (line). Each panel is scaled to the height where mean transmittance equals 1.0.

across stands, though the mean openness over all angles appeared to be lowest in the older stands (155- and 500-year-old). Variation in the degree of openness also decreased toward the horizon.

Inferred canopy profile

The vertical profile of canopy surfaces estimated from the transmittance profile was compact and dense in the youngest stand, and the height of maximum canopy surface was near the ground. In intermediate-aged stands this maximum rose in

height and depth and a second maximum developed in the lower canopy (a “top-heavy” shape). In the oldest stand, the majority of the canopy surface was in the lower half or third of the maximum canopy height (a “bottom-heavy” shape) (Figure 8). Note that the estimate for the 500-year-old stand differs somewhat from that given in Parker (1997) because it was recalculated to conform to the uniform smoothing method.

Estimations of LAI from light

The LAI values derived from inversion of the different radia-

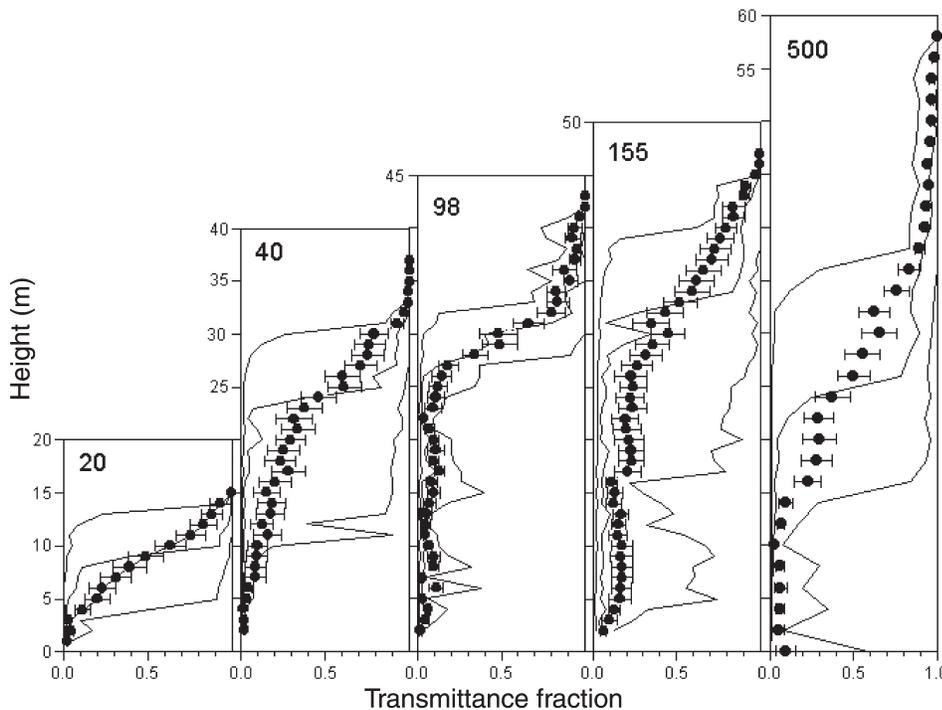


Figure 3. Vertical profile of PAR transmittance in the canopies of five stands in a chronosequence of Douglas-fir forests. The values plotted are the means (●) and standard errors. The three solid lines are the 10th, 50th and 90th percentiles of the distribution at each level.

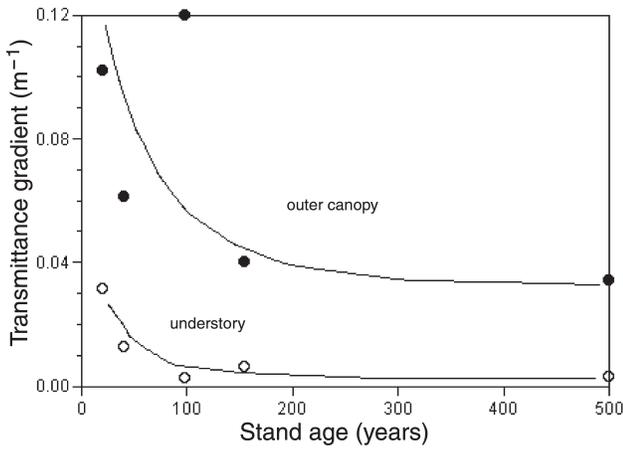


Figure 4. Vertical transmittance gradient in the upper canopy (●) and in the understory (○) of Douglas-fir stands of increasing age in the vicinity of the Wind River Canopy Crane Research Facility.

tion measurements differed markedly (Table 3). The variation in LAI values related more to method than to stands. For example, each method yielded a small range of values (8.61–6.28 (Beer-Lambert method), 5.92–1.72 (sunfleck-size) and

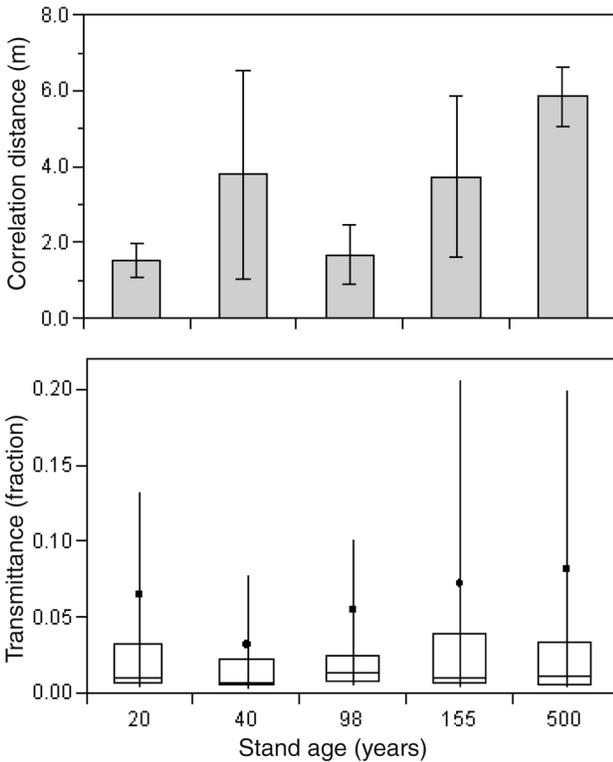


Figure 5. Statistics on understory PAR transmittance from light readings across transects in five Douglas-fir stands. The upper panel gives the correlation distance (error bars are standard errors across transects within a stand). The lower panel gives the 10th (bottom of vertical line), 25th (bottom horizontal line of box), 50th (middle line of box), 75th (top line of box) and 90th (top of vertical line) percentile of the transmittance distribution in each stand, and ■ denotes the mean.

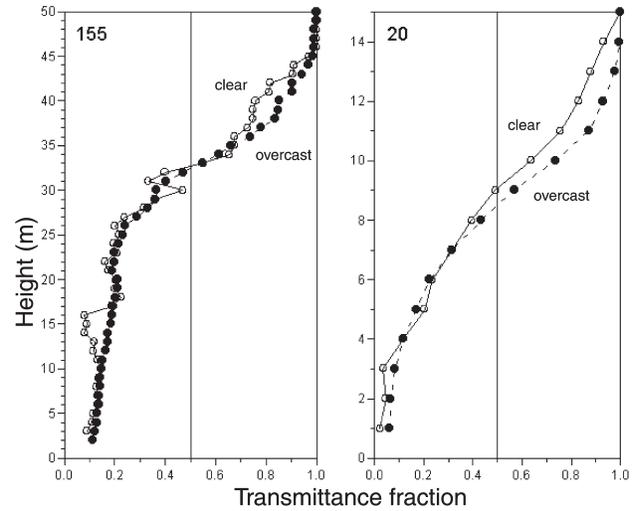


Figure 6. A comparison of mean transmittance profiles taken at the same heights in a 20- and a 155-year-old stand under overcast and clear conditions.

1.07–0.85 (gap-frequency)). Although there was much overlap in estimates between stands there was no overlap between methods.

Discussion

Differences in access systems may have affected vertical light sampling. For example, the crane gondola, with a footprint of 1.3×1.3 m, could not be inserted into small spaces in the 500-year-old stand and likely sampled more of the brighter light environments. Sampling intensity was not uniform across stands and was sometimes inadequate, as suggested by the reversal in the mean at 16 m in the 155-year-old stand.

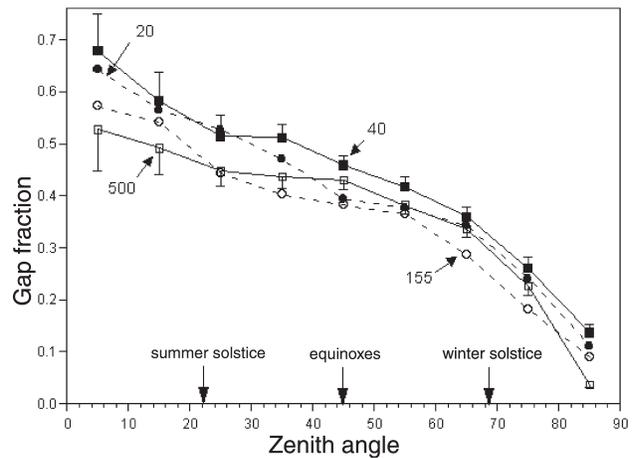


Figure 7. Distribution of openness by zenith angle in each of four Douglas-fir stands based on understory hemispherical images. Bars denote standard errors. The zenith angle (x-axis) values marked by arrows denote maximum sun elevation at the solstices and equinoxes at the sites.

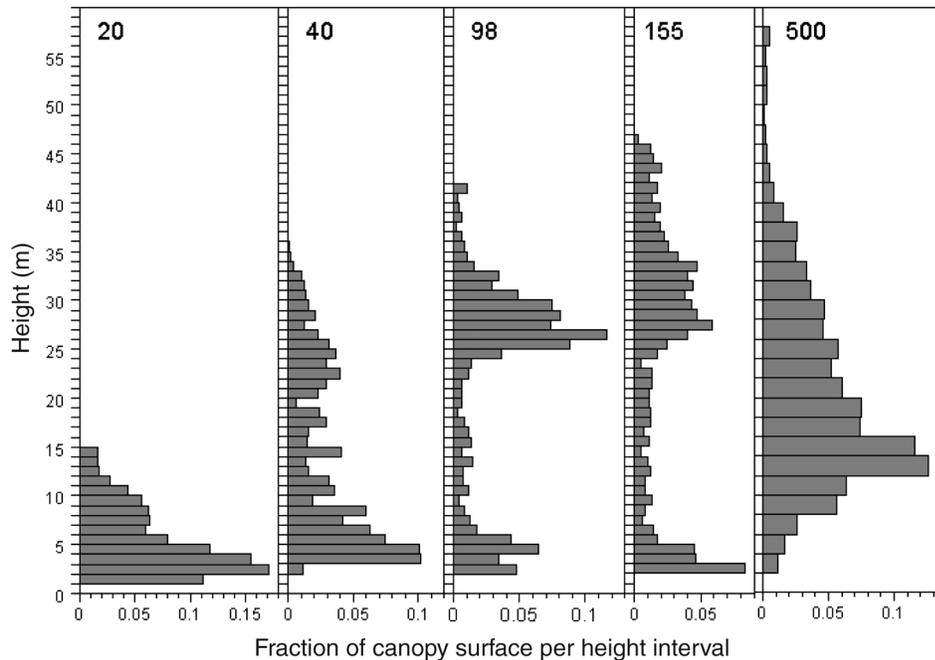


Figure 8. Relative canopy height profile ($L_r(h)$) in five forests of different ages, estimated by Beer-Lambert inversion of the transmittance profile.

However, the sampling required to overcome sun-fleck distortion of the mean pattern (i.e., to faithfully sample highly skewed distributions) is likely to be substantial and impractical for most field studies. The access system with the least bias was the telescoping pole; because it had the smallest sensor platform (about 5×1 cm), it was the least restricted in the canopy locations it could enter. Active remote sensing systems capable of probing the canopy with photons (such as lidar, e.g., Parker et al. 2001) may overcome such biases, but measurements of in-canopy light are probably always distorted to some extent.

The aggregate result of this bias in vertical transmittance sampling is the overestimation of whole-stand means and altered estimation of other statistics. How these are altered will depend on location: variance and skewness would be overestimated above the lumicline and underestimated below. These differences could shift some defined limits of the light environment zones. The effect of this bias on the canopy surface profiles depends not only on the deviation in the shape of the measured and actual profiles but also on the corresponding difference in bulk canopy transmittance (Lefsky et al. 1999, Har-

ding et al. 2001). Generally, where mean measured transmittance is greater than actual transmittance, the vertical rate of attenuation has been underestimated at that level, implying an underestimation of $L_r(h)$.

Limitations of inference

Variations in light environment are ultimately controlled by stand structural features, not the rate of development or the time elapsed since stand initiation. These few examples cannot alone establish detailed patterns, considering the uncertainties inherent in chronosequence studies including differing initial conditions, chance events, historical influences and ecological context (Pickett 1987). Nonetheless, the development of forests in the central Cascades is well studied (including direct, long-term observations of individual stands in this region) and the stands we studied are characteristic of major development stages (e.g., Franklin 1972). We believe the patterns found are generally representative.

The extreme variability in canopy light has long been appreciated for the demands it makes on sampling (e.g., Acock et al. 1969, Thompson and Hinckley 1977). Our findings that the

Table 3. Predictions of leaf area index (LAI) and its standard deviation in five Douglas-fir–western hemlock stands based on three inversion methods relying on different aspects of light environment. As used here, the Beer-Lambert method provides only one estimate per stand.

Stand age (years)	Estimation method		
	Beer-Lambert inversion	Gap-fraction inversion	Sunfleck-size inversion
20	6.80	0.96 ± 0.27	5.92 ± 3.57
40	8.61	0.85 ± 0.18	4.10 ± 0.25
98	7.16	Not available	1.72 ± 0.11
155	6.58	1.03 ± 0.16	3.68 ± 0.88
500	6.28	1.07 ± 0.27	2.10 ± 0.07

distributions of transmittance values never conformed to normal distributions and that they changed in shape vertically in all stands have implications for interpretation of canopy light measurements. First, because of the extreme skewness of the distributions, means are never reliable indicators of common conditions. Second, both the manner and degree to which the mean misrepresents those conditions vary spatially. However, knowing that the pattern in skewness is associated with changes in height should help in constraining the shape of distributions used to predict light environments (Baldocchi and Collineau 1994).

The canopy surface profiles derived from transmittance profile inversion were sensitive to some variations in smoothing. For example, if a discontinuity in the mean transmittance profile remained after smoothing, a high $L_r(h)$ would be estimated. Alternatively, too much smoothing of the transmittance profile would tend to remove vertical details of structure. Because the smoothing is a compromise between minimal modification and the reduction of aberrant observations, the derived $L_r(h)$ profiles shown in Figure 8 should be considered general and approximate.

Sky conditions

Sky condition affects the penetration of light in canopies because it alters the amount and source of illumination. Diffuse light from overcast skies comes from the entire hemisphere, whereas under clear skies most light comes from the direct beam of the sun. A greater proportion of the diffuse light, on cloudy days, has been found to penetrate canopies than does direct light, on clear days (Vezina and Pech 1964, Anderson 1970, Chazdon and Fetcher 1984). However, in the 20- and 150-year-old stands, where such a comparison can be made, we found little difference in transmittance profiles between clear and overcast skies (Figure 6). In the 155-year-old stand, the diffuse profile was smoother. Brown et al. (1994) and Parker (1997) found that within-canopy profiles of broadband UVB light, which is largely diffuse, were often smoother than those of PAR. If vertical growth of the whole canopy follows the extension of the growing points, annual vertical growth might account for the difference in the transmittance profiles of the 20-year-old stand. N.G. McDowell (Oregon State University, Corvallis, OR, unpublished data) found that mean height growth of Douglas-fir in this stand was about 1 m.

Understory openness and vertical transmittance

We found little relationship between canopy openness measured at understory sites and transmittances obtained in vertical profiles directly above those locations, in the stands where both measurements were made at the same sites (Ages 20, 40, 155 and 500). Other unrelated measurements included the mean transmittance at all or the lowest 5 m of the vertical transects with various combinations of zenithal bands, with or without weighting by band area. None of the correlations examined between vertical transmittance and understory openness explained more than 11% of the variance. Many authors have estimated potential light at a location from analysis of

hemispherical images. However, such methods have a variety of sensitivities and often provide poor estimates of light in darker forest environments, such as were encountered in this study (Chazdon and Field 1987, Chazdon et al. 1988, Whitmore et al. 1993, Roxburgh and Kelly 1995). Many features of canopy structure could affect the weak coupling between light conditions at understory locations with those overhead: a single understory branch can reduce the zenithal openness (even under a large upper canopy gap) and bright spots from lateral light are possible even in dark locations.

Understory transmittance and its variation

The understories of these stands were dark. Mean understory transmittances were low, whether calculated as medians (range 0.007–0.02) or means (range 0.03–0.08). Because of the spatial variability in these averages, differences in mean transmittances between stands were not significant. However, the variation itself seemed to increase with stand age, as can be seen from the change in the inter-quartile range in Figure 5 (bottom panel).

The distance at which the autocorrelation fell to zero (the correlation distance, CD), generally increased with stand age. These distances were less than 6 m in all stands, suggesting that the structural feature controlling light variation is not related to the height of the canopy, but to the size of crowns, gaps or other features of the understory. The magnitude of CD was roughly related to the size of some structural features across the stands. For example, CD was always greater than the mean inter-tree distance, D (assuming regular spacing in circular zones) ($CD = -0.40 + 1.6D$; $r = 0.55$, $P < 0.10$). The CD was numerically about 10 times the basal area-weighted mean stem diameter ($CD = 0.11 + 0.113\text{dbh}$; $r = 0.94$, $P < 0.05$). However, CD, mean stem diameter and stem density are each closely related to stand age in this series, and age may be a confounding variable in this analysis. Several authors (Becker and Smith 1990, Smith et al. 1992, Clark et al. 1996, Walter and Gregoire Himmler 1996, Thrichon et al. 1998, A. Ambrose, Humboldt State University, Arcata, CA, personal communication) have measured spatial variation in understory light, but differences in methods (kinds of measurements, spatial resolution, and means of extracting the scale length) make their results difficult to compare.

Transmittance profile

The gradient of attenuation estimated from the mean profile declined with stand age (Figure 1). That is, PAR changed rapidly over a narrow vertical range in young stands, but over a wide range in older stands. A similar pattern was found in a five-stand age sequence of eastern broadleaf forests, but in that study the overstory attenuation gradients exceeded those of the current study (G.G. Parker and Beaty, unpublished observations). The vertical zone of intermediate light flux density, where the majority of light absorption and much photosynthesis occurs, broadens with stand age (Figure 9). We interpret the gradient of vertical PAR attenuation as reflecting crown competition for direct light at the stand level. This intensity of

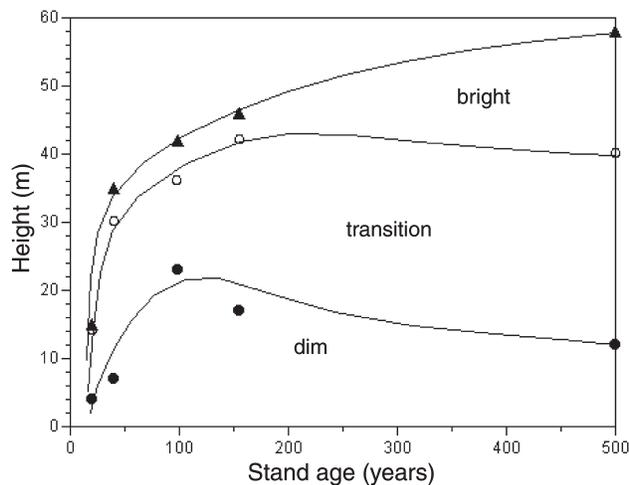


Figure 9. Change in the vertical limits of light environment zones during stand development from an age-series of Douglas-fir forests.

competition progressively diminishes as crowns differentiate, large holes appear from the death of dominant stems, and the outer canopy elaborates. Similarly, we interpret the decline in the understory attenuation gradient to reflect the progressive opening of the lower canopy through the formation of gaps.

Stem heights, canopy heights and radiation heights

The heights of the physical features of these forests are not coincident with significant levels extracted from transmittance measurements. For example, in the 500-year-old stand, the tallest tree is 64.6 m. The mean height of the 100 tallest trees, a common measure of canopy height, is 56.3 m, close to the height at which the mean transmittance reached 1.0 (58 m), but well above the mean treetop height of 48.9 m. The difference between height where mean transmittance equals 1.0 and the mean local height is small for the youngest stand (1.5 m) and increases with stand stature (to 9.1 m in the tallest stand). The low elevations of radiation-effective heights suggest that, particularly in older forests, the uppermost canopy has little influence on canopy light environment. Also, little light is absorbed and little photosynthetic activity takes place in the upper 5 to 10 m of the old-growth canopy.

Estimation of LAI

Variation in the estimates of stand LAI across methods are more likely a reflection of the variety of methodologies rather than of real differences between stands (Table 3). Here, the estimates most comparable with direct estimates of LAI are from the Beer-Lambert inversion. In the 500-year-old stand, for example, only the Beer-Lambert estimate of 6.28 is close to the stand LAI estimates ranging from 8.1 to 9.3 for 3 years made by Thomas and Winner (2000). However, because we used the same, literature-derived extinction coefficient for all stands, the differences in LAI estimates reflect the variation in bulk transmittance averages. Extinction coefficients are best estimated empirically for each stand (Smith 1991, Brown and Parker 1994). The estimates from the sunfleck-size inversion,

and particularly for the gap-frequency inversion, seem unreasonably low.

Each method estimates LAI based on field measurements of light, one or more parameter values (often to adjust for clumping of canopy elements), and a convolution process. The failure of the estimates to converge could lie in the adequacy of the field observations, the appropriateness of parameter values used, the convolution process, or some combination of these. The different field instruments sense very different aspects of canopy structure; e.g., the quantum sensor perceives a different projection of the light environment than does a hemispherical image. Accordingly, the clumping factors needed for the different inversions have different meanings. The parameter for the Beer-Lambert inversion is the extinction coefficient, which summarizes the effects of leaf optical properties and arrangement, including clumping, on a whole canopy basis. For the sunfleck-size inversion one parameter is the “characteristic element size” along the sampling transect. For the gap frequency inversion a required parameter includes the effect of clumping, in the direction of the sun.

Conclusions

Several trends in light environment change are suggested from five Douglas-fir–western hemlock forests. Vertical profiles of PAR transmittance depend on stand height, but various significant heights indicated by the light profiles were more closely associated with stand age than with heights of structural features. As stands increased in age and height, light profiles became progressively steeper and the inferred vertical structure became less bottom-heavy. Neither the angular distribution of openings nor mean transmittance in the understory varied much across the stands. However, the spatial scale of covariation in transmittance appeared to increase with age. Overhead openness near the ground and transmittance in the canopy directly overhead were generally poorly coupled. The LAI estimates provided by these methods were neither reasonable nor consistent across stands, and likely reflected the effect of the methodology and the lack of empirically measured parameters, such as the clumping factor. Many aspects of the change in light environment appear to be influenced by developmental changes in stand structure: the increasing size and diversity of crowns (objects) and gaps (object-free spaces); the differentiation in heights; and the elaboration of the outer canopy.

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