Geoffrey G. Parker, Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037

Canopy Structure and Light Environment of an Old-growth Douglas-fir/ Western Hemlock Forest

Abstract

The three-dimensional light environment within the canopy of a tall coniferous forest was sampled to quantify its variation and localize the sites of radiation absorption. Broadband visible (PAR) and ultraviolet radiation (UVB) were measured around mid-day in midsummer in an old-growth Douglas-fir/Western Hemlock forest in the Cascade Range in southern Washington using sensors suspended from the gondola of a large tower crane. Patterns of vertical transmittance varied greatly between locations and showed abrupt transitions from bright to dark conditions at varying heights. The average light field in this canopy with trees to 60 m was resolved into three functional zones. Above 40 m from the ground is a "bright zone," where light was reliably intense and predominantly in the direct beam component, and below 12 m, a "dim zone," where light was reliably low and mostly diffuse. Between these levels is a "transition zone," with a steep vertical gradient in light transmittance, high horizontal variation, and a mixture of beam and diffuse components. The pattern of UVB light was very similar to that of PAR. From the general transmittance profile the vertical structure of the canopy was estimated to have a peak density of foliage at 12 m (less than one quarter of the stand height) with declining densities above and below. The "bottom-heavy" canopy structure found in this study differs markedly from the "top-heavy" profiles reported from managed or young stands.

Introduction

Vegetation canopies influence the intensity, quality and distribution of radiation. The production of dry matter in forests is closely related to the amount of visible light absorbed in the canopy (Monteith 1977, Linder 1985, Cannell et al. 1987, Monteith 1994), which is related to the three-dimensional organization of canopy elements (e.g., Monsi et al. 1973, Jarvis and Leverenz 1983, Norman and Campbell 1989). Often, aspects of canopy structure are inferred from measurements of canopy light. However, estimation of whole-canopy structure requires information on light on the scale of the whole canopy. Yet studies of forest light environments are usually limited to observations from fixed structures (such as towers) or from the ground (e.g., Pierce and Running 1988, Parker 1995) and can rarely yield patterns representative of the whole canopy. Thus there is little understanding of the general attenuation of light with depth in the canopy, of the point-to-point variation in within-canopy light, or of the relation between canopy structure and light environment in three dimensions.

Stand-level measurements of variation in light within the canopy are uncommon. Most attempts to account for variation have been made over limited ranges, such as within the reach of a tower (e.g., Acock et al. 1969, Thompson and Hinckley 1977, Ellsworth and Reich 1993, Vose et al. 1995) or an individual large tree (Yoda 1978). Suitably extensive observations have been obtained using balloon-mounted sensors (Parker et al. 1996). However, wind shear often makes it difficult to acquire measurements near the top of the canopy. In principle, a tall construction crane could provide the horizontal coverage and stability for truly three-dimensional radiation measurements (Parker et al. 1992) but this application has not been reported.

The objectives of this study were to: 1) assess the suitability of a tower crane system for obtaining light measurements within the canopy of a tall old-growth conifer forest; 2) quantify the vertical pattern of attenuation and the spatial variation of the radiation field; and, 3) infer some aspects of average canopy structure from such radiation measurements.

Materials and Methods

Vertical transects of within-canopy light measurements were obtained 27 and 28 July 1995, within the circle of the tower crane of the Wind River Canopy Crane Research Facility (WRCCRF). The stand is an old-growth Douglas-fir/Western Hemlock forest in the Thornton T. Munger Research Natural Area of the Gifford Pinchot National Forest (Wind River Ranger District) in the Cascade range of southern Washington (45°49'N, 121°58'W). The site, near the upper limits of the western hemlock zone (Franklin and Dyrness 1973), is relatively flat - the elevation range within the crane circle is 6 m (D. Shaw, personal communication). The stand is about 400-500 years old (Franklin and DeBell 1988) with a Douglas-fir (*Pseudotsuga menziesii*) overstory (to 60 m), a western hemlock (*Tsuga heterophylla*) midcanopy and an understory of Pacific silver fir (*Abies amabilis*) and Pacific yew (*Taxus brevifolia*) (DeBell and Franklin 1987).

A Liebherr 550 HC tower crane (Morrow Crane Inc., Salem OR) was used to access the canopy (Holden 1995). The crane center is about 550 m north into the stand along forest road N400. The jib of the crane stands 74.5 m above the tower base and has a range of 85 m, providing access to 2.3 ha of the stand. A suspended personnel platform ("gondola") allowed virtually unrestricted access to any point in the canopy space.

Two radiation sensors were attached to a 15 x 30 cm plexiglass platform suspended 10 m below the rail of the crane gondola. The sensors included a quantum sensor (model LI-190 SB; Li-Cor, Inc., Lincoln NB) which yielded photosynthetic quantum flux (PAR, in $\mu mol\ m^{-2}s^{-1}$) and a Robertson-Berger type UVB meter (model 2D; Solar Light, Inc., Philadelphia PA), which gave biologically-effective UV dosage (UVB, in minimal erythemal doses hr^{-1} [see Berger 1976]). Cables from the sensors led to the gondola where readings were noted from the appropriate display. The sensor platform could be inverted to yield measurements of upwelling light. The platform was leveled with a bull's eye level before and after each transect. In all, 16 vertical transects were made of downwelling light; at four of these locations, transects of upwelling light were also made. Figure 1 shows the transect locations relative to

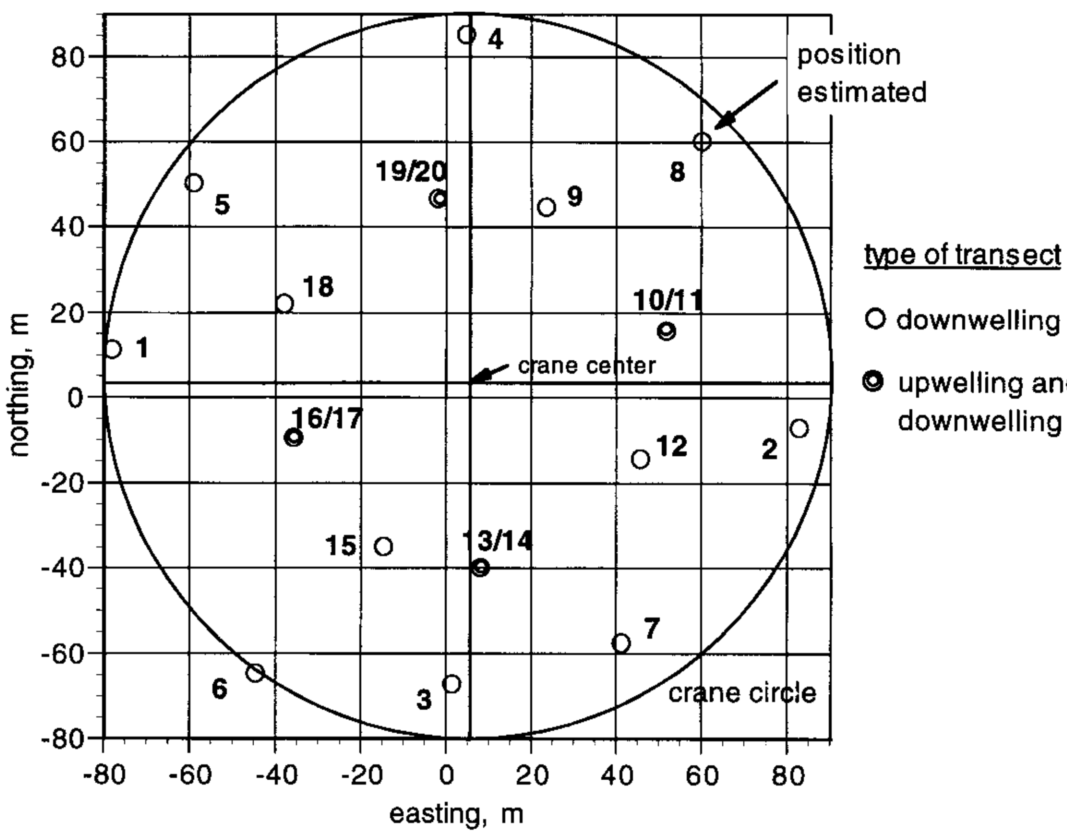

Figure 1. Sixteen locations within the WRCCRF crane circle used for measurements of radiation in vertical transects. Twelve were used for downwelling light only and four for both upwelling and downwelling light. The numbers identify the individual transects.

the coordinate system of the site stem map (see http://cqs.washington.edu/people/eliz/sitemap.html). Most of the transects were in gaps of different sizes; relative sizes of these openings were noted.

To avoid damage to the crane hoisting motor with repeated stopping and starting, measurements were taken at regular intervals during a continuous hoist from the ground to maximum height. Hoisting in "clutch 2, step 2" gave a reliably constant vertical velocity (ranging 0.18 - 0.20 m s^{-1}). Measurements were taken every 10 seconds; the vertical position calculated from time and velocity gave a mean resolution of about 1.9 m. Height above ground was noted and depth below a reference plane (including a correction for the deflection of the jib when loaded by a gondola and three people) was calculated for each measurement.

Measurements were taken within 2.5 hr of solar noon (range 1147-1528 PDT). These corresponded to a mean sun elevation angle of 60.5 ± 3.4° (range 51.7-63.5). PAR and UVB values were all converted to fractions of the maximum above-canopy values for each transect. This ratio is called transmittance here.

Layer Budget of Radiation Components

To obtain mean profiles, the data were grouped by 2 m height intervals (centered on even heights) and statistics for both upwelling (sensors pointed down) and downwelling (sensors pointed up) measurements and both wavebands were calculated. The components of the radiation budget (absorbance [A], transmittance [T], and reflectance [R]) for each canopy layer between measurement levels were then estimated:

$$A[n+1,n] = D_{n+1} - D_n + U_n - U_{n+1},$$
$$T[n+1,n] = D_n + U_{n+1}, \text{ and,}$$
$$R[n+1,n] \approx U_{n+1} - U_n,$$

where the U and D denote the measured upwelling and downwelling components of either PAR or UVB from level n to level n+1; n increases with height from the ground. For each waveband these values were in turn scaled by the maximum D_{n+1} at the top of each transect.

Vertical Foliage Distribution

To estimate the vertical distribution of radiation-occluding material (assumed to be foliage mostly), the mean vertical pattern of PAR attenuation and the general relationship describing light attenuation in turbid media, the Beer-Lambert (B-L) law, was used. Because the absolute leaf area index (LAI) of the study stand was not available, the estimation focused on the relative profile, the fraction of the cumulative downward LAI at a given canopy depth.

First, the normalized extinction coefficient, k_r (the subscript r denotes a normalized variable), was estimated by inverting the B-L law:

$$k_r = - \frac{\ln(I(z)/I(0)}{L_r(z)},$$

where I(0) and I(z) are the radiation flux at the top of the canopy and at depth z, respectively. $L_r(z)$ is the normalized profile, i.e., the fraction of all PAR-absorbing area from the top of the canopy (z=0) to depth z. At the bottom of the canopy, $L_r(z)$ equals 1. Whereas the usual k is the logarithm of the fractional reduction in light per unit area, k_r is normalized over all the absorbing area (k_r is the product of k and LAI). As shown later, the mean penetration of PAR at the forest floor was about 0.05, yielding a bulk k_r of ≈ 3.0 (because $k_r = \ln(I(z)/I(0))$ when $L_r(z) = 1$). Using this value, $L_r(z)$ was calculated from the normalized B-L relation,

$$L_r(z) = - \frac{\ln(I(z)/I(0))}{k_r},$$

where I(z)/I(0) is the mean penetration at depth z. The profile of I(z)/I(0) was smoothed with a 4-point moving average. Finally, the fraction of absorbing area at each level z was extracted from the downward cumulative $L_r(z)$.

Results

Transmittance profiles of PAR (Figure 2) varied greatly among locations. In most of the profiles, there were abrupt transitions from nearly full sunlight to very dark conditions. There was little evidence of the gradual diminution of radiation intensity with depth reported from profiles in other stands (Yoda 1978, Parker et al. 1995). The height above ground where light changed swiftly (the "lumicline") varied greatly among transects. The height of the lumiclines (where the transmittance profile first declines below half of the incident flux) varied from about 12 m (transect 9) to 36 m

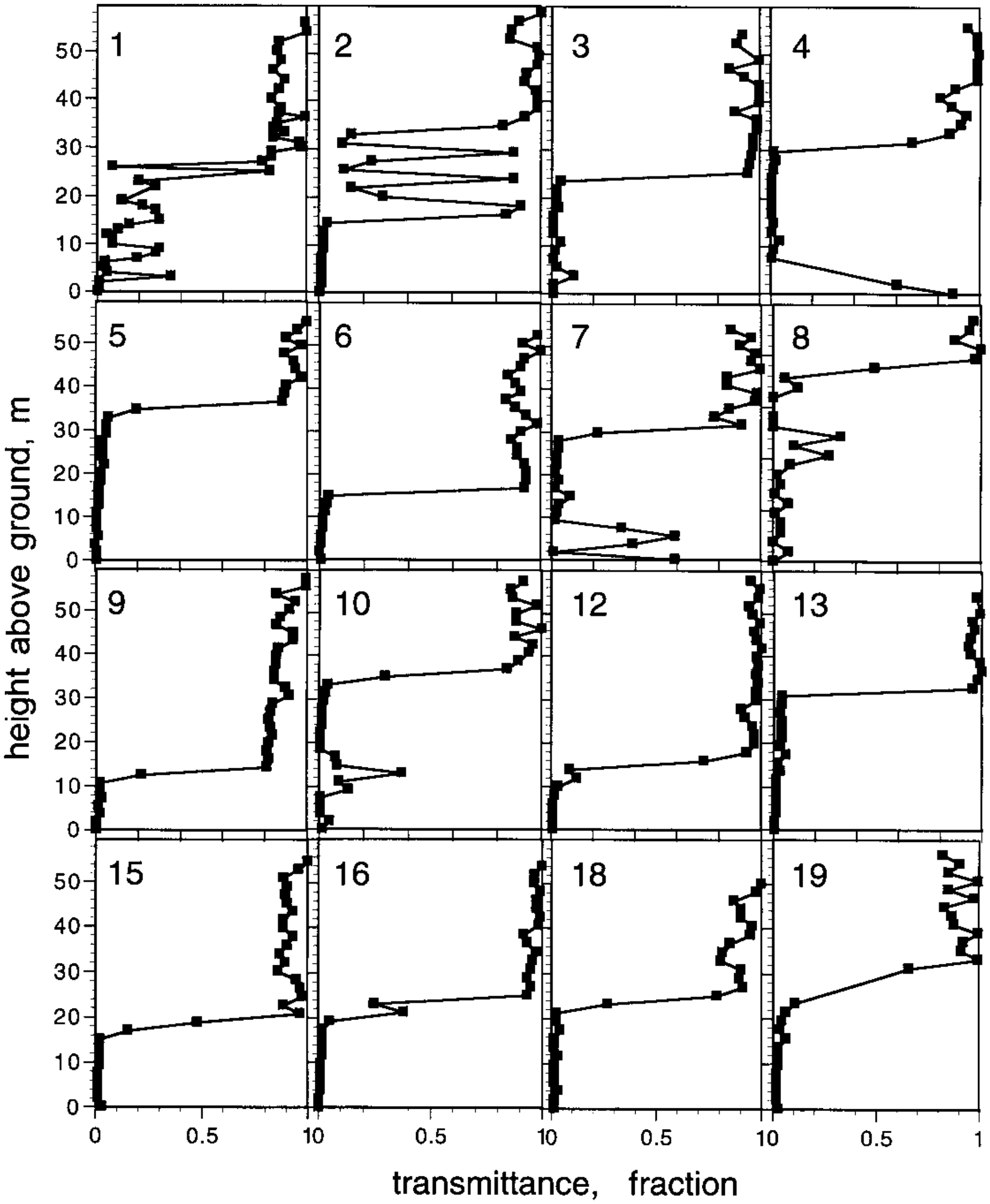

Figure 2. Variation in PAR transmittance profiles. The numbers identify each downwelling light transect in sequence. Transects 1, 6, and 15 were in large gaps; 2, 5, 12, 16, 19 in medium-sized gaps; 9 and 13 in small-medium gaps; 3, 4, 7, and 18 in small gaps; number 10 was in a very small gap.

(transects 5 and 10). The vertical patterns for UVB transmittance were similar to those of PAR.

The pattern of illumination in individual profiles was generally consistent with the size of the canopy opening: big gaps had lower lumiclines and deeper penetration of bright light than did small ones (Figure 2). However, not all transects conformed to this rule - transect 1 was in a large gap with a high lumicline and transect 4 was in a small gap but had a low lumicline.

The general vertical patterns of mean PAR flux and its variability are illustrated in Figure 3a. Transmittance near the forest floor averaged about 5%, though at the very bottom there was an increase in light. Note that, at any canopy level, almost any flux was possible, even relatively high transmittances near the forest floor (e.g., transect 4 in Figure 2). This general pattern was also apparent for UVB (Figure 4a). The mean upwelling light in both bands also diminished with canopy depth. However, in contrast to the curved mean pattern for downwelling light, upwelling light had a nearly linear decline with depth. The reflectances implied by these measurements were very low in both wavebands (maximum of <1% for UVB and <3% for PAR).

The horizontal variation in transmittances, as estimated by the standard deviation of observations at a given height, was low in the upper canopy and in the deepest layers of the forest, but high in the midcanopy (Figures 3b and 4b). Thus, PAR and UVB are the least predictable where they change most rapidly. The relative variability, estimated by the coefficient of variation (standard deviation/mean) was very low in the outer canopy and grew steadily greater with depth in the canopy, to more than 200% near the forest floor. PAR showed more variability at almost all layers than did UVB (Figure 5). The patterns in spatial variation in upwelling measurements were similar to those of the downwelling portion.

The components of the layer budget of radiation (Figure 6) illustrated that reflectance was nearly zero in all layers, and that absorbance was most

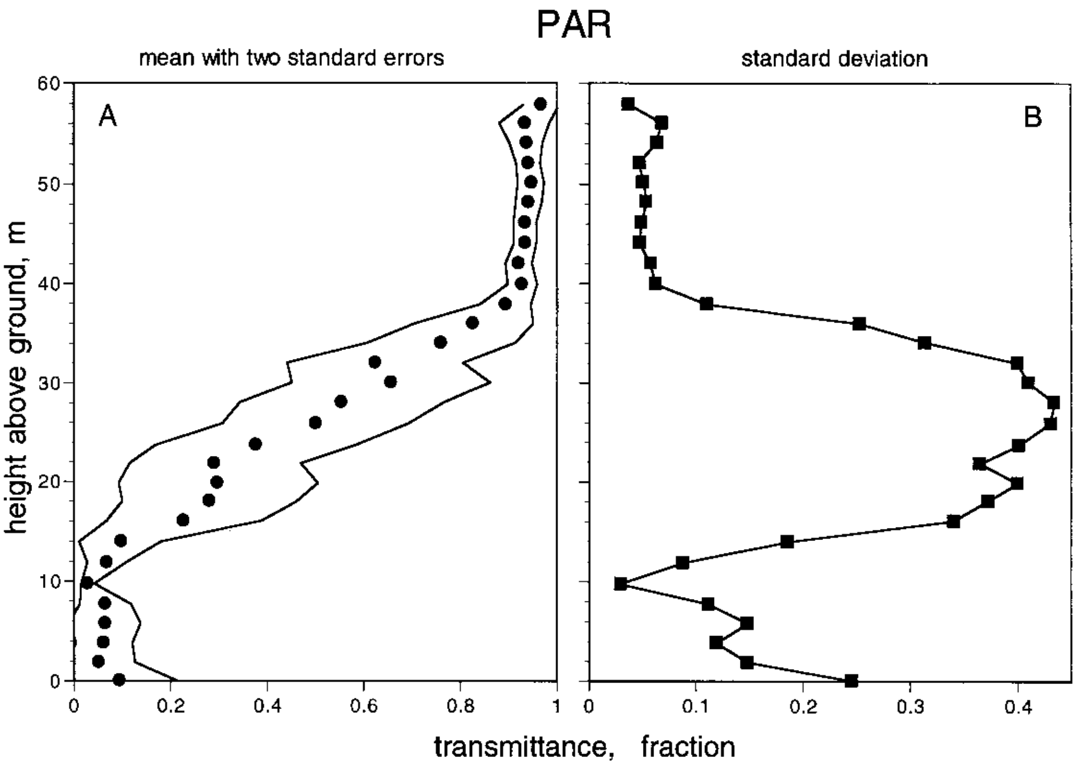

Figure 3. The profile of mean PAR transmittance with two standard error bounds (A) and of the spatial variability of PAR transmittance with height, indicated by the standard deviation (B).

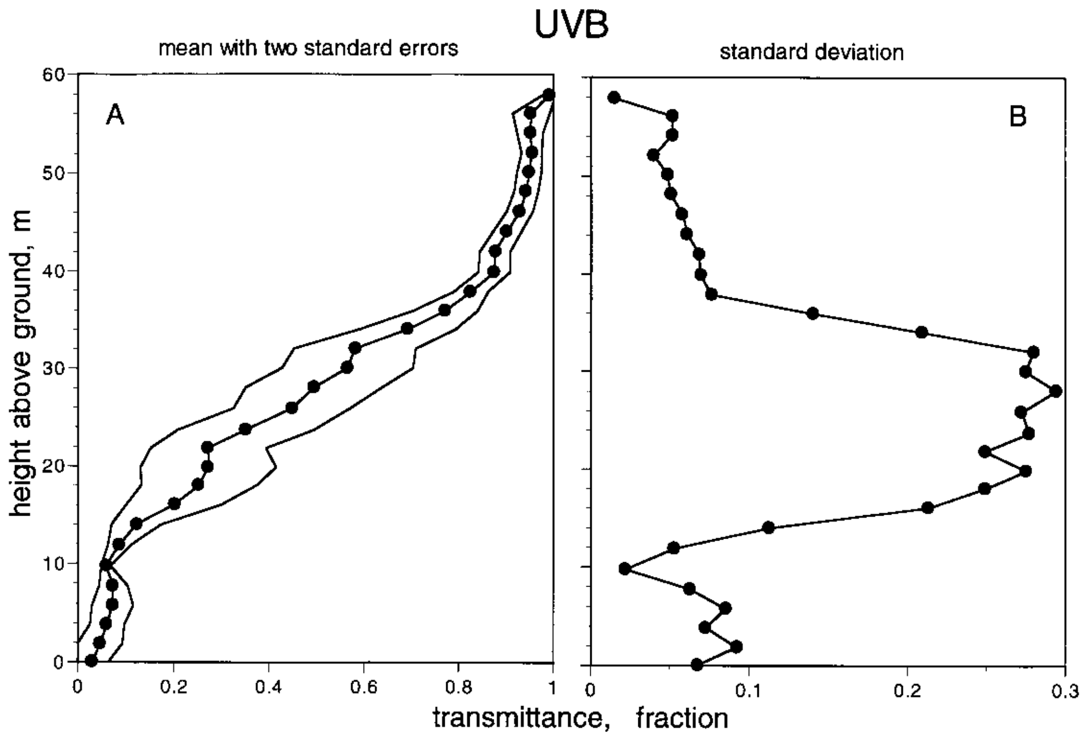

Figure 4. The profile of mean UVB transmittance with two standard error bounds (A) and of the spatial variability of UVB transmittance with height, indicated by the standard deviation (B).

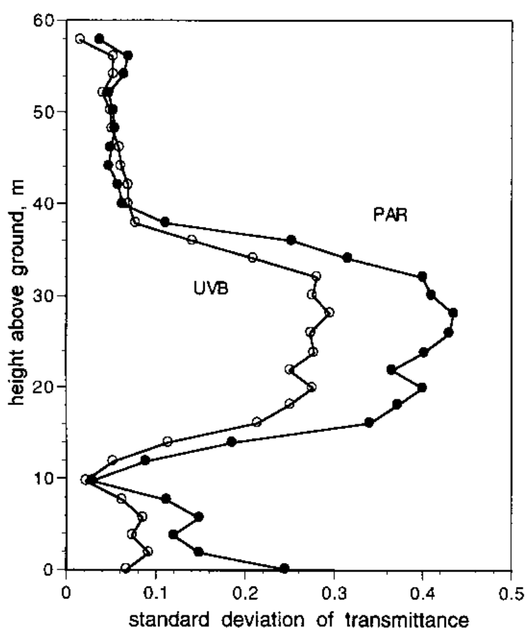

Figure 5. Spatial variation of vertical transmittance compared between the PAR (filled circles) and UVB (open circles) wavebands.

pronounced in the layers of greatest change in transmittance (between 14 and 40 m). The separation into these components is very similar for the PAR and UVB bands.

The inferred vertical distribution of PAR-absorbing material (including foliage, epiphytes, cones, branches, and stems) has a prominent mode between 9-15 m. Above this point to nearly 50 m, a gradual decline with height occurs and below, a rapid decline in PAR-absorbing material was noted (Figure 7b). The level adjacent to the forest floor had little effect on light attenuation. The median height of PAR-absorbing material in this stand is at about 16 m (Figure 7a).

Discussion

Measurements were taken only under the clearest conditions; observations that were obviously influenced by clouds or the shadow of the crane jib were deleted. However, occasional wispy clouds and haziness could have diminished the values of incident light and affected the calculation of transmittances. The small effect of such cloudiness

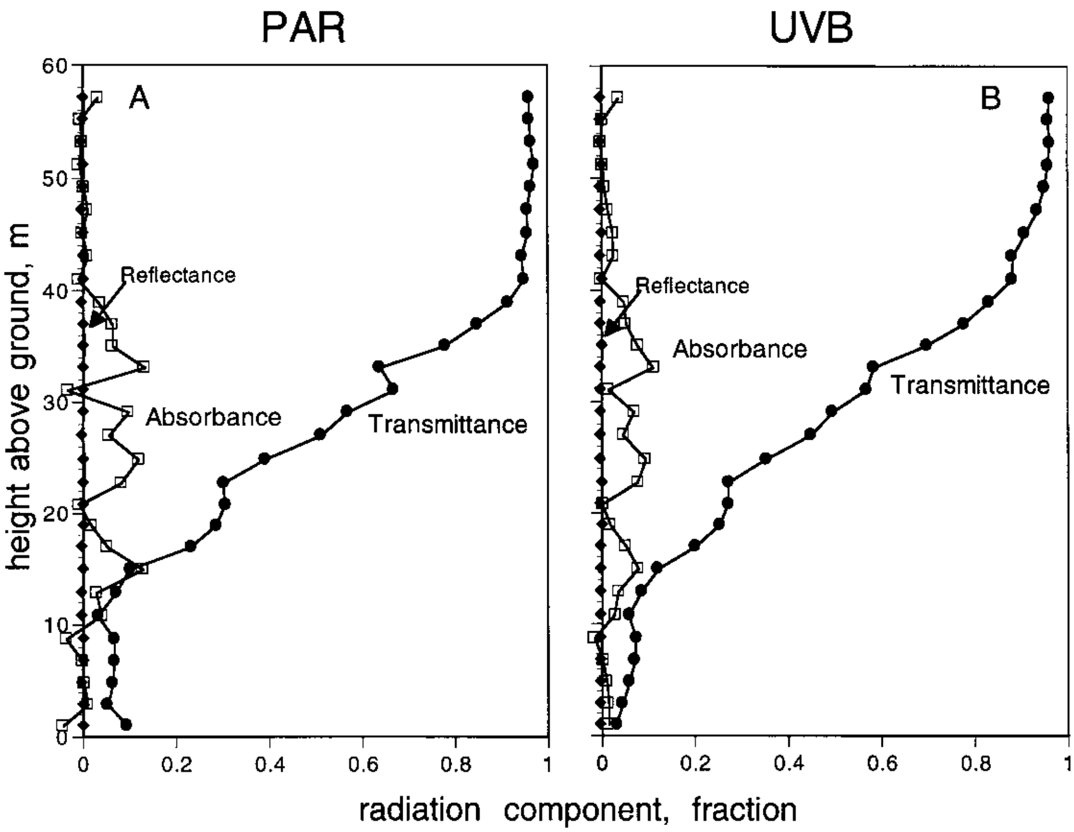

Figure 6. The estimated radiation budget for each 2m layer of the canopy, as defined in the text, for the absorbance, transmittance, and reflectance components for PAR (A) and UVB (B).

is suggested by the variability in transmittance at heights above the canopy (Figure 2).

Observations were taken in openings between crowns where the sensor platform could be inserted. Many, but not all, were gaps caused by the death of overstory trees. It was not possible to sample in the near-bole region with the sensor platform. This restriction to more open areas means that the profiles presented are biased to the brighter regions of this canopy. The mean profile is likely somewhat brighter than would be found in an unrestricted survey.

The calculation of the layer radiation balances assumes that the upwelling and downwelling measurements account for all the light exchanges with a given layer, that lateral light is negligible at this scale. However, mean transmittances can sometimes increase with depth (e.g., in this study the forest floor was brighter in PAR than the level just above it). It is more likely that the reverses in the mean profile reflect inadequate sampling, since an additional source of light is questionable in extensive forests. With more samples the mean transmittance pattern would likely become monotonic. However, since upwelling fluxes were very small, the separation of radiation components is apparent from the transmittance profile: transmittance is mostly the light downwelling from a layer; absorbance is essentially the change in downwelling light; and, reflectance is negligible.

Three distinct functional zones of radiation may be recognized in this stand by considering the vertical pattern of the mean and variability of transmittance of both wavebands (Figure 8). In the outer canopy, more than 40 m above the ground, is a zone of consistently bright light (the "bright zone") and in the lower canopy, below 12 m, is a zone of reliably dark conditions (the "dim zone"). Between these limits is a region where the mean light levels diminish rapidly with depth, with

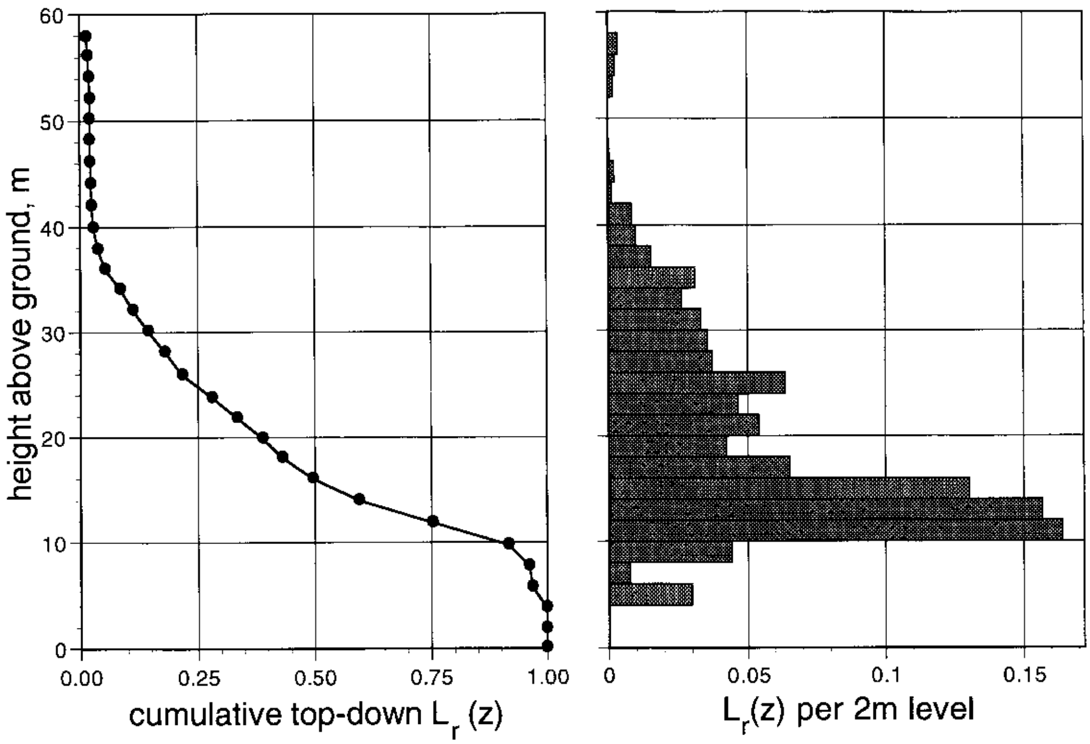

Figure 7. The vertical profile of relative leaf area (L_r(z)), as inferred from the bulk absorbance, the normalized extinction coefficient (k_r), and the mean profile of transmittance. The left panel (A) gives the cumulative downward L_r(z); the right (B) gives L_r(z) by 2m layer.

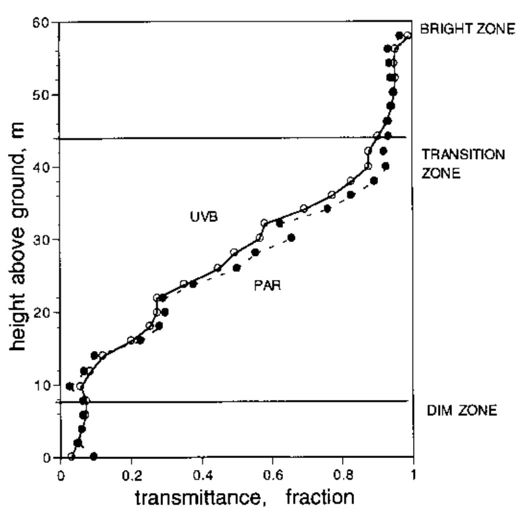

Figure 8. A proposed organization of the canopy light environment at the WRCCRF based on the average and variability in the vertical transmittance of PAR and UVB radiation.

extremely high horizontal variation (the "transition zone"). The abrupt transitions from bright light to deep shade (the lumicline), suggest that the transition zone (Figure 8) is where two extreme light regimes (bright and dim) are mixed in varying proportions. Light in the bright zone is mostly direct and, in the dim zone, predominantly diffuse; light in the transition zone is a mixture of these. The limits of these zones probably vary over daily and annual cycles but those given are probably applicable when the sun is highest above the horizon and radiation income is greatest. At least one-fifth of the annual light input at this latitude is received in the range of sun angles observed in this study.

It is surprising that the mean pattern of transmittance is so smooth, given the abrupt shapes of the individual profiles, the small number of profiles averaged, and the structural heterogeneity of the stand. Because the lumicline is not a feature of the mean light environment, an individual transmittance profile in this stand is likely not to be representative of the average. The shape of profiles in the WRCCRF canopy differs from patterns reported in other, non-coniferous forests where individual profiles are often smoother (e.g., Yoda 1978, Parker et al. 1996). The abrupt transitions from light to dark along the vertical transects are a consequence of moving into the shade of individual crowns. Conical-crowned trees with needle-leaf foliage can have a very high foliage density and be efficient absorbers of lateral light.

The pattern of UVB radiation was smoother in vertical attenuation, with less spatial variation in both upwelling and downwelling components than was the pattern for PAR. This is consistent with Brown et al. (1994) who found UVB varied less abruptly in space than PAR in a variety of forest light environments, probably because UVB derives from diffuse (sky) radiation and not primarily from the direct beam of the sun (as for PAR).

The inference of vertical structure from the pattern of radiation relies on several assumptions. It requires a monotonic transmittance profile (for small data sets, where increases in light with depth could be observed, smoothing might be necessary). It also assumes that the extinction coefficient inferred from ground-level transmittance (the bulk extinction coefficient) may be applied throughout the canopy. However, such a lumped descriptor may not apply where the foliage characteristics (tissue makeup, species composition, orientation angles, clumping) are not average. This problem applies whether using a conventional extinction coefficient (k) or the normalized version (k_r) presented here. Note also that since the sampling was somewhat biased to brighter canopy regions, the vertical distribution of PAR-absorbing surfaces will be shifted to higher elevations than is estimated here (Figure 7). The extent of this shift is probably small.

It has been assumed that most of the radiation absorption was by foliage, however this was not determined in this study. Other sorts of canopy components (epiphytes of various sorts, reproductive tissues, twigs, branches, and stems) undoubtedly absorb some light. But foliage probably dominates absorption: it has the greatest area of canopy components and is positioned to intercept light. However, until direct measurements of $L(z)$ are available, the relative profile ($L_r(z)$) provided by the normalizing method can serve as a hypothesis on the mean vertical structure of the WRCCRF canopy.

The proposed vertical structure is consistent with that expected for a collection of conical crowns having a smooth and declining diameter distribution. The height of the maximum, however, depends on the distribution of PAR-absorbing area within crowns. By aggregating idealized crowns van Pelt and North (1996) estimated the vertical distribution of crown volume in this stand had a single peak at 30 m above ground. The disparity between their estimate of the height of canopy maximum and that of the present study ($\approx$ 12 m) is probably because the density of PAR-absorbing material is not constant within a volume of crown.

The canopy structure inferred in this work differs from others reported for old-growth or conifer forests: the distribution of PAR-absorbing material has a maximum at a relatively low height above ground - around one quarter of the total canopy height - a "bottom-heavy" canopy distribution. In the more commonly reported pattern the majority of canopy area is nearer the top ("top-heavy" structure). However, the novelty of this finding may reflect the choice of stands usually studied: many canopy studies intentionally focus on stands of simple structure (such as conifer plantations) which almost always have top-heavy canopy structure (e.g., Stephens 1969, Ford and Newbould 1971, Kellomäki and Oker-Blom 1983). Older forests examined for canopy structure have been broad-leaved stands, where the vertical structure may be even (e.g., Aber 1979, Brown and Parker 1994) or complex (Parker 1995). Additional observations of canopy structure are needed in older, non-plantation, conifer forests.

Acknowledgements

The research was performed in whole at the Wind River Canopy Crane Research Facility located within the T.T. Munger Research Natural Area in Washington state, USA. The facility is a cooperative scientific venture among the University of Washington, the USFS Pacific Northwest Research Station, and the USFS Gifford Pinchot National Forest. Peter Stone designed and built the sensor platform. Carrie Bayless and Dave Shaw helped with logistical coordination. Mark Creighton operated the crane. Andrew Baker, Mark

Sumera, and Esther Capouano helped in the field data collection. Nalini Nadkarni, Martin Brown, and Thomas Hinckley made comments on a draft of this report. Financial support for this project was provided by the Smithsonian Environmental Research Center, the NASA-Goddard University Research Program and the Wind River Canopy Crane Research Facility. This is a contribution to the Global Change Program of the Smithsonian Institution.

Literature Cited

Acock, B., J.H.M. Thornley, and J. Warren Wilson. 1969. Spatial variation of light in the canopy. *In* I. Setlik. (ed.) *Prediction and Measurement of Photosynthetic Productivity*. PUDOC, The Netherlands, pp. 91-102.

Berger, D.S. 1976. The sunburning ultraviolet meter: design and performance. Photochem. Photobiol. 24: 587-593.

Brown, M.J., G.G. Parker, and N. Posner. 1994. A survey of ultraviolet-B radiation in forests. J. Ecol. 82: 843-853.

Brown, M.J. and G.G. Parker. 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. Can. J. For. Res. 24: 1694-1703.

Cannell, M.G.R., R. Milne, L.J. Sheppard, and M. H. Unsworth. 1987. Radiation interception and productivity of willow. J. Appl. Ecol. 24:261-278.

DeBell, D.S. and J.F. Franklin. 1987. Old-growth Douglas-fir and western hemlock: a 36-year record of growth and mortality. West. J. Appl. For. 2: 111-114.

Ellsworth, D.S. and P.B. Reich. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96:169-178.

Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Technical Report PNW-8. Pac. Northw. For. Range Exp. Sta., Portland OR.

Franklin, J.F. and D.S. DeBell. 1988. Thirty-six years of tree population change in old-growth *Pseudotsuga-Tsuga* forest. Can. J. For. Res. 18: 633-639.

Holden, C. 1995. Canopy open for business. Science 268: 645-647.

Linder, S. 1985. Potential and actual production in Australian forest stands. *In* J.J. Landsberg and W. Parsons (eds.) *Research for Forest Management*. CSIRO Publ., Melbourne, pp. 11-35.

Monteith, J.L. 1977. Climate and efficiency of crop production in Britain. Phil. Trans. R. Soc. London. B 281:277-294.

_____. 1994. Validity of the correlation between intercepted radiation and biomass. Agric. For. Meteorol. 68:213-220.

Parker, G.G, A.P. Smith, and K.P. Hogan. 1992. Access to the upper forest canopy with a large tower crane. BioScience 42: 664-670.

_____. 1995. Structure and microclimate of forest canopies. *In* M. Lowman and N. Nadkarni (eds.) *Forest Canopies - A Review of Research on a Biological Frontier*. Academic Press, San Diego, pp. 73-106.

Parker, G.G., P.J. Stone, and D. Bowers. 1996. A balloon for microclimate observations in the forest canopy. J. Appl. Ecol. 33: 173-177.

Pierce, L.L. and S.W. Running. 1988. Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. Ecol. 69: 1762-1767.

Thompson, D.R. and T.M. Hinckley. 1977. Spatial and temporal variations in stand microclimate and the water status of several species in an oak-hickory forest. Amer. Midl. Nat. 94:373-380.

van Pelt, R. and M.P. North. 1996. Analyzing canopy structure in Pacific Northwest Old-Growth forests with a stand-scale crown model. Northwest Sci. 70 (Special issue): 15-31.

Vose, J.M., N.H. Sullivan, B.D. Clinton, and P.V. Bolstad. 1995. Vertical leaf area distribution, light transmittance, and application of the Beer-Lambert law in four mature hardwood stands in the southern Appalachians. Can. J. For. Res. 25:1036-1043.

Yoda, K. 1978. The three-dimensional distribution of light intensity in a tropical rain forest in West Malaysia. Jap. J. Ecol. 24: 247-254.

Received 4 December 1996
Accepted for publication 29 July 1997