4

Structure and Microclimate of Forest Canopies

Geoffrey G. Parker

I. Introduction

The canopy is both a unique subsystem of the forest and the site of fundamental interactions between vegetation and the physical environment. Other authors in this volume view the canopy as a habitat and discuss the distribution, abundance, and ecological relations of its associated species. In this chapter, I explore canopy–atmosphere interactions for common environmental parameters and the influence of canopy organization on forest environment.

I summarize the general structural features and microclimates peculiar to forest canopies, compare how some forests differ in these characteristics, and explore how structure affects microclimate. I do not discuss the processes or rates of exchange of matter and energy between the forest and the atmosphere (see Chapter 3), nor consider the issue of scaling observations from leaf to canopy or from canopy to region. My principal focus is on the structure and environment of closed, continuous forests. More detail on forest influence on environment is in Kittredge (1948), Geiger (1965), and Lee (1983). The environments and atmospheric interactions of forests are considered in several volumes on physiological plant ecology (Gates, 1980; Landsberg, 1986), micrometeorology or microclimatology (Rosenberg, 1974; Monteith, 1975, 1976; Jones, 1983; Oke, 1987; Arya, 1988), and specialized multiauthored works (Hutchison and Hicks, 1985; Pearcy *et al.*, 1989; Russell *et al.*, 1989).

I will advance several themes. First, forest canopy structure, though broadly understood, has not been clearly defined and is rarely represented in a manner allowing cross-system comparisons. Second, measurements of microclimate have concentrated on mean values of selected environmental characteristics, usually at few locations and short time scales. Spatial variation is rarely assessed and the capacity to predict ecologically meaningful variation is limited. Finally, studies of the relation between canopy structure and function, though increasing in number, are still uncommon. Theories of several canopy–atmosphere interactions (e.g., interception of radiation, momentum, and precipitation) are well developed; data relevant to these interactions are less abundant.

I will illustrate aspects of the structure and function of canopies with examples from several studies in temperate deciduous forests. Reference is made to work in tall, mixed-species forest on the U.S. coastal plain dominated by *Liriodendron tulipifera* (Parker et al., 1989) and in mixed-oak forests in the southern Appalachian Mountains (Parker et al., 1993).

II. Structure of Forest Canopies

A. Definitions

The canopy is the combination of all leaves, twigs, and small branches in a stand of vegetation; it is the aggregate of all the crowns. The canopy is a region as well as a collection of objects (Carroll, 1980). "Canopy structure" is the organization in space and time, including the position, extent, quantity, type and connectivity, of the aboveground components of vegetation (e.g., Maser, 1989; Norman and Campbell, 1989; Nobel et al., 1993). It is often useful to consider the open spaces between canopy elements and the atmosphere contained within and between crowns as part of the canopy.

This definition of canopy departs from other concepts that are restricted to the uppermost covering of vegetation, that is, the "roof" of the forest, the layer above the living limbs of the larger stems (e.g., Norse, 1990). This distinction is useful because in many stands, structural elements are distributed throughout the height of the forest; the covering layer is not always clearly definable. Similarly, the forest environment changes continuously from top to bottom; it is not clear how the gradient should be objectively subdivided. Finally, the dynamic nature of both canopy structure and environment makes the discrimination of boundaries difficult.

Separate study objectives require different operational representations of canopy structure, even for the same forest. For an investigation focused on organisms inhabiting woody surfaces (e.g., epiphytes), the canopy may be conceived as a network of connecting limbs (Nychka and Nadkarni, 1994). The canopy also could be conceptualized as a community of leaves and

studied demographically (Harper, 1989). To consider the patterns of environment and whole-canopy exchange of matter and energy, I will consider the canopy as a three-dimensional porous medium, having both passive and active surfaces.

Many terms have been used interchangeably in reference to canopy structure, but they emphasize different aspects. *Physiognomy* focuses on the shapes of individual crowns. *Architecture* describes the growth patterns and resultant forms of stems (e.g., Hallé et al., 1978; Oldeman, 1990). *Organization* has implied the statistical distribution of canopy components (or important characteristics) in space or time (e.g., Hollinger, 1989). Canopy *texture* refers to the sizes of the crown units composing the overstory that are apparent from above the stand.

B. The Units of Canopy Structure

The proximate units of canopy structure are the crowns of trees; the ultimate units are its leaves and twigs (Evans, 1972). However, as a hectare of closed canopy forest may have millions of leaves and many kilometers of twigs, most studies deal with these units statistically or focus on other levels of organization. Many scales of organization are evident (e.g., Kruijt, 1989): foliage may be clumped (often along branches and branch tips) and/or arranged in clusters, branch systems, and crownlets (Kira et al., 1969; Hallé et al., 1978; Bourgeron, 1983; Whitmore, 1984). Crowns are themselves sometimes grouped (Oldeman, 1990).

Canopy structure can be characterized at several levels of detail. It is most commonly summarized by a characteristic dimension or descriptor, for example, maximum tree height (h_{max}) or the mean height of the dominant trees (h), number or biomass density of the elements (stems ha^{-1} or Mg ha^{-1}), canopy cover (the fraction of sky not obscured by vegetation), or the leaf area index (LAI, m^2 m^{-2}), the ratio of the total one-sided leaf area to the projected ground area. Branch area index (BAI) is the area index of nonleafy material, and the total plant area index (PAI) integrates the two (i.e., PAI = LAI + BAI). Another common descriptor is the mean leaf area per unit volume (leaf area density, LAD, m^2 m^{-3}). Less common are one-dimensional summaries of spatially averaged vertical conditions, such as the height distribution of leaf area [$L(z)$, the foliage–height distribution, $\sum L(z) =$ LAI], the total foliage or branch area, and the leaf angle distribution. Rarely is it possible to specify the three-dimensional organization of canopy elements [i.e., $L(x,y,z)$]. Whatever characteristic is emphasized, canopy structure is usually described by mean conditions, without an assessment of variation.

Forests tend to have higher LAI and lower LAD than other community types in a given environment (Tadaki, 1977). LAD is inversely related to stand height. LAD in herbaceous stands ranges from 2 to 4 m^2 m^{-3}, whereas

Table I Ranges of Leaf Biomass, Left Area Index (LAI), and Mean Leaf Area Density (LAD) Observed in Different Forest Types[a]

Forest type	Leaf biomass (Mg ha^{-1})	LAI (ha ha^{-1})	LAD (m^2 m^{-3})
Deciduous broadleaf	2–3	4–6	0.1–0.3
Evergreen broadleaf	7–11	7–12	0.2–0.5
Deciduous conifer	2–3	5–7	0.1–0.4
Pinus	5–6	7–12	0.2–0.5
Evergreen conifer	9–15	15–20	0.3–0.7

[a]Extended from Tadaki (1977).

the values in forests are typically much lower, 0.2–0.4 m^2 m^{-3} (Kira *et al.*, 1969; Monsi *et al.*, 1973; Parker *et al.*, 1989); LAD in individual foliage layers can exceed these ranges (Table 1).

The surfaces of the canopy are the most important feature for atmospheric interactions. The height distribution of surface area and biomass for leaves and stems has been measured in a midsuccessional, mixed-species deciduous forest (Fig. 1). Biomass of stem tissues, which decreases steeply with height in the forest, far exceeds that of leaves. However, leaf area domi-
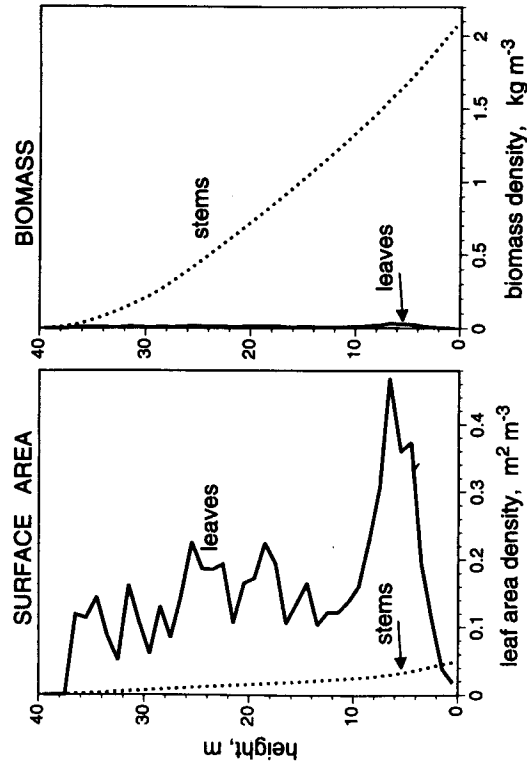

Figure 1 Mean vertical structure of canopy surfaces (left) and biomass (right) in a mixed-species deciduous forest on the mid-Atlantic coastal plain, United States. (From Parker *et al.*, 1989. Reprinted by permission of Kluwer Academic Publishers.)

nates the total aboveground surface area at all canopy levels. This multimodal vertical distribution of leaf area is common in mixed-species stands. The leaf area/total area ratio declines with increasing stem size (Whittaker and Woodwell, 1968). Thus, in older stands a larger proportion of total aboveground surface area is in stems and bark than in younger ones (i.e., LAI/PAI declines).

C. Vertical Organization

Canopy elements (tree height, species, or foliage) may be nonuniformly distributed with height (Smith, 1973; Richards, 1983; Oliver and Larson, 1990). Such patterns derive from species differences in growth form and shade tolerance, and on the stand developmental stage (Wierman and Oliver, 1979; Guldin and Lorimer, 1985; Terborgh, 1985). The vertical divergence of species height during forest development is called *differentiation* (Bicknell, 1982; Oliver and Larson, 1990). Vertical sorting of species leaf area has been demonstrated in mixed-species stands (Fig. 2).

In some stands, canopy leaves and branches are organized into distinct, nonoverlapping layers (*strata*). Such stratification is most easily recognized in single-species forests (especially managed stands) or in single-cohort stands, particularly at early stages of development. Early work in tropical rain forests suggested that stratification was a conspicuous characteristic of vegetation (e.g., Davis and Richards, 1933; Newman, 1954). Because vertical
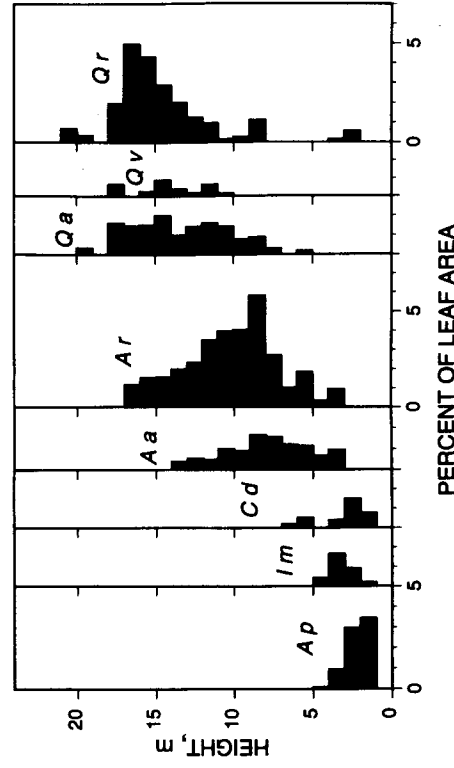
Figure 2 Foliage–height profile for a mixed-species forest in the southern Appalachian Mountains, United States, giving the percentage of leaf area for the major species. Species are coded Ap (*Acer pennsylvanicum*), Im (*Ilex montana*), Cd (*Castanea dentata*), Aa (*Amelanchier arborea*), Ar (*Acer rubrum*), Qa (*Quercus alba*), Qv (*Quercus velutina*), and Qr (*Quercus rubra*). (Reproduced from Parker *et al.*, 1993, with permission.)

organization was rarely quantified, the identification of strata tended to be subjective (Richards, 1983), and distinct vertical layering has not been universally recognized (Hallé et al., 1978; UNESCO/UNEP/FAO, 1978; Whitmore, 1984).

The question of stratification was a contentious issue (Bourgeron, 1983; Brünig, 1983; Longman and Jenik, 1987) partly because at least three distinct characteristics were confused in reference to vertical layering: tree height, species, and biomass (Smith, 1973). For silviculture and forest dynamics, the distribution of crown heights was the important characteristic (Oliver and Larson, 1990). Forest community studies referred to the layering of species within the forest (e.g., Heinsdijk, 1957; Ogawa et al., 1965). The literature on forest microclimate and physiology has concentrated on the vertical organization of biomass and surface area (e.g., Nobel et al., 1993).

Several categories of canopy levels (stories) are recognized. The *overstory* comprises the crowns that are fully (dominant) or largely (codominant) illuminated from above. The *understory* (or *subcanopy*) includes the woody plants in the lowest shady layers. The *midcanopy* is a transitional region between understory and overstory and has crowns that are partly (intermediate) illuminated or overtopped (suppressed). The *ground layer* includes the seedlings of woody plants and other, herbaceous vegetation just above the *forest floor*, which includes the litter. In some stands, an irregular zone of extremely tall crowns (*emergents*) rises above the main canopy. The *outer canopy* is the canopy surface immediately adjacent to the atmosphere; it has variable height and irregular shape.

Richards (1952) distinguished and named distinct layers in tropical rain forests: the more or less continuous canopy of larger trees comprising the main canopy is the B layer. In the A layer are the occasional emergents rising above the B layer. The C and D layers, usually less continuous than the B, are also defined for midcanopy and understory. The ground vegetation is called the E layer. Similar schemes are employed in other forest types, particularly in silvicultural applications (Smith, 1962; Oliver and Larson, 1990).

Height is the most tractable axis for representing forest structure; many models of canopy–atmosphere interactions are one dimensional. Vertical variation in structure, environment, or flux is conventionally represented in graphs with height on the vertical axis. Height is only a crude proxy for environment characteristics in forests; for photosynthetically active radiation (PAR), for example, absolute height is less important than proximity to the outer canopy. Canopy position is usually measured from the ground surface (z, height) but is often scaled to the canopy height (z/h). Others reference canopy position to the top of the forest [depth, $h - z$, or scaled depth $(h - z)/h$].

In many stands, particularly in crops and plantations, the foliage height distribution is unimodal and elevated; the leaf area below $0.25h$ is ignored in some studies (Munn, 1966). However, the vertical distribution of leaf area in mixed-species or multicohort stands is rarely this simple and can have one or more peaks (Monsi et al., 1973; Ross, 1975; Rauner, 1976; Aber, 1979; Franklin et al., 1981; Hedman and Binkley, 1988; Parker et al., 1989). In some older forests stands, $L(z)$ may be nearly uniform (Aber, 1979).

Leaf size, thickness, shape, and tissue chemistry differ between forest understory and overstory (e.g., Boardman, 1977; Kramer and Kozlowski, 1979). The display of foliage is also dependent on canopy position. Leaves tend to be held more vertically in the upper canopy than in the understory (Ford and Newbould, 1971; Hutchison et al., 1986; Hollinger, 1989; leaf azimuth tends not to be preferentially oriented. De Wit (1965) described distributions of leaf inclination angles, including *planophile* (preferentially horizontal), *erectophile* (mostly vertical), *plagiophile* (mostly oblique), and *extremophile* (both horizontal and vertical).

D. Horizontal Variation

Forests are not spatially uniform, but are horizontally heterogeneous at various scales (e.g., Kira et al., 1969; Fritschen, 1985; Krujit, 1989). The various sizes of features of canopy organization are mirrored in corresponding distributions of foliage-free spaces. Light gaps are holes in the canopy extending to the forest floor that permit the penetration of unscattered light (Runkle, 1985; Canham et al., 1990). Gaps of various sizes originate from a variety of causes; their numbers are inversely related to size (e.g., Brokaw, 1985; Sanford et al., 1986). Intercrown spacing and horizontal variation in leaf density increase greatly with height as the number of crowns declines (Ishizuka, 1984; Hubbell and Foster, 1986).

Categories of local organization are nonetheless readily recognized in forests. There are small clearings; open areas with little understory and high overstory ("cathedral" type of organization); places with extremely dense understories only; and other areas thick with leaves at all levels. As many as four tree crowns may overlap at any one position. In older forests, such variations may reflect the mosaic of patch ages (Whitmore, 1984; Oldeman, 1990). Crowns of adjacent trees may overlap like roof shingles (*imbrication*) on hillsides; older forest edges may present a wall of foliage ("river edge effect," Hallé et al., 1978).

J. H. Connell, M. D. Lowman, and I. R. Noble (unpublished data) suggested that variation in canopy vertical structure can be classified with regard to the presence or absence of canopy stories. A three-tiered stand could have as many as eight distinct structural classes (Fig. 3). The classical light gap, vegetation-free at all levels (Brokaw, 1982), is a relatively rare form of several vertical structures that occur in closed-canopy stands. This
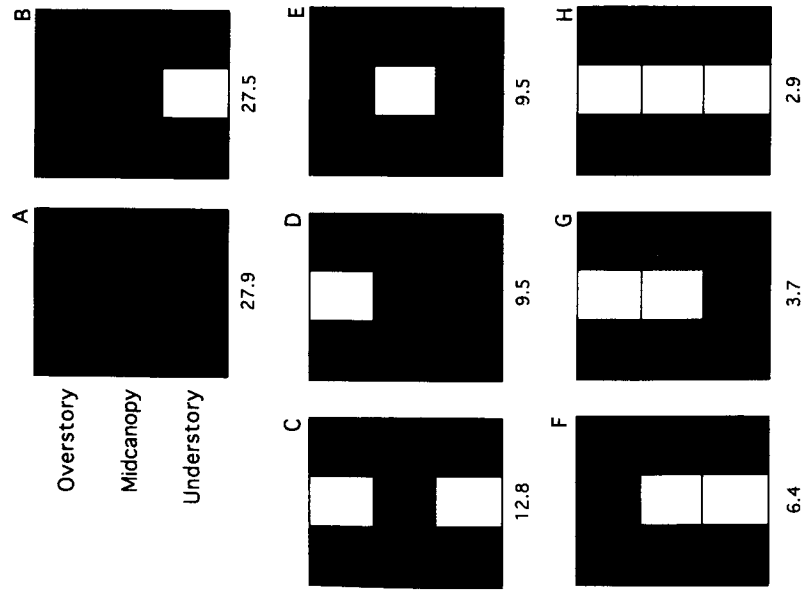
Figure 4   Topography of the outer canopy (left) and of the ground beneath the forest (right) in a young dry forest near Panama City, Panama. The contour intervals are 1 m for the ground surface and 5 m for the canopy. (From G. Parker, unpublished data.)

Figure 3   Forest layer spectrum for the stand in Fig. 2 giving the percentage of the stand in each of eight categories of vertical structure characterized by the presence or absence of overstory, midcanopy, or understory (following the approach of J. H. Connell, M. D. Lowman, and I. R. Noble, unpublished data). Unshaded segments indicate absent strata. Numbers give the percentage of the stand in each structural class. For example, panel H indicates a location without foliage at any level (the classical gap), which represents 2.9% of the forest.

E.   The Outer Canopy

The outer canopy is the layer of leaves and branches at the atmospheric interface; its undulating surface can slope laterally and may intersect the ground (e.g., in forest openings). The complex topography of this region, with features such as steep walls, canyons, and broad ridges (Parker, 1993; and Fig. 4), is generally not apparent from the ground. The surface area of the outer canopy is usually far greater than (e.g., more than twice) the area of ground below (Ford, 1976; Miller and Lin, 1985; Parker *et al.*, 1992). The surface is often punctuated with gaps, but can be very smooth in forests that experience recurring strong winds.

F.   Quantification of Canopy Structure

The difficulties of canopy access impose severe limitations on the quantification of canopy structure (Denison *et al.*, 1972; Moffett and Lowman, Chapter 1). Direct sampling within the intact canopy space is rarely possible in forests (but see Ford and Newbould, 1971; Beadle *et al.*, 1982; Hutchison *et al.*, 1986). Consequently, most structural descriptions are simplifications, often one-dimensional representations of a spatially averaged characteristic, such as $L(z)$.

The appropriate characteristic of canopy structure ultimately depends on the phenomenon studied. The height distribution of leaf surface area, optical properties, and inclination angles are purported to be sufficient to describe critical features of radiation absorption (Campbell and Norman,

approach, however, does not yield information on the spatial scale of individual open spaces.

In some forests, individual subcrowns and crowns are clearly separated, with intervening vegetation-free borders (Kira *et al.*, 1969). This "crown shyness" (Jacobs, 1955; Ng, 1977) is most common in single-species and single-cohort stands (especially plantations) and in stands on windy sites. It is probably maintained by wind-induced abrasion between adjacent crowns (Putz *et al.*, 1984).
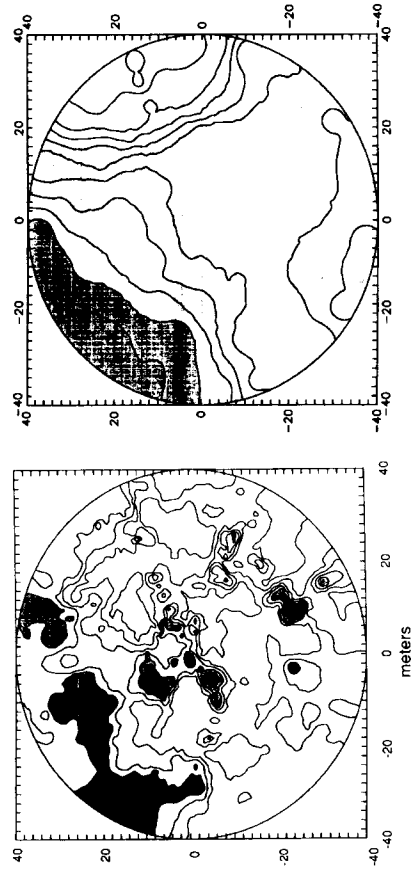
1989; Norman and Campbell, 1989). However, information on leaf angle is not essential for understanding wind velocities or momentum absorption.

Early characterizations of canopy structure were caricatures of the crowns of larger trees in a representative strip of forest, usually including both side and top views (e.g., Richards, 1952; Holdridge et al., 1971). These *profile diagrams* are useful descriptions, particularly for illustrating structural aspects of stand classification (e.g., Kuiper, 1988; Oldeman, 1990), variation along environmental gradients (e.g., Beard, 1944), or changes during succession (e.g., Uhl and Jordan, 1984). Others employed diagrams of vertical structure, idealized by life form and habit (e.g., Dansereau, 1951) or by patterns of growth (Hallé et al., 1978). However, such profiles tend to reflect the peculiarities of the chosen plot and provide little quantification of vertical organization of the whole stand.

Whole-canopy L(z) may be estimated by assembling structural measurements of individual crowns made from observations taken from the ground (e.g., Kruijt, 1989) or from harvested stems (Beadle et al., 1982; Massman, 1982). Foliage–height distributions of individual crowns have been summarized with various distributions: (a) triangular (Kinerson and Fritschen, 1971; Shaw and Pereira, 1982); (b) Gaussian (Stephens, 1969; Jarvis et al., 1976); (c) Weibull (Yang et al., 1993); and (d) beta (Massman, 1982). The assembly of canopy structure from crown measurements works best for crowns with "well-behaved" shapes (e.g., conifers in plantations). Mixed-species stands, which have diverse growth forms, ages, and heights, are difficult to quantify structurally (Campbell and Norman, 1989).

Although L(z) can be sampled directly in grass, crop, or shrub canopies (e.g., Warren-Wilson, 1965), it is rarely possible to obtain *in situ* measurements in forests (but see Miller and Lin, 1985). The method of optical point-quadrats (MacArthur and Horn, 1969) can yield the relative L(z) in forests (e.g., Aber, 1979; Hedman and Binkley, 1988; Parker et al., 1989) but the method is time-consuming. Hemispheric (fish-eye) photography can assess the potential light environment at a point (Chazdon and Field, 1987; Becker et al., 1989; Rich, 1990; Smith et al., 1992) or, in some cases, estimate the LAI (Neumann et al., 1989; Chen et al., 1991; Martens et al., 1993).

Forest structural attributes have been inferred from the effects of the canopy on measurements of environmental variables. These *inversion* techniques (e.g., Welles, 1990), depend on a robust relationship between structure and behavior. The expression describing behavior as a function of structure can sometimes be inverted and solved, yielding aspects of structure as a function of performance. Such methods are extensively developed for radiation-specific attributes (Norman, 1979, 1982; Lang, 1987; Perry et al., 1988; Pierce and Running, 1988). Several devices are now available to facilitate the estimation of LAI from in-canopy light measurements (Welles, 1990; Martens et al., 1993).

Kinerson and Fritschen (1971) inferred some aspects of canopy vertical structure [L(z)] in a Douglas-fir forest from its effect on mean wind profiles. The difference between the predicted logarithmic wind profile and the measured wind profile had a shape similar to the downward cumulative L(z). Wind profiles are not routinely employed to estimate canopy structure.

Some features of canopy structure can be estimated from the spectral quality of canopy light. Jordan (1969) used the ratio of red and far-red light transmitted through a tropical forest canopy to estimate its LAI. Remotely sensed reflectance can provide estimates of regional canopy structure (e.g., Leckie, 1990; Gholz et al., 1991). Several measures calculated from combining different reflectance bands relate to the amount of green canopy biomass, such as the normalized difference vegetation index (NDVI), or "greenness," index:

$$NDVI = \frac{R_{nir} - R_{red}}{R_{nir} + R_{red}}$$

where R_{nir} and R_{red} are the canopy reflectances in the near-infrared and red wavelength bands, respectively. This index takes advantage of the strong reflectance in the near-infrared but weak reflectance in the red wavelengths of green canopies (Smith et al., 1991). Other remote-sensing techniques use a similar approach, with sensors of different wavebands on several airborne or satellite platforms. Though certain interferences (correction for atmospheric absorption, phenological differences in canopy reflectance, reflectance of ground beneath the canopy) must be considered, such methods can be calibrated to yield reasonable predictions of LAI or leaf biomass (e.g., Spanner et al., 1990). Other techniques can yield information beyond the amount of foliage biomass. For example, a profiling airborne laser can simultaneously sense the elevation of both the ground and canopy, yielding the contour of canopy height over a long transect (Krabill et al., 1984; Leckie, 1990).

Paralleling the advances in access methodology (Moffett and Lowman, Chapter 1), the means for quantifying and visualizing canopy structure are growing in diversity and sophistication. The canopy surface has been described as a fractal object (Zeide and Pfeifer, 1991) and as a sum of numerous spatial wavelets (Bradshaw and Spies, 1992). Canopies have also been examined with two-dimensional spectral analysis (Ford, 1976) and three-dimensional tomography (Vanderbilt, 1985).

G. Temporal Changes

Canopy structure changes seasonally in all forests but is most dramatic in completely deciduous stands (e.g., Parker et al., 1989; Fig. 5). Even in evergreen forests, the quantity of leaf area varies over the year (Ford and New-
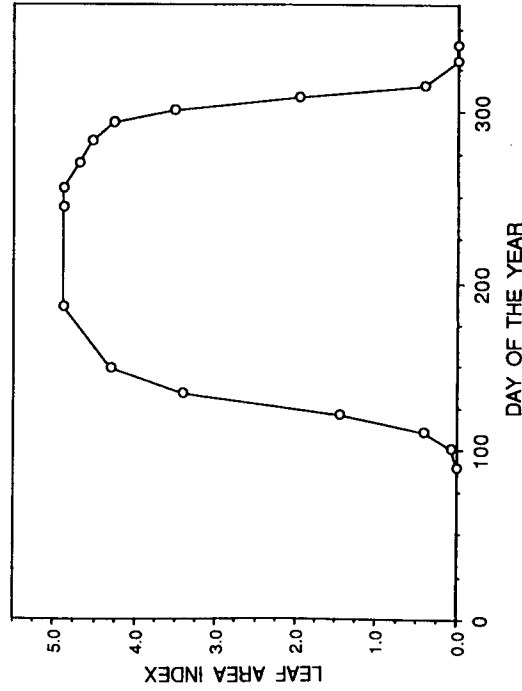
cal and horizontal distributions alter more slowly (Tadaki, 1977; Aber, 1979; Covington and Aber, 1980; Waring and Schlesinger, 1985; Oliver and Larson, 1990). Growing crowns ultimately come into contact with each other; when this happens throughout the stand, the canopy is said to be closed (the height of this contact is called the closure height). Subsequent differences in crown elongation cause height differentiation. The appearance of understory and shade-tolerant species initiates another layer of leaves. As overstory trees begin to die, stand leaf area declines slightly. Older stands may have crowns throughout vertical canopy space, but exhibit much spatial variation in canopy structure.

III. Microclimate

A. General Considerations

Canopy microclimate is ultimately determined by the stand macroclimate; the rhythms of change above and within the forest are set by the cycles of annual and diurnal heating and by the movements of air masses and clouds. Additionally, very short-term events associated with large penetrating eddies recurring on the time scale of less than a minute are important in exchange processes and the ventilation of lower canopy layers. Because most observations of forest environment are taken from measurements at a single location with averaging times of 5–30 minutes, important high-frequency events may be missed.

Some environmental variables (e.g., wind) are influenced by broad-scale canopy features whereas others (e.g., irradiance of visible light) depend more on the local arrangement of elements. The amount of *throughfall* (precipitation reaching the forest floor) depends on the pathways of droplet percolation. The amount of beam radiation received at a point depends on the obstructions along the path of the sun over time. Wind speed and direction depend on the disposition of obstacles upwind and can be very complex in the vicinity of isolated crowns, *windbreaks* (crowns in rows), or vegetation boundaries (McNaughton, 1989).

Several distinct aerodynamic regimes of the surface boundary layer are recognized above and within the canopy. In the *inertial sublayer* (up to several canopy heights above the stand), wind profiles tend to be semilogarithmic, the mean flow is largely horizontal, and turbulent transport of momentum is negligible (i.e., turbulence production is balanced by dissipation). In the *roughness sublayer* (close to and within the forest), profiles are complex and flows are three dimensional, and because the production and dissipation of turbulence are not balanced, net transport may be upward or downward. Additional microclimatic strata may be defined within

Figure 5 Change in total LAI over the course of a year for the stand in Fig. 1.

bould, 1971; Kinerson *et al.*, 1974; Gholz *et al.*, 1991; Hollinger *et al.*, 1994). More substantial changes occur on a successional time scale (Fig. 6); the total amount of leaf area stabilizes early in stand development, but its verti-
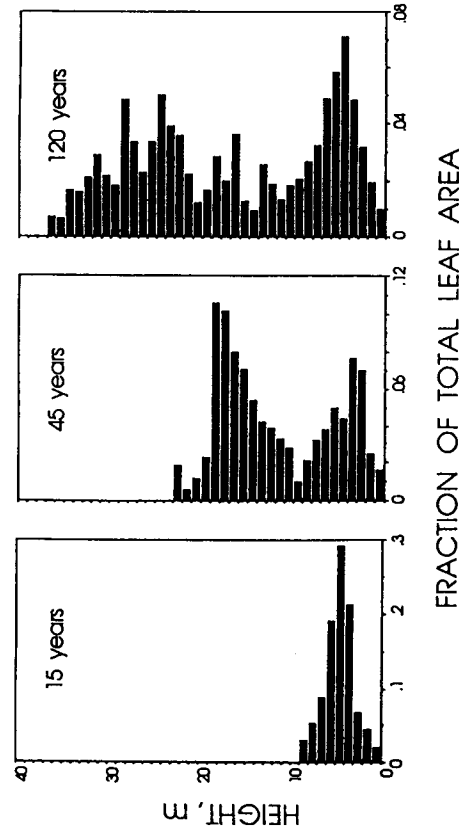

Figure 6 Examples of vertical canopy structures in different-aged stands of the tulip–poplar association in the mid-Atlantic coastal plain, United States. (From G. Parker, unpublished data.)

the canopy based on the direction of the heat and momentum fluxes (e.g., Raupach and Thom, 1981).

B. Precipitation

Precipitation is intercepted, retained, and redistributed by the canopy. Water ultimately evaporates from the canopy (*interception*) or drips through (*throughfall*) or runs down the stems (*stemflow*) to the forest floor (e.g., McCune and Boyce, 1992). The chemical composition of precipitation may also be altered dramatically by the canopy. Parker (1983) and Coxson and Nadkarni (Chapter 20) discuss the acquisition and cycling of solutes by canopies.

In general, between 10 and 30% of incident precipitation is intercepted and evaporated from the canopy. From 1 to 3 mm of water can be retained in the canopy at a given time (*interception capacity*), with greater amounts held in coniferous than in broad-leaved stands. Of the water eventually reaching the forest floor, up to 85% is throughfall and 0–30% is stemflow. Many crown and canopy characteristics affect the retention and redistribution of the amount of precipitation, including species, leaf shape, leaf texture, stem branching, bark roughness, canopy height, and canopy closure (e.g., Kittredge, 1948; Doley, 1981). Models of the precipitation interception by canopies are well developed (e.g., Rutter et al., 1971, 1975; Gash, 1979).

C. Radiation

Radiation absorption in the canopy is dependent on the distribution of leaves and leaf optical properties in the path of direct, diffuse, and scattered light. In general, forest leaves absorb most (≥80%) of the incident short-wave radiation (<700 nm); they transmit and reflect the remainder (e.g., Gates, 1980). More than half the radiation of the longer wavelengths (>700 nm) penetrates canopy leaves; the remainder is largely reflected. The absorption and transmission spectra of leaves depend on species, leaf surface, age, and the angle of light (Gates, 1980).

Endler (1993) distinguished five types of light environment within forests, each with a characteristic color. Shade light in forests is depleted in the blue and red wavelengths relative to incident radiation; green wavelengths are less strongly absorbed (Federer and Tanner, 1966; Holmes, 1981). Understory light in coniferous forests appears to be slightly "bluer" than under broad-leaved hardwoods (Morgan and Smith, 1981). Most dramatic is the relative depletion in the far-red wavelengths; the red:far-red ratio is much narrower in the understory than outside the forest (Smith, 1982; Lee, 1987). The light quality of sunflecks resembles that of direct beam light (less blue and more reddish than shade light). Ultraviolet (UV)

light is strongly absorbed by leaves except in open or disturbed canopies, where diffuse light richer in UV can penetrate (Brown et al., 1994).

Because their surface roughness reduces backscattering to the atmosphere, forest canopies are generally more efficient absorbers of shortwave radiation than are other forms of vegetation (Shuttleworth, 1989). The reflection coefficient (*albedo*) of temperate forests ranges from 0.08 to 0.13 in conifers (Jarvis et al., 1976), 0.10 to 0.12 in growing-season hardwoods, and ≈0.13 for tropical rain forest (Shuttleworth, 1989). Stanhill (1970) found that albedo decreased with vegetation height, from about 0.25 when less than 1 m high to 0.11 for stands above 20 m. This effect may reflect the dependence of roughness on height. Albedo also increases at higher solar zenith angles.

Light transmission decreases rapidly below the level of canopy closure. Average light levels decline with depth thereafter, but there is substantial spatial variability in canopy light environments, particularly in the overstory (Fig. 7). However, transmittance at any level is closely related to the total leaf area from the top of the forest. Monsi and Saeki (1953) proposed a general description of light in canopies, following the Beer–Lambert law for transmission in turbid media:

$$\frac{I}{I_0} = e^{-kL}$$

where I and I_0 are the illuminance at level z and the top of the canopy, L is the total leaf area downward through level z, and k is the light extinction
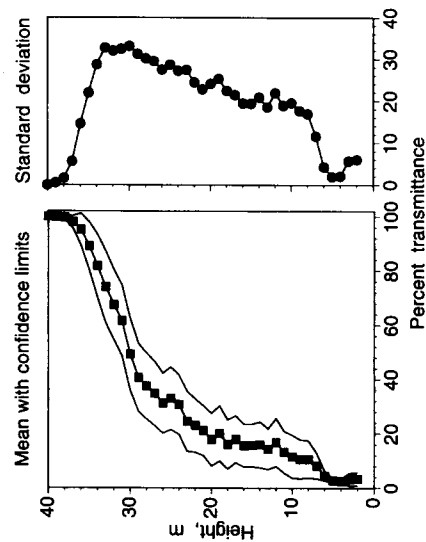

Figure 7 Vertical profile of the transmittance of photosynthetically active radiation (PAR) averaged over profiles at 26 different locations measured from a helium balloon at midday in the forest of Fig. 1. (From G. Parker, unpublished data.)

coefficient. A considerable theory of optics in vegetation canopies has developed with many modifications and extensions to this expression (e.g., Ross, 1975; Norman, 1979). The distribution of leaf angles has a very strong effect on light penetration (e.g., de Wit, 1965): theoretically, the coefficient of extinction, k, ranges from 0.5 for canopies of randomly distributed leaves with spherical orientation to 1.0 in planophile canopies.

Although this expression was originally intended only for monochromatic, direct-beam light interacting with a homogeneous medium of randomly oriented elements, it has been used widely for empirical estimates of canopy leaf area from measurements of light transmittance. The relationship must generally be calibrated for a given stand (e.g., Chason et al., 1991; Brown and Parker, 1994). It also satisfactorily represents the attenuation of global (direct plus diffuse) radiation in canopies (Fig. 8). In some complex forests (e.g., woodlands or canopies with emergent crowns), however, the relation is not so smooth (e.g., Yoda, 1978).

The annual changes in light transmittance in a completely deciduous forest illustrate the influence of foliage on the distribution of PAR in time and height (Fig. 9). Whereas 30–40% of incident light reaches the forest floor in the leafless season, only 1–2% penetrates when the canopy is complete. Some suggest the one-dimensional interception of radiation can be adequately characterized with information on $L(z)$, leaf angle distributions,
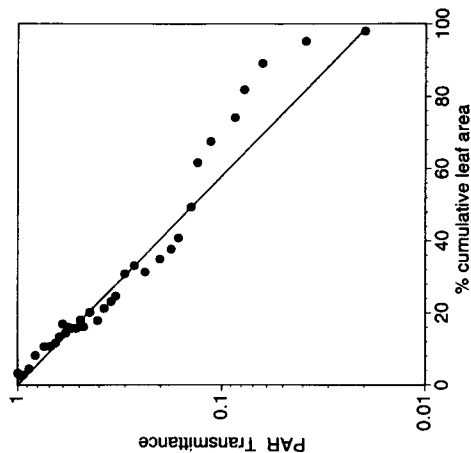

Figure 9 Height–time section showing the seasonal change in light transmittance in the forest of Fig. 1.

Figure 8 Relation between the mean PAR transmittance and the cumulative downward fraction of leaf area by 1-m height intervals in the stand of Fig. 1. The slope of the relation between transmittance and cumulative leaf area index is the empirical extinction coefficient, k (=0.63 here; for LAI=6).
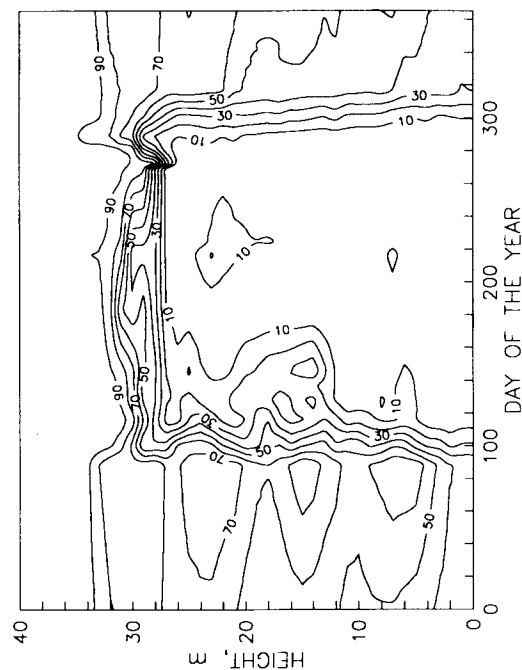
leaf optical properties, and leaf clumping (Norman 1979, 1982; Jarvis and Leverenz, 1983). However, such measurements are available for few stands.

D. Wind Speed

Wind is rapidly decelerated in the layer just above the forest (Fig. 10). The velocity profile in this layer is commonly described as though the wind were reacting to a rough surface displaced above the ground by a distance d (the zero plane displacement). This is equivalent to the mean height of momentum absorption (Thom, 1971), with a gradient controlled by the roughness of the surface (described by the roughness length for momentum, z_0) (e.g., Raupach and Thom, 1981). The mean wind velocity at height z is given by

$$u(z) = \frac{u_*}{k} \ln \left(\frac{z-d}{z_0} \right)$$

where u_* is the friction velocity and k is von Karman's constant (0.41). This expression applies only under neutral conditions and must be corrected when the air is stable or unstable.

Both the roughness and displacement height of canopies depend on the amount and distribution of canopy material, and also on wind speed itself (Brünig, 1970; Thom, 1971). Estimates are often based on the canopy
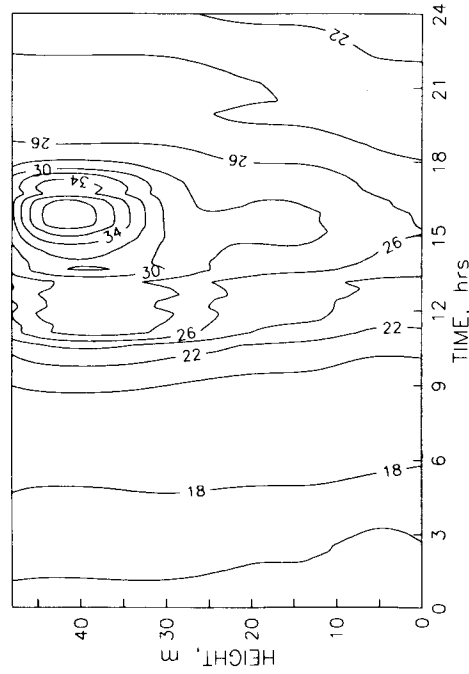
th canopy density and
iption of canopy wind
opy (<0.2 *h*).

onically with depth but
anopy levels, often at
arvis *et al.*, 1976; Shaw,
ple structure that lack
r at forest boundaries,
several canopy heights

s, arresting small-scale
eddies (Baldocchi and
which eddies penetrate
ly, and, especially, the
dley, 1985; Shaw *et al.*,
e of leaves affected dif-
iduous forest.

ng a small fraction of
uated with gusts that
cy sensors, rapid verti-
coherent structures) may
y levels (Crowther and
oore, Chapter 3). Dur-
lines) are followed by
ions have been identi-
low air from near the
ely fast air from above
1988; Bergström and
momentum transport
ical above the canopy
nized structures have
. They may last tens of
er of 30–100 seconds.
30 minutes) are insuf-
985; Finnigan, 1985).

g transport in the can-
ients tend to be weak
bsolute humidity can
d of days. Because of
y. The *saturation deficit*
hout the forest, from

Figure 13 Temperature and humidity covariation just above the forest (solid circles) and at 14 m (open squares) height on the same day as Fig. 10, plotted as loci of successive points 15 minutes apart. Also shown are isolines of water vapor content (solid lines, g m^{-3}) and vapor deficit (dashed lines, g m^{-3}).

humidity relation at two levels in a deciduous canopy over the course of a day show the relative constancy of water vapor content despite wide variation in temperature, relative humidity, and vapor deficit (Fig. 13).

Most incident short-wavelength radiation is absorbed in the outer canopy, the *active layer* for heat exchange. This layer reradiates heat more readily than lower levels in the forest and cools rapidly on clear, still nights. The cooling at the top can establish a stable inversion, which effectively divides the canopy into two thermal zones. When heating resumes in the morning, the stability is broken up. This stratification is weaker than that observed in the temperature cycle of monomictic lakes. It can be punctuated by ventilating events, even at night (Raupach, 1989; Fitzjarrald et al., 1990; Fitzjarrald and Moore, 1990).

Profiles of temperature and moisture have been simulated (e.g., Waggoner, 1975; Norman, 1979; Meyers and Paw U, 1987), but the estimation

Figure 11 Height–time section of diurnal air temperature on the same day as Fig. 10. Temperature contours are 2 degrees. Note the hot spot in the upper canopy in the midafternoon and the weak gradients at night.

highly unsaturated during the day to near saturation at some levels at night (e.g., Cachan, 1963; Lemon et al., 1970; Aoki et al., 1978; Elias et al., 1989). This often stimulates dew formation. Measurements of the temperature–
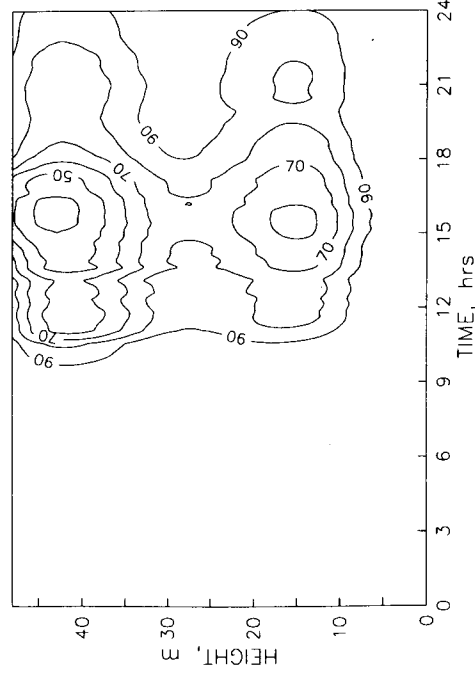

Figure 12 Height–time section of diurnal relative humidity (RH) on the same day as Fig. 10. Contours are 10% RH units. Humidities were near saturation (>95%) in the rest of the day outside the contours shown. Note the decline in RH in the midafternoon.
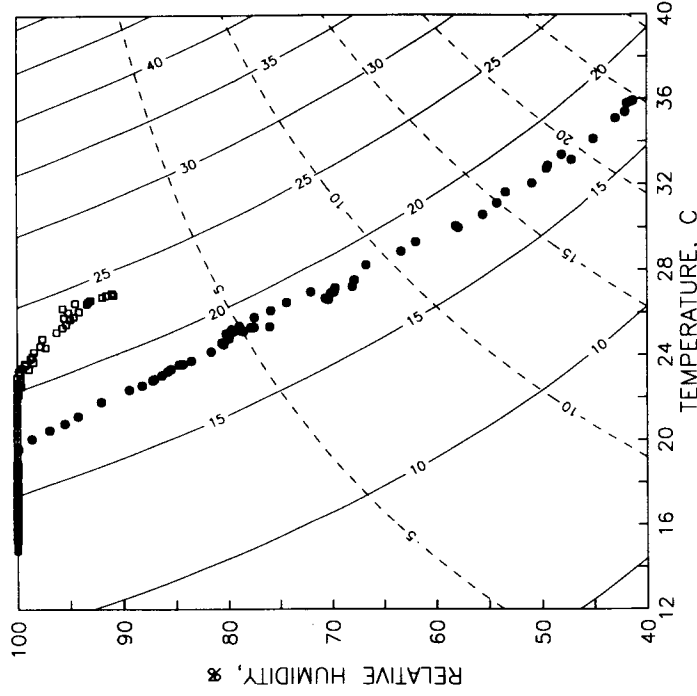
depends strongly on leaf stomatal behavior and is difficult to achieve. When present, forest understories can make a large contribution to the stand evapotranspiration (Black and Kelliher, 1989; Kelliher et al., 1990; Baldocchi and Meyers, 1991).

F. Trace Gases and Particles

Trace gas and particle concentrations often have relatively weak gradients within the canopy, but mean concentrations are typically lower in the understory than in the overstory (but see Lovett and Lindberg, 1992). For models of particle, gas, and vapor gradients in canopies, see Wiman and Agren (1985), Wiman et al. (1985), and Lovett and Lindberg (1992).

For CO_2, however, the active layer of the canopy is an enormous sink, and CO_2 concentrations are often slightly depressed in the overstory during the daytime (Lemon et al., 1970; Saeki, 1973; Allen and Lemon, 1976; Aoki et al., 1978; Elias et al., 1989). The layer near the ground is a source of CO_2, arising from root and soil respiration and decomposition. A pronounced CO_2 maximum often develops in the understory late at night, especially under stable conditions (Odum et al., 1970; Landsberg, 1986; Kira and Yoda, 1989; Shuttleworth, 1989; Bazzaz and Williams, 1991) (Fig. 14). The rate of increase in understory carbon dioxide concentrations during nighttime inversions was employed by Woodwell and Dykeman (1966) to estimate whole-forest respiration.
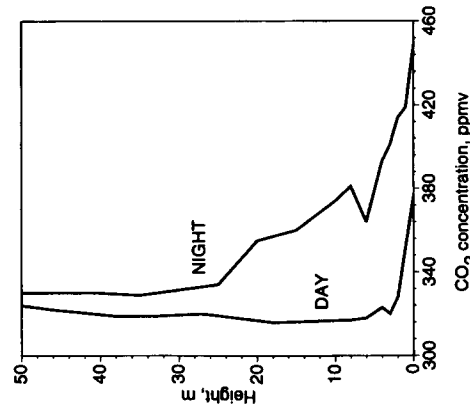

Figure 14 Daytime and nighttime profiles of CO_2 concentration (parts per million) in the forest of Fig. 1.

G. The Complex Vertical Gradient

The environment just above and within the canopy is a transition region between the free atmosphere and conditions near the forest floor. The mean values of many quantities change continuously with height, though often in a complicated and nonmonotonic manner. Because separate atmospheric parameters have different sinks and sources, their profiles are not identical. For example, leaf stomates are sources of water vapor but net sinks for CO_2. The active layer for radiation exchange is not necessarily coincident with that for momentum.

The range of variation in environment also differs between the upper and lower canopy layers (e.g., Fig. 13). The top has a marked diurnal fluctuation in almost every characteristic; variation is progressively reduced with depth in the canopy (Richards, 1952; Whitmore, 1984; Longman and Jenik, 1987). Relative to the outer canopy, the understory is reliably moist, dark, and still.

Also within the canopy is a gradient of connectivity: the outer canopy is clearly more closely coupled with the free atmosphere than is the understory. Cionco (1983, 1985) described a measure of the coupling of air flow in the canopy to that in the surface layer above (the *coupling ratio parameter*, R_c), defined as the ratio of mean wind speed within the canopy to that above it [$R_c = u(0.25h)/u(1.4h)$].

The connectivity between within-canopy layers and the forest exterior depends on the degree to which the large-scale environment is perceived at the level of individual canopy elements. For some environmental variables (e.g., the humidity at the leaf surface), the coupling is mediated by biological processes (largely stomatal control). Jarvis and McNaughton (1986) proposed an index, Ω, of the connection between leaf surface and free airstream values of water vapor deficits, for the case of transpiration. Omega reflects the decoupling of the two environments and ranges between 1 (completely uncoupled) and 0 (extremely strong coupling).

H. Transport in Canopies

Vertical profiles of important environmental parameters are related to the disposition of canopy material. The turbulent exchange of material between forest and atmosphere is in turn related to the stability of the atmosphere, the canopy structure, and the biological controls at canopy surfaces. The broad-scale atmosphere, canopy structure, and biological responses together influence and are influenced by canopy environments and transport processes.

The inference of canopy environment from canopy structure and of atmospheric exchanges from structure and environment is difficult. For example, because of the large scale of the eddies transporting material be-

tween canopy and atmosphere, neither the direction nor the magnitude of fluxes can be inferred from the curvature of profiles within the canopy (e.g., Denmead and Bradley, 1985; Paw U and Meyers, 1989). Fitzjarrald and Moore (Chapter 3) discuss why environmental gradients in forests are not reliable for predicting fluxes, as was once believed.

IV. Canopy Structure of Different Forest Types

There is enormous diversity within latitudes in canopy structure. Most temperate-zone work has focused on younger stands, often conifer plantations, and evergreen lowland rain forests have preoccupied most tropical researchers. Although few suitable measurement sets exist to compare forests in different places, some aspects of the archetypal tropical and temperate forest stands can be compared.

Tropical rain forests have greater annual leaf production (Medina and Klinge, 1983), standing canopy biomass (O'Neill and DeAngelis, 1981), and a higher leaf area index (Tadaki, 1977; DeAngelis et al., 1981; Anderson, 1981). Foliage–height profiles [$L(z)$] are rarely reported for tropical forest (see Kira and Yoda, 1989), but they are commonly presumed to be relatively uniform (e.g., Shuttleworth, 1989). Temperate canopies are often pictured as unimodal and elevated.

Rain forests tend to have lower relative illuminance of visible light at the forest floor (often <1%, Grubb and Whitmore, 1967; Leigh, 1975; Chazdon and Fetcher, 1984), whereas temperate canopies tend to permit higher transmittance (hardwoods in leaf: 1–3%, pines: >5%, hemlocks: <5%). Shuttleworth (1989), however, claimed that many of the bulk characteristics of temperate and tropical canopies (albedo, aerodynamic roughness, illuminance, interception capacity, and the behavior of stomatal conductance) may be roughly similar, given the reliability of the estimates. He suggested that more important distinctions between forests of different latitudes arise in the interaction of structure and local microclimate. Although structures may not differ significantly, the manner by which structure affects energy partitioning, transport, and microclimate may be quite distinct.

V. Summary, Conclusions, and Recommendations

The canopy is the primary site of interaction between the biosphere and atmosphere. The amount and spatial organization of aboveground plant parts influence both the atmospheric environment within canopies and the exchange of material and energy with the lower atmosphere. In the forest,

atmospheric characteristics are strongly modified by canopy structure in two general ways. First, canopy surfaces act as passive drag elements and exchange surfaces for the absorption of wind energy, the dissipation of turbulence, and the exchange of radiation. Second, canopy surfaces actively participate in exchanges of biologically important compounds, such as CO_2 and water vapor.

Forest canopies are distinct from other forms of vegetation because they are "dense, extensive, tall and perennial" (Shuttleworth, 1989). They have more biomass, greater surface area, and lower average leaf area density. The structural complexity of forests makes them aerodynamically rougher than other forms of vegetation (except possibly woodlands). This increases the effectiveness of daytime turbulent mixing, which in turn may reduce environmental gradients within forests.

Forest structure is generally recognized as consisting of the amount and distribution in space of leaves, stems, twigs, and branches, but there are nearly as many distinct measures of canopy structure as there are canopy research programs. Because of the variation in attributes considered, comparisons are restricted to the most commonly measured attributes. Environmental variables are usually measured at only a few locations; spatial variation is rarely assessed (e.g., Kinerson and Fritschen, 1971; Hutchison and Baldocchi, 1989). Representativeness of long-term measurements is unknown and processes that react to structural heterogeneity, such as local convection induced by differences in heat penetration, cannot be assessed.

The bulk of observations of canopy environment are average descriptions of processes and average descriptions of motivating structures. Quantification of structure has been inadequate, even for studies directly focused on forest–atmosphere interactions (Fritschen, 1985). The lack of detailed information limits our capacity to generalize about the importance of canopy structure and climate in controlling canopy environment.

The theoretical basis of canopy–environment interactions is better developed than the observations to test or validate them. Most current models deal with ideal cases and yield predictions about mean conditions. There is a need to extend these predictions to the understanding of particular environments. More empirical studies could be focused on transitional environments, transient regions such as within forest clearings (gaps), and environments that exhibit wide variation, such as the outer forest canopy. The success in understanding mean conditions should be extended to appreciating the variation that organisms undoubtedly perceive.

Much canopy micrometeorology has focused on stands of simple structure, particularly single-species, single-aged forests or crops with elevated, unimodal canopies. Studies of such situations have propelled the development of several useful descriptive and predictive models. However, many

stands are not so simple. There is a need to focus attention on the "non-ideal" canopies—mixed-species forests, multiple-cohort stands, and those with partial or complete deciduous seasons.

Acknowledgments

References

Aber, J. D. (1979). Foliage–height profiles and succession in northern hardwood forest. *Ecology* 60, 18–23.

Allen, L. H., Jr. (1968). Turbulence and wind speed spectra within a Japanese larch plantation. *J. Appl. Meteorol.* 7, 73–78.

Allen, L. H., Jr., and Lemon, E. R. (1976). Carbon dioxide exchange and turbulence in a Costa Rican tropical rain forest. *In* "Vegetation and the Atmosphere" (J. L. Monteith, ed.), Vol. 2, pp. 265–308. Academic Press, London.

Anderson, M. C. (1981). The geometry of leaf distributions in some south-eastern Australian forests. *Agric. Meteorol.* 25, 195–205.

Aoki, M., Yabuki, K., and Koyama, H. (1978). Micrometeorology of Pasoh forest. *Malay. Nat. J.* 30, 149–159.

Arya, S. P. (1988). "Micrometeorology." Academic Press, San Diego.

Baldocchi, D. D., and Meyers, T. P. (1988). Turbulence structure in a deciduous forest. *Boundary-Layer Meteorol.* 43, 345–364.

Baldocchi, D. D., and Meyers, T. P. (1991). Trace gas exchange above the floor of a deciduous forest. 1. Evaporation and CO_2 flux. *J. Geophys. Res.* 96(D4), 7271–7285.

Bazzaz, F. A., and Williams, W. E. (1991). Atmospheric CO_2 concentrations within a mixed forest: Implications for seedling growth. *Ecology* 72, 12–16.

Beadle, C. L., Talbot, H., and Jarvis, P. G. (1982). Canopy structure and leaf area index in a mature Scots pine forest. *Forestry* 55, 105–123.

Beard, J. S. (1944). Climax vegetation in tropical America. *Ecology* 25, 127–158.

Becker, P., Erhart, D. W., and Smith, A. P. (1989). Analyses of forest light environments. Part I. Computerized estimation of solar radiation from hemispherical canopy photographs. *Agric. For. Meteorol.* 44, 217–223.

Bergen, J. D. (1971). Vertical profiles of windspeed in a pine stand. *For. Sci.* 17, 314–321.

Bergström, H., and Högström, U. (1989). Turbulent exchange above a pine forest. II. Organized structures. *Boundary-Layer Meteorol.* 49, 231–263.

Bicknell, S. H. (1982). Development of canopy stratification during early succession in northern hardwoods. *For. Ecol. Manage.* 4, 41–51.

Black, T. A., and Kelliher, F. M. (1989). Processes controlling understory evapotranspiration. *Philos. Trans. R. Soc. London, Ser. B* 324, 207–231.

Boardman, N. K. (1977). Comparative photosynthesis of sun and shade plants. *Annu. Rev. Plant Physiol.* 28, 355–377.

Bourgeron, P. S. (1983). Spatial aspects of vegetation structure. *In* "Tropical Rain Forest Ecosystems: Structure and Function" (F. B. Golley, ed.), pp. 29–47. Elsevier, Amsterdam.

Bradshaw, G. A., and Spies, T. A. (1992). Characterizing gap structure in forests using wavelet analysis. *J. Ecol.* 80, 205–215.

Brokaw, N. V. L. (1982). The definition of treefall gap and its effects on measures of forest dynamics. *Biotropica* 14, 158–160.

Brokaw, N. V. L. (1985). Treefalls, regrowth, and community structure in tropical forests. *In* "The Ecology of Natural Disturbances and Patch Dynamics" (S. T. A. Pickett and P. S. White, eds.), pp. 53–69. Academic Press, Orlando, FL.

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

Brown, M. J., Parker, G. G., and Posner, N. (1994). A survey of ultraviolet-B radiation in forests. *J. Ecol.* 82, 843–854.

Brünig, E. F. (1970). Stand structure, physiognomy and environmental factors in some lowland forests in Sarawak. *Trop. Ecol.* 11, 26–43.

Brünig, E. F. (1983). Vegetation structure and growth. *In* "Tropical Rain Forest Ecosystems: Structure and Function" (F. B. Golley, ed.), pp. 49–75. Elsevier, Amsterdam.

Cachan, P. (1963). Signification écologique des variations microclimatiques verticales dans la forêt sempervivente de basse Côte d'Ivoire. *Ann. Fac. Sci. Dakar* 8, 89–155.

Campbell, G. S., and Norman, J. M. (1989). The description and measurement of plant canopy structure. *In* "Plant Canopies: Their Growth, Form and Function" (G. Russell, B. Marshall, and P. Jarvis, eds.), pp. 1–19. Cambridge Univ. Press, Cambridge, UK.

Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A., and White, P. S. (1990). Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20, 620–631.

Carroll, G. L. (1980). Forest canopies: Complex and independent subsystems. *In* "Forests: Fresh Perspectives from Ecosystem Analysis" (R. H. Waring, ed.), pp. 87–107. Oregon State Univ. Press, Corvallis.

Chason, J. W., Baldocchi, B. B., and Huston, M. A. (1991). A comparison of direct and indirect methods for estimating canopy leaf area. *Agric. For. Meteorol.* 57, 107–128.

Chazdon, R. L., and Fetcher, N. (1984). Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. *J. Ecol.* 72, 553–564.

Chazdon, R. L., and Field, C. B. (1987). Photographic estimation of photosynthetically active radiation: Evaluation of a computerized technique. *Oecologia* 73, 525–533.

Chen, J. M., Black, T. A., and Adams, R. S. (1991). Evaluation of hemispherical photography for determining plant area index and geometry of a forest stand. *Agric. For. Meteorol.* 56, 129–143.

Cionco, R. M. (1965). A mathematical model for air flow in a vegetation canopy. *J. Appl. Meteorol.* 4, 517–522.

Cionco, R. M. (1972). A wind profile index for canopy flow. *Boundary-Layer Meteorol.* 3, 255–263.

Cionco, R. M. (1983). On the coupling of canopy flow to ambient flow for a variety of vegetation types and densities. *Boundary-Layer Meteorol.* 26, 325–335.

Cionco, R. M. (1985). Modeling windfields and surface layer wind profiles over complex terrain and within vegetation canopies. *In* "The Forest–Atmosphere Interaction" (B. A. Hutchison and B. B. Hicks, eds.), pp. 501–520. Reidel Publ., Dordrecht, The Netherlands.

Covington, W. W., and Aber, J. D. (1980). Leaf production during secondary succession in northern hardwoods. *Ecology* 61, 200–204.

Crowther, J. M., and Hutchings, N. J. (1985). Correlated windspeeds in a spruce forest. *In* "The Forest–Atmosphere Interaction" (B. A. Hutchison and B. B. Hicks, eds.), pp. 543–561. Reidel Publ., Dordrecht, The Netherlands.

Dansereau, P. (1951). Description and recording of vegetation upon a structural basis. *Ecology* 32, 172–229.

Davis, T. A. W., and Richards, P. W. (1933). The vegetation of Moraballi Creek, British Guiana: An ecological study of a limited area of tropical rain forest. *J. Ecol.* 21, 350–384.

DeAngelis, D. L., Gardner, R. H., and Shugart, H. H. (1981). Productivity of forest ecosystems studied during the IBP: The Woodlands data set. In "Dynamic Properties of Forest Ecosystems" (D. E. Reichle, ed.), pp. 567–672. Cambridge Univ. Press, Cambridge, UK.

Denison, W. C., Tracey, D. M., Rhoades, F. M., and Sherwood, M. (1972). Direct, non-destructive measurements of biomass and structure in living, old-growth Douglas-fir. In "Research on Coniferous Forest Ecosystems" (J. F. Franklin, L. J. Dempster, and R. H. Waring, eds.), pp. 147–158. Pacific Northwest and Range Experiment Station, Portland, OR.

Denmead, O. T., and Bradley, E. F. (1985). Flux–gradient relationships in a forest canopy. In "The Forest–Atmosphere Interaction" (B. A. Hutchison and B. B. Hicks, eds.), pp. 421–442. Reidel Publ., Dordrecht, The Netherlands.

de Wit, C. T. (1965). "Photosynthesis of Leaf Canopies." Agric. Res. Rep. No. 663. Cent. Agric. Publ. Doc., Wageningen.

Doley, D. (1981). Tropical and subtropical forests and woodlands. In "Water Deficits and Plant Growth" (T. T. Kozlowski, ed.), pp. 209–307. Academic Press, New York.

Dolman, A. J. (1986). Estimates of surface roughness length and zero plane displacement for a foliated and non-foliated oak canopy. *Agric. For. Meteorol.* 36, 241–248.

Eliáš, P., Kratochvílová, I., Janouš, D., Marek, M., and Masarovičová, E. (1989). Stand microclimate and physiological activity of tree leaves in an oak–hornbeam forest. I. Stand microclimate. *Trees* 4, 227–253.

Endler, J. A. (1993). The color of light in forests and its implications. *Ecol. Monogr.* 63, 1–27.

Evans, G. C. (1972). "The Quantitative Analysis of Plant Growth." Blackwell, London.

Federer, C. A., and Tanner, C. B. (1966). Spectral distribution of light in the forest. *Ecology* 47, 555–560.

Finnigan, J. J. (1985). Turbulent exchange in flexible plant canopies. In "The Forest–Atmosphere Interaction" (B. A. Hutchison and B. B. Hicks, eds.), pp. 443–480. Reidel Publ., Dordrecht, The Netherlands.

Fitzjarrald, D. R., and Moore, K. E. (1990). Mechanisms of nocturnal exchange between the rain forest and atmosphere. *J. Geophys. Res.* 95(D10), 16839–16850.

Fitzjarrald, D. R., Moore, K. E., Cabral, O. M. R., Scolar, J., Manzi, A. O., and de Abreu Sa, L. D. (1990). Daytime turbulent exchange between the Amazon forest and the atmosphere. *J. Geophys. Res.* 95(D10), 16825–16838.

Ford, E. D. (1976). The canopy of a Scots pine forest: Description of a surface of complex roughness. *Agric. Meteorol.* 17, 9–32.

Ford, E. D., and Newbould, P. J. (1971). The leaf canopy of a coppiced deciduous woodland. I. Development and structure. *J. Ecol.* 59, 843–862.

Franklin, J. F., Cromack, K., Jr., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F., and Juday, J. (1981). Ecological characteristics of old-growth Douglas fir forests. *USDA For. Serv. Gen. Tech. Rep.* PNW-118.

Fritschen, L. J. (1985). Characterization of boundary conditions affecting forest environmental phenomena. In "The Forest–Atmosphere Interaction" (B. A. Hutchison and B. B. Hicks, eds.), pp. 3–23. Reidel Publ., Dordrecht, The Netherlands.

Gao, W., Shaw, R. H., and Paw U, K. T. (1989). Observation of organized structure in turbulent flow within and above a forest canopy. *Boundary-Layer Meteorol.* 47, 349–377.

Gash, J. H. C. (1979). An analytical model of rainfall interception by forests. *Q. J. R. Meteorol. Soc.* 105, 43–55.

Gates, D. M. (1980). "Biophysical Plant Ecology." Springer-Verlag, New York.

Geiger, R. (1965). "The Climate near the Ground." Harvard Univ. Press, Cambridge, MA.

Gholz, H. L., Cropper, W. P., Jr., McKelvey, K., Ewel, K. C., Teskey, R. O., and Curran, P. J.

(1991). Dynamics of canopy structure and light interception in *Pinus elliotii* stands in northern Florida. *Ecol. Monogr.* 61, 33–51.

Grubb, P. J., and Whitmore, T. C. (1967). A comparison of montane and lowland forest in Ecuador. III. The light reaching the ground vegetation. *J. Ecol.* 47, 33–57.

Guldin, J. M., and Lorimer, C. G. (1985). Crown differentiation in even-aged northern hardwood forests of the Great Lakes region, U.S.A. *For. Ecol. Manage.* 10, 65–86.

Hallé, F., Oldeman, R. A. A., and Tomlinson, P. B. (1978). "Tropical Trees and Forests: An Architectural Analysis." Springer-Verlag, Berlin.

Harper, J. L. (1989). Canopies as populations. In "Plant Canopies: Their Growth, Form and Function" (G. Russell, B. Marshall, and P. Jarvis, eds.), pp. 105–128. Cambridge Univ. Press, Cambridge, UK.

Hedman, C. W., and Binkley, D. (1988). Canopy profiles of some Piedmont hardwood forests. *Can. J. For. Res.* 18, 1090–1093.

Heinsdijk, D. (1957). The upper story of tropical forests. *Trop. Woods* 107, 66–83; 108, 31–45.

Holdridge, L. R., Grenke, W. C., Hatheway, W. H., Liang, T., and Tosi, J. A., Jr. (1971). "Forest Environments in Tropical Life Zones: A Pilot Study." Pergamon, Oxford.

Hollinger, D. Y. (1989). Canopy organization and foliage photosynthetic capacity in a broad-leaved evergreen montane forest. *Funct. Ecol.* 3, 53–62.

Hollinger, D. Y., Kelliher, F. M., Byers, J. N., Hunt, J. E., McSeveny, T. M., and Weir, P. L. (1994). Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology* 75, 134–150.

Holmes, M. G. (1981). Spectral distribution of radiation in plant communities. In "Plants and the Daylight Spectrum" (H. Smith, ed.), pp. 147–158. Academic Press, London.

Hubbell, S. P., and Foster, R. B. (1986). Canopy gaps and the dynamics of a neotropical forest. In "Plant Ecology" (M. J. Crawley, ed.), pp. 77–96. Blackwell, Boston.

Hutchison, B. A., and Baldocchi, D. D. (1989). Forest meteorology. In "Analysis of Biogeochemical Cycling Processes in Walker Branch Watershed" (D. W. Johnson and R. I. Van Hook, eds.), pp. 21–95. Springer-Verlag, New York.

Hutchison, B. A., Matt, D. R., McMillen, R. T., Gross, L. J., Tajchman, S. J., and Norman, J. R. (1986). The architecture of a deciduous forest canopy in eastern Tennessee, U.S.A. *J. Ecol.* 74, 635–646.

Ishizuka, M. (1984). Spatial pattern of trees and their crowns in natural mixed forests. *Jpn. J. Ecol.* 34, 421–430.

Jacobs, M. R. (1955). "Growth Habits of the Eucalypts." Forestry and Timber Bureau, Commonwealth Government Printer, Canberra.

Jarvis, P. G., and Leverenz, J. W. (1983). Productivity of temperate, deciduous and evergreen forests. In "Physiological Plant Ecology. IV. Ecosystem Processes: Mineral Cycling, Productivity and Man's Influences" (O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, eds.), pp. 233–280. Springer-Verlag, Berlin.

Jarvis, P. G., and McNaughton, K. G. (1986). Stomatal control of transpiration: Scaling up from leaf to region. *Adv. Ecol. Res.* 15, 1–49.

Jarvis, P. G., James, G. B., and Landsberg, J. J. (1976). Coniferous forests. In "Vegetation and the Atmosphere" (J. L. Monteith, ed.), Vol. 2, pp. 171–240. Academic Press, London.

Jones, H. G. (1983). "Plants and Microclimate." Cambridge Univ. Press, Cambridge, UK.

Jordan, C. F. (1969). Derivation of leaf area index from quality of light on the forest floor. *Ecology* 50, 663–666.

Kelliher, F. M., Whitehead, D., McAneney, K. J., and Judd, M. J. (1990). Partitioning evapotranspiration into tree and understory components in two young *Pinus radiata* D. Don stands. *Agric. For. Meteorol.* 50, 211–227.

Kinerson, R. S., and Fritschen, L. J. (1971). Modeling a coniferous forest. *Agric. Meteorol.* 8, 439–445.

Kinerson, R. S., Higgenbotham, K. O., and Chapman, R. C. (1974). The dynamics of foliage distribution within a forest canopy. *J. Ecol.* 11, 347–353.

Kira, T., and Yoda, K. (1989). Vertical stratification in microclimate. *In* "Tropical Rain Forest Ecosystems" (H. Lieth and M. J. A. Werger, eds.), pp. 55–71. Elsevier, Amsterdam.

Kira, T., Shinozaki, K., and Hozumi, K. (1969). Structure of forest canopies as related to their primary productivity. *Plant Cell Physiol.* 10, 129–142.

Kittredge, J. (1948). "Forest Influences." McGraw-Hill, New York.

Krabill, W. B., Collins, J. G., Link, L. E., Swift, R. N., and Butler, M. L. (1984). Airborne laser topographic mapping results. *Photogramm. Eng. Remote Sens.* 50, 685–694.

Kramer, P. J., and Kozlowski, T. T. (1979). "Physiology of Woody Plants." Academic Press, Orlando, FL.

Kruijt, B. (1989). Estimating canopy structure of an oak forest at several scales. *Forestry* 62, 269–284.

Kuiper, L. C. (1988). "The Structure of Natural Douglas-fir Forests in Western Washington and Western Oregon." Paper 88-5. Agric. Univ. Wageningen, Wageningen.

Landsberg, J. J. (1986). "Physiological Ecology of Forest Production." Academic Press, London.

Landsberg, J. J., and James, G. B. (1971). Wind studies in plant canopies: Studies on an analytical model. *J. Appl. Ecol.* 8, 729–741.

Lang, A. R. G. (1987). Simplified estimate of leaf area index from transmittance of the sun's beam. *Agric. For. Meteorol.* 41, 179–186.

Leckie, D. G. (1990). Advances in remote sensing technologies for forest surveys and management. *Can. J. For. Res.* 20, 464–483.

Lee, D. W. (1987). The spectral distribution of radiation in two neotropical rainforests. *Biotropica* 19, 161–166.

Lee, R. (1983). "Forest Microclimatology." Columbia Univ. Press, New York.

Leigh, E. G., Jr. (1975). Structure and climate in tropical rain forest. *Annu. Rev. Ecol. Syst.* 6, 67–86.

Lemon, E., Allen, L. H., Jr., and Müller, L. (1970). Carbon dioxide exchange of a tropical rain forest. Part II. *BioScience* 20, 1054–1059.

Longman, K. A., and Jenik, J. (1987). "Tropical Forest and its Environment." Longman, London.

Lovett, G. M., and Lindberg, S. E. (1992). Concentration and deposition of particles and vapors in a vertical profile through a forest canopy. *Atmos. Environ.* 26A, 1469–1476.

MacArthur, R. H., and Horn, H. S. (1969). Foliage profiles by vertical measurements. *Ecology* 50, 802–804.

Martens, S. N., Ustin, S. L., and Rousseau, R. A. (1993). Estimation of the canopy leaf area index by gap fraction analysis. *For. Ecol. Manage.* 61, 91–108.

Maser, C. (1989). "Forest Primeval: The Natural History of an Ancient Forest." Sierra Club Books, San Francisco.

Massman, W. J. (1982). Foliage distribution in old-growth coniferous tree canopies. *Can. J. For. Res.* 12, 10–17.

McCune, B. C., and Boyce, R. L. (1992). Precipitation and the transfer of water, nutrients and pollutants in tree canopies. *Trends Ecol. Evol.* 7, 4–7

McNaughton, K. G. (1989). Micrometeorology of shelter belts and forest edges. *Philos. Trans. R. Soc. London, Ser. B* 324, 351–368.

Medina, E., and Klinge, H. (1983). Productivity of tropical forests and tropical woodlands. *In* "Physiological Plant Ecology. IV. Ecosystem Processes: Mineral Cycling, Productivity and Man's Influences" (O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, eds.), pp. 281–303. Springer-Verlag, Berlin.

Meyers, T. P., and Paw U, K. T. (1987). Modelling the plant canopy microenvironment with higher-order closure principles. *Agric. For. Meteorol.* 41, 143–163.

Miller, D. R., and Lin, J. D. (1985). Canopy architecture of a red maple edge stand measured by a point drop method. *In* "The Forest–Atmosphere Interaction" (B. A. Hutchison and B. B. Hicks, eds.), pp. 59–70. Reidel Publ., Dordrecht, The Netherlands.

Monsi, M., and Saeki, T. (1953). Über den Lichtfaktor in den Pflanzegesellschaften und seine Bedeutung für die Stoffproduktion. *Jpn. J. Bot.* 14, 22–52.

Monsi, M., Uchijima, Z., and Oikawa, T. (1973). Structure of foliage canopies and photosynthesis. *Annu. Rev. Ecol. Syst.* 4, 301–327.

Monteith, J. L., ed. (1975). "Vegetation and the Atmosphere," Vol. 1. Academic Press, London.

Monteith, J. L., ed. (1976). "Vegetation and the Atmosphere," Vol. 2. Academic Press, London.

Monteith, J. L., and Unsworth, M. H. (1990). "Principles of Environmental Physics." Edward Arnold, London.

Morgan, D. C., and Smith, H. (1981). Non-photosynthetic responses to light quality. *In* "Physiological Plant Ecology. I. Responses to the Physical Environment" (O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, eds.), pp. 109–134. Springer-Verlag, Berlin.

Munn, R. E. (1966). "Descriptive Micrometeorology." Academic Press, New York.

Neumann, H. H., den Hartog, G., and Shaw, R. H. (1989). Leaf area measurements based on hemispheric photographs and leaf-litter collection in a deciduous forest during autumn leaffall. *Agric. For. Meteorol.* 45, 325–345.

Newman, I. (1954). Locating strata in tropical rain forest. *J. Ecol.* 42, 218–219.

Ng, F. S. P. (1977). Shyness in trees. *Nat. Malays.* 2, 34–37.

Nobel, P. S., Forseth, I. N., and Long, S. P. (1993). Canopy structure and light interception. *In* "Photosynthesis and Production in a Changing Environment: A Field and Laboratory Manual" (D. O. Hall, J. M. O. Scurlock, H. R. Bolhàr-Nordenkampf, R. C. Leegood, and S. P. Long, eds.), pp. 79–90. Chapman & Hall, London.

Norman, J. M. (1979). Modelling the complete crop canopy. *In* "Modification of the Aerial Environment of Crops" (B. Barfield and J. Gerber, eds.), pp. 249–277. Am. Soc. Agric. Eng., St. Joseph, MO.

Norman, J. M. (1982). Simulation of microclimates. *In* "Biometeorology in Integrated Pest Management" (J. L. Hatfield and I. J. Thomason, eds.), pp. 65–99. Academic Press, New York.

Norman, J. M., and Campbell, G. S. (1989). Canopy structure. *In* "Plant Physiological Ecology: Field Methods and Instrumentation" (R. W. Pearcy, J. R. Ehleringer, H. A. Mooney, and P. W. Rundel, eds.), pp. 301–325. Chapman & Hall, London.

Norse, E. A. (1990). "Ancient Forests of the Pacific Northwest." Island Press, Washington, DC.

Nychka, D., and Nadkarni, N. M. (1994). Spatial analysis of points on tree structures: The distribution of epiphytes on tropical trees. *Biometrics* (in press).

Odum, H. T., Drewry, G., and Kline, J. R. (1970). Climate at El Verde. *In* "A Tropical Rain Forest: A Study of Irradiation and Ecology at El Verde, Puerto Rico" (H. T. Odum and R. F. Pigeon, eds.), pp. B347–B418. U.S. Atomic Energy Commission, Oak Ridge, TN.

Ogawa, H., Yoda, K., Kira, T., Ogino, K., Shidei, T., Ratanawongse, D., and Apasutaya, C. (1965). Comparative ecological study on three main types of forest vegetation in Thailand. I. Structure and floristic composition. *Nat. Life Southeast Asia* 4, 13–49.

Oke, T. R. (1987). "Boundary Layer Climates." Methuen, London.

Oldeman, R. A. A. (1990). "Forests: Elements of Silvology." Springer-Verlag, Berlin.

Oliver, C. D., and Larson, B. C. (1990). "Forest Stand Dynamics." McGraw-Hill, New York.

Oliver, H. R. (1975). Wind speeds within the trunk space of a pine forest. *Q. J. R. Meteorol. Soc.* 101, 168–169.

O'Neill, R. V., and DeAngelis, D. L. (1981). Comparative productivity and biomass relations of forest ecosystems. *In* "Dynamic Properties of Forest Ecosystems" (D. E. Reichle, ed.), pp. 411–449. Cambridge Univ. Press, Cambridge, UK.

Sanford, R. L., Jr., Braker, H. E., and Hartshorn, G. S. (1986). Canopy openings in a primary neotropical lowland forest. *J. Trop. Ecol.* 2, 277–282.

Shaw, R. H. (1977). Secondary wind speed maxima inside plant communities. *J. Appl. Meteorol.* 16, 514–521.

Shaw, R. H., and Pereira, A. R. (1982). Aerodynamic roughness of a plant canopy: A numerical experiment. *Agric. Meteorol.* 26, 51–56.

Shaw, R. H., den Hartog, G., and Neumann, H. H. (1988). Influence of foliar density and thermal stability on profiles of Reynolds stress and turbulence intensity in a deciduous forest. *Boundary-Layer Meteorol.* 45, 391–409.

Shuttleworth, W. J. (1989). Micrometeorology of temperate and tropical forests. *Philos. Trans. R. Soc. London, Ser. B* 324, 299–334.

Sigmon, J. T., Knoerr, K. R., and Shaughnessy, E. J. (1983). Microscale pressure fluctuations in a mature deciduous forest. *Boundary-Layer Meteorol.* 27, 345–358.

Smith, A. P. (1973). Stratification of temperate and tropical forest. *Am. Nat.* 107, 671–683.

Smith, A. P., Hogan, P., and Idol, J. R. (1992). Spatial and temporal patterns of light and canopy structure in a lowland tropical moist forest. *Biotropica* 24, 503–511.

Smith, D. M. (1962). "The Practice of Silviculture." Wiley, New York.

Smith, H. (1982). Light quality, photoreception and plant strategy. *Annu. Rev. Plant Physiol.* 33, 481–518.

Smith, N. J., Borstad, G. A., Hill, D. A., and Kerr, R. C. (1991). Using high-resolution airborne spectral data to estimate forest leaf area and stand structure. *Can. J. For. Res.* 21, 1127–1132.

Spanner, M. A., Pierce, L. L., Peterson, D. L., and Running, S. W. (1990). Remote sensing of temperate coniferous forest leaf area index—The influence of canopy closure, understory vegetation and background reflectance. *Int. J. Remote Sens.* 11, 95–111.

Stanhill, G. (1970). Some results of helicopter measurements of albedo. *Sol. Energy* 13, 59–66.

Stephens, G. R. (1969). Productivity of red pine. 1. Foliage distribution in tree crown and stand canopy. *Agric. Meteorol.* 6, 275–282.

Tadaki, Y. (1977). Some discussions on the leaf biomass of forest stands and trees. *Tokyo For. Exp. Stn. Bull.* 184, 135–161.

Terborgh, J. (1985). The vertical component of plant species diversity in temperate and tropical forests. *Am. Nat.* 126, 760–776.

Thom, S. (1971). Momentum absorption by vegetation. *Q. J. R. Meteorol. Soc.* 97, 414–428.

Uhl, C., and Jordan, C. F. (1984). Vegetation and nutrient dynamics during the first five years of succession following forest cutting and burning in the upper Rio Negro region of Amazonia. *Ecology* 65, 1476–1490.

UNESCO/UNEP/FAO (1978). "Tropical Forest Ecosystems." UNESCO-UNEP, Paris.

Vanderbilt, V. C. (1985). Measuring plant canopy structure. *Remote Sens. Environ.* 18, 281–294.

Waggoner, P. E. (1975). Micrometeorological models. In "Vegetation and the Atmosphere" (J. L. Monteith, ed.), Vol. 1, pp. 205–228. Academic Press, London.

Waring, R. H., and Schlesinger, W. H. (1985). "Forest Ecosystems: Concepts and Management." Academic Press, Orlando, FL.

Warren-Wilson, J. (1965). Stand structure and light penetration. 1. Analysis by point quadrats. *J. Appl. Ecol.* 2, 383–390.

Welles, J. M. (1990). Some indirect methods for evaluating canopy structure. *Remote Sens. Environ.* 5, 31–43.

Whitmore, T. C. (1984). "Tropical Rain Forests of the Far East." Oxford Univ. Press, Oxford.

Whittaker, R. H., and Woodwell, G. M. (1968). Surface area relations of woody plants and forest communities. *Am. J. Bot.* 54, 931–939.

Wierman, C. A., and Oliver, C. D. (1979). Crown stratification by species in even-aged mixed stands of Douglas-fir—Western hemlock. *Can. J. For. Res.* 9, 1–9.

Wiman, B. L. B., and Agren, G. I. (1985). Aerosol depletion and deposition in forests—A model analysis. *Atmos. Environ.* 19, 335–347.

Parker, G. G. (1983). Throughfall and stemflow in the forest nutrient cycle. *Adv. Ecol. Res.* 13, 57–133.

Parker, G. G. (1993). Structure and dynamics of the outer canopy of a Panamanian dry forest. *Selbyana* 14, 5.

Parker, G. G., O'Neill, J. P., and Higman, D. (1989). Vertical profile and canopy organization in a mixed deciduous forest. *Vegetatio* 89, 1–12.

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

Parker, G. G., Hill, S. M., and Kuehnel, L. A. (1993). Decline of understory American chestnut (*Castanea dentata* (Marsh.) Borkh.) in a southern Appalachian forest. *Can. J. For. Res.* 23, 259–266.

Paw U, K. T., and Meyers, T. P. (1989). Investigations with a higher-order canopy turbulence model into mean source–sink levels and bulk canopy resistances. *Agric. For. Meteorol.* 47, 259–271.

Pearcy, R. M., Ehleringer, J. R., Mooney, H. A., and Rundel, P. W. eds. (1989). "Plant Physiological Ecology: Field Methods and Instrumentation." Chapman and Hall, London, UK.

Perry, S. G., Fraser, A. B., Thomson, D. W., and Norman, J. M. (1988). Indirect sensing of plant canopy structure with simple radiation measurements. *Agric. For. Meteorol.* 42, 255–278.

Pierce, L. L., and Running, S. W. (1988). Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. *Ecology* 69, 1762–1767.

Putz, F. E., Parker, G. G., and Archibald, R. M. (1984). Mechanical abrasion and intercrown spacing. *Am. Midl. Nat.* 112, 24–28.

Rauner, J. L. (1976). Deciduous forests. In "Vegetation and the Atmosphere" (J. L. Monteith, ed.), Vol. 2, pp. 241–264. Academic Press, London.

Raupach, M. R. (1989). Stand overstory processes. *Philos. Trans. R. Soc. London, Ser. B* 324, 175–190.

Raupach, M. R., and Thom, A. S. (1981). Turbulence in and above plant canopies. *Annu. Rev. Fluid Mech.* 13, 97–129.

Rich, P. M. (1990). Characterizing plant canopies with hemispherical photographs. *Remote Sens. Environ.* 5, 13–29.

Richards, P. W. (1952). "The Tropical Rain Forest." Cambridge Univ. Press, Cambridge, UK (with corrections in 1975).

Richards, P. W. (1983). The three dimensional structure of tropical rain forest. In "Tropical Rain Forest: Ecology and Management" (S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, eds.), pp. 3–10. Blackwell, Oxford.

Rosenberg, N. J. (1974). "Microclimate: The Biological Environment." Wiley, New York.

Ross, J. (1975). Radiative transfer in plant communities. In "Vegetation and the Atmosphere" (J. L. Monteith, ed.), Vol. 1, pp. 13–52. Academic Press, London.

Runkle, J. R. (1985). Disturbance regimes in temperate forest. In "The Ecology of Natural Disturbances and Patch Dynamics" (S. T. A. Pickett and P. S. White, eds.), pp. 17–33. Academic Press, Orlando, FL.

Russell, G., Marshall, B., and Jarvis, P., eds. (1989). "Plant Canopies: Their Growth, Form and Function." Cambridge Univ. Press, Cambridge, UK.

Rutter, A. J., Kershaw, K. A., Robins, P. C., and Morton, A. J. (1971). A predictive model of rainfall interception in forests. I. Derivation of the model and comparison from observations in Corsican pine. *Agric. Meteorol.* 9, 367–384.

Rutter, A. J., Morton, A. J., and Robins, P. C. (1975). A predictive model of rainfall interception in forests. II. Generalizations of the model and comparison with observations in some coniferous and hardwood stands. *J. Appl. Ecol.* 12, 367–380.

Saeki, T. (1973). Distribution of radiant energy and CO_2 in terrestrial plant communities. In "Photosynthesis and Productivity in Different Environments" (J. P. Cooper, ed.), pp. 297–327. Cambridge Univ. Press, Cambridge, UK.

Wiman, B. L. B., Agren, G. I., and Lannefors, H. O. (1985). Aerosol concentration profiles within a mature coniferous forest—Model versus field results. *Atmos. Environ.* 19, 363–367.

Woodwell, G. M., and Dykeman, W. R. (1966). Respiration of a forest measured by CO_2 accumulation during temperature inversions. *Science* 154, 1031–1034.

Yang, X., Miller, D. R., and Montgomery, M. E. (1993). Vertical distribution of canopy foliage and biologically active radiation in a defoliated/refoliated hardwood forest. *Agric. For. Meteorol.* 67, 129–146.

Yoda, K. (1978). The three-dimensional distribution of light intensity in a tropical rain forest in West Malaysia. *Jpn. J. Ecol.* 24, 247–254.

Zeide, B., and Pfeifer, P. (1991). A method for estimating the fractal dimension of tree crowns. *For. Sci.* 37, 1253–1265.