

PLANT CANOPIES: THEIR GROWTH, FORM AND FUNCTION

Edited by

G. Russell,

University of Edinburgh

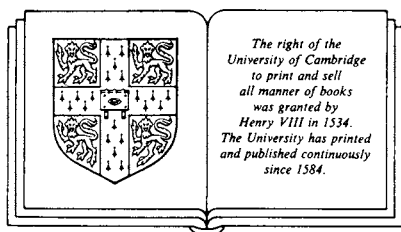
B. Marshall,

Scottish Crop Research Institute

and

P.G. Jarvis,

Professor of Forestry and Natural Resources, University of Edinburgh



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G.S. CAMPBELL AND J.M. NORMAN

1. The description and measurement of plant canopy structure

Introduction

Plant canopy structure is the spatial arrangement of the above-ground organs of plants in a plant community. Leaves and other photosynthetic organs on a plant serve both as solar energy collectors and as exchangers for gases. Stems and branches support these exchange surfaces in such a way that radiative and convective exchange can occur in an efficient manner. Canopy structure affects radiative and convective exchange of the plant community, so information about canopy structure is necessary for modelling these processes.

In addition to considering how canopy structure and environment interact to affect the processes occurring in the plant community, the influence of the canopy on the environment should also be considered. The presence and structure of a canopy exert a major influence on the temperature, vapour concentration, and radiation regime in the plant environment. Interception and transmission of precipitation are also affected, as are soil temperature and soil heat flow. Canopy structure can therefore be important in determining the physical environment of other organisms within the plant community, and can strongly influence their success or failure. Plant canopy structure can indirectly affect such processes as photosynthesis, transpiration, cell enlargement, infection by pathogens, growth and multiplication of insects, photomorphogenesis, and competition between species in a plant community. The indirect influence on soil moisture and temperature can also affect root growth, evaporative water losses from the soil, residue decomposition and other soil microbial processes.

A complete and accurate description of a canopy would require the specification of the position, size and orientation of each element of surface in the canopy. Such a description is clearly impossible to obtain, except for very simple canopies, so that data needs in terms of specific applications must be carefully considered. Canopy properties are generally described statistically as appropriate space or time averages. In some cases additional statistical parameters are needed for an adequate description of the canopy.

Canopies vary on spatial scales ranging from millimetres to kilometres, and on time scales ranging from milliseconds to decades. The description of this variation is an important part of understanding and using canopy structure information. Consideration of variation in structure can be useful in recognizing patterns which

may exist, and using these patterns to maximize sampling efficiency or minimize sampling errors.

Application of the principle of least work (Monteith, 1985) is particularly appropriate to measurements of canopy structure. Because it is possible to invest a lot of time and effort in measurements of canopy structure, it is particularly desirable to determine data requirements before an extensive measurement programme is undertaken.

Phytometric characteristics of plant canopies

The characterisation of plant canopies using various statistical parameters has been presented in considerable detail by Ross (1981). The material presented here is intended to be a brief summary. The reader is referred to the original work for additional detail.

Ross (1981) recommends that descriptions of plant canopies should include measurements at four levels of organisation: individual organs, the whole plant, the pure stand, and the plant community. Each higher level of organisation is intended to include elements from the next lower level, and to add parameters of its own.

At the individual organ level, parameters such as typical length, width, area, dry mass, specific water content, and radiative properties of phytoelements are measured. Whole plants are often symmetric, and have outlines which can be represented by some geometric shape. The parameters which describe the geometric shape are therefore useful as parameters for describing average characteristics of individual plants. Ellipsoidal shapes have been suggested as good approximations to plant outlines (Charles-Edwards & Thornley, 1973; Mann, Curry & Sharpe, 1979; Norman & Welles, 1983). Plants which cannot be represented by a complete ellipsoid can often be represented by a truncated ellipsoid. In addition to plant height and other parameters which relate to the overall geometric shape of the plant, it may be useful to record stem diameter at one or more locations, total number of leaves per plant, number of nodes per plant, number of living leaves per plant, numbers of stems and reproductive organs per plant, and spatial distribution of organs within the plant outline.

In an attempt to maximise return for a given sampling effort, Ross (1981) suggested a two-stage sampling process in which primary statistical characteristics such as plant height, height of the top and bottom of the foliage canopy, stem height and diameter, number of leaves (where possible) and number of living leaves (where possible) are determined on an initial sample of 150–300 plants. These primary characteristics are then examined to select 15–30 plants to be analysed in greater detail to determine average characteristics of individual organs, spatial locations of organs, and orientation of surfaces. If it is not possible to determine spatial locations of organs within the plant envelope, parameters for simple models of foliage distribution should be obtained. Mann *et al.* (1979) suggested three possible idealised distribution

functions. The uniform, the quadratic, and the truncated normal. The uniform distribution is based on the assumption that the probability of finding an element at any location within the plant envelope is independent of position. The other two distribution functions assume a higher density of foliage near the centre of the envelope. Norman & Welles (1983) assumed a uniform density of foliage within the ellipsoidal envelopes within which individual plants are contained, but allowed for the possibility that ellipsoids with different densities could be placed concentrically. Variations of area density within a given plant envelope were described by specifying the dimensions of the various ellipsoidal shells and the average foliage density within each shell.

At the pure stand and plant community levels of organisation, Ross (1981) suggested four types of plant dispersion: regular, semi-regular, random, and clumped. Regular dispersion results when plants are located at the vertices of a regular parallelogram. An example of this would be an orchard planting, or a square or hexagonally sown crop. Semi-regular dispersion results when plants are in rows, but spacing within the row is random, as in many agricultural crops. In random dispersion, there is an equal probability of finding a plant at any location, and with clumped dispersion the probability of finding a plant in a given location is related to the presence or absence of plants in the surrounding area.

A description of canopy organisation at the pure stand or plant community level requires, at least, a measurement of the plant population density, i.e. the number of each species of plant per unit area. For regular or semi-regular dispersion, plant or row spacings are needed and for regular dispersion, angles of the vertices of the parallelogram should also be determined. For random dispersion, only the plant population density is relevant, while for clumped dispersion, it may be possible to assume random dispersion within clumps, and define the size and distribution of the clumps.

As plants grow, they may begin to overlap so that it is difficult to discern the outline of a particular plant or row of plants. The time at which this occurs is termed 'canopy closure'. After canopy closure, radiative exchange and heat and mass transfer processes can be treated using one-dimensional theory. Large plant communities, where the horizontal dimensions are much larger than the vertical dimension, can also be treated as one-dimensional. A one-dimensional model allows dramatic simplification of the convective and radiative exchange processes. It may then be assumed that the phytoelements are randomly distributed in space (rather than within the plant envelope) or grouped around shoots which may themselves be randomly distributed in space.

Canopies which can be modelled as a series of horizontal layers, using one-dimensional models, are important in many agricultural and forest applications, and much of the following analysis will deal with this simplified canopy type. Such canopies are often described in terms of two parameters, the average area density of

component j , $\mu_j(z)$ (m^2m^{-3}), and the angle distribution function of component j , $g(z, r_j)$. The index j is intended to apply to leaves (l), stems (s), and reproductive parts (f) of the plant. The variable z , represents height in the canopy, and r_j represents the direction of a normal to the canopy element (i.e. azimuth, ϕ_j , and inclination θ_j , angles). The function, $g(z, r_j)$ represents the probability of a normal to a canopy element falling within an angle increment, $d\theta, d\phi$. It is normalised so that the integral of $g(z, r_j)$ over all angles in a hemisphere is unity.

Integrals of these parameters are often used. The downward cumulative area index of component j in a canopy is

$$L_j(z) = \int_z^h \mu_j(z) dz \quad (1)$$

where h is the height of the top of the canopy, and z the height from the ground. The leaf area index of a canopy (L_0) is the total area of leaves above unit area of soil, and is given by eqn (1) when $j = l$ and the lower limit of integration is equal to zero.

The integral of the angle distribution function $g(z, r_j)$, is the canopy extinction coefficient for a beam of radiation. This integral can be thought of as the average projected area of canopy elements or the ratio of projected to actual element area. Ross & Nilson (1965) define a G -function, which is the average projection of canopy elements onto a surface normal to the direction of the projection. If the projection zenith angle is θ and azimuth angle ϕ , then the G -function is calculated from the weighted integral of $g(z, r_j)$ over the hemisphere:

$$G(z, r) = \frac{1}{2\pi} \iint g_j(z, r_j) |\cos(r_j, r)| d\theta_j d\phi_j, \quad (2)$$

where

$$\cos(r_j, r) = \cos \theta_j \cos \theta + \sin \theta_j \sin \theta \cos(\theta - \theta_j), \quad (3)$$

θ_j is the inclination angle of the canopy elements (angle between the vertical and a normal to the element) and θ_j is the azimuth angle of the normal to the foliage element. The integral is taken over azimuth angles from 0 to 2π and inclination angles from 0 to $\pi/2$.

A different extinction coefficient, the K -function, has been used by a number of authors (Warren-Wilson, 1965, 1967; Anderson, 1966, 1970). It is the average projected area of canopy elements when they are projected onto a horizontal plane. It is related to the G -function by

$$K(z, r) = G(z, r) / \cos \theta. \quad (4)$$

Simplifications and idealizations

Having established some of the fundamental parameters that can be used to characterise canopy structure, attention is now given to simplifications and assumptions that reduce the number of measurements needed to describe the canopy.

The equations presented in this section will be useful in the analysis of the methods of measurement which will be covered later. We will begin by assuming a closed, horizontally homogeneous canopy with canopy elements randomly spaced in the horizontal. We will therefore be concerned only with the total area and vertical distribution of canopy elements, and the angular distribution of canopy elements. We will assume azimuthal symmetry of the plants, since measurements (Ross, 1981; Lemeur, 1973) indicate that canopies often approximate to this.

Many of the models that are used for calculating radiant energy interception by canopies require information only on area index and angle distribution, but models for the turbulent exchanges of heat and mass, and calculations of the size of penumbra also require a knowledge of the vertical distribution of area within the canopy. Ross (1981) presented a number of examples of area density functions, $u(z)$, for various canopies. Norman (1979) and Pereira & Shaw (1980) modelled $u(z)$ as a simple triangle (Figure 1.1). In such a case, the area density is given by

$$u(z) = \mu_m (z - z_1)/(z_m - z_1), \quad z_1 \leq z \leq z_m,$$

$$u(z) = \mu_m (h - z)/(h - z_m), \quad z_m \leq z \leq h, \quad (5)$$

with $u(z)$ assumed zero outside this range. The maximum leaf area density, μ_m is calculated from

$$\mu_m = 2L_0/(h - z_1). \quad (6)$$

In eqns. (5) and (6), h is the canopy height, z_1 is the lower boundary of the canopy, z_m is the height of maximum leaf area density, and L_0 is the leaf area index of the canopy.

The relationship between downward cumulative area index and height for such a triangular area density distribution is found by integration of eqn (1). For the triangular distribution assumed in eqn (5) the solution is

$$L/L_0 = (1 - z/h)^2 / [(1 - z_m/h)(1 - z_1/h)], \quad z_m \leq z \leq h,$$

$$L/L_0 = 1 - (z - z_1)^2 / [(h - z_1)(z_m - z_1)], \quad z_1 \leq z \leq z_m. \quad (7)$$

These equations allow one to describe the spatial distribution of canopy elements using four easily measured parameters: h , z_m , z_1 , and L_0 . Fig. 1.1 compares measured and predicted $u(z)$ and $L(z)$ for a maize canopy and indicates that these simple descriptions are adequate for many of the purposes for which spatial distribution information is needed.

Idealized leaf angle distribution functions have been widely used to approximate actual leaf angle distributions. Several formulae have been given for constant leaf inclination angles (but randomly distributed azimuthal angles). If all the leaves are

inclined at a constant angle, θ_0 , then the angle distribution function is given by (Ross, 1981):

$$g(\theta_j) = \delta(\theta_j - \theta_0) \sin \theta_j, \quad (8)$$

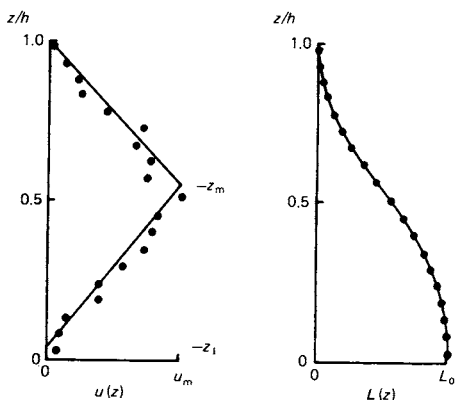
where $\delta(\theta_j - \theta_0)$ is the Dirac delta function, the value of which is unity when $\theta_j = \theta_0$ and zero otherwise. A horizontal distribution results when $\theta_0 = 0$, a vertical or cylindrical distribution when $\theta_0 = \pi/2$, and a conical distribution when θ_0 is between these values. It is useful to think of the distribution of leaf angles in a canopy as being similar to the distributions of areas on various geometric objects. For example, if the surface area of a cone, cylinder or horizontal plane were divided into small elements, and the angle distribution of normals to the elements were determined, the angle distribution of these normals would form a conical, cylindrical or horizontal distribution function.

Another useful distribution function is the spherical, or uniform distribution. The distribution of angles in a canopy with a spherical leaf angle distribution is similar to the distribution of angles for small surface elements of a sphere. The angle distribution function is

$$g(\theta_j) = \sin \theta_j. \quad (9)$$

With the exception of the spherical distribution, the distribution functions described so far are discontinuous, and not at all representative of real canopies. Lemeur (1973) suggested simulating real canopies as weighted sums of conical canopies having a range of inclination angles. This has been useful in providing approximations to canopy angle distributions, but requires many parameters to quantify the inclination angle distribution. A more general form of the spherical distribution function, which is continuous over the entire range of leaf angles, but which has horizontal or vertical

Fig. 1.1. Triangular distribution of canopy area density and the resulting leaf area index distribution. Data points are for a maize canopy, and are taken from Pereira & Shaw (1980).



tendencies would be useful. The ellipsoidal distribution (Campbell, 1986) provides such a function. It is based on the assumption that the leaf angles in a canopy are distributed like the angles of normals to small area elements on the surface of an ellipsoid. A single parameter, $x = b/a$, is required to describe the shape of the distribution; b is the horizontal semi-axis of the ellipsoid, and a is the vertical semi-axis. When $x = 1$, the ellipsoidal distribution becomes the spherical distribution given by eqn (9). When $x > 1$ (oblate spheroid),

$$g(\theta_j) = \frac{2 x^2 \sin \theta_j}{A_1 (\cos^2 \theta_j + x^2 \sin^2 \theta_j)^2} \quad (10)$$

and when $x < 1$ (prolate spheroid),

$$g(\theta_j) = \frac{2 x^2 \sin \theta_j}{A_2 (\cos^2 \theta_j + x^2 \sin^2 \theta_j)^2} \quad (11)$$

Here,

$$A_1 = 1 + \frac{\ln[(1+\epsilon_1)/(1-\epsilon_1)]}{2\epsilon_1 x^2}, \quad \epsilon_1 = (1-x^{-2})^{1/2} \quad (12)$$

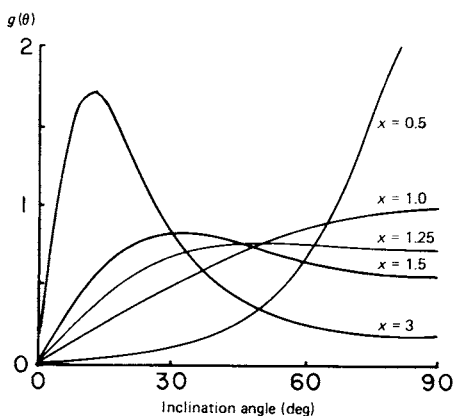
and

$$A_2 = 1 + (\sin^{-1} \epsilon_2)/(x\epsilon_2), \quad \epsilon_2 = (1-x^2)^{1/2} \quad (13)$$

Figure 1.2 shows examples of the ellipsoidal angle distribution function for several values of x .

For most purposes the extinction coefficients G , or K (eqns (2) or (4)) are more useful than the leaf angle distribution functions. These may be obtained by integrating the distribution functions using eqn (2), but are often easier to derive by considering the projected areas of solids having the angle distributions for the given distribution function (Monteith & Unsworth, 1990). Thus, for a horizontal distribution, G is the

Fig. 1.2. Ellipsoidal inclination angle distributions for several values of x which are typical of plant canopies.



ratio of projected area of a horizontal plane to surface area of the plane, so $G = \cos \theta$. From eqn (4), $K = 1$ for the horizontal distribution. The G and K functions for other angle distributions are given in Table 1.1. Extinction coefficients are plotted as functions of zenith angle for several angle distributions in Figs. 1.3 and 1.4.

The assumption that element normals have random azimuthal distribution is in error for species with heliotropic leaves. Shell & Lang (1975) suggest the use of the von Mises probability density function to model leaf angle distributions for such canopies. Mann *et al.* (1979) propose a much simpler, but less realistic formula based on the assumption that all heliotropic leaves maintain a constant orientation relative to the sun. When they are oriented perpendicular to the sun then

$$g(r_j) = \delta(r_j - r) , \quad (14)$$

where r represents the zenith and azimuth angles of the solar beam.

Table 1.1. *Extinction coefficients for various angle distribution functions. All except the heliotropic assume azimuthal symmetry. The beam zenith angle is θ , and the element inclination angle is θ_j . The parameter, x , for the ellipsoidal distribution, is the ratio of vertical to horizontal projections of canopy elements or $G(0)/G(\pi/2)$*

| | |
|--|---|
| <i>Horizontal inclination</i> $G = \cos \theta$ | $K = 1$ |
| <i>Vertical inclination</i> $G = 2 \sin \alpha/\pi$ | $K = 2 \tan \theta/\pi$ |
| <i>Conical inclination, $\theta + \theta_j \leq \pi/2$,</i> $G = \cos \theta \cos \theta_j$, | $K = \cos \theta_j$ |
| <i>Conical inclination, $\theta + \theta_j > \pi/2$</i> $G = \cos \theta \cos \theta_j [1 + 2(\tan \beta - \beta)/\pi]$ $\cos \beta = 1/(\tan \theta \tan \theta_j)$ | $K = \cos \theta_j [1 + 2(\tan \beta - \beta)/\pi]$ |
| <i>Spherical (uniform) distribution</i> $G = \frac{1}{2}$ | $K = 1/(2 \cos \theta)$ |
| <i>Heliotropic (leaves perpendicular to solar beam)</i> $G = 1$ | $K = 1/\cos \theta$ |
| <i>Ellipsoidal distribution</i> $G = (x^2 \cos^2 \theta + \sin^2 \theta)^{1/2}/(Ax)$ | $K = (x^2 + \tan^2 \theta)^{1/2}/(Ax)$ |
| $A = A_1$ (eqn (12)) for $x > 1$, $A = A_2$ (eqn (13)) for $x < 1$, $A = 2$ for $x = 1$ | |
| A is closely approximated by $A = [x + 1.774(x + 1.182)^{-0.733}]/x$ | |

Fig. 1.3. The extinction coefficient, G , as a function of zenith angle for x values representing various canopy angle distributions.

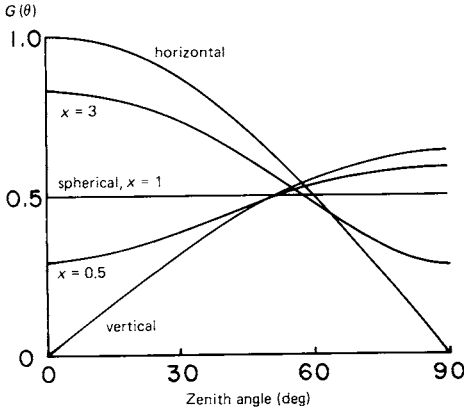
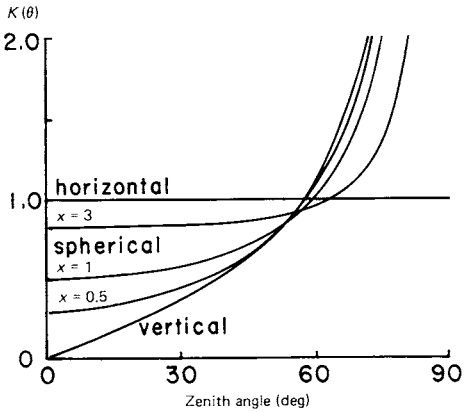


Fig. 1.4. The extinction coefficient, K , as a function of zenith angle for x values representing various canopy angle distributions.



Using the extinction coefficients from Table 1.1, it is possible to determine the probability of a probe encountering 0, 1, 2, ... canopy elements as it passes through a canopy. If canopy elements are randomly dispersed in space, then the number of contacts along a path through the canopy is a random variable which has a Poisson distribution function (Nilson, 1971). For a canopy which approximates the Poisson model, the probability of a probe traversing a distance through the canopy, s , in direction, r , without intersecting any canopy elements is

$$P_0(z,r) = \exp[-s u(z) G(\theta)] , \tag{15}$$

where $u(z)$ is the area density of canopy elements, and $G(\theta)$ is the appropriate extinction coefficient from Table 1.1. The probability of encountering n canopy elements in a transect of length s in direction r is

$$P_n(z,r) = [s u(z) G(\theta)]^n \exp[-s u(z) G(\theta)]/n! . \quad (16)$$

The mean number of intersections is

$$\mu(z,r) = s u(z) G(\theta) , \quad (17)$$

and the variance of the number of contacts is equal to the mean.

For a canopy which approximates a Poisson model, relative variance, or ratio of the variance to the mean is unity. Measurements of relative variance for a canopy are, therefore, useful for determining how closely real canopies approximate the Poisson model. When the relative variance for a canopy exceeds unity, the canopy is said to be clumped or underdispersed, and if it is less than unity, the canopy is overdispersed. Nilson (1971) discusses positive and negative binomial models to describe such canopies. Such models have been used by Monteith (1965) and others to describe the interaction of radiation with canopies.

The most obvious departure from a uniform dispersion of canopy elements occurs when leaves are clumped around a shoot, or when leaves are clumped around individual plants or rows of plants, as in a row crop, an orchard, or a sparse forest stand. Such situations were modelled by Allen (1974), Norman & Jarvis (1975) and Norman & Welles (1983) as clumps of vegetation, regularly or randomly dispersed, within which the foliage distribution did follow the Poisson model. Eqns (15) and (16) may therefore be used to model transmission and absorption of radiation by individual clumps.

Measurement of canopy structure

We now consider some methods which can be used to obtain the canopy parameters discussed in the previous sections. Recording of phenological data, plant populations, locations, and dimensions, heights, and leaf numbers is straightforward, though tedious, and will not be discussed further here. We will consider the determination of the area density function, $u(z)$, or its integral, $L(z)$ and the angle density function, $g(z,\theta_j)$, or its integrals, $G(\theta)$ or $K(\theta)$. We will also discuss some methods for determining the mean and variance of the number of intersections of a probe with canopy elements. Techniques for determining these parameters fall into three broad categories: direct measurement, indirect measurement, and allometric determination. Direct measurement methods are those where area and angle measurements are made directly on canopy elements to determine canopy parameters. Indirect methods require a model which relates some canopy response, such as light transmission or reflection, to the canopy structure parameters. The response is measured under appropriate conditions, and the model is inverted to determine the

canopy structure parameters. Allometric methods are those which relate easily measured canopy properties to parameters which are more difficult to determine using empirically derived relationships. The best known of these are the relationships between sapwood area and leaf area in trees. We now briefly consider several direct methods and allometric methods, and then will treat indirect methods in some detail since they are not widely published elsewhere.

Direct measurement methods

Two methods have been suggested for direct determination of canopy properties. The stratified-clip method was introduced by Monsi & Saeki (1953), and has been widely used in studies of canopy structure. Briefly, it consists of defining a representative volume of foliage, usually using a wire frame, and dividing the volume into layers which can be clipped to determine area and leaf orientation. The sampling volume should be large enough to include a relatively large number of plants. (ground areas of 0.25–2 m² are typical). The canopy is then stratified according to height, leaf inclination angle, and leaf azimuth angle. A study such as that of Lemeur (1973) is typical, where up to six canopy layers were defined, with six elevation angle classes of 15 degrees each, and eight azimuth angle classes of 45 degrees each. Inclination and azimuth angles may be measured with a protractor and compass for each canopy element, and then that element is clipped and placed in a labelled polythene bag to await area measurement. The stratified-clip method is most useful in canopies such as grasses or small legumes, where plant population densities are high, and studies of individual plant characteristics would be difficult. This method is obviously not suitable for forests and other canopies where plants are widely spaced and large.

The second method is called the dispersed-individual-plant (DIP) method (Ross, 1981). The method consists of selecting 10–30 plants which are representative of the canopy and measuring characteristics of those plants, such as leaf area, spatial distribution of area, leaf angles, node heights, stem diameters, etc. Leaves are again cut from the plant as their locations and angles are determined. Samples are stratified at least according to height, inclination angle, and azimuth angle, and may also be stratified according to distance from the plant axis, to obtain some information on area density functions for individual plants. The DIP method is well suited to situations where plant densities are low and plants are large.

Several modifications have been suggested for decreasing the difficulty and improving the accuracy of these direct methods. Lang (1973) and Lang & Shell (1976) used a device consisting of three arms connected such that a pointer could be located at any point within a given canopy volume. Angles between the arms were measured using precision potentiometers and the voltages from the potentiometers were sensed using a computer-controlled data logger. The locations of points defining triangles on the surface of canopy elements are directly entered into the computer, and the areas, inclinations, and azimuths of the canopy elements are calculated. A number

of portable logging devices with adequate computing capability for this application are now commercially available.

Allometric measurement methods

Allometric methods are discussed by Ross (1981), and some have been used extensively for obtaining the leaf area index of forest canopies (e.g. Grier & Waring, 1974; Kaufmann & Troendle, 1981; Marchand, 1983). Measurements show a linear relationship between sapwood area and leaf area for a given species and environment. Sapwood area is estimated, nondestructively, using increment borings. The primary difficulty of the method is the need to calibrate each species and to make adjustments for environment. Whitehead, Edwards & Jarvis (1984) suggested a refinement of the method which appears to eliminate some of the species variability. Water permeability of the sapwood was measured in addition to area. This accounted for the differences observed in the relationship between the two species studied. The height distribution of leaf area can be determined by measuring sapwood area at various heights.

Indirect measurement methods

There are many possible methods for indirect determination of canopy structure. Those to be discussed here all rely on the insertion of a physical or optical probe into the canopy to determine either the number of intersections of the probe with canopy elements within a given canopy volume, or the probability of traversing a given volume of canopy without intersecting any canopy element.

The first method is called the method of inclined point quadrats. It was first used in New Zealand by Levy & Madden (1933). Reeve, in an appendix to Warren–Wilson (1959) provided the necessary analysis for the method to be used to determine area density and mean inclination angle of canopy elements. Philip (1965) extended the analysis to determination of the inclination angle distribution function.

The second method is gap fraction analysis. Bonhomme *et al.* (1974) analysed fisheye photographs of canopies to determine the distribution of the gap fraction, and then used a simple method of mathematical inversion to estimate leaf area index. More sophisticated inversion methods can be used to determine both leaf area index and leaf angle distributions of canopies (e.g. Norman *et al.*, 1979).

The original inclined point quadrat method made use of a thin, pointed probe, which was inserted into the canopy at various zenith and azimuth angles. The location of contacts with canopy elements was recorded for a large number of insertions of the probe into a given canopy volume. Eqn (17) gives the relationship between the mean number of intersections of foliage elements, $\mu(z,r)$, and the area density, $u(z)$. For canopies with azimuthal symmetry, the relationship between area density and intersections with foliage elements is found by multiplying both sides of eqn (17) by $2 \sin \theta d\theta$, integrating from 0 to $\pi/2$, and noting that

$$\int_0^{\pi/2} G(\theta) \sin \theta d\theta = 1 .$$

This gives

$$u(z) = \int_0^{\pi/2} (\mu(z,\theta)/s) \sin \theta \, d\theta . \quad (18)$$

The quantity $\mu(z,\theta)/s$ is the mean number of hits at height z in the canopy, averaged over all azimuth angles, per unit distance, s , traversed by the probe in direction θ . Once $u(z)$ is known, $G(\theta)$ may be obtained from eqn (17) by plotting $\mu(z,\theta)/[s u(z)]$ as a function of θ .

As previously noted, the relative variance, or ratio of variance of number of hits to mean number of hits, should be unity for a canopy which meets the assumption of uniform dispersion. The inclined point quadrat method could be used to estimate the variance needed for this calculation, though the number of probe insertions required to accurately determine the variance may be so large as to make the method impractical.

Several modifications to the inclined point quadrat method have been suggested. A laser probe was substituted for the pointed metal probe by Vanderbilt, Bauer & Silva (1979). The laser probe can be used for measurements on forest canopies where the use of the metal probe becomes practically impossible, but the data obtained are limited to just the location of the first intersection with the canopy. A second modification was suggested by Caldwell, Harris & Dzurec (1983) who used a motor-driven probe shaft with an encoder, and a fibre-optic device to record contacts with canopy elements, thus allowing automatic recording of the contacts.

The main disadvantage of the inclined point quadrat method is the labour required to obtain the data. Large numbers of probe insertions are needed to obtain reliable estimates of the canopy structure parameters. Also, the height of a canopy which can be analysed with the method is limited, unless the laser probe is used.

Gap fraction analyses for determining canopy properties are similar to inclined point quadrat analyses, except that only the probability of zero intersections (P_0 in eqn (15)) is known. Since the argument in the exponent of eqn (15) is just the mean number of intersections, the analyses presented here of gap fraction information could as well apply to inclined point quadrats.

Gap fraction measurements have generally been obtained using light as the probe. A measurement of the fractional length of a transect under a plant canopy that is exposed to direct beam radiation is sufficient for the calculation. Measurements can be made manually, by measuring the total length of sunflecks along a tape or metre stick, or with light sensors. In tall canopies, penumbral effects smudge the boundaries and only methods using sensors that differentiate between beam and diffuse are suitable. Lang, Xiang Yuequin & Norman (1985) describe a sensor that can be used to determine the gap fraction along a transect. Briefly, it consists of a filtered silicon cell at the end of a collimating tube. Filters limit the response of the silicon cell to wavelengths around 430 nm, and the collimator limits the view angle to 0.302 sr. A sighting tube aids in the alignment of the sensor so that it only sees beam radiation. The sensor is mounted on a track or cable so that it can be moved through the canopy

at various heights. The gap fraction of the canopy is determined by measuring the mean transmission for beam radiation along the transect. Transects are made at several times on clear days with the sun at different elevation angles.

Fisheye photographs made either from below (Anderson, 1970; Bonhomme & Chartier, 1972; Fuchs & Stanhill, 1980) or from above the canopy (Bonhomme, Varlet Grancher & Chartier, 1974) can also be used for determining the gap fraction of canopies. A single fisheye photograph shows the gaps for all azimuth and zenith angles of the hemisphere seen by the lens, but measurements from several photographs are needed to give reliable estimates of gap fraction functions because of the variability of canopies. The photographs may be analysed, either manually (Anderson, 1970) or automatically (Bonhomme & Chartier, 1972) to determine the gap fraction. The photographs should be taken only under diffuse light (on an overcast day, or just before sunrise or after sunset). Beam radiation reflected from canopy elements, or the presence of the solar beam in the photograph can cause such non-uniform exposure that analysis of the photograph is difficult or impossible.

A modified form of eqn (15) is used to find the leaf area index and leaf angle distribution from the gap fraction data. If $G(\theta)$ is constant throughout the canopy, a canopy transmission coefficient, $\tau(z)$, for beam radiation can be defined as:

$$\tau(z) = \exp[-K(\theta, \theta_j) L(z)] . \quad (19)$$

Eqn (19) can be used in various ways to determine the leaf area index, and possibly also the leaf angle distribution function for a canopy. The simplest application is that of Bonhomme *et al.* (1974). Fig. 1.4 shows that the extinction coefficients for all angle distribution functions are near unity when the zenith angle is around 60 degrees. Bonhomme *et al.* used fisheye pictures, taken from above the canopy to determine the gap fraction at zenith angle of 57.5 degrees. They determined that the average K value for this zenith angle for all canopy types was 1.12 so leaf area index was calculated from eqn (19) using the measured gap fraction at 57.5 degrees and a K value of 1.12. Excellent agreement was observed between measured and predicted leaf area index up to L_0 of about 1.

Additional information about the canopy can be obtained from measurements of gap fractions at other zenith angles. If we consider the canopy to be composed of independent elements, each having a given area index, L_i , a given inclination angle, θ_i , and a given extinction coefficient, $K(\theta, \theta_i)$, then the probability of a ray penetrating the entire canopy is the product of the probabilities of a ray penetrating each of the populations or classes of individual canopy elements. Using eqn (19), we can therefore write

$$-\ln[\tau(\theta)] = \sum_i L_i K(\theta, \theta_i) . \quad (20)$$

If values for $\tau(\theta)$ are known for a number of values of θ , and $K(\theta, \theta_i)$ is computed for each zenith angle and leaf angle class then eqn (20) can be solved to give the L_i

values. If the number of angle classes, i , is equal to the number of zenith angles, eqn (20) represents a set of m linear equations in m unknowns, which is readily solved. If the number of zenith angles is greater than the number of angle classes, the problem is a linear least squares problem, and values of L_i are sought which minimise the sum of squares of differences between measured and predicted values of $\ln[\tau(\theta)]$. The sum of the values of L_i obtained in this way is the leaf area index, and the leaf angle distribution function can be estimated from the fraction of the leaf area in each leaf angle class. It is appropriate to minimise differences in $\ln \tau$ rather than τ because errors in the τ measurement are likely to be a fairly constant fraction of the measurement, and τ is therefore likely to have a log-normal distribution.

The values for L_i determined by standard least squares procedures are not constrained to physically realistic values, and can therefore be positive or negative. A negative leaf area index may give a good fit to the data, but is obviously not an acceptable solution. The least squares solution to eqn (20) must therefore be constrained to give only positive values for the L_i . Methods for constraining the solution are given by Menke (1984) and Lang *et al.* (1985). Menke gives FORTRAN code for implementing a least squares fit to data with positivity constraints.

A simpler method for finding area index assumes the ellipsoidal distribution and solves eqn (19) by a least squares method for x and L . We would like to find values for x and L which minimise

$$F = \Sigma (\ln \tau_i + K(\theta_i, x) L)^2, \quad (21)$$

subject to the constraint, $x > 0$. The minimum can be found by solving $\partial F/\partial L = 0$ and $\partial F/\partial x$, simultaneously. From the first equation we obtain

$$L = -\Sigma [K(\theta_i, x) \ln \tau_i] / \Sigma K(\theta_i, x)^2, \quad (22)$$

and from the second,

$$L = -\Sigma [\ln \tau_i \partial K(\theta_i, x) / \partial x] / \Sigma [K(\theta_i, x) \partial K(\theta_i, x) / \partial x]. \quad (23)$$

To solve the equations, L can be eliminated between them, and x found by the bisection method. Once x is known, L is found from eqn (22). Fig. 1.5 is a BASIC computer program which illustrates the bisection method and finds L and x from measured transmission coefficient data.

All of the inversion methods discussed so far rely on the assumption that the canopy elements are randomly dispersed in space. This is obviously not a good assumption for row crops before canopy closure, for coniferous trees or for canopies which never close, such as in desert vegetation. Canopies with heliotropic leaves or regular dispersion also violate this assumption. Lang *et al.* (1985) show examples of the errors that can arise when gap fraction inversion methods are applied to both row crops and crops with heliotropic leaves. In such cases a more sophisticated model and inversion method is needed. For row crops, the model of Mann *et al.* (1979) or