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Edited by G. Russell, B. Marshall and P. G. Jarvis
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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

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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

$$L_j(z) = \int_z^h \mu_j(z)\ \mathrm{d}z \qquad (1)$$

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:

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

where

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

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

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

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

$$u(z) = u_m\,(z - z_l)/(z_m - z_l), \quad z_l \leqq z \leqq z_m\,,$$

$$u(z) = u_m\,(h - z)/(h - z_m), \quad z_m \leqq z \leqq h, \tag{5}$$

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

$$\mu_m = 2L_0/(h - z_l)\,. \tag{6}$$

In eqns. (5) and (6), h is the canopy height, z_l 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

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

$$L/L_0 = 1 - (z - z_l)^2/[(h - z_l)(z_m - z_l), \quad z_l \leqq z \leqq z_m\,. \tag{7}$$

These equations allow one to describe the spatial distribution of canopy elements using four easily measured parameters: h, z_m, z_l, 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):

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

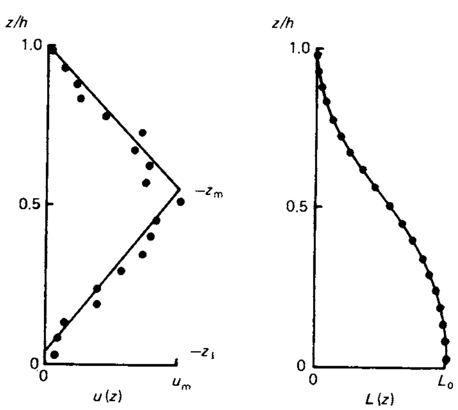
where $\delta(\theta_j - \theta_0)$ is the Dirac delta function, the value of which is unity when $\theta_j = \theta_0$ and zero otherwise. A horizontal distribution results when $\theta_0 = 0$, a vertical or cylindrical distribution when $\theta_0 = \pi/2$, and a conical distribution when θ_0 is between 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),

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

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

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

Here,

$$A_1 = 1 + \frac{\ln[(1+\varepsilon_1)/(1-\varepsilon_1)]}{2\varepsilon_1 x^2}\ , \quad \varepsilon_1 = (1-x^{-2})^{1/2} \qquad (12)$$

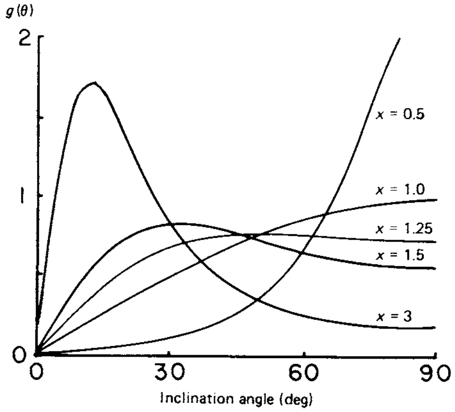
and

$$A_2 = 1 + (\sin^{-1}\varepsilon_2)/(x\varepsilon_2)\ , \quad \varepsilon_2 = (1-x^2)^{1/2}\,. \qquad (13)$$

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

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

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

Table 1.1. *Extinction coefficients for varous 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(π/2)*

Horizontal inclination $G = \cos\theta$	$K = 1$
Vertical inclination $G = 2\sin q/\pi$	$K = 2\tan\theta/\pi$
Conical inclination, $\theta+\theta_j \leq \pi/2$, $G = \cos\theta\cos\theta_j$,	$K = \cos\theta_j$
Conical inclination, $\theta+\theta_j > \pi/2$ $G = \cos\theta\cos\theta_j\,[1+2(\tan\beta - \beta)/\pi]$ $\cos\beta = 1/(\tan\theta\tan\theta_j)$	$K = \cos\theta_j\,[1+2(\tan\beta - \beta)/\pi]$
Spherical (uniform) distribution $G = \frac{1}{2}$	$K = 1/(2\cos\theta)$
Heliotropic (leaves perpendicular to solar beam) $G = 1$	$K = 1/\cos\theta$
Ellipsoidal distribution $G = (x^2\cos^2\theta + \sin^2\theta)^{1/2}/(A\,x)$	$K = (x^2 + \tan^2\theta)^{1/2}/(Ax)$

$A = A_1$ (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.

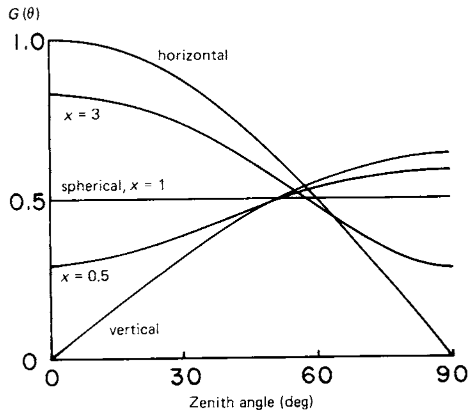
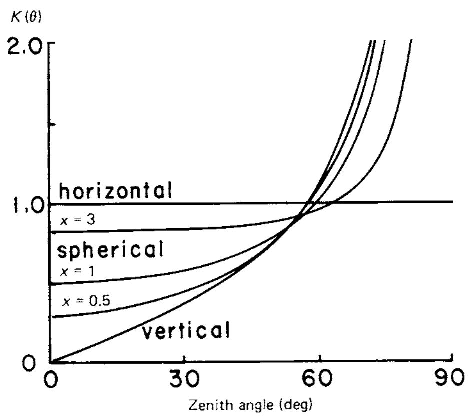


Fig. 1.4. The extinction coefficient, K, as a function of zenith angle for x values representing various canopy angle distributions.



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

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

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

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

The mean number of intersections is

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

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