Foliage area and architecture of plant canopies from sunfleck size distributions

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(Received 24 February 1992; accepted 3 March 1992)

ABSTRACT

Chen, J.M. and Black, T.A., 1992. Foliage area and architecture of plant canopies from sunfleck size distributions. Agric. For. Meteorol., 60: 249–266.

A Poisson model is developed to describe sunfleck or gap size distributions beneath clumped plant canopies. This model is based on the assumption that foliage clumps are randomly distributed in space and foliage elements are randomly distributed within each clump. Using this model, the foliage clumping index, leaf area index (L), clump area index, element area index in each clump, and element and clump widths were successfully derived for two artificial canopies and a thinned and pruned Douglas-fir forest stand. It is shown that existing theories for deriving L from measurements of canopy gap fraction have limitations, and the use of canopy architectural information derived from canopy gap size distribution can substantially improve the technique for indirectly measuring L of plant canopies.

INTRODUCTION

Considerable progress has been made in the last decade in the theory and instrumentation for the indirect measurement of leaf area index and architecture of plant canopies because of their importance in studies of physical and physiological processes in plant canopies (Welles, 1990). Indirect methods for determining leaf area index have become popular because of their convenience compared with direct methods, especially for forest stands, but the methods can become very complicated when the spatial distribution of foliage elements is not random. Leaves of plant canopies are generally grouped together to form clumps, such as tree crowns, branches, subbranches, and twigs in the case of coniferous trees. The transmission of radiation through a clumped canopy is determined not only by the leaf area index but also by the size, form and density of foliage clumps. The theory of beam radiation

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transmission through non-random plant canopies was first explored in a systematic fashion by Nilson (1971), who used a Markov chain model to derive a generalized formula as follows

$$P = \exp\left[-G(\theta)\Omega L/\cos\theta\right] \tag{1}$$

where P is the probability of a beam passing through the canopy, $G(\theta)$ is the mean projection of unit leaf area on the plane perpendicular to the beam direction θ from the normal to the ground surface, L is the leaf area index, and Ω is a clumping index. The product of Ω and L can be defined as the effective leaf area index (L_e) (Black et al., 1991). Since the angle distribution of foliage elements is generally unknown, the value of L_e can only be obtained from multiangular radiation transmission measurements. The LAI-2000 Plant Canopy Analyzer (PCA) (LI-COR, Lincoln, NE) serves very well for this purpose. Multiangular measurements can also be obtained from fisheye photography, or from the DEMON (CSIRO, Centre for Environmental Mechanics, Canberra, Australia), the Ceptometer (Decagon Device, Pullman, WA) and a solar radiation tram used at different times on a clear day. All these instruments are based on the measurements of radiation transmittance or gap fraction and generally can only measure L_e. To translate L_e to L, it is necessary to know the clumping index Ω, which is determined by the canopy architecture. The term 'canopy architecture' here includes not only the usual meaning of angle distribution of foliage elements but also the spatial arrangement of the elements.

Gower and Norman (1991) tested the PCA in four coniferous plantations and found that the values of L_e were about 35–40% smaller than L obtained from destructive sampling. They found that the difference could be attributed to the ratio of total projected needle area to shoot silhouette area. The underlying assumption of using this simple multiplier of L_e to obtain L is that shoots are randomly distributed in space. However, in most coniferous canopies, the distribution of shoots is determined by branches, whorls and trees, and the effect of foliage clumping at these larger scales can not be ignored.

Chen and Black (1991b) simplified the description of a 26-year-old dense Douglas-fir canopy with the assumption that needles are confined within branches and branches are randomly distributed in space. Using a Poisson model with this assumption, they calculated the clumping index to be 0.55–0.65, which compared well with the measured value of 0.55. The clumping indices measured for two other Douglas-fir stands, a 28-year-old thinned and pruned stand and a 80-year-old unmanaged stand, were 0.36 and 0.45, respectively (Chen et al., 1991). These values were smaller than the values calculated using the Poisson model considering only branch architecture because foliage clumping at the tree scale was more important in these two stands.

Lang and Xiang (1986) developed a technique for measuring L for discontinuous plant canopies. They showed that the effect of crop row structure and non-randomness of foliage distribution on the indirect measurement of L can be largely reduced when L is measured in many short transects 10 times the leaf width in length. This technique has substantially improved the method of obtaining L from a single spatial average of beam transmittance. However, they showed that the values of L obtained in this way for wheat and sorghum canopies are very sensitive to the averaging length and the correction factor due to the finite averaging length could be very different for canopies of different row width. In applying this technique to coniferous canopies where leaves are small and L is large, there exists an additional problem that the transmittance in many small transects is effectively zero, leading to an infinite value of L. For this reason, Lang et al. (1991) chose 16 cm as the averaging length for *Pinus radiata* canopies. What correction factors to be used for a given averaging length remains a problem.

All these previous studies are based on gap fraction measurements. Neumann et al. (1989) used a Markov chain model to derive the foliage clumping index from the gap size of a deciduous canopy determined by hemispherical photography. The model calculates the clumping index from a conditional probability of a ray passing through the canopy in the same opening separated by a distance Δd. The conditional probability was very sensitive to the choice of Δd, and they found it difficult to justify the particular values used. This approach may deserve further exploration.

There have not been enough attempts to explore and utilize the information contained in the size of the gaps or sunflecks beneath plant canopies. The objective of this paper is to explore the feasibility of using the information in a gap size or sunfleck size distribution to derive the clumping index, and therefore, the leaf area index, and to infer the canopy architecture. The theory presented in this paper provides links between the various approaches mentioned above.

THEORY

Random canopy

For the case that the sun is at the zenith, Miller and Norman (1971) derived an equation for sunfleck (or gap) size distribution beneath a plant canopy with horizontal foliage elements randomly positioned in space

$$P(l) = \exp\left[-\rho(\sigma + wl)\right] \tag{2}$$

where $P(l)$ is the probability of a probe of length l falling completely in a sunfleck, ρ is the number of the elements per unit ground area, σ is the area of an element and w is the element width perpendicular to the long axis of the

probe. If the elements are circular discs, w is the diameter of the discs. If the elements are square plates, w varies from the length of the sides to the length of the diagonals depending on the relative probe position. When $l = 0$, eqn. (2) predicts the gap fraction of the canopy.

Equation (2) can be rearranged to obtain

$$P(l) \; = \; \exp\left[-L(1 + l/W)\right] \tag{3}$$

where $L = \rho\sigma$, which is the total element area per unit ground surface area, and W is defined as the characteristic element width, which is the ratio of element area σ to width w. For example, for discs

$$\sigma \; = \; \frac{\pi}{4} w^2 \tag{4}$$

so that $W = \pi/4\,w$ where w is taken as the diameter of the discs. Generally, for other element shapes,

$$W \; = \; cw \tag{5}$$

where c is a factor depending on the geometrical shape of the elements.

When the sun is at an angle θ to the normal to the plant canopy and the elements are not horizontal, there are several modifications to be made to eqn. (3): (1) the path length of a solar beam passing through the canopy increases by a factor of $1/\cos\theta$ so that the element area index experienced by the entire path becomes $L/\cos\theta$; (2) the average element area projected on a plane M perpendicular to the direction of the beam becomes $LG(\theta)$, where $G(\theta)$ is the mean projection coefficient, being 0.5 for a spherical (random) distribution of the normal to the elements; (3) the length of the probe (l) placed horizontally on the ground surface must be projected on M to be $l\cos\theta_p$, where $\theta_p = \arctan(|\cos\Delta\beta\tan\theta|)$, $\Delta\beta$ being the difference between the azimuth angles of the sun and the probe long axis. With these modifications, eqn. (3) becomes

$$P(l) \; = \; \exp\left[- \frac{L_p}{\cos\theta}\left(1 + \frac{\cos\theta_p}{W} l\right)\right] \tag{6}$$

where $L_p = LG(\theta)$, which is the element area index projected on M.

Clumped canopy

In clumped canopies, sunfleck sizes are determined not only by the width and the number of the elements but also by the width and the number of the clumps. To understand the effect of clumping on sunfleck size distribution, it is useful to simplify the structure of the canopy using the following assumptions:
(1) there exists a characteristic clump width W_c;
(2) spatial distribution of all clumps is random;

(3) foliage elements are randomly dispersed within each clump.

If the sunfleck sampling area is more than an order of magnitude larger than the clump size, eqn (6) can be used to predict the sunfleck size distribution under opaque clumps, i.e.

$$P_c(l) = \exp\left[-\frac{L_c}{\cos\theta}\left(1 + \frac{\cos\theta_p}{W_c}l\right)\right] \tag{7}$$

where L_c is the clump area index, defined as the area enclosed by the smoothed outlines of all clumps projected on M per unit ground area. In this notation, $W_c = \sigma_c/w_c$, where σ_c and w_c are, respectively, the mean area enclosed by the smoothed outlines and mean width of clumps projected on M.

In reality, foliage clumps often contain gaps, and sunflecks under plant canopies result from the gaps both between and within the clumps. For simplicity, we assume that the average path length of solar beams through a clump is independent of the angle of incidence to the clump. To satisfy this assumption, the clumps must be spherical. Although foliage clumps in plant canopies may have various shapes, this assumption is a good approximation when the number of the clumps of various orientations is large. The sunfleck size distribution on the ground within the smoothed outline of a single clump can be predicted by

$$P_{E1}(l) = \exp\left[-L_{Ep}\left(1 + \frac{\cos\theta_p}{W_E}l\right)\right] \tag{8}$$

where W_E is the characteristic element width and L_{Ep} is the sum of the individual element areas within a clump projected on M divided by the area enclosed by the smoothed outline of the clump projected on M. In this equation, L_{Ep} is not divided by $\cos\theta$ because the average path length of a beam passing through a clump does not depend on θ, but $\cos\theta_p$ remains because the probe l must be projected on M.

The probability of a probe of length l totally exposed to the sun within the outline of the intersection of two clumps is the product of the probabilities for both clumps, i.e.

$$P_{E2}(l) = P_{E1}P_{E1}$$

$$= \exp\left[-2L_{Ep}\left(1 + \frac{\cos\theta_p}{W_E}l\right)\right] \tag{9}$$

In general, the probability of the entire probe being exposed to the sun within the intersection of n clumps is

$$P_{En}(l) = \exp\left[-nL_{Ep}\left(1 + \frac{\cos\theta_p}{W_E}l\right)\right] \tag{10}$$

From the Poisson theory, the probability of n clumps overlapping in the

direction of the sun's beam is given by

$$P_{cn} = \frac{\exp(-L_{c\theta}) \times L_{c\theta}^n}{n!} \tag{11}$$

where $L_{c\theta} = L_c/\cos\theta$ and $n \geqslant 1$. The probability that the probe l encounters n clumps and is still completely in a sunfleck is the product of $P_{En}(l)$ and P_{cn}, and the total probability for all possible regimes of exposure is then

$$P(l) = P_c(l) + P_{E1}(l)P_{c1} + P_{E2}(l)P_{c2} + \ldots \tag{12}$$

where n is an integer, which can be infinite. The first term on the right-hand side of eqn. (12) is the probability for probe exposure between the opaque clumps, and the second term is for exposure within one clump and the third term within two overlapping clumps and so on. In most cases, the probability of a beam passing through more than two clumps is very small, and it would be accurate enough to limit n to 2 or 3. If $n = 2$, eqn. (12) becomes

$$P(l) = P_c(l) + L_{c\theta}\exp(-L_{c\theta})P_{E1}(l) + \frac{1+\alpha}{2}L_{c\theta}^2\exp(-L_{c\theta})P_{E1}^2(l) \tag{13}$$

where α is a small correction for the higher order terms. It is approximated by

$$\alpha = L_{c\theta}P_{E1}(l)/3 \tag{14}$$

When $l = 0$, eqn. (13) predicts the total gap fraction beneath the canopy to be

$$P(0) = \exp(-L_{c\theta})\left[1 + L_{c\theta}\exp(-L_{Ep}) + \frac{1+\alpha}{2}L_{c\theta}^2\exp(-2L_{Ep})\right] \tag{15}$$

From this equation and setting $P(0) = \exp(-L_{e\theta})$, it can be shown that

$$L_{Ep} = \ln\{(1+\alpha)L_{c\theta}\exp(-L_{c\theta})/$$
$$\sqrt{2(1+\alpha)\exp[-(L_{e\theta}+L_{c\theta})] - (1+2\alpha)\exp(-2L_{c\theta})} - \exp(-L_{c\theta})\} \tag{16}$$

For the calculation of L_{Ep}, eqn. (16) needs to be used twice, the first time with $\alpha = 0$ and the second time with α estimated from eqn. (14) with $l = 0$. If α is larger than 0.5, a more complicated formula including one or more higher terms should be used for calculating L_{Ep} by computer iteration. This case seldom happens for plant canopies.

If the elements can be identified as leaves, the leaf area index (L) is given by

$$L = L_E L_c \tag{17}$$

where L_E is the sum of half the total individual element areas within a clump
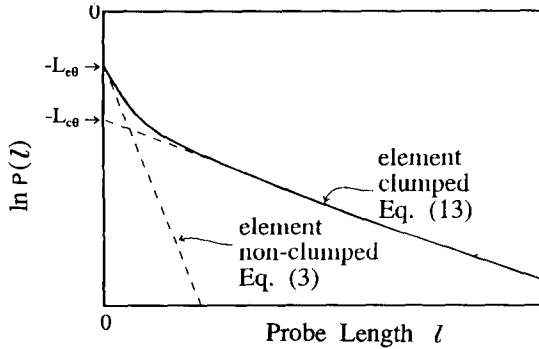
Fig. 1. Schematic sunfleck size distribution beneath a clumped plant canopy.

divided by the area enclosed by the smoothed outline of the clump projected on M. It is given by

$$L_E = L_{Ep}/G_E(\theta) \tag{18}$$

where $G_E(\theta)$ is the mean projection of unit element area on the plane perpendicular to θ. If the element is taken as a group of leaves, the right-hand side of eqn. (17) should be multiplied by the ratio of the total leaf area to the total projected area of the group at a reference angle (to be described in more detail in Experiments). Since the effective leaf area index is obtained from eqn. (1) as follows

$$L_e = \frac{\cos\theta}{G(\theta)} \ln\left[\frac{1}{P(0)}\right] \tag{19}$$

the clumping index for the elements can, therefore, be calculated as

$$\Omega_E = \frac{L_e}{L} = \frac{L_e}{L_E L_c} = \frac{L_{e\theta}}{L_{Ep}L_{c\theta}} \tag{20}$$

where $L_{e\theta} = L_e G(\theta)/\cos\theta = -\ln P(0)$. In eqn. (20), it is assumed that $G(\theta) = G_E(\theta)$.

Techniques for determining $L_{c\theta}$ and $L_{e\theta}$

A technique for determining $L_{c\theta}$ is demonstrated in Fig. 1. When the probe length is several times larger than the element width, the value of $P(l)$ is largely determined by the size (W_c) and the area index (L_c) of the clumps. Extrapolating the curve backwards linearly on a ln $P(l)$ vs. l plot, an intercept on the ordinate is obtained, which from eqn. (7) gives the value of $L_{c\theta}$. This linear extrapolation technique is valid when the element size is much smaller than the clump size. If the sizes are similar, a clear linear portion may not be found and a curve-fitting procedure using two exponential functions can generally produce a good estimate of $L_{c\theta}$. The other broken line in Fig. 1

indicates the distribution which would otherwise be obtained if all elements of area index L_e were randomly distributed in space, i.e. eqn. (2).

The value of $L_{e\theta}$ is the intercept of the probability curve on the ordinate because $P(l)$ at $l = 0$ is the canopy gap fraction. Since L_{Ep} is calculated from $L_{c\theta}$ and $L_{e\theta}$ using eqn. (16), the clumping index for the element (Ω_E) can be obtained from a sunfleck size distribution curve using eqn. (20) without the knowledge of θ.

A sunfleck size distribution not only enables us to calculate Ω_E and L but also provides information on the canopy architecture. The slope of the extrapolated line is determined by the ratio of $L_{c\theta}$ to $W_c/\cos\theta_p$ (eqn. (7)). Since $L_{c\theta}$ is obtained from the intercept, W_c can also be determined. The slope of the tangent on the $\ln P(l)$ curve at $l = 0$ is similarly determined by $L_{e\theta}\cos\theta_p/W_E$. Therefore, W_E can also be obtained in the same way. The curvature of the curve is related to the ratio of W_E to W_c. The difference between $L_{e\theta}$ and $L_{c\theta}$ is dictated by L_{Ep}. The smaller the difference, the larger is the value of L_{Ep} and the smaller is the value of Ω_E (larger clumping). When the difference does not exist, either the clumps are opaque (infinite L_{Ep} or zero Ω_E) or the foliage elements are completely random.

EXPERIMENTS

Artificial canopies

Two artificial plant canopies were created by randomly placing clumps 15.5 cm in diameter on a 91 × 244 cm wire frame. The first had 65 clumps and the second 100 clumps. There were 122 opaque discs (elements) 1.04 cm in diameter randomly scattered in each clump made from a photocopy transparency. The random distributions of the elements and clumps were determined by a random number generator built by Wichmann and Hill (1987). The gaps between the elements either across, or within, the overlapped or non-overlapped clumps were measured on 16 straight lines parallel to the long dimension of the frame.

Douglas-fir canopy

Measurements of sunflecks beneath an extensive 28-year-old Douglas-fir (*Pseudotsuga mensiesii*) stand were made with a radiation tram scanning a transect of 16 m in 10.5 min. The azimuth of the tram transect was 153.5° (clock-wise from the North). The stand was thinned to 575 stems ha^{-1} and pruned 2 years prior to the measurements. Mounted horizontally on the tram were a photon sensor (Li-Cor, Lincoln, NE, Model LI-190SB, 10 µs time constant) and two Moll-Gorczynski pyranometers (Kipp and Zonen, Delft, Netherlands, Model CM5, 1 s time constant), one of which was shaded by an

adjustable oval disc having the short and long axes of 11.2 cm and 14.5 cm, respectively, at a distance of 35 cm from the pyranometer to measure the diffuse irradiance, and a data logger (Campbell Scientific, Logan, UT, Model 21X). The sunfleck measurements were made with the photon sensor, and the direct solar irradiance beneath the canopy was taken as the difference between the measurements of the unshaded and shaded pyranometers. The direct irradiance above the canopy was obtained from another two CM5 pyrano-meters mounted on the top of 16 and 24 m towers, the first of which was equipped with a shadow band to measure the diffuse irradiance above the canopy. The experiment was carried out in July and August 1990 near Browns River 20 km northwest of Courtenay on Vancouver Island, B.C. During the experiment, there were 7 clear days from which the effective leaf area index was determined from the transmittance of the direct solar radiation. Sunfleck measurements were made during the afternoon of 21 July, a clear day, when the photon sensor was sampled at 2 Hz, giving a spatial resolution of 1.2 cm.

The leaf area index of the stand was obtained from intensive destructive sampling. Four trees of selected sizes were felled. A branch was removed from every second whorl. The base diameter of all branches on the four trees and the diameter at breast height (1.3 m) of 250 trees were measured. The needles were removed from these branches, dried (8 h at 80°C) and weighed. The mass ratio of young (< 1 year old) to old ($\geqslant 1$ year old) needles was estimated. The area of fresh needle samples pressed between two glass plates was measured with a video-camera image analysis system (Skye Instruments, Llandrindod Wells, Wales, Model S1700), which was carefully calibrated with opaque paper strips of the same size to remove the edge effect. Leaf area index was calculated using the ratio of the projected needle area to dry needle weight, which decreased from 76 cm^2 g^{-1} at the tree bottom to 52 cm^2 g^{-1} at the tree top for young needles and from 64 to 45 cm^2 g^{-1} for old needles, and the relationships between the square of branch diameter and dry needle weight ($r^2 = 0.81$) and between the tree basal area and the foliage area per tree ($r^2 = 0.98$). The leaf area index was 5.6, which has been converted from the projected to half the total needle area using a factor of 1.18. The ratio of the total needle area to the total vertically projected shoot area was measured with the video-camera system to be 1.77 on average. The total vertically projected shoot area (L_s) is defined as the vertically projected area of a horizontally placed shoot multiplied by π since the projected area does not change much with rotation of the shoot about its longer axis (i.e. its projection can be approximated by a circular cylinder). The projected area is the indented shadow area (the intercepted area seen on a video screen) and is smaller than the area enclosed by the smoothed outer boundary. It will be shown later that shoots of Douglas-fir trees could be treated as the elements responsible for sunfleck size distribution beneath the canopy, and hence L_E in eqn. (18) was taken as L_s in this study. When L_E is re-projected in the canopy in the direction of the
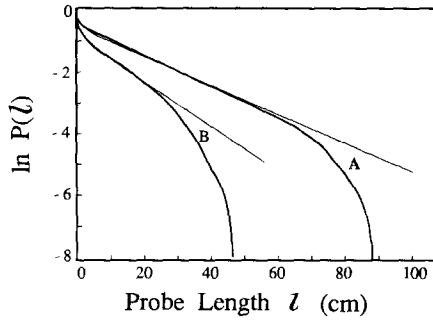
Fig. 2. Gap size distribution of two artificial plant canopies with circular clumps of 15.5 cm diameter randomly placed on a 91 × 244 cm^2 frame. There were 122 small discs of 1.04 cm diameter randomly scattered in each clump. (A) 65 clumps with clump area index $L_c = 0.55$, and (B) 100 clumps with $L_c = 0.85$. ————, measured; ———, theoretical. The theoretical lines were calculated using eqn. (13).

sun, it should be multiplied by a mean projection coefficient $[G_E(\theta)]$ to obtain L_{Ep} (eqn. (18)). The mean projection coefficient of a randomly oriented circular cylinder is 0.5 based on half the total cylinder surface area (Lang, 1991; Chen and Black, 1991a).

RESULTS

Artificial canopies

Figure 2 shows the measured gap size distribution of the artificial canopies in comparison with the theoretical distribution calculated using eqn. (13) with $W_c = 12.2$ cm, $W_E = 0.82$ cm, $L_{Ep} = 0.5$, $\theta = \theta_p = 0$ and the respective values of L_c in Table 1. The agreement between the measured and the theoretical results is satisfactory. The dropoff of the measured curves at the large values of l is expected for any actual measurements because the gap size in reality is always finite. The actual and derived values of each of the canopy attributes compare well (Table 1). The leaf area index derived for both canopies was about 10% larger than the respective actual value. This difference resulted partly from a negative bias in determining the value L_c because

TABLE 1

Comparison of the actual and derived values for two artificial canopies

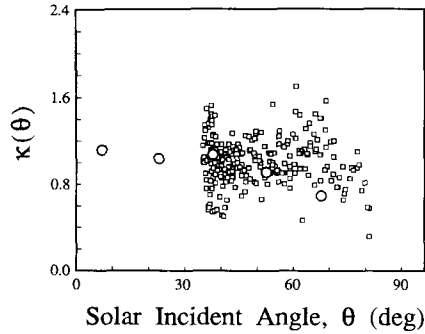| Canopy	Value	L_e	L_c	L_{Ep}	Ω	L	W_c	W_E
1	Derived		0.52	0.59	0.75	0.31	9.9	0.89
	Actual	0.234	0.55	0.50	0.84	0.28	12.2	0.82
2	Derived		0.83	0.55	0.76	0.48	11.1	0.87
	Actual	0.369	0.85	0.50	0.85	0.43	12.2	0.82

Fig. 3. Mean contact number $\kappa(\theta)$ of a thinned and pruned 28-year-old Douglas-fir stand measured with a solar radiation tram (□) and the LI-COR LAI 2000 Plant Canopy Analyzer (O).

the slope of the curves was slightly affected by the dropoff at the lower end of the curves. In spite of this problem, the measurements are considered to be an experimental validation of the Poisson model and the techniques developed in this study.

Douglas-fir canopy

Determining L_e

Figure 3 shows the mean contact number $\kappa(\theta)$ of the stand obtained from the measurements of the direct irradiance above, and below, the canopy on the 7 clear days. The large scatter of the data results from the finite length of the tramway and the dynamic movement of sunflecks beneath the thinned and pruned canopy. However, the large body of the data supplemented by the PCA measurements at $\theta = 7°$, 23° and 38° allows a reliable determination of L_e using Miller's (1967) equation

$$L_e = 2 \int_0^{\pi/2} \kappa(\theta) \sin \theta \, d\theta \tag{21}$$

The value of L_e was determined to be 2.0 ± 0.2.

Determining Ω and L

Figure 4 shows instantaneous measurements of the photosynthetically active photon flux density (PPFD) beneath the canopy for one tram run on a clear day. The values of PPFD in small sunflecks were much smaller than that above the stand owing to the penumbra effect and the movement of the foliage in the wind. The width of each of these sunflecks was obtained from dividing the integrated PPFD over the apparent sunfleck width by the direct PPFD above the canopy. This integrating approach ensures that the gap fraction equals the mean beam transmittance (Norman et al. 1971).

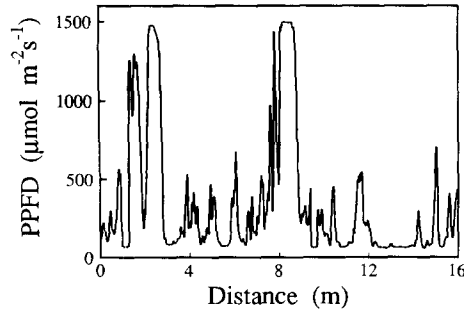The calculated sunfleck size distribution for this and the two following tram

Fig. 4. Instantaneous PPFD beneath a thinned and pruned 28-year-old Douglas-fir stand for a complete tram run between 15:35 and 15:44 h Pacific standard time (PST) on 21 July 1990.

runs is shown in Fig. 5. The upward curvature of the distribution is expected for a clumped plant canopy. Similar curvature was found for sumac and sunflower canopies by Norman et al. (1971). From the distribution curve, the value of $L_{c\theta}$ can be accurately determined to be 3.2. The projected element area index within a clump (L_{Ep}) calculated from eqn. (16) is 1.17 and the clumping index calculated from eqn. (20) is 0.59. The slopes of the extrapolated line and the tangent at $l = 0$ were $0.0333\,\text{cm}^{-1}$ and $0.17\,\text{cm}^{-1}$, respectively. The angle θ_p is calculated from arctan $[|\cos(251.3° - 153.5°)\tan(55°)] = 11°$, where 55° is the sun's incidence angle to the canopy, and 251.3° and 153.5° are the sun's and tram's azimuth angles, respectively. (In calculating W_E and W_c in Table 2, the sun's azimuth angle changed from 181.7° for the first period to 251.3° for the last period.) From the slopes, area indices and θ_p, it is found that $W_E = 11.8\,\text{cm}$ and $W_c = 94\,\text{cm}$. Table 2 summarizes all the results derived from sunfleck measurements in this and other periods. The following points can be made from the results in Table 2.

(1) The element width W_E represented reasonably well the characteristic
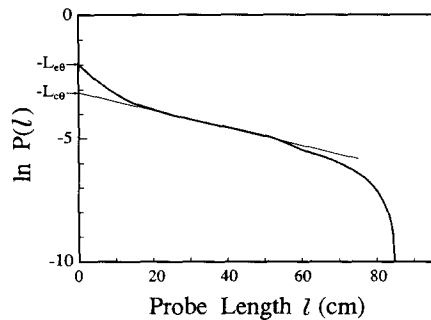

Fig. 5. Sunfleck size distribution beneath a thinned and pruned 28-year-old Douglas-fir stand between 15:35 and 16:15 h PST on 21 July 1990.

TABLE 2

Foliage clumping index and canopy architecture parameters derived from the measured sunfleck size distribution in a thinned and pruned Douglas-fir stand

	Time (PST)					
	12:03– 12:50 h	12:51– 13:25 h	13:26– 14:07 h	14:08– 14:50 h	14:50– 15:34 h	15:35– 16:15 h
θ	36°	38°	42°	45°	51°	55°
$L_{e\theta}$	0.83	1.43	1.98	1.34	1.77	2.22
L_e	1.34	2.25	2.94	1.89	2.23	2.54
$L_{c\theta}$	1.30	2.40	3.00	2.10	3.00	3.20
L_c	1.05	1.89	2.22	1.48	1.88	1.83
L_{Ep}	1.02	0.89	1.06	1.01	0.87	1.17
L_E	2.02	1.78	2.12	2.02	1.74	2.34
Ω_E	0.629	0.668	0.620	0.630	0.678	0.592
L	3.77	5.96	8.40	5.31	5.82	7.59
W_E (cm)	9.4	10.6	6.9	16.0	12.7	11.8
W_c (cm)	137	321	139	157	85	94

Leaf area index (L) is calculated from $L = \gamma L_E L_c$ with $\gamma = 1.77$. In calculating L_E (eqn. (18)), $G_E(\theta) = 0.5$ is assumed, and in L_e (eqn. (19)), $G(\theta) = 0.5$ is assumed.

width of shoots rather than needles. The characteristic width of an average shoot of 17 cm in length and 4 cm in diameter would be 6.5 cm if its longitudinal axis were randomly inclined and oriented. The average value of W_E was 11.2 cm, which is somewhat larger than the value of 6.5 cm, but much larger than the characteristic width of 0.3 cm for an average needle of 2.5 cm in length, 0.18 cm in width and 0.08 cm in thickness.

(2) The clump width W_c was much larger than the element width and changed with time. This change reveals that the beam transmission through the canopy was affected by different structure of the foliage at different times. When the solar elevation was high, the clump width was comparable with the average horizontal width of tree crowns, indicating that the individual tree crowns were distinct foliage clumps responsible for most of the sunflecks seen on the forest floor. As solar elevation decreased (or θ increased) with time, the clump width decreased, revealing that the tree crowns began to break down to branches. Douglas-fir trees have a large proportion of horizontal branches (Chen and Black, 1991b). This branch structure becomes more apparent when seen from a near horizontal direction.

(3) As expected from Fig. 3, the value of L_e in different periods varied considerably from its mean value of 2.0. For the same reason the values of L determined from each individual period also changed significantly. However, the clumping index obtained in the various periods varied very little and seemed to be less affected by limitations of measurements. This suggests that a reliable procedure for obtaining L would be combining L_e from multi-

angular radiation measurements and Ω from sunfleck measurements at a few solar angles, i.e.

$$L = \frac{L_e}{\Omega} \tag{22}$$

where $\Omega = \Omega_E/\gamma$, γ being the ratio of total needle area in a shoot to total shoot projected area (defined in Experiments).

(4) The average projected clump area index (L_c) is 1.7 and the average projected element area index within a clump (L_{Ep}) is 1.0. If the elements are assumed to have a spherical angle distribution, half the total element area index within a clump (L_E) would be 2.0. Since the measured ratio of half the total needle area to half the total shoot (element) area is 1.77, half the needle area per projected clump area is 3.5, suggesting that tree crowns might have been the major foliage clumps.

On the floor of the forest stand with average tree height of 16 m, only reasonably large sunflecks could be seen. Small sunflecks resulting from the gaps between the needles in a shoot disappeared because of the penumbra effect. (The sun is not a point source but a disc of finite size, which casts a fuzzy edge of approximately 1 cm in width only 1 m away from an object). This is the reason that only shoots could be resolved from the sunfleck size distribution. The fact that W_E equals shoot width rather than needle width suggests that shoots of the Douglas-fir trees can be considered as the effective foliage elements and the values of Ω_E shown in Table 2 should be taken as the clumping index for the shoots. This index includes the effect of foliage clumping at scales larger than a shoot, i.e. tree, branch and sub-branch scales. The remaining task for obtaining the clumping index for the needles would, therefore, be to find how much needle area is in an average shoot, or more precisely what is the ratio of the total needle area in a shoot to the total shoot projected area (defined in Experiments). Using the measured ratio of 1.77 and the mean Ω_E value of 0.64, the total clumping index Ω for the needles becomes 0.36, which happened to be the same as the independently determined value of 0.36. The error in Ω determined both directly and indirectly is estimated to be 10–20%.

The approach of treating shoots as foliage elements is similar to that of Gower and Norman (1991), who found that radiation in four coniferous canopies is affected by the shoot shadow (silhouette) area rather than the needle area. Our definition of one half of the total projected shoot area (see experiments) is similar to Gower and Norman's shoot shadow area, except that ours is greater by a factor of $\pi/2$. By using the projected shoot area and estimating the sunfleck size with the PPFD-integrating technique, the effect of the gaps between needles is appropriately taken into account.

DISCUSSION

The results derived using the sunfleck size distribution theory presented in this paper have the following implications.

(1) The basic foliage size directly responsible for the interception of radiation, referred to as 'element' in this paper, may be a group of leaves rather than individual leaves. This size can be found from the sunfleck size distribution. When a group of leaves can be treated as an element, Lang and Xiang's (1986) technique of finite sampling area can be used more effectively if the sampling area is related to the size of the elements. The spatial separation Δd used in the calculation of the conditional probability by Neumann et al. (1989) may also be related to the element size. When the elements are groups of leaves, the ratio of the total leaf area to the total projected area element should be measured before the leaf area is determined.

(2) In clumped canopies, there exists a continuous distribution of gap or sunfleck size resulting from the gaps both between and within the clumps. The effect of foliage clumps on the indirect measurements of element area is inevitable no matter how small a sampling area is chosen. The more clumped a canopy is, the larger is the effect on the measurements. This is the reason for the correction factor for the finite averaging length being different for crops of different row widths as found by Lang and Xiang (1986). In essence, by taking a finite averaging length, the effect of foliage clumping at scales larger than the averaging length is eliminated, but the effect remains for scales smaller than the averaging length. A further study may be useful to explore the possibility of obtaining a correction factor for any finite averaging length from a sunfleck (or gap) size distribution.

(3) The fact that the clump width derived at high solar elevation angles was comparable with the projected width of Douglas-fir tree crowns indicates that clumping at the tree scale had an important effect on light transmission through the thinned and pruned canopy. This is why the clumping index for this stand is smaller (more clumped) than that calculated by Chen and Black (1991b) considering only the clumping at the branch scale.

(4) In principle, theories and techniques developed based on the canopy gap fraction are incapable of treating the effect of non-randomness of foliage spatial distribution. To avoid this shortcoming, the information contained in the canopy gap sizes should be explored. No specialized instrument is presently available for this purpose, although the DEMON may be used as a portable tram when it is carried at a fixed angle with a constant speed. We suggest that future research on the design of instruments for measuring L from radiation transmission be directed toward obtaining canopy gap size information.

Like many other theories for indirect measurement of L, the sunfleck size distribution theory developed in this paper makes a number of assumptions. The successful use of this theory depends on how well these assumptions are

met. The most important assumption made in deriving the theory is the random spatial distribution of foliage clumps. The spatial distribution of tree crowns has been assumed to be random for natural conifer stands (Li and Strahler, 1988), and branches in a Douglas-fir stand with overlapping tree crowns have been assumed to be approximately randomly distributed (Chen and Black, 1991b). When the spacing between trees is more regular than random, such as in an orchard or a plantation, the theory has to be modified. The other limitation of the theory is that it is basically a one-scale clumping model, whereas foliage clumping of plant canopies can occur at more than one scale. The model was successfully used for the Douglas-fir stand because the clumping at the tree and branch scales was effectively combined to form a characteristic clump width at a given solar incident angle. Further studies are required to see if this approach is generally correct for other plant canopies.

Although the curvature of the sunfleck or gap size distribution shown in Fig. 1 is general for clumped canopies, the simple technique of obtaining the clump area index can only be reliably applied when there is a flat 'shoulder' in the middle of the curve. If the characteristic clump width is not substantially larger than the element width, the shoulder may not be flat and a computer iteration procedure would be required to obtain $L_{c\theta}$. If clumps at one level are very dense and effectively opaque, they should be treated as elements.

CONCLUSIONS

It is feasible to extract information on plant canopy architecture from the sunfleck size distribution beneath the canopy. A truncated Poisson model has been used successfully to derive the foliage clumping index and the leaf area index of two artificial canopies and a thinned and pruned Douglas-fir forest canopy. Other information which can be derived from the sunfleck or gap size distribution includes the clump area index, element area index within individual clumps, clump width and element width. This information can be used to improve techniques of indirectly measuring leaf area index of plant canopies based on canopy gap fraction or radiation transmittance. A convenient instrument for measuring canopy gap sizes is required for this purpose.

canopies. We are greatly indebted to Dr. A.R.G. Lang for his careful review of the manuscript and for his valuable and constructive comments. Dr. H.H. Neumann helped improve comments on their work.

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APPENDIX: LIST OF SYMBOLS

c shape correction factor (ratio of W to w)

$G(\theta)$ projection of unit leaf area on a plane M perpendicular to the direction θ

l probe length

L leaf area index

L_c clump area index projected on M

$L_{c\theta}$ $L_c/\cos\theta$

L_e effective leaf area index

$L_{e\theta}$ $L_e G(\theta)/\cos\theta$

L_E sum of half the individual element areas within a clump divided by the area enclosed by the smoothed outline of the clump projected on M

L_{Ep} sum of the individual element areas within a clump projected on M divided by the area enclosed by the smoothed outline of the clump projected on M

M plane perpendicular to the solar beam

P probability of a beam passing through a canopy

$P(l)$ probability of a probe l being completely exposed to the sun

$P_c(l)$ $P(l)$ for a canopy composed of opaque clumps

$P_E(l)$ $P(l)$ within the smoothed boundary of a clump

w element maximum width perpendicular to probe l

W characteristic width, e.g. for horizontally oriented circular discs, it is $\pi/4$ times the diameter

W_c characteristic width of clumps

W_E characteristic width of elements

α correction factor for higher order Poisson terms

$\Delta\beta$ difference between azimuth angles of the sun and the probe axis

θ angle of incidence of the solar beam

θ_p angle between the axis of the probe l and plane M

$\kappa(\theta)$ mean contact number at angle θ

ρ number of foliage elements per unit ground surface area

σ foliage element area

Ω clumping index for leaves (needles)

Ω_E clumping index for elements (shoots)