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PHOTOSYNTHETIC RADIATION REGIME AND
CANOPY STRUCTURE IN MODELED FOREST STANDS

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Tiivistelmä

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The relationships between canopy structure and photosynthetic radiation regime are studied on a theoretical basis. In modeling the canopy structure a statistical approach is applied and the radiation field inside a stand is described in terms of random variables and their distributions. A comparison is made between horizontally homogeneous stands and grouped forest stands in order to assess the influence of grouping of foliage on the irradiance distribution in a forest stand. Results show that grouping considerably reduces the interception of radiation and causes a large spatial variation. In coniferous stands the grouping of needles into shoots and the effect of penumbra are shown to have an important influence on the distribution of radiation on the needle area.

Tutkimuksessa tarkastellaan teoreettisesti latvuston rakenteen ja valoilmaston välistä suhteita fotosynteesin kannalta. Latvuston rakenne kuvataan tilastollisilla malleja käyttäen ja säteilykenttään liittyvät suureet käsitellään satunnaismuuttujina. Lehtien ryhmittymisen vaikutus metsikön valoilmastoon tutkitaan vertaamalla metsiköitä ns. horisontaalisesti homogeenisiin kasvustoihin, joissa ryhmittäisyyttä ei esiinny. Tulokset osoittavat, että ryhmittyminen selvästi vähentää säteilyn pidättymistä ja lisää säteilyn paikallista vaihtelua. Havumetsiköissä erityisesti neulasten ryhmittymisen versoihin sekä puolivarjoefekti ovat tekijöitä, joilla on huomattava vaikutus säteilyn jakautumiseen neulaspinnoilla.

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PREFACE

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LIST OF MAIN SYMBOLS

Symbols connected to stand structure

$g(r_1)$	density function for leaf orientation
$G(r)$	mean projection of unit leaf area
$G_s(r)$	mean projection of unit shoot area
k	extinction coefficient
LAI	leaf area index (= leaf area per unit ground area)
$L(z)$	cumulative leaf area index above z
$L_p(z)$	projected leaf area index above z
$L_T(z)$	leaf area of crown above z
l_r	mean orthogonal projection area of a leaf, projected in direction r
$P = (x, y, z)$	point in space
P_1	point on the surface of a leaf
$p_0(P, r)$	gap probability at P in direction r
$p_0(z, r)$	mean probability of a gap in direction r , at depth z
$p_{00}(P, r, r')$	probability of gaps in directions r and r' , at point P
$p_{00}(z, r, r')$	mean probability of gaps in directions r and r' , at depth z
$r = (\theta, \varphi)$	direction in space
$r_1 = (\theta_1, \varphi_1)$	direction of leaf normal
\hat{r}_1	angle between directions r and r_1
$S(z, r)$	horizontal projection of crown envelope
$T(z, r)$	horizontal crown projection area at depth z , in direction r
$t_r(P)$	path length within crown from point P in direction r
$Y(r, L)$	number of contacts (random variable)
$\delta(P, r)$	random function for gap distribution
θ	inclination angle
λ	stand density
ρ	number density of leaves
φ	azimuth angle
Ω_1	hemisphere facing a leaf

Symbols connected to the radiation regime

F	rate of photosynthesis
H_P	distribution function of irradiance at P
H_L	spatial distribution of irradiance on the leaf area L
I_0	irradiance of incoming radiation (on a horizontal plane)
I_s	incoming direct solar irradiance
I_d	incoming diffuse irradiance
$I(P)$	mean irradiance at point P
$I_d(P)$	mean direct solar irradiance at P
$I_d(P)$	mean diffuse irradiance at P
$I(P_1)$	mean irradiance at P_1 on a leaf
$I(z)$	mean horizontal irradiance at depth z
$I(z, L)$	mean irradiance on the leaf area, at depth z
$i(r)$	total radiance in direction r
$i_d(r)$	radiance of direct solar radiation
$i_d(r)$	radiance of diffuse sky radiation
i_λ	monochromatic radiance
k_λ	monochromatic attenuation coefficient
m	air mass
NIR	near infra-red radiation
PAR	photosynthetically active radiation
S	solid angle of the sun
S_0	solar constant
u	optical thickness of the atmosphere
$X(P)$	irradiance at P (random variable)
$X_s(P)$	direct solar irradiance at P
$X_d(P)$	diffuse irradiance at P
$X_s(P)$	irradiance of the scattered component at P
$X(P_1)$	irradiance at P_1 on a leaf
θ_s	solar elevation

λ	wavelength
τ	transmittance of the atmosphere
Ω	solid angle of the upper hemisphere
$d\omega$	elemental solid angle, $d\omega = \cos\theta d\theta d\phi$

Mathematical abbreviations

cov	covariance
E	expectation value
Prob	probability
var	variance

1. INTRODUCTION

Solar radiation is the only source of energy for the process of photosynthesis by green vegetation. In order to calculate the photosynthetic production of a crop canopy, the temporal variation in the amount of radiation absorbed by leaves must be known. Moreover, because the dependence of photosynthesis upon irradiance is non-linear, not only the amount of radiation absorbed by leaves but the spatial distribution of photosynthetically active radiation on the leaf surface must be known.

Two main phenomena may be identified when dealing with radiation field in plant canopies: the incident radiation field, i.e. the transfer of solar radiation in the atmosphere, and the transfer of radiation within the plant canopy (Niilisk et al. 1970). The incident radiation field depends upon sun position and cloud type and pattern. Temporal variation is induced by the sun's passage along its path and by cloud movement. During completely clear or overcast days the temporal variation is slow. A large and rapid temporal variation in the direct component of incident radiation is, however, caused by cloud movement in partly clouded skies. Also, on an apparently clear day invisible high-level cloud near the sun can cause considerable variation (Anderson 1964). Inside the canopy, the temporal variation is further increased by foliage movement (cf. Smolander 1984).

For a fixed incident radiation field, however, the structure of a canopy determines the patterns of radiant flux and interception occurring within the canopy. The canopy radiation field is characterised by a large spatial variation. It is suitable to separate two components of the spatial variation, one being the gradient of mean irradiance over a certain area (along a transect) and the other being the microvariation in a specific (small) part of the canopy.

The attenuation of radiation passing through a canopy, resulting from absorption, transmission and reflection of foliage ele-

ments, causes a vertical gradient of mean irradiance. In addition, a horizontal gradient in mean irradiance results from a non-random (grouping) distribution of foliage – in a horizontally homogeneous canopy there would be no horizontal gradient in mean irradiance.

The spatial microvariation is of a more stochastic nature and is mainly due to the highly directional distribution of incoming radiation during clear skies when up to 90 % enters as direct solar radiation. Direct solar radiation creates a very uneven distribution of irradiance which, except for the often small penumbral area, is formed of "sunflecks" (receiving full sunlight) and "shaded areas" (receiving no direct solar radiation) (cf. Miller and Norman 1971a, b).

Theoretical canopy models have an important role in analysing the dependence between canopy structure and radiation regime. The models describe the radiation conditions with mathematical equations, using properties of incident radiation and a description of canopy structure as input data.

Canopy radiation models can be divided into two general types based on either a geometrical or a statistical approach (Lemeur and Blad 1974). In the geometrical approach the stand is modeled as an arrangement of shapes with characteristic geometrical dimensions, while in the statistical approach the positions of plant elements are stochastic variables with some given statistical distribution.

Geometrical models are most appropriate for predicting the interception of radiation by a stand on a daily or seasonal basis (cf. Lemeur and Blad 1974). Statistical models on the other hand are particularly useful in the study of penetration and spatial and temporal variation of radiation at different times and different levels within a specific canopy – characteristics which are relevant for estimating photosynthesis.

With respect to photosynthesis the most

important structural characteristics are connected with the leaves, the photosynthetically active elements. The description of canopy structure is therefore primarily concerned with the amount of leaves (leaf area index), the distributions of leaf position and orientation, and geometrical and optical properties of the leaves.

An infinite number of statistical distributions are available for describing leaf position and orientation, each one resulting in a different model. Most of the various statistical models are, however, based on the assumption of a horizontally homogeneous stand. A comprehensive model, taking into account all components of radiation, is presented by Ross (1981) who described the stand as a horizontally homogeneous anisotropic plate medium where the radiative transfer equation is applied.

In modeling the radiation regime of a coniferous stand there are two important considerations: (a) the effect of penumbra and (b) the effect of grouping of foliage on the spatial

distribution of irradiance on the foliage area. The small size of conifer needles creates a considerable penumbral area which strongly levels out the distribution of direct solar radiation. On the other hand, horizontal heterogeneity caused by grouping of foliage into individual crowns and shoots creates a large spatial variation on the horizontal plane. The gradients of irradiance exist not only within crowns but even more so within the individual shoots.

This study deals with the relationships between canopy structure, radiation and photosynthesis. In modeling the canopy structure, a statistical approach is applied. The radiation field within the canopy is thus described in terms of random variables and their distributions. The aim of the study is to analyse how the characteristic features of coniferous forest stands affect the canopy radiation regime and photosynthetic production, and to estimate the magnitude of errors introduced by assuming horizontal homogeneity and by disregarding the penumbral effect.

2. STAND STRUCTURE AND ITS MODELING

2.1. Statistical models of leaf dispersion

The structure of a stand is mathematically described by the spatial distribution and orientation of phytoelements (plant parts) and by their geometrical properties. In the statistical approach the location of a phytoelement is a stochastic variable distributed according to some statistical distribution.

Random dispersion: The Poisson model

The spatial distribution of leaves is often assumed to be random. A random dispersion of leaves is a concept usually incorporating the following assumptions: (i) the location of a leaf, determined by the coordinates of a chosen reference point $P = (x, y, z)$, is considered a random variable, (ii) the coordinates x , y and z have a uniform distribution in the canopy space confined between two horizontal levels, and (iii) the positions of leaves are independent of each other.

The probability that any leaf is situated in a subvolume (V) of the canopy space (C) is V/C . When there are N leaves randomly dispersed in the canopy space, the probability of finding n leaves in the subvolume V is then given by the binomial distribution

$$q_n = \binom{N}{n} (V/C)^n (1-V/C)^{N-n} \quad (1)$$

Letting $N \rightarrow \infty$ this distribution tends to the Poisson (qV) distribution (cf. e.g. Cramér 1945)

$$q_n = \exp(-qV) (qV)^n / n! \quad (2)$$

$$q_0 = \exp(-qV)$$

where $q = N/C$ is the number density of leaves in the canopy.

For a large N there is no significant difference between Equations (1) and (2). The random dispersion is therefore usually

characterised by the Poisson distribution and the two concepts are used interchangeably.

The random dispersion is also called "uniform" because of the assumption (ii) that the coordinates x, y and z have a uniform density function. The height coordinate z is often replaced by the cumulative leaf area index $L(z)$ above z , and z is allowed to be non-uniform, i.e. the density of leaves may vary with depth in the canopy. Horizontally, the stand is assumed to be homogeneous in the sense that statistical characteristics of the phytoelements at a given height are independent of the coordinates x and y .

The distribution of gaps in the canopy is an important characteristic of canopy structure with respect to radiation penetration. In Nilson's (1971) analysis, the distribution of the random variable $Y(r, L)$, denoting the number of contacts with foliage made by a vector starting from the level L (downward cumulative leaf area index) and pointing in direction $r = (\theta, \varphi)$ ($\theta =$ inclination, $\varphi =$ azimuth), is derived for different models of leaf dispersion.

For the Poisson model the probability of n contacts ($Y(r, L) = n$) is (cf. Nilson 1971)

$$p_n = \exp(-G(r)L/\mu) (G(r)L/\mu)^n / n! \quad (3)$$

where $G(r)$ is the mean projection of unit foliage area in direction r and $\mu = \sin\theta$.

The probability of a gap ($n = 0$) is then

$$p_0 = \exp(-G(r)L/\mu) \quad (4)$$

Equation (4) can be derived in a large number of slightly differing ways. The basic assumption is that the horizontal locations of leaves are statistically independent and purely random, i.e. the horizontal coordinates (x, y) have a uniform density function in the canopy space. When these conditions are met, the stand is said to be horizontally homogeneous.

Binomial models

The positive and negative binomial distributions are also used to describe leaf dispersion. The positive binomial model can be defined as follows (Nilson 1971): It is assumed that;

- (i) the stand can be divided into a finite number $N = L/dL$ of equal and statistically independent layers,
- (ii) only zero or one contact within a layer dL is possible, and
- (iii) the probability of one contact in direction $r = (\theta, \varphi)$ within a layer is $G(r)dL/\mu$ ($\mu = \sin \theta$)

With these assumptions, the probability of n contacts in direction r , within N layers, is

$$p_n = \binom{N}{n} (1-G(r)dL/\mu)^{N-n} (G(r)dL/\mu)^n \quad (5)$$

The probability of no contact within N layers is, in this case

$$p_0 = (1-G(r)dL/\mu)^N \quad (6)$$

In the negative binomial model more than one contact within a layer is possible and the probability of n contacts within N layers is

$$p_n = \binom{N+n-1}{n} (G(r)dL/\mu)^n (1+G(r)dL/\mu)^{-N-n} \quad (7)$$

and

$$p_0 = (1+G(r)dL/\mu)^{-N}$$

In the binomial models the number, N , of independent layers is a parameter characterising the leaf dispersion. Both models tend to the Poisson distribution when $N \rightarrow \infty$.

Characterisation of leaf dispersion

The dispersion of foliage can be analysed by the point quadrat method originally introduced by Levy and Madden (1933) and further developed by Warren Wilson (cf. e.g.

Warren Wilson 1960, 1963). The method is as follows: A long, thin needle is inserted in a fixed direction $r = (\theta, \varphi)$ (θ = inclination, φ = azimuth) through the stand and all contacts it makes with the foliage elements are recorded. The distribution of the number of contacts $Y(r, L)$ characterises the leaf dispersion.

The relative variance of $Y(r, L)$ is used to characterise the dispersion of foliage (cf. Warren Wilson 1965). The smaller the relative variance is, the more regular is the dispersion. For the Poisson model the relative variance is 1, for the positive binomial model it is $1-GdL/\mu$ and for the negative binomial model it is $1+GdL/\mu$. Compared to the Poisson model, the positive binomial model describes a more regular dispersion of foliage while the negative binomial model describes a more clumped dispersion. A decreasing number (N) of independent layers leads to an increasing degree of clumping in the negative binomial model and to increasing regularity in the positive binomial model.

In real stands, deviations from a random dispersion, both towards a more clumped or a more regular form, have been observed (cf. e.g. Warren Wilson 1965, Ross 1981). Within a single plant the dispersion of leaves is semi-regular as a rule, whereas the distribution of individual plants tends to be clumped (Ross 1981).

Markov models

Nilson (1971) introduced the so-called Markov model. In this model, the probability of a contact in one horizontal layer depends on whether there has been a contact in the previous layer (the Markov property). The Markov model thus accounts for cases where horizontal layers in the canopy are not statistically independent – a very realistic assumption. This general model covers a wide variety of leaf patterns from regular to clumped ones. The "cost" of this generality, however, is that it involves three unknown parameters which have no obvious interpretation.

2.2. Grouping models

Statistical models describing horizontally homogeneous stands are not applicable in stands where the foliage is grouped into individual plant crowns.

In geometrical models, considering single shapes or regularly arranged shapes with characteristic geometrical dimensions, this kind of grouping is taken into account. Geometrical figures such as cylinders, cones, ellipsoids and spheres are used to describe the crown shape (cf. e.g. Jahnke and Lawrence 1965, Brown and Pandolfo 1969, Terjung and Louie 1972) and the crown is assumed to be opaque or to have some given (non-statistical) transmission coefficient.

Purely geometrical models considering regularly spaced or individual opaque shapes do not consider any statistical properties of the stand structure. Geometrical and statistical models are often combined in such a way that statistical distributions are applied at some level(s) of the structural hierarchy, for example in describing the spatial pattern of plants or the dispersion of foliage within crowns (cf. Charles-Edwards and Thornley 1973, Szwarcbaum and Shaviv 1976, Satterlund 1983).

Norman (1975) defines the stochastic-regular or weighted-random approach as a method combining random theory with what he calls the "regularly-spaced-opaque-obstacle" approach. These models are at least partly statistical but consider non-random foliage dispersion caused by grouping of foliage at different levels. The term "grouping models" will therefore, in the following, be used to characterise these kinds of models.

Characteristics of grouping models

The degree of grouping in a stand is mainly determined by the density and spatial pattern of trees. The spatial distribution of trees on the ground can be defined as a spatial point pattern on the plane by assuming that each tree occupies one point on the plane corresponding to the growing area.

The simplest and most widely used model for the spatial pattern of trees is that gener-

ated by a purely random (Poisson) process. The common use of the Poisson model reflects the fact that the dynamics of spatial pattern of plants is extremely difficult to describe. When plants are naturally regenerated there is a tendency for the offspring to be concentrated in the neighbourhood of the parent plant, thus resulting in a "contagious" (clustered) distribution (Cole 1946). A common course of the development of spatial pattern is from a heterogeneous, clustered distribution towards a more homogeneous (regular) distribution brought about by competition.

Quantitative descriptions of spatial pattern can be made using (a) distance methods or (b) methods based on sample quadrats of constant size (cf. Skellam 1952, Clark and Evans 1954). Based on these methods, different indices used for characterising the spatial pattern and for testing its departure from randomness can be defined.

A study of the development of spatial pattern of Scots pine stands in northern Finland was presented by Pohtila (1980). The spatial pattern of naturally regenerated stands, classified using the cluster index of Cox (1971), developed from a very heterogeneous, clustered distribution towards a distribution more homogeneous than the Poisson in the saw-timber stage. Artificially regenerated stands are usually established with a spatial pattern more regular than the Poisson. However, the spatial pattern of sown or planted stands was also found to frequently approach the Poisson distribution at a later stage of development (Pohtila 1980).

There is more to canopy structure than the density and spatial pattern of trees. Crown shapes and dimensions and the distribution of leaves within the crowns are important characteristics of models describing forest structure. Although the characteristic crown shape for a wide variety of species has been extensively studied (cf. e.g. Horn 1971, Brunig 1976), the spatial distribution of leaves within individual crowns has proved difficult to describe. As a first approximation, the models of leaf dispersion treated above have been used in describing the inner structure of tree crowns.

The model of Norman and Jarvis (1975) for Sitka spruce (*Picea sitchensis* (Bong.) Carr.) considers grouping of foliage at two levels: the grouping of needles in shoots and of shoots into whorls. Shoots, described as semi-transparent cylinders, are randomly dispersed in the (cylindrical) whorls. The whorls are assumed to be Poisson distributed in the canopy space.

In Nilson's (1977) general model the stand is composed of tree crowns represented by geometrical figures (cones, ellipsoids, parabolae or rectangles) and the spatial pattern of trees on the ground follows the Poisson distribution. The crowns have a transmission coefficient which depends on the viewing direction.

The approach of Oker-Blom and Kelomäki (1983) applied to Scots pine (*Pinus sylvestris* L.) stands is similar to that of Nilson (1977), except that the inner structure of crowns is considered as well. The spatial pattern of trees (conical crowns) is Poisson and needles are grouped into shoots which are randomly dispersed in the crowns and have a spherical orientation.

In a subsequent paper (Oker-Blom et al. 1983), the shoot structure is modeled. The outer shape of a shoot is described by a cylinder, the dimensions of which are determined by the shoot length, needle length and angle between needle and shoot axis. The inner structure of the shoot cylinder is described on the basis of following assumptions: (1) the location of a needle on the shoot axis is random, (2) the angle between needle and shoot axes is constant and the azimuthal orientation of a needle relative to the shoot axis is uniform, and (3) the shape of a needle is described as a cylinder.

2.3. Leaf orientation and projection area

In addition to leaf dispersion, the orientation of leaves is an important characteristic of canopy structure. The orientation of a planar (infinitely thin) leaf is defined by the direc-

tion $r_1 = (\theta_1, \varphi_1)$ of its normal. The mean projection of unit leaf area in direction $r = (\theta, \varphi)$ is given by (cf. Ross and Nilson 1965)

$$G(r) = \int_{\Omega} 1/(2\pi)g(r_1) \cos r_1 d\omega_1 \quad (8)$$

where $1/(2\pi)g(r_1)$ is the (normalized) probability density function for the leaf normal (to the leaf's upper side), Ω is the upper hemisphere and ω_1 a solid angle around r_1 ($d\omega_1 = \cos \theta_1 d\theta_1 d\varphi_1$).

A spherical distribution is defined by $g=1$. The leaves then have a random direction in space, i.e. the leaf normal has equal probability of pointing in any direction. For the spherical distribution

$$G(r) = \int_{\Omega} 1/(2\pi) \cos r_1 d\omega_1 = 1/2 \quad (9)$$

For leaves with constant inclination θ_0 and uniform azimuthal distribution (cf. Warren Wilson 1967)

$$G(r) = \begin{cases} \sin\theta \cos\theta_0, & \text{when } \theta \geq \theta_0 \\ \sin\theta \cos\theta_0 (1 + 2(\tan\tau - \tau)/\pi), & \text{when } \theta < \theta_0 < \pi/2 \\ 2\cos\theta/\pi, & \text{when } \theta_0 = \pi/2 \end{cases} \quad (10)$$

where $\tau = \arccos(\tan\theta \cot\theta_0)$.

G as a function of θ for different values of θ_0 is shown in Figure 1.

For non-planar leaves (needles) these formulae do not apply. Some "G-values" for conifer needles, modeled as bisected cylinders, are presented by Oker-Blom and Kelomäki (1981, 1982a). In the case of randomly oriented needles the value is 0.25 when total ("two-sided") surface area of needles is considered. This value equals that of randomly oriented leaves (0.5) based on one-sided leaf area.

When shoots are taken as the basic foliage elements the mean shoot projection per unit needle area, i.e. the G -value for shoots (G_s), is considerably smaller than those of planar leaves due to mutual shading of needles on a shoot. In addition to being dependent on the directions of the shoot and that of the projection, the shoot projection area depends on shoot structure.

Ross (1981) presents extensive data on the orientation of foliage for many different ag-

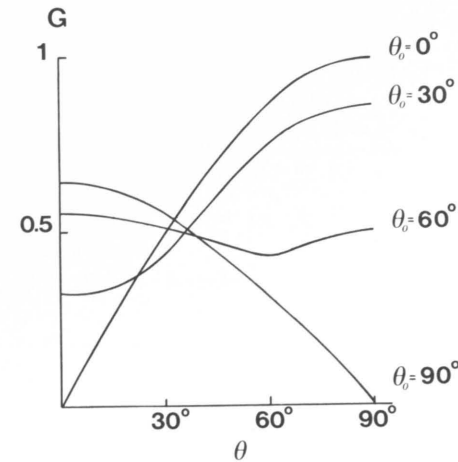


Fig. 1. The mean projection of unit foliage area (G) for leaves with constant inclination (θ_0) and uniform azimuthal distribution.

ricultural species. In terms of the "inclination index of foliage area", which measures the departure from a spherical distribution, many stands are shown to have a leaf orientation rather close to the spherical. Generally, the mean inclination angle of foliage depends on the stage of development and on the position in the canopy. As a rule, the azimuthal distribution is rather uniform.

For trees, the branching pattern and branch angles have been studied (cf. Hallé et al. 1978, Fisher and Honda 1979 a,b). These data, however, give very little information on the actual leaf or shoot orientation. The mean shoot inclination angle in Scots pine crowns decreases with shoot age and depth in the crown (J. Ross, unpublished data). For the total crown, however, the shoot orientation was fairly well described by the spherical distribution, for which the shoot axis has no preferred direction in space.

The G_s -values for shoots, i.e. the ratio between projected shoot area and needle area of the shoot, depend on shoot structure and direction of projection.

Ratios of projected and total needle area measured by Norman and Jarvis (1974) for Sitka spruce varied between 0.13 and 0.5 depending on the direction of projection. The total needle area in this case referred to the outline area of all needles when detached and laid on the horizontal. For flat needles this silhouette area closely corresponds to the one-sided leaf area of planar leaves but for thicker needles it may be considerably smaller (cf. Johnson 1984).

Carter and Smith (1985) define the ratio of silhouette to total leaf area (STAR) as the silhouette area of a shoot (orthogonal projection) divided by the total surface area of all needles on the shoot. Their STAR-values thus correspond to one half of the G -values for planar leaves.

The projection area of a Scots pine shoot with given structural characteristics can be calculated with help of the previously mentioned model of shoot structure (Oker-Blom et al. 1983). Photographically measured and calculated values of the projection area of eight Scots pine shoots inclined at the angles 0°, 45° and 90° to the plane of projection are presented in Figure 2 (Smolander et al. 1986). The corresponding G_s -values, based on total needle surface area, varied between 0.06 and 0.18.

On the basis of photographically measured projection areas of 260 Scots pine shoots (unpublished data), the mean G_s -value assuming spherical orientation of the shoot axis was 0.14, i.e. less than 60% of the G -value (0.25) for a spherically oriented needle. These values are of the same magnitude as those measured by Carter and Smith (1985) for three different conifer species, *Abies lasiocarpa* ((Hook) Nutt.), *Pinus contorta* (Engelm.) and *Picea engelmannii* (Parry ex Engelm.).

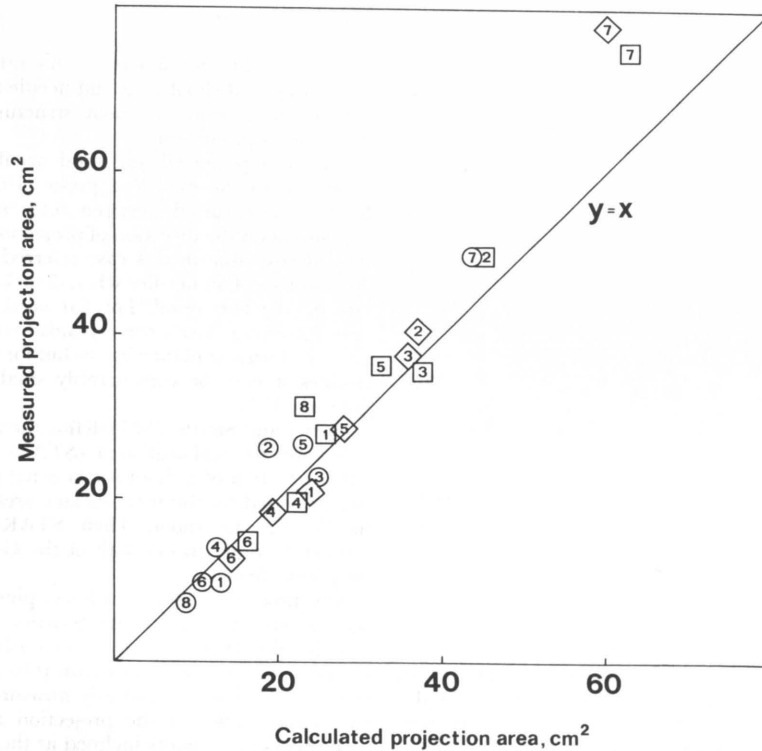


Fig. 2. Photographically measured and calculated projection areas of eight Scots pine shoots at different inclinations to the plane of projection: 0° (□), 45° (◇) and 90° (○). Numbers inside the symbols refer to specific shoots. (Smolander et al. 1986).

3. THE RADIATION FIELD INSIDE A STAND

3.1. Properties of incident radiation

The irradiance of solar energy received on an exposed surface normal to the sun's rays at the mean sun-earth distance and in the absence of atmosphere is known as the solar constant (S_0) and has a value of ca. 1380 Wm^{-2} (Ross 1981). In traversing the atmosphere, part of the radiation is scattered and absorbed, whereby radiation is attenuated and the spectrum and direction of radiation are changed. Total incident radiation is divided into two components:

- (1) direct solar radiation consisting of the transmitted unscattered part of radiation, the direct beam, and
- (2) diffuse sky radiation consisting of scattered radiation reaching the ground from all directions of the sky.

The monochromatic transmittance τ_λ^m is (cf. Gates 1980)

$$\tau_\lambda^m = \exp(-k_\lambda u m) \quad (12)$$

The mean atmospheric transmittance (averaged over all wavelengths) is correspondingly

$$\bar{\tau}^m = (\int S_{0\lambda} \tau_\lambda^m d\lambda) / (\int S_{0\lambda} d\lambda) \quad (13)$$

For a solar elevation of θ_s , the horizontal irradiance of incident direct solar radiation can then be expressed as

$$I_d = S_0 \bar{\tau}^m \sin \theta_s \quad (14)$$

where the air mass may be approximated as $m \approx 1/\sin \theta_s$, when $\theta_s \geq 30^\circ$ (Gates 1980).

Values of τ along the zenith path ($m=1$) are normally between 0.4 and 0.7. During midday hours in middle latitudes the direct solar irradiance at a surface perpendicular to the solar beam ranges from about 700 to 1000 Wm^{-2} (Ross 1975).

The sun elevation depends on the hour angle, geographical latitude and declination (cf. Paltridge and Platt 1976). In southern Finland (latitude $61^\circ N$) the maximum solar elevation is 53.4° and the elevational distribution of sunshine hours during the growing season (April 15 to October 15) is rather uniform (cf. Oker-Blom and Kellomäki 1982b).

Direct solar radiation reaching the earth is in the spectral range of 290–4000 nm. In terms of energy the share of ultraviolet radiation (290–380 nm) is about 2%, the share of photosynthetically active radiation (PAR, 380–710 nm) is 42% and the share of near infra-red radiation (NIR, 710–4000 nm) is 56% (Ross 1975). According to west-European standards PAR is in the spectral range of 400–700 nm.

Direct solar radiation

The attenuation of direct solar radiation in the atmosphere is spectrum-selective and depends on the optical thickness (u), denoting the mean concentration of attenuating particles in the way of the beam, and on the pathway length of the solar beam through the atmosphere, characterised by the air mass (m) (Gates 1980). The attenuation of a beam of monochromatic radiation of spectral radiance can be expressed by Beer's law as

$$i_\lambda = S_{0\lambda} \exp(-k_\lambda u m) \quad (11)$$

where $S_{0\lambda}$ is the monochromatic radiance outside the atmosphere, i_λ the monochromatic radiance reaching the earth and k_λ is the monochromatic attenuation coefficient. The air mass is the ratio of the pathway length through the atmosphere in the direction of the sun to the pathway length in the zenith direction.

Diffuse sky radiation

The irradiance and spectral composition of incident diffuse radiation depend on solar elevation and on the character of scattering.

Scattering below a cloudless sky (Rayleigh scattering) occurs on small particles and increases with decreasing wavelengths. The spectral composition of radiation is shifted towards shorter wavelengths, with a maximum in the blue ($\lambda \approx 450$ nm). The shares of ultraviolet radiation, PAR and NIR are 10 %, 65 % and 25 %, respectively (Ross 1975).

In the presence of clouds, scattering occurs on larger particles (Mie scattering) and is less selective. The spectrum of a cloudy sky is nearly that of direct solar radiation.

The irradiance of diffuse radiation depends on cloud type and amount. On a clear day the share of diffuse radiation amounts to ca. 10 % of the direct solar radiation. The maximum irradiance of diffuse radiation, occurring at midday below middle level clouds, reaches 400–500 Wm^{-2} , while the minimum values in the case of low level clouds are between 30 and 70 Wm^{-2} (Ross 1981).

The share of diffuse radiation from total incident radiation depends on climatological factors which vary with time and geographical position. In southern Finland the share of diffuse radiation between April 15 and October 15 (the growing season) was about 40 % in terms of energy, as calculated by the author on the basis of the yearly reports (1975–79) presented by the Meteorological Institute in Finland.

Denoting the radiance of diffuse sky radiation in the direction $r = (\theta, \varphi)$ by $i_d(r)$, the horizontal irradiance of diffuse sky radiation is

$$I_d = \int_{\Omega} i_d(r) \sin\theta \, d\omega \quad (15)$$

The directional distribution of skylight is non-isotropic. Under clear-sky conditions the sky is brightest near the sun and darkest in a zone approximately 90° from the sun in the plane of the sun and observer.

Under a totally cloudy sky the brightness decreases from zenith towards the horizon. A theoretical distribution SOC (Standard OverCast) has been developed for this overcast condition (Moon and Spencer 1942).

The radiance $i_d(r)$ for the SOC distribution is given by

$$i_d(r) = 3I_d(1+2\sin\theta)/(7\pi) \quad (16)$$

In the most common situation of partly cloudy skies a quantification of the distribution of sky radiation is particularly difficult due to the poor accuracy of cloud specification, and no theoretical distribution of diffuse radiation is available. The large multiple scatter within clouds, however, tends to induce isotropy and the sky is commonly assumed to be isotropic in practical meteorological problems (Paltridge and Platt 1976). For an isotropic (Uniformly OverCast, UOC) sky $i_d(r)$ is independent of the direction r , $i_d(r) = I_d/\pi$.

3.2. Components of radiation in a stand

The radiation inside a stand can be divided into three components (Niilisk et al. 1970):

- (1) direct solar radiation penetrating through gaps in the stand,
- (2) diffuse solar radiation penetrating through gaps in the stand, and
- (3) complementary radiation due to scattering of radiation on the foliage and the ground.

Consider a point $P = (x, y, z)$ on a hypothetical horizontal plane inside the stand. The irradiance $X(P)$ at P can be expressed as

$$X(P) = X_s(P) + X_d(P) + X_c(P) \quad (17)$$

where $X_s(P)$ is the irradiance of unscattered direct radiation, $X_d(P)$ the irradiance of unscattered diffuse radiation and $X_c(P)$ the irradiance of scattered radiation.

The components X_s and X_d depend on the stand structure, i.e. on the proportion of gaps in different directions of the upper hemisphere as seen from P , while the scattered component X_c mainly depends on stand density, soil albedo and spectral properties of the phytoelements. The spectral properties of green leaves depend on the species and on the

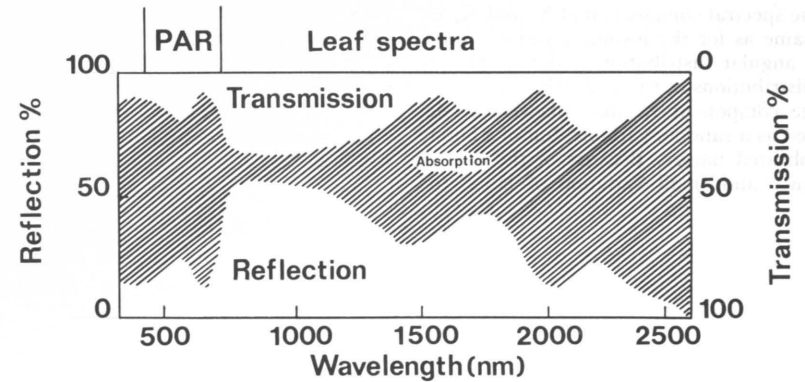


Fig. 3. The absorption, transmission and reflection coefficients of an "average" green leaf. (Monteith 1965).

leaf age and structure. The absorption, transmission and reflection coefficients of an "average" green leaf are presented in Figure 3 (Monteith 1965). In the PAR-region the absorption coefficient is ca. 85 % (Ross 1975) for broadleaves and over 90 % for conifer needles (Gates et al. 1965).

When the stand structure is described in statistical terms, the distribution of gaps in the hemisphere as seen from a point P can be expressed by the random variable $\delta(P, r)$, for which

$$\delta(P, r) = \begin{cases} 1, & \text{when there is a gap in direction } r = (\theta, \varphi) \\ 0, & \text{when the direction } r \text{ is obstructed} \end{cases} \quad (18)$$

The expectation value of $\delta(P, r)$ then equals the probability of a gap, $p_0(P, r)$, in direction r (cf. Chapter 2).

Using the random function δ , the components X_d and X_s can now be expressed as random variables given by

$$X_d(P) = \int_{\Omega} i_d(r) \delta(P, r) \sin\theta \, d\omega \quad (19)$$

$$X_s(P) = \int_S i_s(r) \delta(P, r) \sin\theta \, d\omega$$

where i_d (i_s) is the radiance of diffuse sky radiation (direct solar radiation) in direction

r , Ω is the upper hemisphere and S the solid angle of the sun.

The assumption that P is situated on a horizontal plane was made in order to simplify the notations. The irradiance at a point (P_1) on an (inclined) leaf is obtained by replacing $\sin\theta$ by the cosine of the angle between the direction of radiation and the direction of the leaf normal (r_1) at P_1 . The upper hemisphere is correspondingly replaced by the hemisphere facing the leaf at P_1 . If not otherwise stated, a point denoted by P is assumed to be situated on a horizontal surface while the notation P_1 specifically refers to a point on the surface of a leaf (needle).

At any point on the leaf area the irradiance is defined as a random variable with a value which depends on the distribution of incident radiation and on stand structure. The spatial distribution on the leaf surface is induced by the irradiance distributions at all points belonging to the leaf area. At a point P_1 on the leaf surface the distribution function H_{P_1} of the irradiance is defined by

$$H_{P_1}(I) = \text{Prob}(X(P_1) \leq I) \quad (20)$$

The spatial distribution of irradiance H_L , over the leaf surface area L is defined as

$$H_L(I) = (1/L) \int_L H_{P_1}(I) dL \quad (21)$$

The spectral composition of X_s and X_d are the same as for the incoming radiation and their angular distribution is determined by the distributions of $i(r)$ and $\delta(P,r)$.

The component X_c may likewise be described as a random variable, but of a highly complicated nature. Because of the low irradiance and small variation of X_c in the

PAR-region (cf. Fig. 3) the scattered component is usually treated as a diffuse flux or is neglected. In the following analysis, photosynthetically active radiation is considered and the penetration of radiation is treated as a problem of shading, i.e. it is assumed that $X_c=0$.

4. THE PENETRATION OF RADIATION INTO A STAND

4.1. Mean irradiance and its spatial variation

The irradiance of unscattered radiation at a given point P was expressed as a random variable depending on the distributions of sun and sky radiation and the distribution of gaps in the hemisphere facing P. The mean irradiances of diffuse and direct solar radiation at P are then the expectation values, EX_d and EX_s , of the random variables X_d and X_s and are obtained from Equation (19) by replacing $\delta(P,r)$ with its expectation value which equals the probability of a gap, $p_0(P,r)$.

Thus, at a point P on a horizontal surface the mean irradiance of diffuse radiation is

$$I_d(P) = EX_d(P) = \int_{\Omega} i_d(r)p_0(P,r) \sin\theta \, d\omega \quad (22)$$

and the mean irradiance of direct solar radiation is

$$I_s(P) = EX_s(P) = \int_{\Omega} i_s(r)p_0(P,r) \sin\theta \, d\omega \quad (23)$$

The total mean irradiance $I(P)$ may consequently be written as

$$I(P) = \int_{\Omega} i(r)p_0(P,r) \sin\theta \, d\omega \quad (24)$$

where $i(r) = i_d(r) + i_s(r)$ and $i_s(r) = 0$ in the part of the upper hemisphere not belonging to the solid angle of the sun.

Averaged over the horizontal (coordinates x and y) $I(P)$ yields the mean horizontal irradiance $I(z)$ at depth z . The interception of radiation by the canopy above z is then $I_0 - I(z)$, where I_0 is the total horizontal irradiance above the stand, $I_0 = I_s + I_d$.

4.1.1. Horizontally homogeneous stand

In a horizontally homogeneous stand the probability of a gap, $p_0(P,r)$, is independent

of the horizontal coordinates x and y . The Poisson model gives (cf. Eqn. 4)

$$p_0(P,r) = \exp(-G(r)L(z)/\sin\theta) \quad (25)$$

and the mean horizontal irradiance is then (cf. Eqn. 24)

$$I(z) = \int_{\Omega} i(r) \exp(-G(r)L(z)/\sin\theta) \sin\theta \, d\omega \quad (26)$$

The quantity $k = G(r)/\sin\theta$ is called the extinction coefficient and it varies with the direction r (Fig. 4, Anderson 1966). Therefore, the attenuation of radiation is not strictly exponential except for horizontal leaves, in which case $k=1$ ($G(r)=\sin\theta$), or when radiation enters from one specified direction. In

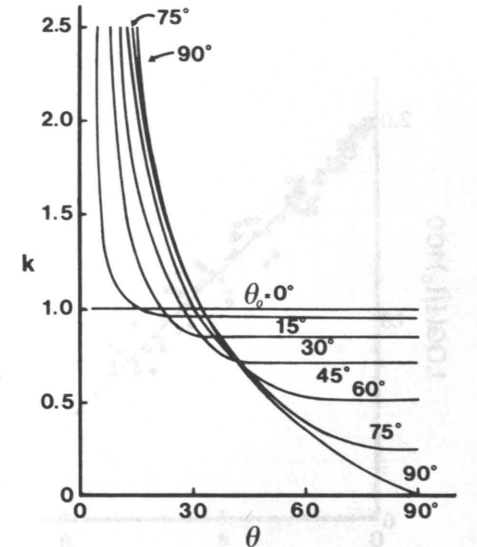


Fig. 4. The extinction coefficient (k) as a function of the inclination angle (θ) of incoming radiation for leaves with constant inclination (θ_0) and uniform azimuthal distribution. (Anderson 1966).

those cases we have

$$I(z) = I_0 \exp(-kL(z)) \quad (27)$$

which is the formula introduced by Monsi and Saeki (1953) as an application of Beer's law in plant stands. According to Equation (27) the mean horizontal irradiance decreases exponentially with the projected foliage area index $L_p(z) = kL(z)$.

Equation (27) applies to the attenuation of direct solar radiation (entering as a nearly parallel beam) in a horizontally homogeneous stand. The attenuation of direct solar radiation at a given moment (fixed sun elevation) is very dependent upon the leaf orientation, determining the extinction coefficient k (cf. Fig. 4).

De Wit (1965) uses the term "planophile orientation" for a largely horizontal leaf arrangement and the term "erectophile orientation" for a predominantly vertical leaf arrangement. Generally speaking, the rate of attenuation is large in a planophile canopy

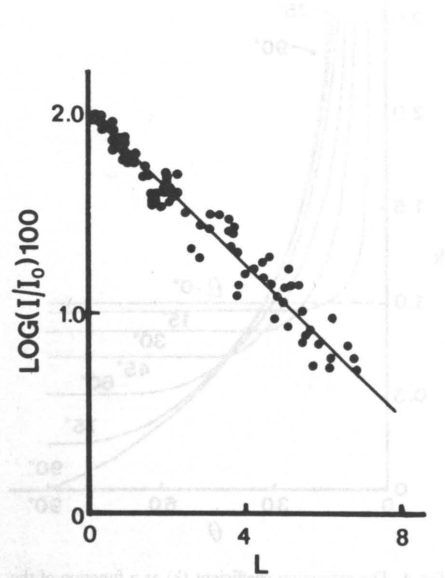


Fig. 5. The logarithm (I/I_0) of the relative irradiance in a rice community as a function of the cumulative leaf area index (L) . (Takeda 1961).

and small in an erectophile canopy when the directional distribution of radiation is confined to large inclination angles. The situation is reversed when the directional distribution of radiation is predominantly one of small inclination angles. Since the sun moves continuously along its path, the integrated effect of leaf orientation on the attenuation during a longer period is, however, much smaller (cf. Oker-Blom and Kellomäki 1982a).

Equation (27) is commonly used also to describe the attenuation of diffuse radiation which is not (by theory) strictly exponential. In that case an "average" k -value is used as the extinction coefficient. For agricultural crops where the horizontal distribution of leaves is rather uniform, Equation (27) has been found to approximate well the attenuation of radiation (Fig. 5, Takeda 1961).

Mean irradiance on the leaf area

The irradiance at a point $P_1 = (x, y, z)$ on the surface of a leaf is expressed as (cf. Eqn. 19)

$$X(P_1) = \int_{\Omega_1} i(r) \delta(P_1, r) \cos^2 r_1 d\omega \quad (28)$$

where Ω_1 is the solid angle of 2π facing the leaf at P_1 and r_1 is the direction of the leaf normal at P_1 .

The mean irradiance at P_1 (the mean of the irradiance distribution at P_1) is the expectation value of $X(P_1)$, obtained by replacing $\delta(P_1, r)$ (Eqn. 28) with its expectation value (cf. Eqn. 25), i.e.

$$I(P_1) = \int_{\Omega_1} i(r) \exp(-G(r)L(z)/\sin\theta) \cos^2 r_1 d\omega \quad (29)$$

In a horizontally homogeneous stand, the gap distribution characterised by $\delta(P, r)$ is horizontally independent. The distribution function H_P of $X(P_1)$ therefore depends only on the depth (z) and leaf orientation (determined by r_1) and not on the coordinates x and y . At any two points at the same depth, different orientations of the respective leaf surfaces cause differences in the mean irradiance (cf. Eqn. 29).

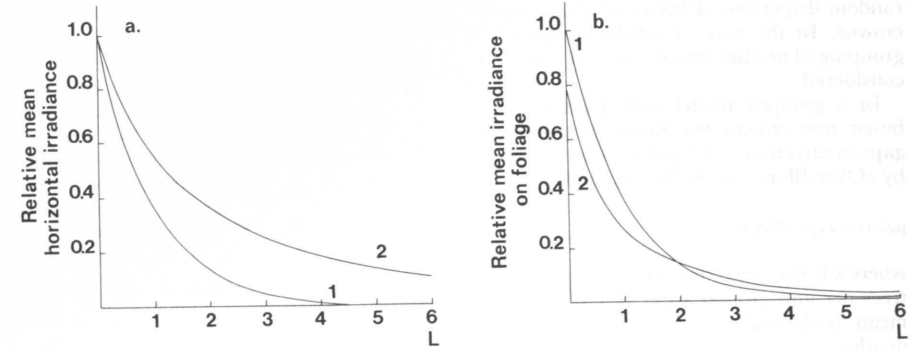


Fig. 6. (a) The relative mean horizontal irradiance and (b) the relative mean irradiance on the foliage area as functions of the leaf area index (L) in a horizontally homogeneous canopy with (1) horizontal leaves and (2) vertical leaves. (Oker-Blom and Kellomäki 1982a).

The expectation value of $I(P_1)$ with respect to the leaf orientation density (probability density for r_1) yields the mean irradiance on the leaf area (total surface area) at depth z . The mean irradiance on the leaf area at depth z can be interpreted as the interception of radiation per unit leaf area in the layer $(L(z), L(z) + dL(z))$ and can be obtained by differentiating $I(z)$ (Eqn. 26) with respect to $L(z)$ and changing the sign, i.e.

$$I(z, L) = \int_{\Omega} i(r) \exp(-G(r)L(z)/\sin\theta) G(r) d\omega \quad (30)$$

When $L(z)$ and $G(r)$ refer to one-sided leaf area, the mean irradiance $I(z, L)$ also denotes the interception per one-sided leaf area. The mean irradiance based on total surface area is obtained by differentiating with respect to total surface area.

From Equation (30) it can be concluded that $I(z, L)$ equals $I(z)$ (Eqn. 26) only for $G(r) = \sin\theta$ (horizontal leaves). Thus, only in the case of horizontal, randomly dispersed leaves is the mean irradiance on the leaf area equal to the mean horizontal irradiance.

Figure 6 (Oker-Blom and Kellomäki 1982a) shows calculated values of (a) the mean horizontal irradiance $(I(z))$ and (b) the mean irradiance on the foliage area $(I(z, L))$, relative to the horizontal irradiance (I_0) above the canopy, as a function of the cumulative leaf area index $(L(z))$ for (1) hori-

zontal leaves and (2) vertical leaves in a modeled homogeneous canopy during a standard overcast sky (SOC).

Radiance increases from the horizontal to the vertical in the SOC model (Eqn. 16). Therefore, vertical leaves enable more radiation to penetrate and the mean horizontal irradiance is consequently higher in the canopy model with vertical leaves (Fig. 6a). For the same reason, the mean irradiance on the leaf area in the upper part of the canopy is lower in the case of vertical leaves (Fig. 6b). Horizontal leaves situated above a leaf area index of about 2 are in a favourable position during a SOC. For positions in the canopy below large values of the cumulative leaf area index the mean irradiance on foliage is nearly the same in both cases. Differences in mean irradiance on the foliage area are much smaller than differences in the mean horizontal irradiance.

4.1.2. Grouped stand

A real forest stand is characterised by grouping of foliage into individual crowns, resulting in a horizontally heterogeneous foliage area distribution. The effect of grouping on the mean irradiance and its spatial variation will be analysed for a model stand composed of Poisson distributed trees with a

random dispersion of leaves or shoots in the crowns. In the case of coniferous trees the grouping of needles into shoots will further be considered.

In a grouped model with Poisson-distributed tree crowns the mean proportion of gaps in direction r at depth z , $p_0(z,r)$, is given by (Oker-Blom and Kellomäki 1983)

$$p_0(z,r) = \exp(-\lambda T(z,r)) \quad (31)$$

where λ is the stand density (mean number of trees per unit ground area) and $T(z,r)$ is the mean horizontal crown projection area at depth z .

The mean horizontal irradiance is then

$$I(z) = \int_{\Omega} i(r) \exp(-\lambda T(z,r)) \sin \theta \, d\omega \quad (32)$$

The crown projection area $T(z,r)$ is given by (cf. Mann et al. 1977)

$$T(z,r) = \int_{S(z,r)} (1 - \exp(-c_r(z) f_r(x,y))) \, dx \, dy \quad (33)$$

where $S(z,r)$ is the projection of the crown envelope at height z (the region onto which the crown is projected), $c_r(z)$ the total projected foliage area (the sum of the horizontal projection areas of the individual foliage elements) and $f_r(x,y)$ the density function of the projected foliage over $S(z,r)$.

If leaves (shoots) are randomly dispersed (i.e. have a uniform spatial density within the crown), $f_r(x,y)$ is proportional to the path length $t_r(x,y)$ within the crown in direction r and $c_r f_r = c_r \sin \theta t_r / V$ where V is the crown volume (Oker-Blom and Kellomäki 1982b). The quantity $c_r \sin \theta$ is the total orthogonally projected foliage area and equals $G(r) L_T(z)$ ($G_s(r) L_T(z)$ in the case of shoots), where $L_T(z)$ is the leaf (needle) area of the crown above z .

The cumulative leaf area index is $L(z) = \lambda L_T(z)$ and Equation (31) may be written

$$p_0(z,r) = \exp(-T(z,r) L(z) / L_T(z)) \quad (34)$$

The ratio $T(z,r) / L_T(z)$ between crown projection area and leaf area of the crown then corresponds to the extinction coefficient (cf. Eqns. 25–27) of the stand in direction r . Due to mutual shading of leaves in the crown its

value is, however, considerably smaller than the mean horizontal projection of unit foliage area (k) for an individual foliage element. At the same leaf area index the interception of radiation is consequently smaller in a non-homogeneous grouped stand. In coniferous stands the interception per unit needle area is further reduced due to grouping of needles into shoots, giving small values of the mean projection per unit of foliage area (G_s).

The effect of grouping is illustrated in Figure 7 (Kellomäki et al. 1986). Model 1 describes a horizontally homogeneous canopy with randomly dispersed needles. In Model 2 shoots are randomly dispersed in the canopy space, i.e. the grouping of needles into shoots is considered. The grouping of shoots in the individual crowns is further considered in Model 3.

The attenuation of direct radiation for a solar elevation of 45° was calculated for the stands described by Models 1–3. In the horizontally homogeneous canopy with randomly dispersed needles (Model 1) the attenuation of mean horizontal irradiance is an exponential function of the projected needle area index.

In the stand described by Model 2 shoots are randomly dispersed in the canopy space and the ratio between projected shoot area and projected needle area is assumed to be 0.6 (cf. Oker-Blom and Kellomäki 1983). The stand is horizontally homogeneous with respect to shoots and the mean horizontal irradiance decreases exponentially with the "projected shoot area index".

In the stand described by Model 3, shoots are randomly dispersed in the conical crowns of Poisson distributed trees. The stand density is assumed to be 0.2 m^{-2} (2000 trees per ha) and the height/width -ratio of the crowns is equal to 2. The mean horizontal irradiance decreases exponentially with the "projected crown area index" (cf. Eqn. 31), i.e. the stand density times the crown projection area.

The attenuation of radiation as a function of the projected needle area index (L_p) for Models 1–3 is given in Figure 8 (Kellomäki et al. 1986), showing a slower attenuation (smaller interception) for an increased degree of grouping.

Measurements of the penetration of radiation in forest stands (e.g. Norman and Jarvis 1975, Baldocchi et al. 1985) confirm that the

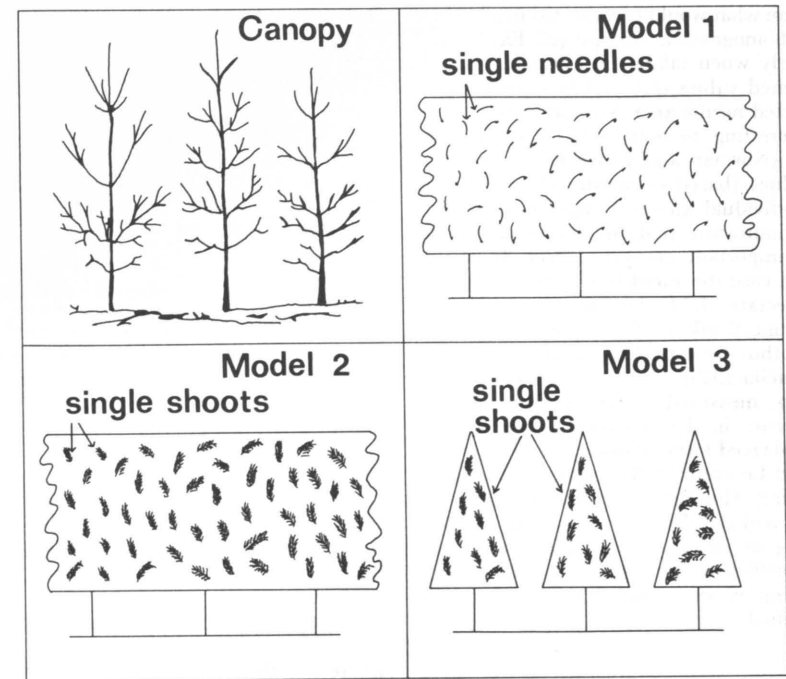


Fig. 7. Models of canopy structure showing different degrees of grouping (Kellomäki et al. 1986).

random theory underestimates the transmission, i.e. that the extinction coefficients for forest stands are smaller than those obtained by assuming horizontal homogeneity. Consequently, Norman and Jarvis (1975) found that their model, incorporating grouping into shoots and whorls, agreed better with measurements than the random theory. When the woody plant parts (stems and branches) were included in the leaf area index, the agreement was further improved.

Norman and Jarvis (1974) give values of the extinction coefficient (k) at different levels in a Sitka spruce stand, calculated from measured PAR transmission data and leaf area index (cf. Eqn. 27). During clear sky conditions k varied between 0.50 and 0.80 when the sun elevation was 42° , and between 0.41 and 0.91 for a solar elevation of 25° . The corresponding G -values ($G = k \sin \theta_s$) are then between 0.17 and 0.54, and are clearly small-

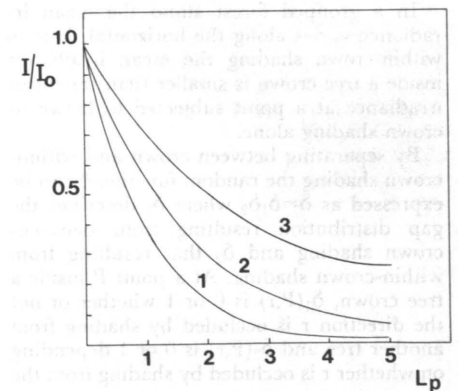


Fig. 8. Relative horizontal irradiance (I/I_0) as a function of the projected needle area index (L_p) for the canopy models presented in Fig 7 (Kellomäki et al. 1986).

ler than what would be expected in a horizontally homogeneous canopy (cf. Fig. 1.), particularly when taking into account that the presented values of k and G were based on projected needle area (silhouette area).

Interesting to note is that, in the same study (Norman and Jarvis 1974), measured G_s -values (based on needle silhouette area) for individual shoots ranged from 0.13 to 0.50, indicating that the shoots caused the most important grouping effect. In the reported case the stand was dense (4000 trees per hectare, LAI close to 10), and a less pronounced effect of grouping into crowns could thus be expected (cf. Oker-Blom and Kellomäki 1983).

Also, measured values of the extinction coefficient in 13 different coniferous and broad-leaved forest stands, presented by Jarvis and Leverenz (1983), indicate an effect of grouping. However, since the orientation of leaves and the directional distribution of incoming radiation strongly affect the extinction coefficient (cf. Fig. 4), the influence of grouping in the reported cases cannot be quantified.

Mean irradiance on the leaf area

In a grouped forest stand the mean irradiance varies along the horizontal. Due to within-crown shading the mean irradiance inside a tree crown is smaller than the mean irradiance at a point subjected to between-crown shading alone.

By separating between-crown and within-crown shading the random function δ can be expressed as $\delta = \delta_1 \delta_2$ where δ_1 describes the gap distribution resulting from between-crown shading and δ_2 that resulting from within-crown shading. At a point P inside a tree crown, $\delta_1(P, r)$ is 0 or 1 whether or not the direction r is occluded by shading from another tree and $\delta_2(P, r)$ is 0 or 1 depending on whether r is occluded by shading from the same tree.

If leaves are randomly dispersed in the crown, the probability of a free line of sight through the crown from a point P inside the crown is (cf. Oker-Blom and Kellomäki 1983)

$$\text{Prob}(\delta_2(P, r) = 1) = \exp(-\varrho l_r t_r(P)) \quad (35)$$

where ϱ is the number density of leaves in the crown, l_r the average orthogonal projection area of a leaf and $t_r(P)$ the length of the path within the crown from P in direction r . The quantity ϱl_r equals $G(r)L_T(z)/V$.

The probability of a free line of sight through the other crowns is (cf. Oker-Blom and Kellomäki 1983)

$$\text{Prob}(\delta_1(P, r) = 1) = \exp(-\lambda T(z, r)) \quad (36)$$

According to the assumptions, the random functions δ_1 and δ_2 are independent of each other and the probability of a gap is equal to their product, i.e.

$$p_0(P, r) = \exp(-\varrho l_r t_r(P)) \exp(-\lambda T(z, r)) \quad (37)$$

The mean irradiance at the point $P_1 = (x, y, z)$ on a leaf inside the crown is thus (cf. Eqn. 29)

$$I(P_1) = \int_{\Omega_1} i(r) \exp(-\varrho l_r t_r(P_1)) \exp(-\lambda T(z, r)) \cos r_1 d\omega \quad (38)$$

where r_1 is the direction of the leaf normal at P_1 and Ω_1 the hemisphere facing the leaf at P_1 .

The expectation value of $I(P_1)$ with respect to the leaf orientation density yields the mean irradiance on foliage (based on total surface area) at depth z . The mean irradiance can also be obtained by differentiating $I(z)$ (Eqn. 32) with respect to $L(z)$ and changing the sign.

In Figure 9 (Oker-Blom and Kellomäki 1983) the mean irradiance on foliage, here expressed as mean interception per projected foliage area, as a function of depth in the canopy, is compared for a horizontally-homogeneous model and a grouped model. In the grouped model the stand was composed of Poisson distributed trees with conical crowns of a height two times the width. Leaves were randomly distributed in the crowns. In the horizontally homogeneous model the vertical density of leaves was similar to that in the grouped model, i.e. the cumulative leaf area index at a given depth was similar in both stands. The calculations were made for direct solar radiation and the elevation of the sun was assumed to be 45°.

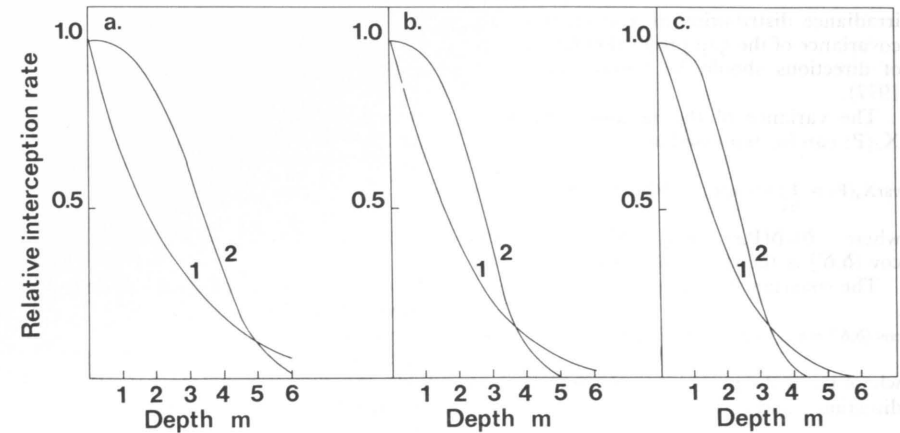


Fig. 9. Relative interception rates as a function of canopy depth for varying stand density (a=1000 ha⁻¹, b=2000 ha⁻¹, c=3000 ha⁻¹) and canopy models (1=grouped stand, 2=horizontally homogeneous stand). (Oker-Blom and Kellomäki 1983).

In the horizontally-homogeneous model the interception rates are high in the upper canopy and decrease very rapidly. In the grouped-canopy model the rates are considerably lower in the upper canopy as a result of within-crown shading. The difference in interception rates increases as the stand density decreases. In the lowest part of the canopy, however, the interception rates are increased as a result of grouping which enables more radiation to penetrate through the upper canopy.

When the foliage consists of coniferous shoots, the mutual shading of needles on a shoot must further be considered. Apart from being reduced by shading from another tree crown and shading from shoots of the same tree crown, the irradiance at a point within a shoot is reduced by within-shoot shading. At a point P within a shoot the random function δ can thus be expressed as $\delta = \delta_1 \delta_2 \delta_3$ where $\delta_3(P, r)$ is 0 (1) whether or not a needle of the same shoot is shading P . The probability of a gap in direction r is then reduced by the factor $\text{Prob}(\delta_3(P, r) = 1)$ and the mean irradiance at P_1 is

$$I(P_1) = \int_{\Omega_1} i(r) \exp(-\lambda T(z, r)) \exp(-\varrho l_r t_r(P_1)) \times \text{Prob}(\delta_3(P_1, r) = 1) \cos r_1 d\omega \quad (39)$$

The reduction in irradiance due to within-shoot shading then depends on the shoot structure which determines the distribution of δ_3 . In a specified direction (r) the mean value of $\text{Prob}(\delta_3(P_1, r) = 1) \cos r_1$ over the needle surface area of a shoot equals the mean shoot projection per unit of needle area ($G_s(r)$). Normally G_s -values are considerably smaller than the corresponding G -values for planar leaves and the reduction in mean irradiance on the foliage caused by within-shoot shading is consequently large. This fact emphasizes the need for a description of shoot structure in the general description of stand structure.

4.2. Distribution of diffuse irradiance

The diffuse component X_d of the irradiance at a point P can in many cases be considered as the sum of many nearly independent variables (cf. Eqn. 19) and therefore, according to the central limit theorem (cf. e.g. Cramér 1945), has a distribution tending to the normal one (Ross 1981). The mean and variance of diffuse radiation thus characterise its distribution. In order to get the variance of the

irradiance distribution at a given point the covariance of the gap proportion for any pair of directions should be known (cf. Nilson 1977).

The variance of the random component $X_d(P)$ can be expressed as

$$\text{var}X_d(P) = \iint_{\Omega} i_d(r)i_d(r')\text{cov}(\delta,\delta')\sin\theta\sin\theta'd\omega d\omega' \quad (40)$$

where $\delta=\delta(P,r)$ and $\delta'=\delta(P,r')$ and $\text{cov}(\delta,\delta')$ is the covariance of δ and δ' .

The covariance is obtained as

$$\text{cov}(\delta,\delta') = p_{00}(P,r,r') - p_0(P,r)p_0(P,r') \quad (41)$$

where p_{00} is the probability of a gap both in direction r and r' , given by

$$p_{00}(P,r,r') = \text{Prob}(\delta(P,r)=1 \mid \delta(P,r')=1)p_0(P,r') \quad (42)$$

When $i_d(r)$ and $\delta(P,r)$ are known, the remaining problem is to find the conditional probability $\text{Prob}(\delta=1 \mid \delta'=1)$ of a gap in direction r given that there is a gap in direction r' , for any pair of directions r and r' .

4.2.1. Horizontally homogeneous stand

The variance of diffuse radiation will be derived for a model canopy composed of randomly dispersed, horizontal and circular leaves (Fig. 10a). The probability $p_0(P,r)$ of a free line of sight from $P=(x,y,z)$ in direction r is (cf. Eqns. 2 and 25)

$$p_0(P,r) = \exp(-L(z)) = \exp(-\rho\pi R^2 z) \quad (43)$$

where ρ is the number density of leaves per unit volume and R is the leaf radius. $V=\pi R^2 z$ represents the volume outside which the mid-point of a leaf must be situated in order not to shade the direction r (see Fig. 10a). The corresponding volume around direction r' is denoted V' .

The conditional probability, $\text{Prob}(\delta=1 \mid \delta'=1)$, is easily found to be

$$\begin{aligned} \text{Prob}(\delta=1 \mid \delta'=1) &= \exp(-\rho(V-V_c(r,r'))) \\ &= \exp(-L(z))\exp(\rho V_c(r,r')) \end{aligned} \quad (44)$$

where $V_c(r,r')$ is the intersection of V and V' (Fig. 10b).

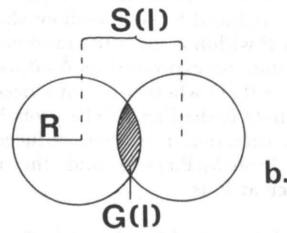
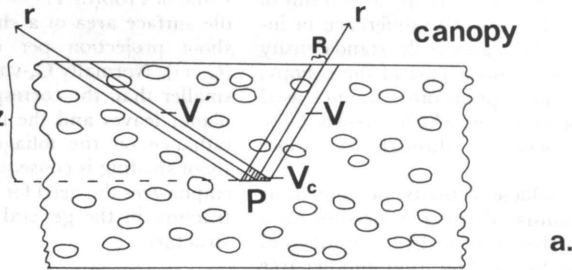


Fig. 10. (a) Representation of a horizontally homogeneous canopy. (b) Volume V_c and its horizontal cross-section $G(1)$. (See text for further explanation).

V_c is a measure of the degree of statistical dependency between $\delta(P,r)$ and $\delta(P,r')$. The horizontal cross-section $G(1)$ of V_c at the vertical distance l above P (Fig. 10b) is given by

$$G(l) = 2R^2(\arccos t(1)-t(1)(1-t^2(1))^{1/2}) \quad (45)$$

where $t(1)=s(1)/(2R)$ and $s(1)$ (Fig. 10b) is the horizontal distance between r and r' given by

$$s(1) = 1(\cot^2\theta + \cot^2\theta' - 2\cot\theta \cot\theta' \cos(\varphi - \varphi'))^{1/2} \quad (46)$$

The vertical height of V_c is $h(r,r') = \min(z, 2R/d(r,r'))$, where

$$d(r,r') = (\cot^2\theta + \cot^2\theta' - 2\cot\theta \cot\theta' \cos(\varphi - \varphi'))^{1/2}.$$

Thus,

$$V_c(r,r') = \int_0^{h(r,r')} G(l)dl \quad (47)$$

which can be solved analytically.

When $h = 2R/d$, Equation (47) yields $V_c = 8R^3/3d$ and ρV_c is then proportional to the product of R and the leaf area density $L(z)/z = \rho\pi R^2$.

Combining Equations (41)–(44) gives

$$\text{cov}(\delta,\delta') = \exp(-2L(z))(\exp(\rho V_c(r,r')) - 1) \quad (48)$$

Given the distribution of sky brightness the variance of the distribution of diffuse irradiance at P can now be calculated from Equations (40) and (48). For an isotropic sky, $i_d(r)$ is constant ($=I_d/\pi$) and the variance is

$$\text{var}X_d(P) = (I_d/\pi)^2 \iint_{\Omega} \iint_{\Omega'} (\exp(-2L(z)) \times \exp(\rho V_c(r,r')) - 1) \sin\theta \sin\theta' d\omega d\omega' \quad (49)$$

In a horizontally homogeneous canopy the irradiance distribution at any point P on the horizontal plane is independent of the coordinates x and y and is equal to the horizontal irradiance distribution (the spatial distribution of irradiance on the horizontal plane). The variance of the irradiance distribution at P therefore characterises the horizontal variance. In the case of horizontal leaves the

horizontal variance further equals the variance of the irradiance distribution on the leaf area.

Table 1 and Figure 11 show some values of the mean horizontal irradiance (relative to the irradiance above the canopy), the standard deviation and the coefficient of variation in different situations, assuming an isotropic distribution of sky radiation. Depth (z), leaf radius (R) and leaf area density (l.a.d.) are the parameters which are varied. At a given depth in the canopy the coefficient of variation increases with leaf size and leaf area density (Fig. 11). With increasing depth (leaf area index) the variance (standard deviation) decreases (Table 1) due to a decreasing mean irradiance but the coefficient of variation increases (Fig. 11).

In the case of non-circular, inclined leaves the geometry becomes more complicated but the same theory is applicable. The important parameters, however, affecting the variance are the leaf size and leaf area density which are varied in the present case. The expression for the variance at a point on an inclined leaf is obtained from Equation (40) by substituting the upper hemisphere by the hemisphere facing the leaf and $\sin\theta$ by the cosine of the angle between the direction of radiation and the leaf normal at the point considered.

4.2.2. Grouped stand

Nilson (1977) gives an expression for the horizontal variance of diffuse radiation in a stand composed of Poisson-distributed trees. At depth z , the mean probability of a free line of sight in both the directions r and r' , denoted $p_{00}(z,r,r')$, is derived as

$$\begin{aligned} p_{00}(z,r,r') &= P_0(S_1+S_2-S_c) + P_0(S_1)P_1(S_2-S_c)a(r') + \\ &P_0(S_2)P_1(S_1-S_c)a(r) + \\ &P_0(S_1+S_2-2S_c)P_1(S_c)p_{00}^{(1)} + \\ &P_1(S_1-S_c)P_1(S_2-S_c)P_0(S_c)a(r)a(r') + \dots \end{aligned} \quad (50)$$

The quantities $S_1=S(z,r)$ and $S_2=S(z,r')$ are the horizontal projections of a crown envelope in directions r and r' , $S_c=S_c(r,r')$ is the

Table 1. Values of the relative mean (r.i.), standard deviation (s.d.) and coefficient of variation (c.v.) of the horizontal irradiance distribution in a horizontally homogeneous stand under isotropic sky radiation conditions, for different values of the depth in the canopy (z), the leaf radius (R) and the leaf area density (l.a.d.).

z	R	l.a.d.	L(z)	r.i.	s.d.	c.v.
0.5	0.025	1	0.5	0.607	0.0777	0.128
1	0.025	1	1	0.368	0.0475	0.129
2	0.025	1	2	0.135	0.0176	0.130
0.5	0.025	2	1	0.368	0.0758	0.206
1	0.025	2	2	0.135	0.0285	0.211
2	0.025	2	4	0.018	0.0039	0.215
0.5	0.025	4	2	0.135	0.0410	0.304
1	0.025	4	4	0.018	0.0058	0.322
2	0.025	4	8	0.0003	0.0001	0.380
0.5	0.050	1	0.5	0.607	0.1214	0.200
1	0.050	1	1	0.358	0.0758	0.206
2	0.050	1	2	0.135	0.0285	0.211
0.5	0.050	2	1	0.368	0.1071	0.291
1	0.050	2	2	0.135	0.0410	0.304
2	0.050	2	4	0.018	0.0058	0.322
0.5	0.050	4	2	0.135	0.0591	0.438
1	0.050	4	4	0.018	0.0088	0.490
2	0.050	4	8	0.0003	0.0002	0.694

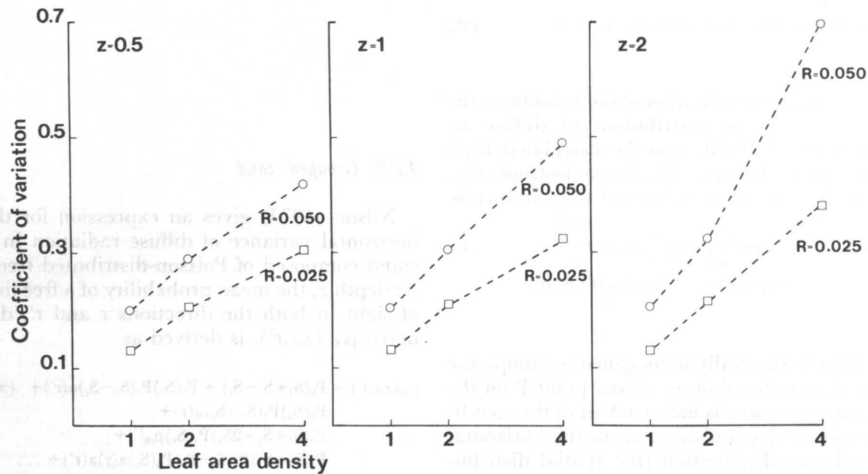


Fig. 11. The coefficient of variation of the horizontal irradiance distribution as a function of the leaf area density in a horizontally homogeneous stand at different depths ($z = 0.5, 1, 2$) and for different values of the leaf radius ($R = 0.025 \text{ m}, 0.050 \text{ m}$).

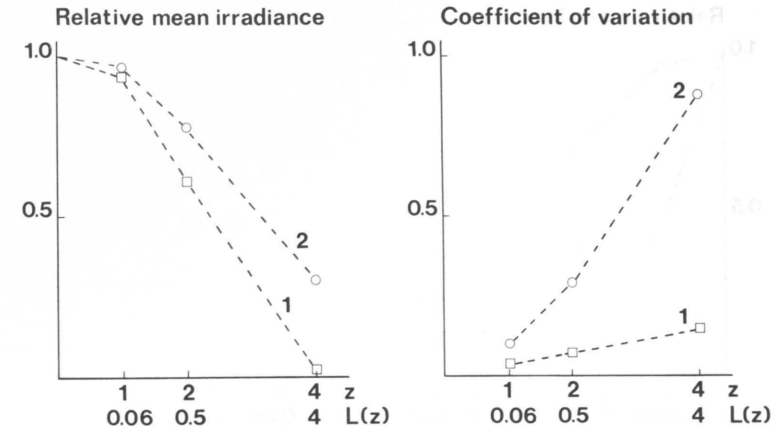


Fig. 12. The relative mean and the coefficient of variation of the horizontal irradiance distribution at different depths (z) (leaf area index $L(z)$) in (1) a horizontally homogeneous stand and (2) a grouped stand.

area of the common part of S_1 and S_2 , $P_i(S)$ is the probability of i stems located on the area S , $a^i(r)$ is the probability of a free line of sight through i tree crowns in direction r and $p_{00}^{(i)}$ is the probability of a free line of sight in both direction r and r' , through i crowns.

When trees are Poisson-distributed, the probability $P_i(S)$ is by definition

$$P_i(S) = (\lambda S)^i \exp(-\lambda S) / i! \quad (51)$$

If it is assumed that $p_{00}^{(i)} = a^i(r) a^i(r')$, where $a(r)$ is the crown transparency in direction r , Equation (50) may be written

$$p_{00}(z, r, r') = \exp(-\lambda(S_1 + S_2 - S_c)) \sum_i \sum_j \sum_k \frac{\alpha^i}{i!} \frac{\beta^j}{j!} \frac{\gamma^k}{k!} \quad (52)$$

where $\alpha = \lambda a(r)(S_1 - S_c)$, $\beta = \lambda a(r')(S_2 - S_c)$ and $\gamma = \lambda a(r) a(r') S_c$. Noting that $e^x = \sum (x^i / i!)$, Equation (52) further reduces to

$$p_{00}(z, r, r') = \exp(-\lambda((1-a(r))S_1 + (1-a(r'))S_2)) \times \exp(\lambda(1-a(r))(1-a(r'))S_c) \quad (53)$$

With present notations $(1-a(r))S_1 = T(z, r)$, $(1-a(r'))S_2 = T(z, r')$ and $(1-a(r))(1-a(r'))S_c = T_c(z, r, r')$ (= the shaded part of S_c). The covariance may thus be written

$$\text{cov}(\delta, \delta') = \exp(-\lambda(T(z, r) + T(z, r')) \times \exp(\lambda T_c(z, r, r')) - 1) \quad (54)$$

and T_c is obtained as

$$T_c(z, r, r') = \int_{S(z, r)} ((1 - \exp(-\phi l, t_r(x, y))) \times (1 - \exp(-\phi l, t_{r'}(x, y)))) dx dy \quad (55)$$

Equation (54) was derived assuming that the basic elements, the crowns, are randomly distributed and have a non-statistical transmission coefficient $a(r)$, i.e. within a crown the probabilities of gaps in two different directions are independent of each other.

For a given distribution of diffuse sky radiation the horizontal variance of diffuse radiation is obtained from Equations (40) and (54). In Figure 12 the relative mean horizontal irradiance of incoming isotropic sky radiation and the coefficient of variation at different depths (leaf area indices) in a horizontally homogeneous and a grouped stand are compared. The grouped stand was assumed to be composed of Poisson distributed trees with conical crowns of height 4 m and width 2 m. The stand density was 0.25 m^{-2} , total (one-sided) leaf area index was 4 and the leaf area was assumed to be randomly dispersed in the

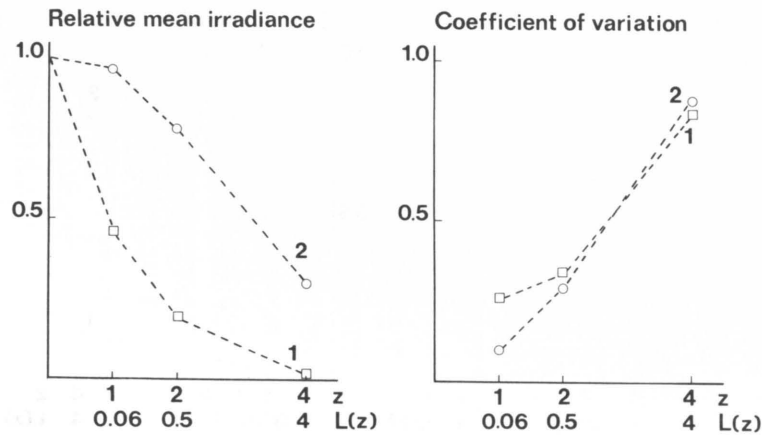


Fig. 13. The relative mean and the coefficient of variation of the irradiance distribution in a grouped stand (1) at a point in the center of a tree crown, and (2) on the horizontal plane, expressed as functions of the canopy depth (z) (leaf area index $L(z)$).

crowns. In the homogeneous stand the leaf area above any given height was equal to that in the grouped stand and the leaves were assumed to be circular with a leaf radius of 0.025 m.

In the grouped stand the mean horizontal irradiance at a given depth in the canopy is higher than in the horizontally homogeneous stand (Fig. 12a) and the coefficient of variation is considerably larger (Fig. 12b). Grouping into crowns thus reduces the mean irradiance and causes an increased spatial variation in the horizontal.

In a grouped stand the irradiance distribution is not horizontally independent and the mean and variance at a point P inside a crown differ from the mean and variance of the horizontal irradiance distribution at the same depth. The probability of gaps in the directions r and r' , from a point P inside a crown can be derived by treating between-crown and within-crown shading separately. Within the crown the probability of a free line of sight in direction r is given by Equation (35). The probability of gaps within the crown in both the directions r and r' is then (cf. Eqns. 42–44)

$$p_{00}^{(1)} = \exp(-q(l_t(P) + l_{t'}(P))) \exp(qV_c(r, r')) \quad (56)$$

where V_c is the volume outside which a leaf must be situated in order not to cause shade in both the directions r and r' (cf. Fig. 10).

The random functions δ_1 and δ_2 are assumed to be independent of each other and the probability of gaps in directions r and r' is then equal to the product of the probability of gaps within the crown (Eqn. 56) and the probability of free lines of sight through the other crowns in the given directions (Eqn. 53), i.e.

$$p_{00}(P, r, r') = \exp(-q(l_t(P) + l_{t'}(P))) \exp(qV_c(r, r')) \times \exp(-\lambda(T(z, r) + T(z, r'))) \exp(\lambda T_c(z, r, r')) \quad (57)$$

and the covariance is (cf. Eqns. (37) and (41))

$$\text{cov}(\delta, \delta') = \exp(-q(l_t(P) + l_{t'}(P))) \times \exp(-\lambda(T(z, r') + T(z, r'))) \times (\exp(qV_c + \lambda T_c) - 1) \quad (58)$$

In Figure 13 the relative mean and coefficient of variation of the irradiance distributions at points situated at different depths in the center of a tree crown are compared to the relative mean and coefficient of variation of the horizontal irradiance distributions at the

same depths. Inside the crown the irradiance is considerably decreased due to within-crown shading (Fig. 13a). The coefficient of variation is initially larger in the center of the crown but gradually the difference levels out (Fig. 13b). At the same mean irradiance, however, the coefficient of variation is smaller in the center of the crown.

4.3. Distribution of direct solar irradiance

The variance of the distribution of direct solar radiation can be expressed in an analogous way as that of diffuse radiation (Eqn. 40) by replacing the upper hemisphere with the solid angle subtended by the sun. Due to the small angular diameter (ca 0.5°) of the sun the degree of statistical dependency is large and the variance of direct solar radiation is considerably larger than that of diffuse radiation. The distribution of direct radiation at a point is usually close to a two-valued distribution, which is obtained by assuming parallel solar beam geometry and cannot therefore be approximated by a normal distribution. Hence, the mean and variance are not sufficient in characterising the distribution.

4.3.1. Penumbra

The penumbral area at a given height of the canopy is the area in which the sun is neither fully visible nor totally obscured. Penumbra occurs when a shading leaf only partly obscures the solar disc as seen from a given point. The solid angle subtended by a shading leaf depends on the leaf size and the distance from the point considered. When the solid angle subtended by a shading leaf is large compared with that of the sun the probability of a penumbra is small. Thus, generally speaking, in low stands with large leaves the occurrence of a penumbra is rare.

Neglecting the penumbra effect, i.e. assuming parallel solar beam geometry, a point either receives full sunlight or no direct radiation. In that case the distribution of direct solar irradiance at a given point can be approximated by a two-valued (0–1) distribution (the sun fully visible or totally obscured).

In tall stands with smaller leaves (needles), however, the penumbra effect has an important influence on the distribution of irradiance. Penumbra does not affect the mean irradiance but results in a more even distribution of irradiance.

4.3.2. Methods for deriving the distribution of direct solar irradiance

Attempts to derive the distribution of direct solar radiation analytically have been made by various authors. Miller and Norman (1971 a,b) developed a model for deriving the size distribution of sunflecks segments in a canopy with randomly dispersed leaves, assuming zero sun diameter. The irradiance distribution along a sunfleck segment was then derived taking into account the penumbra which occurs at the ends of the segment terminated by the edges of the shadow-forming leaves. The transmission value (relative irradiance) at a point on the segment was expressed as a simple function of the distance from the end of the segment and the angle between the segment and the leaf "edge". It was assumed that the leaves terminating a sunfleck lie at the same height. The occurrence of penumbra caused by leaf shadows whose geometrical edges come close to the transect without actually intersecting it and of the penumbra from neighbouring sunflecks is not considered in the model. The edge of a shadow-forming leaf is assumed to be a straight line of infinite length, a reasonable assumption in the case of (non-compound) leaves which are large compared with the apparent solar disc. The theory was tested against measurements of gap-size distribution and irradiance distribution (Norman et al. 1971) in a sumac (*Rhus typhina* L.) and a sunflower (*Helianthus annuus* L.) canopy, showing good agreement.

Denholm (1981 a,b) presents a different method for calculating the penumbra effect. First, the fractional areas of sunflecks (full sunlight), umbra (full shade) and penumbra are calculated. In the penumbral region the probabilities of n -fold penumbra, caused by a penumbral overlap of n leaves, are derived.

The probability distributions of the visible fraction of the sun in the penumbral region is then calculated under the conditional probabilities of n -fold penumbra. The cases of $n \leq 2$ are solved analytically, assuming straight as well as curved leaf edges. The case of a penumbral overlap of more than two leaves, however, becomes too complicated for an analytical solution and in that case it is assumed that the radiation is distributed as diffuse flux.

Common to both the above mentioned models is that they apply to canopies with randomly dispersed (convex) leaves which are large in comparison with the apparent solar disc and where the probability of more than two-fold penumbra is small. Since the penumbral region increases in deep canopies with small leaves it may be argued that these models fail to estimate the influence of penumbra in situations where it can be expected to be of importance. In a coniferous stand the penumbral region is large and the region of umbra is small because a conifer needle is practically unable to totally obscure the sun. In addition, the small gaps between needles grouped into shoots increase the probability of a penumbral overlap of several needles. Penumbra, in coniferous stands, cannot therefore be treated with help of above mentioned methods.

Monte Carlo methods

An alternative method of estimating the distribution of direct solar radiation is by the Monte Carlo method. In the Monte Carlo method the "behaviour" of a process is imitated by simulating random variables connected with the process.

The application of Monte Carlo methods in simulating canopy-radiation interactions was first introduced by Japanese scientists. For example, Tanaka (1969, 1970) used a Monte Carlo simulation to estimate the sunlit leaf area in a tobacco plant community. The stand was described with a geometrical model in which the leaves were divided into triangular sections with given coordinates. Random numbers were produced to hit the indi-

vidual leaf sections and the number of hits was the random variable quantity by which the sunlit leaf area was estimated.

In the works of Oikawa and Saeki (1977) and Oikawa (1977 a,b) the penetration of radiation in plant communities of different geometry (a canopy with randomly distributed foliage and a square-planted population) was estimated by a Monte Carlo simulation. Models including canopy reflectance are presented by e.g. Smith and Oliver (1972), Szwarcbbaum and Shaviv (1976) and Kimes et al. (1980).

Oker-Blom (1984, 1985 a) uses a Monte Carlo simulation method to calculate probability density functions of direct solar irradiance within a hypothetical canopy. At a given point in the canopy the relative irradiance is assumed to be proportional to the visible fraction of the solar disc. The method is as follows: Leaves (shoots) are generated in the crowns of the canopy according to a uniform spatial distribution by means of a random number generator. At any particular point in the canopy the visible fraction of the sun is simulated by dividing the solid angle subtended by the sun into equal portions, each represented by one direction, and testing whether or not the direction is obscured by one of the randomly generated leaves (shoots). The share of unobscured directions is the simulated random variable quantity representing the visible fraction of the sun. By repeating the procedure a number of times a frequency distribution is obtained. This distribution is an estimate of the probability density function of relative direct solar irradiance at the particular point.

The simulated probability density functions of relative direct solar irradiance at some points of a hypothetical canopy are shown in Figures 14 and 15 (Oker-Blom 1984). The stand was composed of cylindrical crowns of height 2.67 m and width 1.33 m. The leaves were assumed to be horizontal discs with a radius of 0.025 m and a number density of 500 m^{-3} .

In Figure 14 the distributions resulting from within-crown and between-crown shading are compared. At a point subjected to only within-crown shading (Fig. 14a-b) the effect of penumbra is small. In the simulations the probabilities of penumbra at the linear depth (=path length within the crown

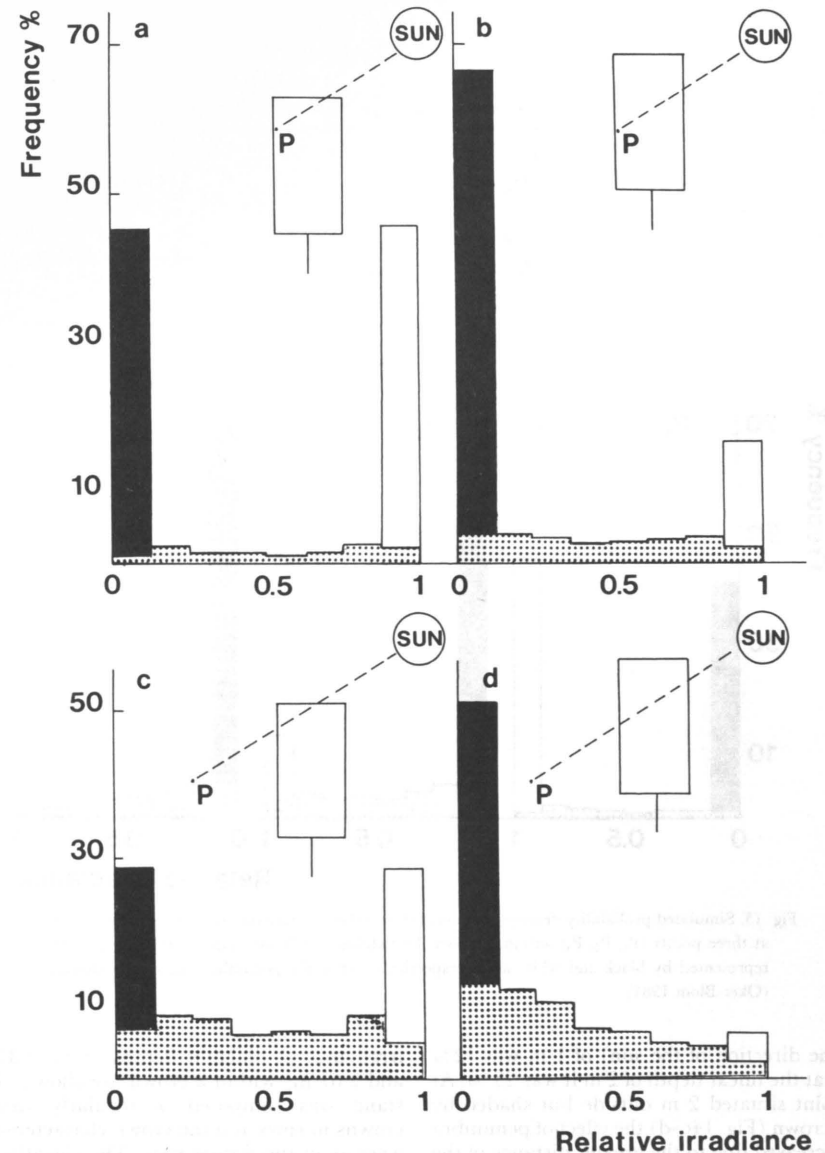


Fig. 14. Simulated probability density functions of the relative irradiance of direct solar radiation at a point P subjected to within-crown shading (a,b) or between-crown shading (c,d). Probabilities of "total shade" and "full sun" are represented by black and white areas respectively, while the penumbral fraction is shaded. (Oker-Blom 1984).

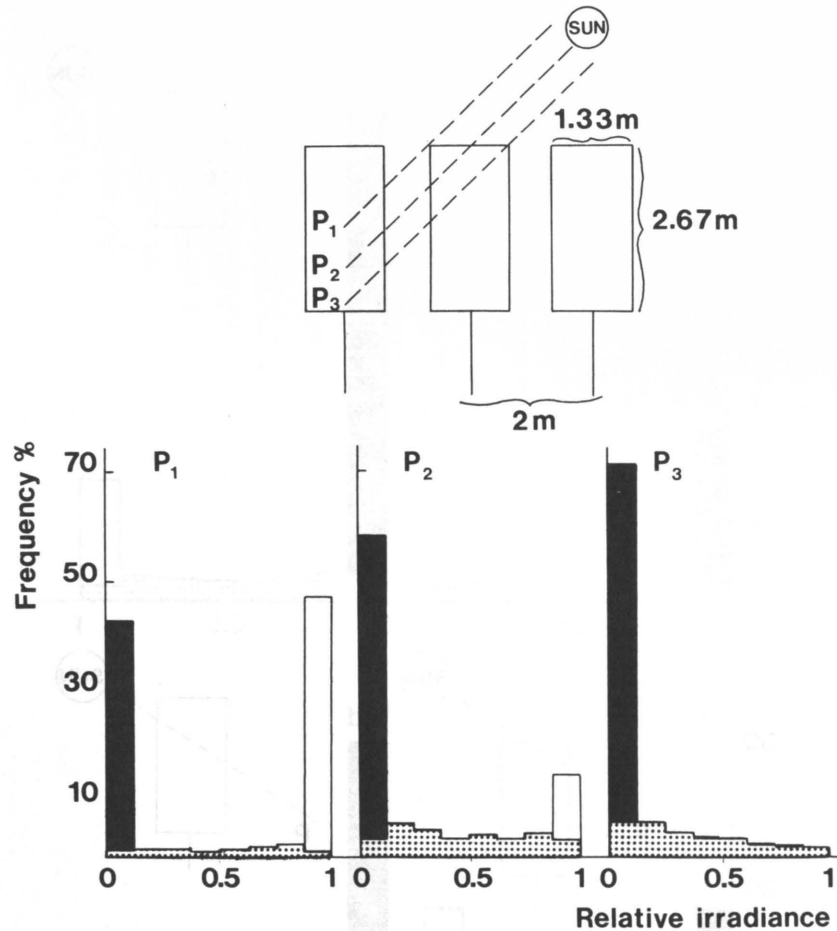


Fig. 15. Simulated probability density functions for the relative irradiance of direct solar radiation at three points (P_1 , P_2 , P_3) within a crown. Probabilities of "total shade" and "full sun" are represented by black and white areas respectively, while the penumbral fraction is shaded. (Oker-Blom 1984).

in the direction of the sun) of 1 m was 12% and at the linear depth of 2 m it was 23%. At a point situated 2 m outside but shaded by the crown (Fig. 14c-d) the effect of penumbra is increased due to the greater distance of the shading elements. The probabilities of penumbra are 54% (linear depth 1 m) and 58% (linear depth 2 m), respectively.

In Figure 15 the simulated probability density functions of the relative direct solar

irradiance at different depths (1 m, 1.33 m and 2.67 m) within a crown are shown. The stand was composed of regularly spaced crowns in rows and the crown characteristics were as in the former case. The elevation of the sun was assumed to be 45° and its azimuth equal to that of the tree row. At the highest point (P_1) subjected to within-crown shading only the distribution is quite similar to a 0-1-distribution, the probability of

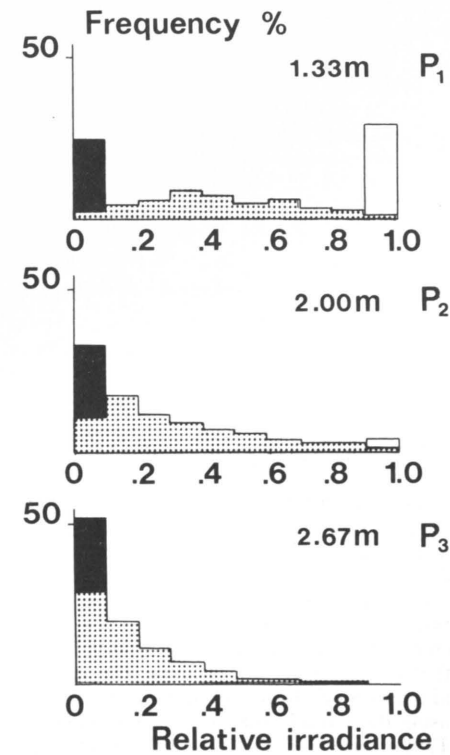


Fig. 16. Simulated probability density functions of the relative irradiance of direct solar radiation at three points (P_1 , P_2 , P_3) in a coniferous crown. Probabilities of "total shade" and "full sun" are represented by black and white areas respectively, while the penumbral fraction is shaded. (Oker-Blom 1985a).

penumbra being only 10%. At the lower points (P_1 and P_2) the between-crown shading results in an increasing penumbra effect, the probabilities being 30% and 33%.

In Figure 16 (Oker-Blom 1985a) the corresponding simulated probability density functions within a crown of a coniferous canopy are shown. The canopy was modeled as above except for the shoot structure. The shoots are described as cylinders of length 0.09 m and width 0.04 m and the orientation of the shoot axes is assumed to be spherical. The transmission coefficient of a shoot was assumed to be a binomially distributed random variable with mean 0.6 and a variance depending on the distance from the shading shoot to the point under consideration. The expected projection area of a shoot then equals that of a circular leaf with radius 0.025 m when projected on a plane making the angle of 45° with the leaf, and the mean irradiances at the points P_1 , P_2 and P_3 are thus equal to those in the leaf canopy (Fig. 15). By comparing the corresponding density functions the influence of shoot structure can be assessed.

In the present case the probabilities of penumbra are 50%, 76% and 77%, i.e. considerably higher than for the leaf canopy which were 10%, 30% and 33%. The probabilities of "total shade" and "full sun" are correspondingly smaller. In the leaf canopy the probability of total shade is large and increases with depth in the crown. In the coniferous canopy, however, the probability of total shade is small throughout the crown, reflecting the fact that a needle rarely is capable of obscuring the total solar disc.

5. RADIATION AND PHOTOSYNTHESIS

5.1. Photosynthetic response to radiation

The dependence of photosynthetic rate (F) on irradiance is known to be non-linear. This non-linearity of the photosynthetic response curve causes problems in estimating the mean rate of photosynthesis (\bar{F}) from the mean irradiance (\bar{I}). Because F is a concave function, $F(\bar{I})$ is always an overestimate of \bar{F} , unless there is no variation in the irradiance.

In order to estimate the mean photosynthesis per unit leaf area during a specific time period, information on the spatial and temporal irradiance distributions are needed. When the temporal variation in irradiance is rapid, i.e. when the fluctuations are fast compared with the response time of photosynthesis, momentary values of the irradiance should not be used in estimating the rate of photosynthesis (cf. Thornley 1974, Percy et al. 1985). In a canopy, this kind of rapid variation in direct solar irradiance may occur, for instance, as a result of branch movement and leaf flutter.

However, when the temporal variation is slow compared with the response time of photosynthesis, the rate of photosynthesis at a given moment can be assumed to be independent of the irradiance at any earlier moment. The temporal mean rate of photosynthesis can then be obtained as the mean of these "momentary" rates (cf. Thornley 1974).

Analogously, the small size of the independently operating photosynthetic units allows one to treat them theoretically as points (Leverenz 1985, personal communication), and the spatial mean rate of photosynthesis can be obtained by integrating over the spatial irradiance distribution.

Thus, the mean steady-state photosynthetic rate of a leaf area L at a given moment is obtained as the expectation value of F with respect to the spatial irradiance distribution H_L . Formally, it can be expressed as

$$\bar{F} = \int_0^{I_{\max}} F(I) dH_L(I) = (1/L) \iint_{0,L} F(I) dH_P(I) dL \quad (59)$$

where H_P is the irradiance distribution at P_i belonging to L and I_{\max} is the maximum value of I .

In order to get an estimate of \bar{F} the spatial irradiance distribution or the distributions of irradiance at various points on the leaf area are thus needed.

5.2. Estimation of photosynthesis

The irradiance distribution at a given point in the canopy is formed as the sum of two nearly independent random variables – the direct and diffuse component. As demonstrated above, the distribution of diffuse radiation is usually rather narrow (see also Gutschick 1984). For overcast sky conditions it is therefore possible to estimate the rate of photosynthesis from the mean and variance using the second order approximation of the Taylor series (cf. Thornley 1976, Hari et al. 1984, Smolander 1984). Alternatively, the irradiance distribution may be approximated by a truncated normal distribution with given mean and variance.

Using a rectangular hyperbola to describe the photosynthetic response, Thornley (1976) shows that the maximum relative error in estimating \bar{F} by $F(\bar{I})$ is

$$(dF/F)_{\max} = -(1/4)v^2 \quad (60)$$

where v is the coefficient of variation for the irradiance distribution. Applied to the values given in Table 1 and Figure 11–13 this approximation in most cases gives maximum relative errors of only a few percent.

Due to the considerably larger variation of the direct solar irradiance this component is the main factor determining the shape of the irradiance distribution while the diffuse component only slightly deforms it (Hari et al. 1985). The variable shape of the irradiance distribution for direct solar radiation at diffe-

rent points causes difficulty in obtaining estimates of the mean rate of photosynthesis during clear sky conditions.

If the penumbra effect is small enough to be neglected the situation is simple. In that case the irradiance distribution at any point is two-valued and the probability of full sunlight equals the probability of a gap in the sun's direction. The irradiance at a point on a leaf receiving full sunlight is determined by the angle between the directions of sun and leaf normal and the spatial distribution of irradiance on the leaf area is then determined by the distribution of gaps in the direction of the sun and by the leaf area orientation.

Among all distributions with a given mean value a two-valued distribution has the maximum possible variance. For a large class of concave functions (e.g. photosynthetic response curves) this distribution gives the lowest expectation value (average rate of photosynthesis) (cf. Lappi and Smolander 1984). The 0–1 distribution is thus highly unfavourable regarding photosynthesis. The influence of penumbra is that of making the distribution more even by creating a penumbral area in which the relative irradiance is between 0 and 1. With increasing depth in the canopy the mean irradiance decreases, the probability of penumbra increases and the probability of "full sun" decreases (cf. Figs. 14–16).

In the leaf canopy model (Fig. 15) rates of photosynthesis calculated with help of the simulated irradiance distributions and using a Blackman-type response curve (Blackman 1905), saturating at one half of full sunlight, were 4 % (P_1), 23 % (P_2) and 42 % (P_3) higher than those obtained by assuming parallel solar beam geometry (cf. Oker-Blom 1984). In the coniferous-canopy model (Fig. 16) the rates increased with 23 %, 60 % and 69 %, respectively (Oker-Blom 1985a).

These results, although based on theoretical calculations for hypothetical canopies, indicate that the influence of penumbra in many situations is too important to be neglected. In coniferous stands this is probably true at practically all levels of the canopy while in canopies with larger leaves the penumbra mainly affects the irradiance distribution and rates of photosynthesis in the lower canopy (cf. Denholm 1981b). The influence of penumbra on rates of photosynthesis

also depends on the photosynthetic characteristics of the leaves, – the more linear is the photosynthetic response curve, the smaller is the influence of penumbra (cf. Norman et al. 1971).

The fact that the distribution of direct radiation is so variable and depends on a large number of structural characteristics of the canopy, however, makes it difficult to define the irradiance distribution with only a few characteristics (mean, moments etc.). By simulation methods the irradiance distribution at certain points of the canopy may be estimated and the effect of penumbra can be quantified. Situations for which the effect of penumbra must be considered can also be identified by simulation. This method is, however, too laborious to be applied on the whole canopy and therefore needs to be combined with a theoretical analysis of the problem.

5.3. Shoot photosynthesis

In the preceding analysis it has been shown that the problems of estimating the mean rate of photosynthesis are particularly difficult for an irradiance distribution formed by the direct solar component in the presence of penumbra. In many situations the diffuse component can be considered as being formed as a sum of a large number of independent variables and thus has a distribution tending to a normal distribution, characterised by the mean and variance. In addition, the variation of diffuse radiation inside a stand is often so small that use of the mean irradiance alone gives satisfactory estimates of the mean rate of photosynthesis.

This is, however, not always the case. As will be shown, the clustering of needles in a shoot creates a radiation field within the shoot which is very different from that surrounding the shoot. The complex structure of a coniferous shoot thus causes some additional difficulties in relating shoot photosynthesis to irradiance. The irradiance distribution on the shoot's needle area is strongly dependent on shoot structure and radiation field geometry.

The irradiance $X(P_1)$ at a point P_1 within the shoot can be expressed as

$$X(P_1) = \int_{\Omega_1} i(r)\delta_1(P_1,r)\delta_2(P_1,r)\delta_3(P_1,r) \cos r_1 d\omega \quad (61)$$

where $\delta = \delta_1\delta_2\delta_3$ is the random function having the value 0 or 1 depending on whether the direction r is occluded or not.

The function δ is divided in components based on the nature of shading: δ_1 describes the gap distribution resulting from between-crown shading, δ_2 that resulting from within-crown shading and δ_3 that resulting from within-shoot shading.

The function δ_1 mainly depends on the density, size and spatial distribution of trees. Between-crown shading is normally caused by foliage elements located at a great distance, thus creating a penumbra effect which considerably levels out the spatial variation in direct solar irradiance.

The function δ_2 is determined by the inner structure of the crown. Within-crown shading causes a gradient in the mean irradiance and the spatial variation caused by within-crown shading is larger than that caused by between-crown shading because the shading elements are located at a smaller distance.

The distribution of δ_3 depends on the shoot structure in the same way as δ_1 and δ_2 depend on canopy and crown structure. This dependency is, however, on a quite different scale due to the fact that at a given point within a shoot a needle of the same shoot is capable of occluding a many times larger fraction of the hemisphere than needles belonging to other shoots. This follows from the fact that the solid angle occluded by a needle is inversely proportional to the square of its distance away from the point considered.

From two separate points on the same shoot, a shoot located at a great distance as compared with the distance between the points is seen in approximately the same direction and occludes solid angles of the same size. From this we can conclude that within the confines of a shoot the distributions of δ_1 and δ_2 are not very variable. Thus, the spatial variation of irradiance within a shoot is mainly determined by the within-shoot shading (Oker-Blom 1986).

For deriving the irradiance distribution on the needle area of a shoot a description of shoot structure is needed. Based on the previ-

ously mentioned model of shoot geometry (Oker-Blom et al. 1983) the spatial distribution of irradiance for a Scots pine shoot was simulated using a Monte Carlo technique (Oker-Blom 1986). In the simulations the two different radiation fields surrounding the shoot were described as (a) isotropic diffuse radiation from the upper hemisphere and (b) isotropic diffuse radiation from the upper hemisphere combined with direct solar radiation. The shoot was assumed to be horizontally lying, sun elevation was 45° and the ratio between direct solar radiation (received normally to the solar beam) and diffuse radiation (received on the horizontal) was 10.

Figure 17 (Oker-Blom 1986) shows the simulated spatial irradiance distributions over the needle area under the radiation conditions (a) and (b). The relative mean irradiances (based on total needle surface area) were 0.233 (a) and 0.146 (b). The coefficients of variation for the spatial irradiance distributions were 0.91 (a) and 1.70 (b), respectively.

Within-shoot shading resulted in a low mean irradiance and a large spatial variation on the shoot's needle area. Both the mean and variance are sensitive to the directional distribution of the surrounding radiation field. In a directional field where the radiation is concentrated to a small solid angle the mean irradiance is highly dependent on the direction of the shoot relative to the direction of radiation. The spatial variation is increasing with the directionality of the surrounding radiation field. At equal irradiance the variance was 3.5 times larger for the simulated irradiance distribution in case (b) than for the isotropic case (a).

With help of the simulated irradiance distributions (Fig. 17), the rates of photosynthesis for the shoot in conditions (a) and (b) were calculated, using a Blackman curve to describe the photosynthetic response of a needle surface area element (cf. Terashima and Saeki 1985). Parameters for the Blackman curve were $a=210 \mu \text{Em}^{-2}\text{s}^{-1}$ (irradiance at which saturation occurs) and $F_m=15.6 \text{mgCO}_2\text{dm}^{-2}\text{h}^{-1}$ (maximum rate), estimated from measurements of a model shoot (Oker-Blom 1985b). Rates expressed as a function of the mean irradiance on the needle area are shown in Figure 18 (Oker-Blom 1986). As a result of the larger spatial variation of ir-

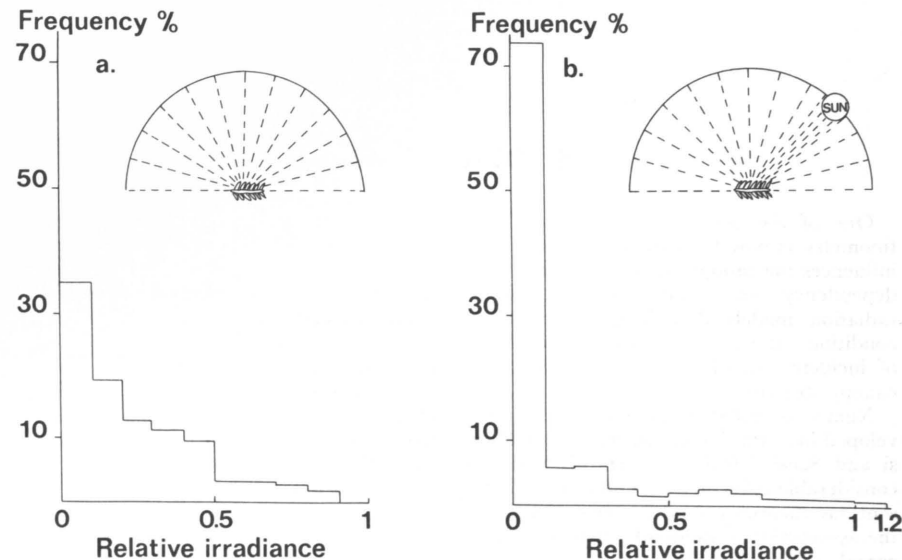


Fig. 17. Simulated irradiance distributions on the needle area of a horizontally lying shoot subjected to (a) isotropic radiation from the upper hemisphere and (b) isotropic diffuse radiation and direct solar radiation. (Oker-Blom 1986).

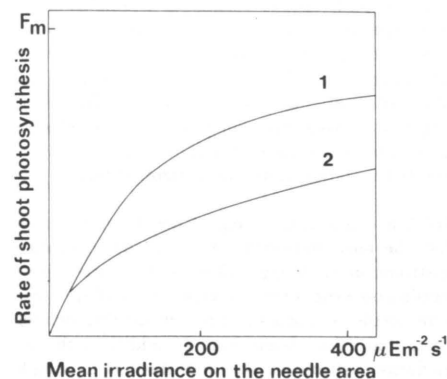


Fig. 18. Rates of shoot photosynthesis, calculated using the simulated irradiance distributions in Fig. 17 (curve 1: condition (a), curve 2: condition (b)) and expressed as a function of the mean irradiance on the needle area. (Oker-Blom 1986).

radiance in the directional field (Fig. 17b), calculated rates of photosynthesis are clearly higher in the isotropic radiation field (Fig. 17a).

The directional distribution of radiation appears to be an important factor regarding the photosynthetic response of a shoot. In a direct radiation field the amount of intercepted radiation, which depends on the direction of the shoot relative to that of radiation, is the major component causing variation in the photosynthetic response (Smolander et al. 1986). In a multidirectional radiation field, however, the irradiance is distributed more evenly on the needle area than in the case of a highly directional radiation field. At an equal mean irradiance rates of photosynthesis are therefore likely to be higher in a multidirectional than in a direct radiation field (cf. Fig. 18). It has also been shown from experimental measurements that, at an equal total flux, the rate of photosynthesis for a shoot is increased for multidirectional radiation compared to direct radiation (cf. Zelawski et al. 1973, Leverenz and Jarvis 1979). Thus, the mean irradiance on the needle area of a shoot is not a sufficient characteristic for the radiation conditions of a shoot and should be combined with knowledge about shoot structure and radiation field geometry.

6. DISCUSSION

One of the main problems in phytoclimatology is how the canopy structure itself influences the canopy radiation regime. This dependency can be analysed with canopy radiation models describing the radiation conditions, and using as input data properties of incident radiation and a description of canopy structure.

Numerous radiation models have been developed since the first classical model of Monsi and Saeki (1953). During this period a considerable refinement has taken place. Present-day theories are no longer restricted by the assumption of randomly dispersed, horizontal and black leaves.

The consideration of non-random leaf dispersion (cf. e.g. Acock et al. 1970, Nilson 1971) and various different leaf orientations (e.g. De Wit 1965, Duncan et al. 1967, Ross and Nilson 1966) is included in many theories. Scattering of radiation is also treated in several models (cf. e.g. Cowan 1968, Norman et al. 1971, Ross 1981).

These models have mostly been developed for agricultural crops, in which the horizontal distribution of leaves has been assumed to be uniform. Thus, in most models the vertical gradient in irradiance is considered while averaging is done along the horizontal, i.e. the horizontal variation and its influence on the statistical characteristics of irradiation at the leaf level are not considered.

The horizontal variation in irradiance results mainly from two sources: (a) horizontal heterogeneity of the canopy due to grouping of foliage and (b) the highly directional distribution of incoming radiation during clear skies. These affect different components of the variation: direct solar radiation causes a large variation from point to point anywhere in the canopy, and horizontal heterogeneity causes gradients in the mean irradiance along the horizontal. The grouping of foliage affects not only the irradiance distribution on hypothetical horizontal planes but, particularly, the distribution of irradiance on the foliage area.

Grouping of foliage into crowns typically occurs in forest stands. In coniferous stands the grouping of needles into shoots further increases the horizontal heterogeneity. Another specific characteristic of a coniferous stand is the small size of needles, causing a penumbra effect which affects the distribution of direct solar irradiance. The influence of these special features of coniferous stands has been treated in the present study. The theoretical results obtained can be summarized as follows.

(a) Grouping of foliage into individual crowns results in a considerable decrease in the interception of radiation per unit leaf area as compared with a horizontally homogeneous stand. This is particularly evident for a stand with low density and a non-regular spatial pattern of trees. While the grouping always results in a smaller total interception per unit leaf area, the interception rates at the lower canopy may be increased by the grouping effect. Thus, both the slope and the shape of the attenuation curve is affected by grouping into crowns. Grouping of foliage results in gradients of the mean irradiance and in an increased variation along the horizontal plane.

(b) For conifers, grouping of needles into shoots has the most important effect on the irradiance distribution on foliage. Due to the clustering of needles on a shoot the interception of radiation per unit needle area of a shoot is considerably smaller than that of a planar leaf. In addition, the irradiance distribution within a shoot is to a high degree determined by the within-shoot shading. The shoot structure creates a very uneven spatial distribution of irradiance on the needle area. The irradiance distribution is further sensitive to the directionality of the radiation field. In a multidirectional field, radiation is distributed more evenly on the needle area, and as a result rates of photosynthesis are higher.

(c) Penumbra has an important effect on the distribution of direct solar irradiance. In coniferous

stands the influence of penumbra is considerable at practically all levels of the canopy and has a large effect on rates of photosynthesis.

The reliability of these results naturally depends on the adequacy of the assumptions involved. The strong dependency between canopy structure and radiation regime particularly emphasizes the need for adequate descriptions of stand structure. A detailed description of a forest stand involves various parameters such as the spatial pattern of trees, crown shape, spatial distribution of leaves (shoots) in the crowns, shoot structure etc., while its usefulness on the other hand presupposes simplification and generalization. So far, realistic and yet simple descriptions of the structure of forest stands have not been developed.

An important application of theoretical modeling, however, is namely to identify the structural characteristics which significantly affect the radiation regime of a stand. The present results show that certain structural properties of forest stands, such as the grouping into crowns and shoots, the complex shoot structure and the needle size largely affect the within-stand radiation regime and therefore should be considered in modeling the stand structure.

The large temporal and spatial variation of radiation in combination with the non-linear photosynthetic response to irradiance makes it difficult to characterise the canopy radiation regime in relation to photosynthesis. In estimating the photosynthetic production during a specified period, the spatial and temporal irradiance distributions over the foliage area are needed. This is not only a problem in theoretical modeling but causes considerable problems in radiation measurements – a very large number of sensors measured simultaneously is needed in order to get reliable estimates of the spatial and temporal variation (cf. Hari et al. 1985).

In addition to the problems of time and space there is a problem of relevance connected with radiation measurements (Ander-

son 1965). Radiation is measured with artificial surfaces which differ from the photosynthetically active elements with respect to size, structure, arrangement and directional distribution. In addition, measurements always involve averaging over space. Thus, for instance, the spatial irradiance distributions during clear skies, formed by sunflecks, shaded areas and penumbral areas cannot be adequately measured. Under these circumstances it is difficult to relate measurements to the actual radiation conditions for the leaf area in the canopy. These difficulties connected with radiation measurements further emphasize the need for developing theoretical radiation models. The same difficulties are, on the other hand, present when testing and verifying radiation models. Therefore, more emphasis should simultaneously be placed on the development of new instruments (cf. Gutschick et al. 1985) that could help test and validate the theory.

There is a great potential for the use of radiation models. In spite of great theoretical advancement in modeling the radiative transfer in a canopy, radiation models have not yet been used as an effective tool for predicting plant productivity or manipulating crop yield. The reason for this is not associated with theoretical problems in modeling the radiative transfer in vegetation. On the contrary, radiation models, considered in isolation, are quite sophisticated. An effective use of radiation models, however, presupposes that consideration given to other important variables is at an equally appropriate level. It seems that our theoretical knowledge of the radiation environment far exceeds, for example, our understanding of a plant's physiological response to radiation. Another restriction to the use of radiation models is the lack of realistic descriptions of the canopy structure which ultimately forms the radiation regime. Any further development of theoretical radiation models therefore should be directed towards a greater realism by integrating knowledge in related disciplines.

REFERENCES

- Acock, B., Thornley, J. H. M. & Warren Wilson, J. 1970. Spatial variation of light in the canopy. In: I. Setlik (Ed.), Prediction and Measurement of Photosynthetic Productivity, pp. 91–102. Centre for Agricultural Publishing and Documentation, Pudoc, Wageningen.
- Anderson, M. C. 1964. Studies of the woodland light climate. 1. The photographic computation of light conditions. *J. Ecol.* 52: 27–41.
- 1965. Some problems of simple characterization of the light climate in plant communities. In: Bainbridge, R., Evans, G. C. & Rackham, O. (Eds.), Light as an ecological factor, pp. 77–90. Blackwell Scientific Publications, Oxford.
- 1966. Stand structure and light penetration. II. A theoretical analysis. *J. Appl. Ecol.* 3: 41–54.
- Baldocchi, D. D., Hutchison, B. A., Matt, D. R. & McMillen, R. T. 1985. Canopy radiative transfer models for spherical and known leaf inclination angle distributions: A test in an oak-hickory forest. *J. Appl. Ecol.* 22: 539–555.
- Blackman, F. F. 1905. Optima and limiting factors. *Ann. Bot.* 19: 281–295.
- Brown, P. S. & Pandolfo, J. P. 1969. An equivalent-obstacle model for the computation of radiative flux in obstructed layers. *Agric. Meteorol.* 6: 407–421.
- Brunig, E. F. 1976. Tree forms in relation to environmental conditions: an ecological viewpoint. In: M. G. R. Cannel & F. T. Last (Eds.), Tree physiology and yield improvement, pp. 139–156. Acad. Press, London.
- Carter, G. A. & Smith, W. K. 1985. Influence of shoot structure on light interception and photosynthesis in conifers. *Plant Physiol.* 79: 1038–1043.
- Charles-Edwards, D. A. & Thornley, J. H. M. 1973. Light interception by an isolated plant, a simple model. *Ann. Bot.* 37: 919–928.
- Clark, P. J. & Evans, F. C. 1954. Distance to nearest neighbour as a measure of spatial relationship in populations. *Ecology* 35 (4): 445–453.
- Cole, L. C. 1946. A theory for analyzing contagiously distributed populations. *Ecology* 27 (4): 329–341.
- Cowan, I. R. 1968. The interception and absorption of radiation in plant stands. *J. Appl. Ecol.* 5: 367–379.
- Cox, F. 1971. Dichtebestimmung und Strukturanalyse von Pflanzenpopulationen mit Hilfe von Abstandsmessungen. *Mitt. Bundesforsch. Anst. Forst- und Holzwirtschaft., Reinbek b. Hamburg*, 87: 1–184.
- Cramér, H. 1945. Mathematical methods of statistics. Hugo Gebers förlag, Uppsala. 575p.
- Denholm, J. V. 1981a. The influence of penumbra on canopy photosynthesis. I. Theoretical considerations. *Agric. Meteorol.* 25: 145–166.
- 1981b. The influence of penumbra on canopy photosynthesis. II. Canopy of horizontal circular leaves. *Agric. Meteorol.* 25: 167–194.
- Duncan, W. G., Loomis, R. S., Williams, W. A. & Hanau, R. 1967. A model for simulating photosynthesis in plant communities. *Hilgardia* 38 (4): 181–205.
- Fisher, J. B. & Honda, H. 1979 a. Branch geometry and effective leaf area: a study of Terminalia-branching pattern. 1. Theoretical trees. *Amer. J. Bot.* 66 (6): 633–644.
- & Honda, H. 1979 b. Branch geometry and effective leaf area: a study of Terminalia-branching pattern. 2. Survey of real trees. *Amer. J. Bot.* 66 (6): 645–655.
- Gates, D. M. 1980. Biophysical ecology. Springer-Verlag, New York Inc. 611p.
- , Keegan, H. J., Schleter, J. C. & Weidner, W. R. 1965. Spectral properties of plants. *Appl. Opt.* 4 (1): 11–20.
- Gutschick, V. G. 1984. Statistical penetration of diffuse light into vegetative canopies: effect on photosynthetic rate and utility for canopy measurement. *Agric. Meteorol.* 30: 327–341.
- , Barron, M. H., Waechter, D. A. & Wolf, M. A. 1985. Portable monitor for solar radiation that accumulates irradiance histograms for 32 leaf-mounted sensors. *Agric. Meteorol.* 33: 281–290.
- Hallé, F., Oldeman R.A.A. & Tomlinson, P. B. 1978. Tropical trees and forests: an architectural analysis. Springer-Verlag, Berlin. 441p.
- Hari, P., Nilson, T., Salminen, R., Kaipainen, L., Korpilähti, E. & Ross, J. 1984. Nonlinear dependence of photosynthetic rate on irradiance and its consequences for estimates of the amount of carbohydrates formed. *Photosynthetica* 18 (1): 28–33.
- , Kaipainen, L., Korpilähti, E., Mäkelä, A., Nilson, T., Oker-Blom, P., Ross, J. & Salminen, R. 1985. Structure, radiation and photosynthetic production in coniferous stands. Research notes 54, University of Helsinki, Department of Silviculture. 233 p.
- Horn, H. S. 1971. The adaptive geometry of trees. Princeton University Press, New Jersey. 144p.
- Jahnke, L. S. & Lawrence, D. B. 1965. Influence of photosynthetic crown structure on potential productivity of vegetation, based primarily on mathematical models. *Ecology* 46 (3): 319–326.
- Jarvis, P. G. & Leverenz, J. W. 1983. Productivity of temperate, deciduous and evergreen forests. In: Lange, O. L., Nobel, P. S., Osmond, C. B. & Ziegler, H. (Eds.), Physiological plant ecology IV, Encyclopedia of plant physiology, vol. 12D, pp. 233–280. Springer Verlag, Berlin.
- Johnson, J. D. 1984. A rapid technique for estimating the total surface area of pine needles. *Forest Sci.* 30 (4): 913–921.
- Kellomäki, S., Oker-Blom, P. & Kuuluvainen, T. 1986. The effect of crown and canopy structure on light interception and distribution in a tree stand. In: Tigerstedt, P. M. A., Puttonen, P. & Koski, V. (Eds.), Crop physiology of forest trees, pp. 107–115. Proceedings of an International Conference on Managing Forest Trees as Cultivated Plants. University Press, Helsinki.
- Kimes, D. S., Ranson, K. J. & Smith, J. A. 1980. A Monte Carlo calculation of the effects of canopy geometry on PAR absorption. *Photosynthetica* 14 (1): 55–64.
- Lappi, J. & Smolander, H. 1984. Intergration of the hyperbolic radiation-response function of photosynthesis. *Photosynthetica* 18 (3): 402–410.
- Lemeur, R. & Blad, B. 1974. A critical review of light models for estimating the short-wave radiation regime of plant canopies. *Agric. Meteorol.* 14: 255–286.
- Leverenz, J. W. & Jarvis, P. G. 1979. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). VIII. The effects of light flux density and direction on the rate of photosynthesis and the stomatal conductance of needles. *J. Appl. Ecol.* 16: 919–932.
- Levy, E. B. & Madden, E. A. 1933. The point method of pasture analysis. *New Zeal. J. Agric.* 46: 267–279.
- Mann, J. E., Curry, G. L., Hartfiel, D. J. & Demichele, D. W. 1977. A general law for direct sunlight penetration. *Math. Biosci.* 34: 63–78.
- Miller, E. E. & Norman, J. M. 1971a. A sunfleck theory for plant canopies. I. Lengths of sunlit segments along a transect. *Agron. J.* 63: 735–738.
- & Norman, J. M. 1971b. A sunfleck theory for plant canopies. II. Penumbra effect: Intensity distribution along sunfleck segments. *Agron. J.* 63: 739–743.
- Monzi, M. & Saeki, T. 1953. Über den Lichtfactor in den Pflanzengesellschaften und seine bedeutung für die Stoffproduktion. *Jap. J. Bot.* 14(1): 22–52.
- Monteith, J. L. 1965. Radiation and crops. *Exp. Agric. Rev.* 1: 241–251.
- Moon, P. & Spencer, D. E. 1942. Illumination from a non-uniform sky. *Trans. Illum. Engng. Soc., N. Y.* 37: 707–712.
- Nilisk, H., Nilson, T. & Ross, J. 1970. Radiation in plant canopies and its measurement. In: I. Setlik (Ed.), Prediction and measurement of photosynthetic productivity pp. 165–177. Centre for Agricultural Publishing and Documentation, Pudoc, Wageningen.
- Nilson, T. 1971. A theoretical analysis of the frequency of gaps in plant stands. *Agric. Meteorol.* 8: 25–38.
- 1977. A theory of radiation penetration into non-homogeneous plant canopies. In: The penetration of solar radiation into plant canopies. *Acad. Sci. Estonian SSR, Tartu (in Russian)*. 145p.
- Norman, J. M. 1975. Radiative transfer in vegetation. In: De Vries, D. A. & Afgan, N. H. (Eds.), Heat and mass transfer in the biosphere. 1. Transfer processes in plant environment, pp. 187–205. Scripta Book, Washington D. C.
- , Miller, E. E. & Tanner, C. B. 1971. Light intensity and sunfleck-size distribution in plant canopies. *Agron. J.* 63: 743–748.
- & Jarvis, P. G. 1974. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). III. Measurements of canopy structure and interception of radiation. *J. Appl. Ecol.* 11: 375–398.
- & Jarvis, P. G. 1975. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). V. Radiation penetration theory and a test case. *J. Appl. Ecol.* 12: 839–878.
- Oikawa, T. 1977a. Light regime in relation to plant population geometry. II. Light penetration in a square-planted population. *Bot. Mag. Tokyo* 90: 11–22.
- 1977b. Light regime in relation to plant population geometry. III. Ecological implications of a square-planted population from the viewpoint of utilization efficiency of solar energy. *Bot. Mag. Tokyo* 90: 301–311.
- & Saeki, T. 1977. Light regime in relation to plant population geometry. I. A Monte Carlo simulation of light microclimates within a random distribution foliage. *Bot. Mag. Tokyo* 90: 1–10.
- Oker-Blom, P. 1984. Penumbra effects of within-plant and between-plant shading on radiation distribution and leaf photosynthesis: A Monte Carlo simulation. *Photosynthetica* 18(4): 522–528.
- 1985a. The influence of penumbra on the distribution of direct solar radiation in a canopy of Scots pine. *Photosynthetica* 19(3): 312–317.
- 1985b. Photosynthesis of a Scots pine shoot: Simulation of the irradiance distribution and photosynthesis of a shoot in different radiation fields. *Agric. For. Meteorol.* 34: 32–40.
- 1986. Irradiance distribution and photosynthesis of a Scots pine shoot as influenced by shoot structure and solar radiation field geometry. In: T. Fujimori & D. Whitehead (Eds.), Crown and canopy structure in relation to productivity, pp. 382–395. Forestry and Forest products Research Institute, Ibaraki, Japan.
- & Kellomäki, S. 1981. Light regime and photosynthetic production in the canopy of a Scots pine stand during a prolonged period. *Agric. Meteorol.* 24: 185–199.
- & Kellomäki, S. 1982a. Effect of angular distribution of light on light absorption and photosynthesis in the plant canopy: Theoretical computations. *Agric. Meteorol.* 26: 105–116.
- & Kellomäki, S. 1982b. Theoretical computations on the role of crown shape in the absorption of light by forest trees. *Math. Biosci.* 59: 291–311.
- & Kellomäki, S. 1983. Effect of grouping of foliage on the within-stand and within-crown light regime: Comparison of random and grouping canopy models. *Agric. Meteorol.* 28: 143–155.
- , Kellomäki, S. & Smolander, H. 1983. Photosynthesis of a Scots pine shoot: The effect of shoot inclination on the photosynthetic response of a shoot subjected to direct radiation. *Agric. Meteorol.* 29: 191–206.
- Paltridge, G. W. & Platt, C. M. R. 1976. Radiative processes in meteorology and climatology. In: Developments in Atmospheric Science, 5. Elsevier Scientific Publishing Company. 318p.
- Pearcy, R. W., Osteryoung, K. & Calkin, H. W. 1985. Photosynthetic responses to dynamic light environments by Hawaiian trees. *Plant Physiol.* 79: 896–902.
- Pohtila, E. 1980. Spatial distribution development in young tree stands in Lapland (in Finnish). *Commun. Inst. For. Fenn.* 98(1): 1–35.
- Ross, J. 1975. Radiative transfer in plant communities.

- In: Monteith, J. L. (Ed.), *Vegetation and the atmosphere*, vol. 1, pp. 13–55. Acad. Press, London.
- 1981. The radiation regime and architecture of plant stands. Dr. W. Junk Publishers, The Hague. 391p.
- & Nilson, T. 1965. The extinction of direct radiation in crops. In: *Questions on radiation regime of plant stand*, pp. 25–64. Acad. Sci. ESSR, Inst. Phys. Astron., Tartu (in Russian).
- & Nilson, T. 1966. A mathematical model of the radiation regime of vegetation. In: V. K. Pyldmaa (Ed.), *Actinometry and Atmospheric Optics*, pp. 253–270. Israel Progr. for Sci. Transl., Jerusalem, 1971.
- Satterlund, D. R. 1983. Forest shadows: How much shelter in a shelterwood? *Forest Ecology and Management* 5: 27–37.
- Skellam, J. G. 1952. Studies in statistical ecology. I. Spatial pattern. *Biometrika* 39: 349–362.
- Smith, J. A. & Oliver, R. E. 1972. Plant canopy models for simulating composite scene spectroradiance in the 0.4 to 1.05 micrometer region. In: *Proceedings of the 8:th International Symposium of remote sensing*, pp. 1333–1353. Environ. Univ. Mich.
- Smolander, H. 1984. Measurement of fluctuating irradiance in field studies of photosynthesis. *Acta For. Fenn.* 187: 1–56.
- , Oker-Blom, P., Ross, J., Kellomäki, S. & Lahti, T. 1986. Photosynthesis of a Scots pine shoot: Test of a shoot photosynthesis model in a direct radiation field. *Agric. For. Meteorol.* 39.
- Szwarcbaum, I. & Shaviv, G. 1976. A Monte Carlo model for the radiation field in plant canopies. *Agric. Meteorol* 17: 333–352.
- Takeda, T. 1961. Studies on the photosynthesis and production of dry matter in the community of rice plants. *Jap. J. Bot.* 17: 403–437.
- Tanaka, S. 1969. Estimation of sunlit leaf area in tobacco plant community by the Monte Carlo method. Estimation of direct sunlight. In: *Photosynthesis and utilization of solar energy*, pp. 76–79. Level III Experiment, 1968. Tokyo.
- 1970. Geometrical distribution of leaves in tobacco plant community. In: *Photosynthesis and utilization of solar energy*, pp. 16–19. Level III Experiments 1969. Tokyo.
- Terashima, I. & Saeki, T. 1985. A new model for leaf photosynthesis incorporating the gradients of light environment and of photosynthetic properties of chloroplasts within a leaf. *Ann. Bot.* 56: 489–499.
- Terjung, W. H. & Louie, S. S. 1972. Potential solar radiation on plant shapes. *Int. J. Biometeorol.* 16: 25–43.
- Thornley, J. H. M. 1974. Light fluctuations and photosynthesis. *Ann. Bot.* 38: 363–373.
- 1976. *Mathematical models in plant physiology*. Acad. Press, London. 318p.
- Warren Wilson, J. 1960. Inclined point quadrats. *New Phytologist* 58: 92–101.
- 1963. Estimation of foliage denseness and foliage angle by inclined point quadrats. *Aust. J. Bot.* 11: 95–105.
- 1965. Stand structure and light penetration. I. Analysis by point quadrats. *J. Appl. Ecol.* 2: 383–390.
- 1967. Stand structure and light penetration. III. Sunlit foliage area. *J. Appl. Ecol.* 4: 159–165.
- Wit, C. T. De. 1965. *Photosynthesis of leaf canopies*. Agric. Res. Report No. 663: 1–57, Wageningen.
- Zelawski, W., Szaniawski, R., Dybczynski, W. & Piechurowski, A. 1973. Photosynthetic capacity of conifers in diffuse light of high illuminance. *Photosynthetica* 7(4): 351–357.

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