

## THE BARE BONES OF LEAF-ANGLE DISTRIBUTION IN RADIATION MODELS FOR CANOPY PHOTOSYNTHESIS AND ENERGY EXCHANGE

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### ABSTRACT

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The effects of leaf-angle distribution in radiation models for canopy photosynthesis and energy exchange can be accurately described by using as few as three leaf-angle classes (0-30°, 30-60° and 60-90°). On this basis, simple equations have been developed and tested for reflectance, extinction and distribution of radiation in leaf canopies. In these equations the spherical leaf-angle distribution, default in most models, serves as a point of reference.

### INTRODUCTION

The equations to represent the effect of leaf-angle distribution on light interception were developed in the nineteen sixties by authors such as de Wit (1965), Cowan (1968), Lemeur (1971) and Ross (1975) to a point where the practical methodology of measuring the leaf-angle distributions in the field hampered further progress. Fortunately, the theory also showed that there is not a strong effect of leaf-angle distribution on light extinction and photosynthesis, so that highly refined data of leaf-angle distribution are not required. A reasonable guess for the leaf-angle distribution of most crops is the spherical or isotropic one. This distribution can serve as a base line and it is therefore used as a standard in most models (de Wit et al., 1978). However, sometimes the need is felt to introduce some detail about deviating leaf-angle distributions, e.g., by breeders to compare performance of cultivars.

The purpose of this paper is to describe the effects of these other distributions, with as few as three leaf-angle classes (0-30°, 30-60° and 60-90°). Naturally, for three classes the empirical data can be provided with less difficulty than for the nine classes employed in most other literature.

Because the photosynthetic and stomatal response to radiation is non-lin-

ear, not only the total absorbed radiation is of interest, but also how it is distributed over the leaf area. Sources of unevenness in distribution of radiation over the leaves are extinction of radiation with depth in the canopy, the presence of sunlit and shaded leaf area, and differences in orientation towards the sun among the sunlit leaves.

In radiation models these three sources of unevenness are treated in the following way: (1) extinction of radiation with depth in the canopy can be handled by stratification of the leaf canopy, or by integration over the profile; (2) within each layer sunlit and shaded leaf area is distinguished on the basis of the extinction coefficients for direct and diffuse radiation; (3) within the sunlit area the distribution of the cosines of incidence of the direct solar radiation (irradiation distribution) is used for a further classification of the sunlit leaves.

#### THE THEORETICAL ATTRACTIVENESS OF THE SPHERICAL LEAF ANGLE DISTRIBUTION

In the spherical leaf-angle distribution, all orientations of the leaf surfaces have equal probability. This lack of directional preference leads to relatively simple solutions of the unevenness problem. In particular, the irradiation distribution of sunlit leaves must be independent of the solar elevation. The distribution of the leaf surfaces can be compared to the distribution of the surface elements of a sphere. The mean projected area of a random set of leaf surfaces into any direction is equal to one half of the total surface area of these leaves. This simple ratio can be derived from the ratio of the base of a hemisphere (the projected area) to its surface (the set of the leaf surfaces). Another simple relationship is the distribution of the cosine of incidence of direct radiation. This distribution is uniform from zero to one, so that the mean cosine is equal to one half, which is in accordance with the mean projected area.

Not only is the spherical leaf-angle distribution theoretically attractive, it also appears a good first-order approximation for real leaf canopies. Therefore, it is desirable to keep the spherical leaf-angle distribution as a point of reference in the description of other distributions.

#### ANGLE OF INCIDENCE AND PROJECTION OF LEAVES, AND EXTINCTION COEFFICIENT

The extinction coefficient  $K$  occurs in the exponential equation for the radiation profile as follows

$$I = I_0 \exp(-KL) \quad (1)$$

where  $I_0$  = incoming radiation flux,  $I$  = radiation flux at canopy depth  $L$ , and  $L$  = leaf area between top of the canopy and considered level. The value of  $K$

for a direct beam of radiation is related to its mean cosine of incidence on the leaf surfaces. For a single flat leaf the cosine  $t$  of the angle of incidence is described by the angle of tilt  $\lambda$  of the leaf (leaf angle), the solar elevation  $\beta$  above the horizon, and the difference in azimuthal orientation  $\alpha$  between leaf normal and sun

$$t = \sin \beta \cos \lambda + \cos \beta \sin \lambda \cos \alpha \quad (2)$$

If the leaf orientations do not have any azimuthal preference, the distribution of  $t$  is uniform with  $\alpha$  and the cumulative distribution function of  $t$  can be found by letting  $\alpha$  increase uniformly from  $-\pi$  to 0 (Fig. 1). The other half of the azimuthal circle from 0 to  $\pi$  can be omitted for reasons of symmetry. The range  $-\pi$  to 0 for  $\alpha$  is now equivalent to the range 0–1 for the cumulative distribution probability  $S$  (Fig. 1).

For light interception, and normally also for photosynthesis, it does not matter whether the upper or the lower side of a leaf is directly illuminated so that negative values of  $t$  are equivalent to their positive counterparts. This fact complicates the dependence of  $t$  on  $S$  if the sun angle  $\beta$  is lower than the leaf angle  $\lambda$  (Fig. 2). In this  $(t, S)$  diagram both axes range from 0 to 1. According to elementary calculus the average value of  $t$  can be found as the integral of  $t$  with respect to the cumulative probability  $S$

$$\bar{t} = \int_0^1 t \, dS \quad (3)$$

Graphically, this quantity is equal to the area under the  $(t, S)$  curve (as a fraction of the total area of the diagram). It is the same quantity as the average projection of the leaves into the direction of the solar beam, called  $O$  by de Wit (1965), and  $G$  by Ross (1975).

The interception and the consequent extinction of radiation can be derived when the value of  $O$  is known, because the extinction coefficient  $K$  is equal to  $O/\sin\beta$ . For constant  $K$ , the extinction of radiation is exponential with leaf area index reckoned from the top of the canopy. The average irradiance of leaves at any depth in the canopy can now be calculated.

The expression for  $O$  can be found by substitution of eq. 2 into 3, and subsequent analytical integration of the absolute value of  $t$ . Again, for uniform azimuthal orientation, the solution is

$$O(\beta, \lambda) = \sin\beta \cos\lambda \quad \beta > \lambda \quad (4a)$$

or

$$O(\beta, \lambda) = \frac{2}{\pi} [\sin\beta \cos\lambda \arcsin(\tan\beta/\tan\lambda) + (\sin^2\lambda - \sin^2\beta)^{0.5}] \quad \beta < \lambda \quad (4b)$$

For horizontal leaves this expression condenses into  $\sin\beta$ , because all cosines

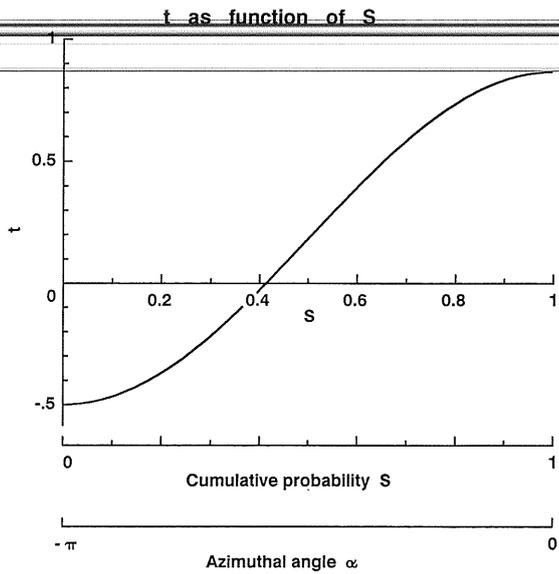


Fig. 1. Cosine  $t$  of incidence of radiation on a leaf surface, as a function of the azimuthal angle  $\alpha$ , for the assumed azimuthal uniformity of leaf orientation (eq. 2). The cumulative probability  $S$  can then be projected directly on the abscissa, so that a  $(t,S)$  diagram emerges. In this example with  $\lambda$  at  $45^\circ$  and  $\beta$  at  $15^\circ$ , negative values of  $t$  occur (illumination of lower side).

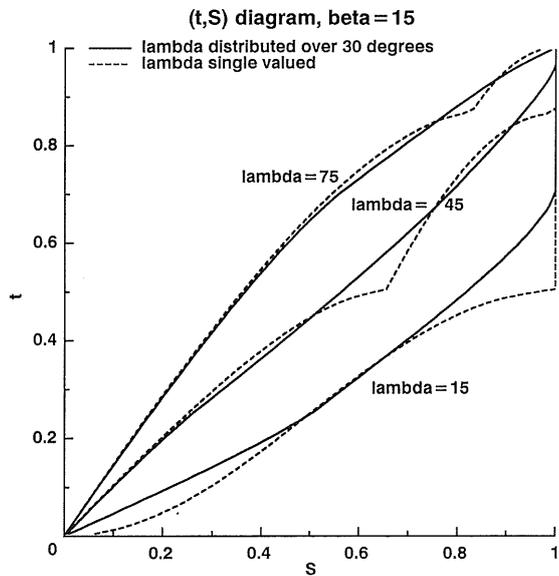


Fig. 2.  $(t,S)$  diagram with only the absolute values of  $t$ , for  $\beta$  at  $45^\circ$  and for three values of  $\lambda$  (dashed lines). When the leaf angles are taken as distributed (proportional to  $\sin \lambda$ ) over the  $30^\circ$  class considered, the relationship is more linear (solid lines).

of incidence are concentrated on to one single value:  $\sin\beta$ . Computation of photosynthesis is then relatively simple.

For composite leaf-angle distributions, the mean value of the projection  $O$  must be found by integration over the leaf-angle distribution  $F$  between zero and  $\pi/2$ :

$$\bar{O}(\beta) = \frac{2}{\pi} \int_0^{\pi/2} F(\lambda) O(\beta, \lambda) d\lambda \quad (5)$$

As a major simplification, of which the accuracy will be discussed below, this expression is approximated by

$$\bar{O}(\beta) = F_1 O_1(\beta) + F_2 O_2(\beta) + F_3 O_3(\beta) \quad (6)$$

where  $F_1$ ,  $F_2$  and  $F_3$  stand for the relative frequencies of leaves in the three inclination classes around  $15^\circ$ ,  $45^\circ$  and  $75^\circ$ , respectively, covering thirty degrees each. In other words,  $F_1$  is defined by the integral of  $F(\lambda)$  from 0 to  $\pi/6$ , divided by the same integral from 0 to  $\pi/2$ . The sum of  $F_1$ ,  $F_2$  and  $F_3$  is unity by definition.

The shape of  $F(\lambda)$  within the class boundaries is taken as sinusoidal with  $\lambda$  in order to ensure a homogeneous density of the leaf normals within the leaf-angle class considered.

In Fig. 3 the dependence of  $O_1$ ,  $O_2$  and  $O_3$  on the solar elevation is drawn as calculated by eq. 4. The shape of the graphs suggests the possibility to approximate  $O_1$  and  $O_2$  as a combination of a sinusoid and a constant lower limit

$$O_1 = \max(0.26, 0.93 \sin\beta) \quad (7a)$$

$$O_2 = \max(0.47, 0.68 \sin\beta) \quad (7b)$$

This approach does not work that easily for  $O_3$ , but instead the expression for  $O_3$  was derived from the constraint that the projection for the spherical leaf-angle distribution must be equal to 0.5, whatever the solar elevation. This value of 0.5 follows immediately from the ratio of the projection of a hemisphere to its surface area. The relative frequencies  $F_1$ ,  $F_2$  and  $F_3$  for a spherical distribution are 0.134, 0.366 and 0.5, respectively, as calculated from  $1 - \cos(30)$ ,  $\cos(30) - \cos(60)$ , and  $\cos(60) - \cos(90)$ . The distribution is similar to that of the surface area on a sphere. With these frequencies, eq. 6 yields the following expression for  $O_3$

$$O_3 = 1 - 0.268 O_1 - 0.732 O_2 \quad (7c)$$

The close agreement of these approximating equations with the exact expression (eq. 4), can be checked in Fig. 3 where these approximations have been drawn as solid lines.

The other curves in Fig. 3 give the  $O$ -values for single leaf angles of  $15^\circ$ ,  $45^\circ$

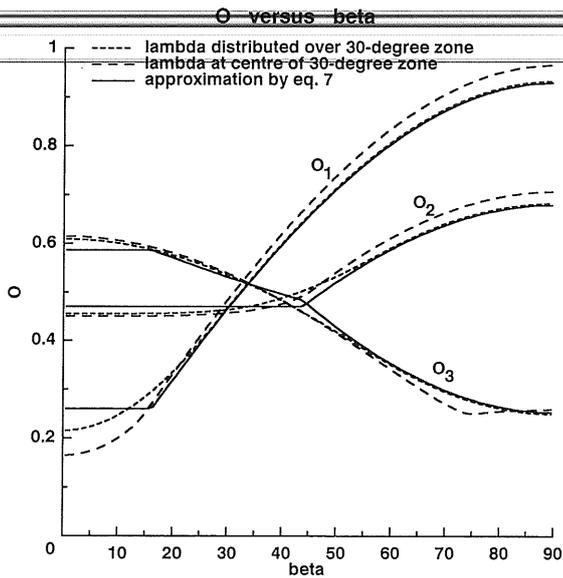


Fig. 3. Leaf projection  $O$  as a function of elevation  $\beta$ , according to the approximating eq. 7 (solid lines), and the exact values of  $O$  calculated for leaf-angle distributed over a  $30^\circ$  zone and for a single leaf angle at the centre of the zone. The three groups of curves stand for the standard leaf-angle classes centred around  $15^\circ$ ,  $45^\circ$  and  $75^\circ$  inclination.

and  $75^\circ$ , respectively. The effect of distributing the leaf angles within each of the  $30^\circ$  classes is also illustrated. For either type of distribution within the  $30^\circ$  class, sharply peaked or distributed, the approximation by eqs. 6 and 7 works very well. Although perhaps the deviation, which occurs for  $\beta < 10^\circ$ , could have been corrected by a more complex formulation of eq. 7a, for reasons of simplicity the deviation is accepted. At such low solar elevations the direct beam is usually weak anyway.

#### EXTINCTION COEFFICIENT $K$

The geometry of incoming radiation can be simplified to stem from two sources: a solar point-source of direct radiation and a uniform sky source of diffuse radiation. The beam of direct radiation follows an exponentially declining curve within the leaf canopy, characterized by an extinction coefficient  $K_{\text{direct}}$ . Within the canopy, however, secondary diffuse radiation is also generated from intercepted direct radiation. The sum of the primary (direct) and secondary (diffused by the leaf canopy) components together also show an approximately exponential extinction, but with a smaller extinction coeffi-

cient. The value of this coefficient  $K_{\text{tot}}$  can be found as  $K_{\text{direct}}(1-\sigma)^{1/2}$  (Goudriaan, 1977). Once  $\bar{O}(\beta)$  is determined by eqs. 6 and 7,  $K_{\text{direct}}$  can be calculated as  $\bar{O}(\beta)/\sin\beta$  (Table 1).

The profile of diffuse sky radiation in the canopy is a summation of profiles each originating from a different ring zone of the sky. The extinction coefficient for the radiation from each of these zones can be found just by substituting zone elevation for solar height. Radiation components from low elevation will decrease faster in the leaf canopy, because of their larger  $K$ -value, than those originating from near the zenith. With increasing leaf area index ( $LAI$ ) the effective  $K$ -value, calculated as  $-\ln(I/I_0)/L$ , will steadily decrease (Fig. 4) because the vertical radiation components will dominate at greater canopy depth.

The accuracy of the calculation of the total profile of sky radiation increases with the number of zones distinguished. In Fig. 4 the results based on nine  $10^\circ$  zones (solid lines) as well as based on three  $30^\circ$  zones (using Table I) have been compared for the horizontal,  $45^\circ$ , vertical and spherical leaf-angle distributions. For low values of  $LAI$ , all  $K$ -values for diffuse radiation tend to unity. With increasing  $LAI$ , the importance of leaf angle also increases. In view of the good performance of the approximation by three  $30^\circ$  zones, as shown in Fig. 4, the profile of diffuse radiation can be described well by the following equation

$$I = I_0 \left[ \frac{1}{4} \exp(-K_{15}L) + \frac{1}{2} \exp(-K_{45}L) + \frac{1}{4} \exp(-K_{75}L) \right] \quad (8)$$

where the subscripts of  $K$  refer to the elevation of incoming radiation. The weights  $\frac{1}{4}$ ,  $\frac{1}{2}$  and  $\frac{1}{4}$  represent the contributions from the three  $30^\circ$  zones of a uniform overcast sky (UOC), which is characterized by equal radiance all over the sky. Each ring zone contributes a fraction given by the integral of  $\sin\beta \cos\beta$  integrated between the zone boundaries. The more realistic standard overcast sky (SOC: Grace, 1971) is characterized by a sky radiance that increases with elevation  $\beta$  according to the function  $1 + 2 \sin \beta$ . Integration of this function (multiplied by the geometrical factors  $\sin\beta \cos\beta$ ) results in the weight coefficients 0.178, 0.514 and 0.308 for the three SOC zones, instead of the values  $\frac{1}{4}$ ,  $\frac{1}{2}$ ,  $\frac{1}{4}$ , respectively, which were used in eq. 8 for the UOC.

TABLE 1

Extinction coefficient  $K$  computed for each leaf-angle class as a function of elevation  $\beta$  of the incoming radiation

	$\beta$		
	$15^\circ$	$45^\circ$	$75^\circ$
$K_1$	1.00	0.93	0.93
$K_2$	1.82	0.68	0.68
$K_3$	2.26	0.67	0.29

## K-diffuse

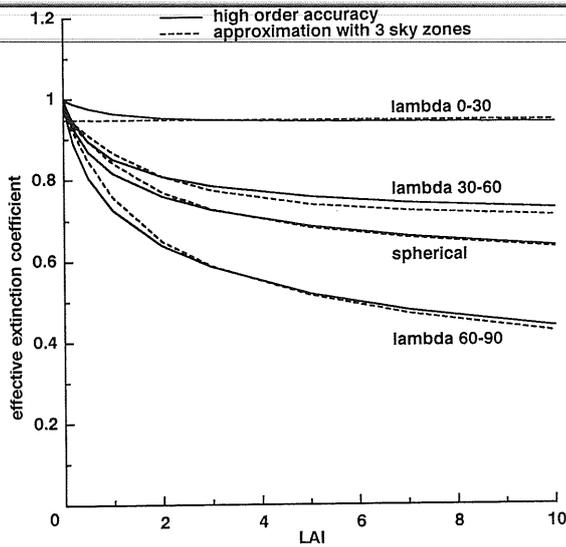


Fig. 4. The effective extinction coefficient, computed as  $-\ln(I/I_0)/L$  on the basis of the approximating eqs. 8 and 9 (dashed lines) and a much more accurate nine-zone method (solid lines). The results include the spherical leaf-angle distribution, and the three standard leaf-angle classes centred round  $15^\circ$ ,  $45^\circ$  and  $75^\circ$  inclination.

On the basis of Table 1 the three  $K$ -values can be found by linear addition of the contributions of the three leaf-angle classes

$$K_{15} = 1.00 F_1 + 1.82 F_2 + 2.26 F_3 \quad (9a)$$

$$K_{45} = 0.93 F_1 + 0.68 F_2 + 0.67 F_3 \quad (9b)$$

$$K_{75} = 0.93 F_1 + 0.68 F_2 + 0.29 F_3 \quad (9c)$$

The first derivative of eq. 8 with respect to  $L$  provides the sky radiation  $H$  absorbed per leaf area at depth  $L$

$$H = I_0 \left[ \frac{1}{4} K_{15} \exp(-K_{15}L) + \frac{1}{2} K_{45} \exp(-K_{45}L) + \frac{1}{4} K_{75} \exp(-K_{75}L) \right] \quad (10)$$

For the SOC the coefficients  $\frac{1}{4}$ ,  $\frac{1}{2}$  and  $\frac{1}{4}$  must be adapted as discussed above. If one prefers to neglect the dependence of the extinction coefficient on sky zone elevation, the value of  $K_{45}$  is the best single approximation.

To account for scattering of radiation, each of these extinction coefficients should have been premultiplied with  $(1-\sigma)^{1/2}$ . Canopy reflection  $\rho$  is included by a factor  $(1-\rho)$  applied to the entire expression.

TABLE 2

Canopy reflection as a function of solar elevation (no diffuse radiation). Comparison of detailed model results (Goudriaan, 1977, table 6) and the approximating eq. 12, for  $\sigma=0.3$ . Then  $\rho_{\text{hor}}$  equals 0.089 for all combinations. For a spherical leaf-angle distribution,  $\bar{O}$  is equal to 0.5

	Solar elevation		
	5°	45°	85°
Detailed model result	0.148	0.072	0.059
Approximation by eq. 12	0.152	0.074	0.059

#### CANOPY REFLECTION

Canopy reflection  $\rho$  for a canopy with horizontal leaves can be calculated (Goudriaan, 1977, p. 14) by the expression

$$\rho_{\text{hor}} = [1 - (1 - \sigma)^{1/2}] / [1 + (1 - \sigma)^{1/2}] \quad (11)$$

An exact mathematical expression for non-horizontal leaves is not possible, but a reasonable approximation is

$$\rho_c = \frac{2\bar{O}}{\bar{O} + \sin\beta} \rho_{\text{hor}} \quad (12)$$

This expression gives a decreasing canopy reflection with increasing solar elevation. Under grazing incidence  $\rho_c$  may even approach twice the standard value of a canopy with horizontal leaves. Under a very high solar elevation on the other hand,  $\rho_c$  may drop to half this value. The dependence on solar elevation is the strongest with an erectophile leaf-angle distribution. As also shown by eq. 12, the dependence disappears with horizontal leaves, because  $\bar{O}$  is then equal to  $\sin\beta$ . A few examples of the result of this equation are given in Table 2, in comparison with results obtained by a detailed model (Goudriaan, 1977).

#### DISTRIBUTION OF RADIATION

Sunlit and shaded leaves can be distinguished by a separate calculation of the profile of the direct solar beam, and of the diffuse and diffused radiation profiles (Goudriaan, 1977; Spitters, 1986). Once this large source of unevenness is accounted for, the unevenness in distribution of radiation within the class of sunlit leaves still remains. This unevenness is completely described by the cumulative distribution of the absolute value of  $t$ , as given in the  $(t, S)$  diagram (Fig. 2). A detailed subdivision of illumination classes of leaves can then be made and used to generate their different rates of photosynthesis.

The basic idea of this paper is to simplify the use of leaf-illumination classes

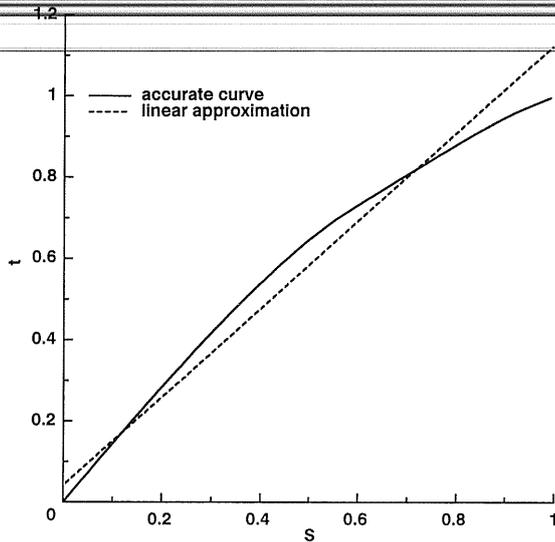
**(t,S) diagram, beta = 15, lambda 60-90**

Fig. 5.  $(t,S)$  diagram for  $\beta$  at  $15^\circ$  and  $\lambda$  distributed in the leaf-angle class from  $60$  to  $90^\circ$ . The linear relationship with mean and variance equal to the accurate curve is also drawn. In the linearized relationship,  $t$  can exceed the range  $0-1$ .

by reducing the description of the distribution of  $t$  to its mean (which is identical to  $\bar{O}(\beta)$ ), and its variance. In fact, this is equivalent to the  $(t,S)$  relationship approximated by a straight line retaining both average  $t$  (or  $O$ ) and the variance of  $t$  (Fig. 5).

The variance of the cosine of incidence follows from the integral of  $(t - \bar{t})^2$  over  $S$

$$V(\beta, \lambda) = \int_0^1 (t - \bar{t})^2 dS \quad (13)$$

which is the same as

$$V(\beta, \lambda) = \int_0^1 t^2 dS - \bar{O}^2 \quad (14)$$

An analytical evaluation of the integral of  $t^2$  leads to a remarkably simple expression

$$\int_0^1 t^2 dS = \frac{1}{2} \sin^2 \lambda + \sin^2 \beta (\cos^2 \lambda - \frac{1}{2} \sin^2 \lambda) \quad (15)$$

This expression can be derived from integration of  $t^2$  (see eq. 2), by considering that the azimuthal distribution is uniform, so that integration over  $S$  from 0 to 1 is equivalent to integration over the azimuthal angle  $\alpha$  from  $-\pi$  to 0. For single values of leaf angle the precise value of  $\lambda$  can be immediately substituted into eq. 14. However, for distributed leaf angles, a weighted integration must be done. Using a sinusoidal distribution within each of the three  $30^\circ$  classes the result is

$$\int_0^1 t^2 dS = 0.06 F_1 + 0.25 F_2 + 0.467 F_3 + \sin^2 \beta (0.81 F_1 + 0.25 F_2 - 0.4 F_3) \quad (16)$$

For reasons of isotropy we know beforehand that for a spherical leaf-angle distribution the  $(t, S)$  diagram is simply a straight line from  $(0, 0)$  to  $(1, 1)$  irrespective of solar height. Indeed, the coefficient of  $\sin^2 \beta$ , the combination  $0.81 F_1 + 0.25 F_2 - 0.4 F_3$ , is practically zero with  $F_1, F_2$  and  $F_3$  at 0.134, 0.366 and 0.5, respectively. The constant portion of eq. 16 is practically equal to  $1/3$ , being the integral of  $t^2$  between 0 and 1.

#### CROP PHOTOSYNTHESIS AND ENERGY EXCHANGE

Instead of a precise integration of leaf photosynthesis over the  $(t, S)$  curve, a linear  $(t, S)$  relationship is now used as an approximation (Fig. 5). At  $S = 0.5$  this line passes through the mean value of  $t$  (or  $O$ ). The slope of the line is equal to the square root of 12 times the variance  $V$ , as calculated by eq. 14. Because  $S$  always varies from 0 to 1, this slope is identical to the range  $r$  of  $t$  in the linear approximation

$$r = \left[ 12 \left( \int_0^1 t^2 dS - \bar{O}^2 \right) \right]^{0.5} \quad (17)$$

For the special situation of the spherical leaf-angle distribution  $\int t^2 dS$  equals 0.333333 and  $\bar{O}^2$  equals 0.25, so that  $r$  is unity. It should be noted that  $t$  calculated according to this straight line can exceed the range  $(0, 1)$ . Although physically impossible, it is perfectly alright to use such values in computations.

Integration of, e.g., photosynthesis, along this straight line for  $S$  ranging from 0 to 1 is very simple with the three-point Gaussian integration method (Goudriaan, 1986)

$$A_{\text{sunlit}} = (A(\bar{O} - \gamma r) + 1.6 A(\bar{O}) + A(\bar{O} + \gamma r)) / 3.6 \quad (18)$$

where  $A(t)$  is the assimilation rate at cosine of incidence  $t$ , and  $\gamma$  is the Gaussian width  $0.15^{1/2}$  that is used in the three-point integration.

The same procedure can be used in the calculation of the transpiration rate of the canopy.

#### APPLICATION

Real leaf-angle distributions have been grouped into classes typified by names such as 'planophile', 'erectophile', etc. (de Wit, 1965). A convenient mathematical equation to describe these distributions is the function  $\sin \lambda \exp(p\lambda)$ . The factor  $\sin \lambda$  in this function can be considered as the isotropy factor of the spherical leaf-angle distribution, the other factor serves to describe the relative deviation from isotropy. Normalized to unity over the range  $(0, \pi/2)$  this function results in the contents of the leaf-angle classes such as given in Table 3.

The values for  $p$  were chosen to yield distributions similar to the typical curves given by de Wit (1965).

The detailed  $10^\circ$  classification in combination with the detailed  $(t, S)$  functions, such as given in Fig. 2 (dashed lines), are used in a model for gross canopy assimilation. Results of this model are here called 'accurate'. Similarly, the  $30^\circ$  classification in combination with the approximating methods, as given in this paper, are used in a model; otherwise the photosynthetic and meteorological descriptions are the same. Results of this model are here called 'approximate'. The comparison of both methods is given in Table 4. For overcast conditions the agreement between both methods is almost perfect, apparently as a result of the absence of direct radiation. For clear sky conditions there is some deviation caused by the approximations discussed in this paper, but very little.

A separate point to be considered is the treatment of diffuse sky radiation. The results used for comparison between the 'accurate' and 'approximate'

TABLE 3

Leaf-angle distribution  $F$  for  $10^\circ$  and  $30^\circ$  class widths generated by the function  $\sin \lambda \exp(p\lambda)$ .  $p$ -Values of  $-3.7$  and  $0.8$  are used as characteristic for planophile and erectophile distributions

Leaf-angle class	Planophile $p = -3.7$	Spherical $p = 0$	Erectophile $p = 0.8$
0-10°	0.148	0.015	0.007
10-20°	0.250	0.045	0.024
20-30°	0.217	0.074	0.045
30-40°	0.156	0.100	0.070
40-50°	0.101	0.123	0.100
50-60°	0.061	0.143	0.133
60-70°	0.036	0.158	0.169
70-80°	0.020	0.168	0.207
80-90°	0.011	0.174	0.245
	0.615	0.134	0.076
	0.318	0.366	0.303
	0.067	0.500	0.621

TABLE 4

Comparison of daily gross CO<sub>2</sub> assimilation in kg CO<sub>2</sub> ha<sup>-1</sup> d<sup>-1</sup>, calculated by the 'accurate' and the 'approximate' models for a number of different circumstances. The chosen photosynthetic properties were  $P=30$  kg CO<sub>2</sub> ha<sup>-1</sup> h<sup>-1</sup>,  $\epsilon=0.11 \cdot 10^{-9}$  kg CO<sub>2</sub> J<sup>-1</sup>. Incoming radiation modelled as in Spitters et al. (1986) for a latitude of 50°N

	'Accurate'	'Approximate'	
	Single $K_{diffuse}$	Single $K_{diffuse}$	Multiple $K_{diffuse}$
<i>LAI=0.1</i>			
June, clear: planophile	39.895	40.739	41.037
spherical	39.779	39.762	40.602
erectophile	39.716	39.630	40.559
June, overcast: planophile	18.559	18.549	20.231
spherical	16.55	16.55	20.188
erectophile	16.279	16.282	20.164
December, clear: planophile	14.912	15.045	15.246
spherical	16.273	16.274	16.589
erectophile	16.476	16.419	16.752
December, overcast: planophile	3.422	3.422	3.841
spherical	2.966	2.966	3.841
erectophile	2.908	2.908	3.838
<i>LAI=5</i>			
June, clear: planophile	675.71	680.25	673.17
spherical	703.06	702.80	690.99
erectophile	709.53	707.63	694.91
June, overcast: planophile	293.25	293.29	289.83
spherical	294.04	294.03	286.00
erectophile	293.84	293.85	284.13
December, clear: planophile	147.19	143.35	142.45
spherical	130.48	130.39	128.08
erectophile	128.24	128.50	125.79
December, overcast: planophile	48.65	48.65	48.60
spherical	48.07	48.07	47.47
erectophile	47.96	47.96	47.05

models were obtained by treating sky radiation according to a single exponential extinction curve, for which  $K_{45}$  (eq. 9b) was used as the mean  $K$ -value. To test the validity of this simplification, extinction was more correctly modelled using eq. 10, so that the effective  $K$ -value decreases with depth (Fig. 4). The

results of this run are listed in the last column under 'multiple  $K_{\text{diffuse}}$ ', and should be compared to the middle column. The most interesting effect is the disappearance of the influence of leaf angle under very low  $LAI$ , and a simultaneous increase of photosynthesis as well. This result can be understood as being caused by convergence of all  $K$ -values to the relatively high value of unity for low  $LAI$  (Fig. 4). For large  $LAI$  on the other hand, photosynthesis is usually decreased due to a higher, but less efficient, concentration of diffuse radiation in the upper layer of leaves.

Further sophistication of the model, using an SOC distribution of sky radiation makes the results (not shown here) slightly return towards the values in the middle column (over about a quarter of the difference), but the effect of leaf angle remains very small under low  $LAI$ . In view of the simplicity of its implementation, use of the SOC seems warranted.

Whether for UOC or SOC, the multiple extinction of diffuse sky radiation should be used when it is necessary to consider the effects of leaf-angle distribution. As shown in Table 4, the error caused by simplifying extinction of diffuse sky radiation to a simple exponential relationship is of at least the same order of magnitude as that of simplifying leaf-angle distribution to a simple spherical one. Indeed, the leaf-angle effect seriously interferes with the presence of multiple extinction of diffuse sky radiation.

## DISCUSSION

This work was inspired by the idea of Ross (1975) that only three classes of leaf angle should give sufficient information for the characterization of extinction of radiation. As shown in this paper, this idea is fruitful and can be elaborated into a form applicable to photosynthesis calculations, largely retaining the accuracy of a more complex model. Ross compressed the information of the two-degrees of freedom contained in three leaf-angle classes into a single coefficient  $\chi_L$  to express the deviation between the actual and the spherical leaf-angle distribution. In this paper, the closest relative to  $\chi_L$  is the factor of  $\sin^2 \beta$  in eq. 16. Another combination of the coefficient  $F$  is used as well, so that the variance of irradiance can be calculated also.

A standard model such as described by Spitters (1986) uses the spherical leaf-angle distribution as default. The possibility to generalize the leaf-angle distributions requires eight lines of coding to be added or modified, those corresponding with the eqs. 6–10, 12, 16 and 17. Equation 18 was already included with the default values of 1 for  $r$ , and 0.5 for  $\bar{O}$ . At the expense of remarkably little coding the model can be expanded to represent the essential features of leaf-angle distribution.

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