

## SEPARATING THE DIFFUSE AND DIRECT COMPONENT OF GLOBAL RADIATION AND ITS IMPLICATIONS FOR MODELING CANOPY PHOTOSYNTHESIS

### PART II. CALCULATION OF CANOPY PHOTOSYNTHESIS.

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#### ABSTRACT

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In a preceding paper, a method was presented to estimate the diurnal courses of total, direct and diffuse radiation from total daily radiation only. In the present paper, these relations are introduced into a simulation model for daily canopy assimilation. With the assimilation—light response of single leaves, assimilation rates of sunlit and shaded leaf area are calculated in relation to vertical position within the canopy and time of day. Numerical integration over canopy layers and over the day yields the daily canopy assimilation.

Neglecting variation in illumination intensity of the leaves overestimates assimilation due to the convex, asymptotic assimilation—light response. For an atmospheric radiation transmission of 0.5 and a canopy with leaf area index of 5, daily canopy assimilation was overestimated by 2% when only the mean leaf angle was considered, 7% when all incoming light was treated as diffuse, 14% when light intensity was averaged over the day, and 23% when light absorption was averaged over canopy layers. These percentages increased sharply with an increase in atmospheric transmission. Neglecting the random variation in irradiance around the diurnal sine wave, overestimated assimilation by only 2–3%.

Daily canopy assimilation was approximated very closely by using a weighted average of the assimilation rates at only three selected canopy depths at three times of day. A more concise model appeared to be satisfactory: a rectangular hyperbola for leaf assimilation—light response, integrated analytically over canopy leaf area index and using the irradiance averaged over the day.

#### INTRODUCTION

Calculation of canopy photosynthesis from the amount of incoming photosynthetically active radiation forms the central part of most crop growth simulation models. Use of average illumination intensities of the leaves in the calculations would overestimate assimilation because of the convex assimilation—light response. Account has therefore to be taken of the temporal and spatial variation in illumination intensity. One of the sources of variation is the discrimination between diffuse skylight and direct sunlight. This partitioning of the incoming radiation into a diffuse and a

direct flux causes a spatial bimodality in illumination of the leaves: shaded leaves receive diffuse light only, while sunlit leaves receive both the diffuse and direct flux.

In Part I of this study (Spitters et al., 1986) a simple approach to estimate the diurnal courses of total, diffuse and direct radiation from daily total radiation was presented. The aim of the present paper is to incorporate the established relationships into a simulation model for daily canopy assimilation.

The modeling of canopy assimilation starts from the approach of de Wit (1965; de Wit et al., 1978), which is representative of many other simulation models in this field. Canopy photosynthesis is calculated from the absorbed amount of photosynthetically active radiation ('light', 400–700 nm) and the photosynthesis–light response of single leaves. The assimilation of shaded and sunlit leaf area is calculated separately. In the de Wit model, canopy assimilation is calculated for a standard clear sky and a standard overcast sky; actual canopy assimilation is obtained by interpolating between both by assuming that the sky is either clear or overcast. Spitters et al. (1986), demonstrated that this approach is not justified because sky conditions are, in reality, much more intermediate. In this paper, therefore, a different procedure is applied in which the direct and diffuse flux for the actual sky are calculated from the measured total radiation according to the regression given in Part I (Spitters et al., 1986).

In the de Wit model, daily canopy assimilation is calculated as the sum of the assimilation rates of the different canopy layers over the different time intervals of the day. Such a numerical approach is adopted here as the standard with which other approaches are compared. The equations are, however, presented with respect to discrete points rather than to intervals of canopy depths and time. Thus, formulations become clearer and become suitable for a simplified method of calculating daily canopy assimilation. As was shown by Goudriaan (1986), a very close approximation of daily canopy assimilation is obtained with a weighted average of the assimilation rates at three selected canopy depths at three times of the day. These discrete points were selected by a Gaussian integration algorithm.

The relevance of taking account of the variation in illumination intensity of the leaves in calculating daily canopy assimilation will be evaluated for the different sources of this variation separately.

#### DESCRIPTION OF THE MODEL FOR CANOPY PHOTOSYNTHESIS

The light profile within the canopy is determined by the amount of light entering the top of the canopy and the extinction coefficients of the different radiation components. On the basis of the light profile, absorption can be derived for any height within the canopy. Substitution into the assimilation–light response of the leaves gives the assimilation per unit leaf area in the studied canopy layer. Integration over layers and over the day-light period yields the daily assimilation rate of the canopy.

### *Incoming light at the top of the canopy*

Daily global irradiance is input for the model. In Part I (Spitters et al., 1986) an equation was presented to partition the total flux into its direct component, with angle of incidence equal to solar angle, and its diffuse component, with incidence under different angles. The diurnal trends of total, direct and diffuse radiation were characterized as well and account was taken of the greater share of the diffuse flux in the photosynthetically active wavebands. On the whole, photosynthetically active radiation amounts to 50% of total radiation.

Incoming light is partly reflected by the canopy. The reflection coefficient  $\rho$  of a green, closed vegetation is:

$$\rho = \left( \frac{1 - (1 - \sigma)^{1/2}}{1 + (1 - \sigma)^{1/2}} \right) \left( \frac{2}{1 + 1.6 \sin \beta} \right) \quad (1)$$

where the first term denotes the reflection of a canopy of horizontal leaves (Goudriaan, 1977, p. 14,31) and the second term is an approximate correction factor for a spherical leaf angle distribution (Goudriaan, personal communication).  $\beta$  = solar elevation above the horizon;  $\sigma$  = scattering coefficient of single leaves and for visible radiation in the order of 0.20. Hence, a fraction  $1 - \rho$  of the incoming flux is potentially available for absorption by the canopy.

### *Light profile within the canopy*

Light intensity, adjusted for crop reflection, decreases approximately exponentially with leaf area index when going deeper into the canopy:

$$I_L = (1 - \rho)I_0 e^{-kL} \quad (2)$$

where  $I_0$  = light intensity at the top of the canopy ( $\text{J m}^{-2} \text{ ground s}^{-1}$ );  $L$  = leaf area index ( $\text{m}^2 \text{ leaf m}^{-2} \text{ ground}$ );  $I_L$  = net light intensity at depth  $L$  ( $L$  reckoned from top downwards);  $k$  = extinction coefficient. Hereafter the subscript  $L$  will be omitted.

Analogously, the profiles of the net diffuse flux (df) and the net flux caused by direct irradiance (dr) are characterized as (Goudriaan, 1982):

$$I_{df} = (1 - \rho)I_{0,df} e^{-k_{df}L} \quad (3)$$

$$I_{dr} = (1 - \rho)I_{0,dr} e^{-(1 - \sigma)^{1/2} k_{bL} L} \quad (4)$$

where  $k_{bL}$  = extinction coefficient of 'black' leaves, i.e. leaves which show neither transmission nor reflection.

On its way through the canopy a part of the direct flux which is intercepted by the leaves is scattered by those leaves; hence, the direct flux segregates into a diffused, scattered component and another component which remains direct. Attenuation of the direct component of the direct

flux proceeds equally to the attenuation of light in a hypothetical canopy of black, non-scattering leaves:

$$I_{\text{dr, dr}} = I_{0, \text{dr}} e^{-k_{\text{bl}} L} \quad (5)$$

The diffused component is obtained as the difference between the total direct flux and its direct component:

$$I_{\text{dr, df}} = I_{\text{dr}} - I_{\text{dr, dr}} \quad (6)$$

### *Extinction coefficients*

For a spherical leaf angle distribution with leaves distributed randomly within the canopy volume, the extinction coefficients of the diffuse flux and that of the direct component of the direct flux are approximated, respectively, by (Goudriaan, 1977, 1982):

$$k_{\text{df}} = 0.8(1 - \sigma)^{1/2} \quad \text{and} \quad k_{\text{bl}} = 0.5/\sin \beta \quad (7)$$

where 0.5 points to the average projection on the ground surface of leaves showing a spherical angle distribution, and 0.8 is the value of  $0.5/\sin \beta$  averaged over inclination  $\beta$  of incident radiation under an overcast sky.

Actual extinction coefficients deviate from the above theoretical values, mainly because leaves are clustered rather than randomly distributed. Assuming that the leaf angle distribution is still spherical, eq. 7 gives as an approximation for the extinction coefficient of black leaves:

$$k_{\text{bl}} = 0.5k_{\text{df}}/(0.8(1 - \sigma)^{1/2} \sin \beta) \quad (8)$$

where the empirical, measured value of  $k_{\text{df}}$  is used rather than the theoretical value of eq. 7.

Absorption is complementary to transmission, hence light absorption at canopy depth  $L$  is obtained from the exponential light profile (eq. 2) as

$$I_{\text{a}} = -dI/dL = (1 - \rho)I_0 k e^{-kL} \quad (9)$$

where  $I_{\text{a}}$  = absorbed light energy per unit leaf area ( $\text{J m}^{-2} \text{ leaf s}^{-1}$ ). (Note that in this paper  $I$  denotes the incident flux, expressed per unit ground surface, whereas  $I_{\text{a}}$  is used for the flux absorbed per unit leaf area.) Similarly, absorption of the diffuse and direct flux are derived from eq. 3 and 4 to be:

$$I_{\text{df, a}} = (1 - \rho)I_{0, \text{df}} k_{\text{df}} e^{-k_{\text{df}} L} \quad (10)$$

and:

$$I_{\text{dr, a}} = (1 - \rho)I_{0, \text{dr}}(1 - \sigma)^{1/2} k_{\text{bl}} e^{-(1 - \sigma)^{1/2} k_{\text{bl}} L} \quad (11)$$

Of the direct component of the direct flux (eq. 5), the non-scattered part  $1 - \sigma$  is absorbed:

$$I_{\text{dr, dr, a}} = (1 - \sigma)I_{0, \text{dr}} k_{\text{bl}} e^{-(1 - \sigma)^{1/2} k_{\text{bl}} L} \quad (12)$$

The absorbed diffused component of the direct flux is obtained by subtracting the direct component (eq. 12) from the total of the direct flux (eq. 11).

Two leaf area classes are distinguished: shaded leaf area and sunlit leaf area. The shaded leaf area absorbs the diffuse flux and the diffused component of the direct flux:

$$I_{\text{sh, a}} = I_{\text{df, a}} + (I_{\text{dr, a}} - I_{\text{dr, dr, a}}) \quad (13)$$

The sunlit leaf area receives diffuse and direct radiation:

$$I_{\text{sl, a}} = I_{\text{sh, a}} + (1 - \sigma)k_{\text{bl}}I_{0, \text{dr}} \quad (14)$$

At every horizon within the canopy, the intensity of the unobstructed direct beam equals its intensity above the crop. Leaves differ in angle, but it can be shown that on the average their illumination intensity is a fraction  $k_{\text{bl}}$  of that at a horizontal plane ( $I_{0, \text{dr}}$ ). A fraction  $1 - \sigma$  of the intercepted flux is absorbed by the leaves. In eq. 12 the absorption of the direct beam is averaged over sunlit plus shaded leaf area, whereas the second part of eq. 14 gives the absorption intensity per unit of sunlit leaf area only.

#### *Instantaneous assimilation per canopy layer*

The assimilation rate of a canopy layer is obtained by substituting the absorbed amount of light energy into the assimilation—light response of single leaves. Of the two-parameter response functions, the asymptotic exponential appears to be the most satisfactory (Peat, 1970; own unpublished results). The assimilation rate of the shaded leaves is thus described by

$$A_{\text{sh}} = A_{\text{m}} (1 - e^{-\epsilon I_{\text{sh, a}}/A_{\text{m}}}) \quad (15)$$

where  $A_{\text{sh}}$  = assimilation rate of shaded leaf area ( $\text{g CO}_2 \text{ m}^{-2} \text{ leaf h}^{-1}$ ),  $A_{\text{m}}$  = asymptote or assimilation rate at light saturation ( $\text{g CO}_2 \text{ m}^{-2} \text{ leaf h}^{-1}$ ),  $\epsilon$  = initial slope or light-use efficiency ( $\text{g CO}_2 \text{ J}^{-1}$  absorbed). Light-use efficiency is about  $12.5 \times 10^{-6} \text{ g CO}_2 \text{ J}^{-1}$  at  $20^\circ\text{C}$  (Ehleringer and Pearcy, 1983) and  $A_{\text{m}}$  is for ruderal  $\text{C}_3$  species in the order of  $4 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ . Evidently, alternative response functions (e.g. Thornley, 1976, p. 94) may be applied in the model.

For the sunlit leaf area, the average absorption intensity given in eq. 14 may be substituted into eq. 15. It is, however, more accurate to account for the variation in leaf angle and thus in illumination intensity. The direct flux is absorbed by a leaf perpendicular to the direct beam with an intensity of:

$$I'_{\text{sl, dr, a}} = (1 - \sigma)I_{0, \text{dr}}/\sin \beta \quad (16)$$

where  $\beta$  = solar elevation,  $I_{0, \text{dr}}$  = direct irradiance on a horizontal plane. With a spherical leaf angle distribution, the sine of leaf angle is distributed uniformly. Hence, equidistant sine classes have an equal frequency, irrespec-

tive of solar elevation. Integration over the sine of incidence gives for the assimilation rate of sunlit leaf area (Goudriaan, personal communication):

$$A_{sl} = A_m [1 - (A_m - A_{sh}) (1 - e^{-\epsilon I'_{sl, dr, a}/A_m}) / (\epsilon I'_{sl, dr, a})] \quad (17)$$

with the assimilation of shaded leaves ( $A_{sh}$ ) given by eq. 15 and the absorption of leaves perpendicular to the direct beam ( $I'_{sl, dr, a}$ ) by eq. 16.

The assimilation rate per unit leaf area, averaged over a canopy layer, is the sum of the assimilation rates of sunlit and shaded leaves, each weighted to their share in that layer:

$$A' = f_{sl} A_{sl} + (1 - f_{sl}) A_{sh} \quad (18)$$

The fraction sunlit leaf area ( $f_{sl}$ ) equals the fraction of the direct beam reaching that layer. According to eq. 5:

$$f_{sl} = e^{-k_{bl} L} \quad (19)$$

Note that the intensity of the direct beam per unit leaf area does not change with canopy depth.

The model predicts the assimilation rate in a dynamic light environment from the steady state rates at the respective light intensities. In a light environment of fluctuating sunflecks, deviations from this assumption occur due to a required induction of photosynthetic capacity and due to post-illumination  $CO_2$  fixation (Percy et al., 1985). These deviations are expected to be small on the whole so that they are not accounted for in the model.

#### *Instantaneous canopy assimilation*

Canopy assimilation is calculated as a weighted average of the assimilation at three horizons within the canopy. The horizons, selected by Gaussian integration (Goudriaan, 1986), are:

$$L = (0.5 + p(0.15)^{1/2})LAI \quad p = 1, 0, 1 \quad (20)$$

with LAI = total leaf area index of the crop. The weighted average of these assimilation rates, to be derived from eq. 18 and 20, is

$$A_h = LAI (A'_{-1} + 1.6 A'_0 + A'_1) / 3.6 \quad (21)$$

where  $A_h$  = hourly canopy assimilation ( $g CO_2 m^{-2} ground h^{-1}$ ).

#### *Daily canopy assimilation*

To integrate the instantaneous canopy assimilation (eq. 21) over the day, again the Gaussian approach of numerical integration was followed. The three selected time points refer to the period from noon to sun set:

$$t_h = 12 + 0.5 D (0.5 + p(0.15)^{1/2}) \quad p = 1, 0, 1 \quad (22)$$

where  $D$  = daylength (h; eq. 17 in Spitters et al., 1986). Daily canopy assimi-

lation is obtained as the weighted average of the instantaneous assimilation rates (eq. 21) at the selected time points:

$$A_d = D (A_{h,-1} + 1.6A_{h,0} + A_{h,1})/3.6 \quad (23)$$

where  $A_d$  = daily canopy assimilation ( $\text{g CO}_2 \text{ m}^{-2} \text{ ground day}^{-1}$ ).

#### CONCISE APPROACHES

In the model, several sources of variation in illumination intensity of the leaves were explicitly accounted for. Neglecting this variation and using the average intensity would overestimate crop assimilation due to the convex asymptotic photosynthesis—light response. This bias may be partly avoided by applying a photosynthesis—light response function which proceeds more gradually than the asymptotic exponential of eq. 15. For this, the rectangular hyperbola is used:

$$A = \left( \frac{\epsilon I_a}{\epsilon I_a + A_m} \right) A_m \quad (24)$$

where  $A$  = assimilation rate ( $\text{g CO}_2 \text{ m}^{-2} \text{ leaf h}^{-1}$ ),  $I_a$  = absorbed light ( $\text{J m}^{-2} \text{ leaf s}^{-1}$ ). The hyperbola is used only to approximate an average assimilation rate. For the initial slope  $\epsilon$  and the saturation level  $A_m$  those values should, therefore, be used which are obtained by fitting an asymptotic exponential, rather than the hyperbola, to the leaf photosynthesis measurements.

Light absorption averaged over daylight period and canopy layers is obtained from eq. 2 as:

$$I_a = (1 - \rho) I_d (1 - e^{-kL})/(LD) \quad (25)$$

where  $I_d$  = daily amount of light incident at the top of the canopy ( $\text{J m}^{-2} \text{ day}^{-1}$ ). Substitution into eq. 24 and multiplication by canopy leaf area index  $L$  and daylength  $D$  yield a very simple expression for daily crop assimilation.

More sophistication is introduced by making allowance for the exponential light profile within the canopy. Substitution of eq. 9 for the light absorption at a certain canopy depth into eq. 24 gives the assimilation rate at that depth. Integration over canopy leaf area index  $L$  gives:

$$A_d = D \frac{A_m}{k} \ln \left\{ \frac{A_m + k\bar{I} \epsilon}{A_m + k\bar{I} \epsilon e^{-kL}} \right\} \quad (26)$$

where  $A_d$  = daily canopy assimilation ( $\text{g CO}_2 \text{ m}^{-2} \text{ ground day}^{-1}$ ),  $\bar{I} = (1 - \rho)I_d/D$  = light intensity averaged over the daylight period and corrected for crop reflection ( $\text{J m}^{-2} \text{ s}^{-1}$ ). Several authors (e.g. Acock et al., 1978) have used a similar equation in crop growth models.

Appropriateness of both approaches is evaluated in Fig. 3.

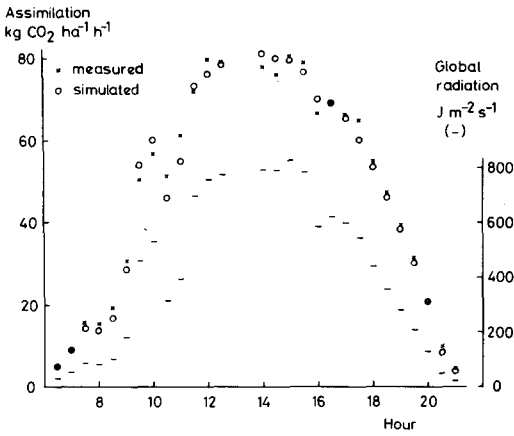


Fig. 1. Daily course of measured (x) and simulated (o) gross assimilation rate of a sugar beet crop in relation to global irradiance (-) (unpublished measurements of L. Sibma and W. Louwse). Gross assimilation rates were obtained from measured net rates by adding the measured dark respiration of  $7.1 \text{ kg CO}_2 \text{ ha}^{-1} \text{ h}^{-1}$ . Experimental details: Day 209 (28 July 1981); location Flevoland, The Netherlands; LAI = 5.26; temperature  $20^\circ\text{C}$ ; data adjusted to a constant concentration of 330 vpm  $\text{CO}_2$ , parameters used in the model:  $A_m = 5.0 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$  (L. Sibma, unpublished data of leaf photosynthesis)  $\epsilon = 12.5 \mu\text{g CO}_2 \text{ J}^{-1}$ ;  $k_{\text{eff}} = 0.7$ . Irradiance at the top of the canopy is obtained by multiplying the plotted global radiation by 0.86, being the transmission of the perspex chamber.

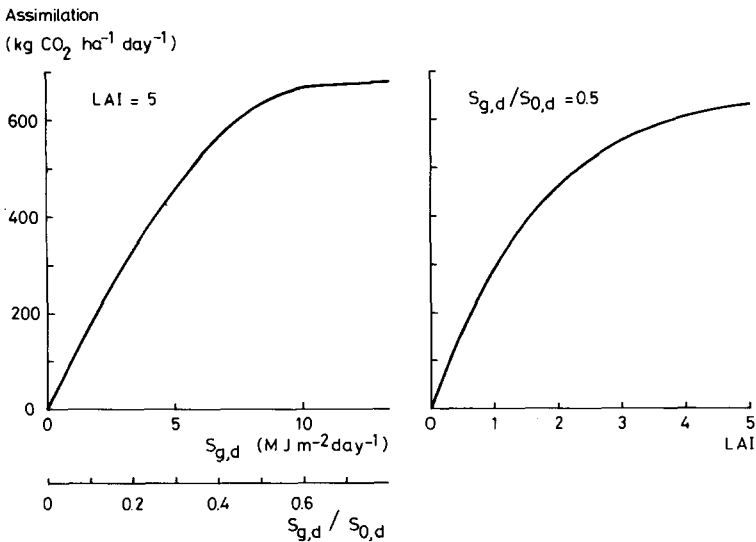


Fig. 2. Daily canopy assimilation simulated with the reference version of the model for different levels of global radiation ( $S_{g,d}$ ), atmospheric transmission ( $S_{g,d}/S_{0,d}$ ) and leaf area index (LAI).



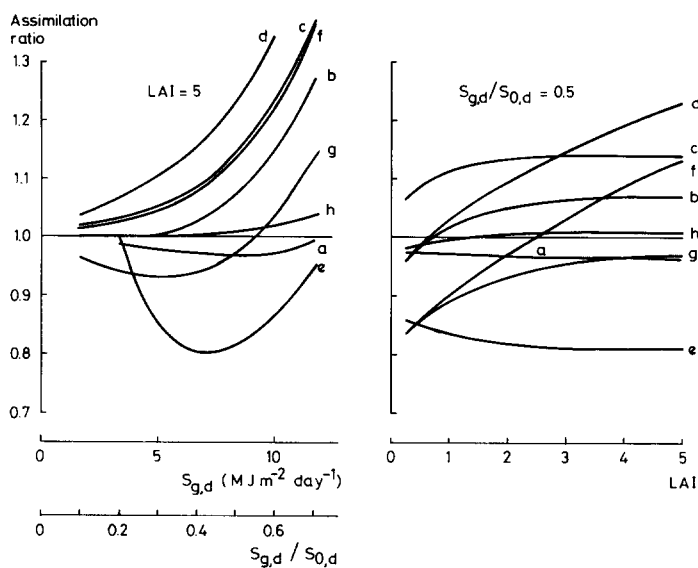


Fig. 3. Daily canopy assimilation as calculated with different versions of the model and expressed relative to the daily canopy assimilation calculated with the reference version. These ratios are given in relation to daily global radiation ( $S_{g,d}$ ), atmospheric transmission ( $S_{g,d}/S_{0,d}$ ) and leaf area index (LAI). Curves a–d illustrate the influence of different sources of variation in illumination intensity of the leaves: (a) accounting for random variation in irradiance around diurnal sine wave, (b) treating all incoming light as diffuse, (c) neglecting the diurnal sine wave by using light intensity averaged over the daylight period, (d) neglecting the exponential light profile within the canopy by using light absorption averaged over canopy layers. Curve e reflects the usual way of discriminating between direct and diffuse light by assuming that the sky is either clear or overcast. Curves f and g use a rectangular hyperbola for the leaf assimilation–light response function: (f) light absorption averaged over daylight period and canopy layers, (g) light absorption averaged over daylight period only. Curve h: canopy assimilation calculated as weighted average of assimilation rates at three selected canopy depths at three moments of the day.

#### SENSITIVITY ANALYSIS AND DISCUSSION

The model yields realistic values, as is illustrated in Fig. 1 where simulated and measured assimilation rates of a sugar beet crop are plotted.

The influence of the different sources of variation in illumination intensity of the leaves will be evaluated with the model. A model version where daily canopy assimilation is computed numerically is taken as a standard. In this version, the canopy is partitioned into 30 horizontal layers and the daylight period into intervals of 15 min. Day 230 (Aug. 18) is considered, being the day with average irradiance for the 200 days of the Dutch growing season (Apr. 1–Oct. 17). At 52° Northern Latitude, daylength is then 14.3 h and extra-terrestrial irradiance  $33.4 \text{ MJ m}^{-2} \text{ day}^{-1}$ . The results of the sensitivity analysis, as presented in Fig. 2, were only slightly influenced by day and latitude.

The standard crop has leaves which are distributed at random within the canopy volume and show a spherical leaf angle distribution. With a scattering coefficient of the leaves of 0.2, the extinction coefficient for the diffuse flux is 0.72 (eq. 7). Light use efficiency  $\epsilon$  is  $12.5 \times 10^{-6} \text{ g CO}_2 \text{ J}^{-1}$  at  $20^\circ\text{C}$  (Ehleringer and Pearcy, 1983) and  $A_m$  is  $4.0 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ , a value typical of ruderal  $C_3$  species. Decrease of  $A_m$  with canopy depth is neglected.

Under good growing conditions, crop growth is mainly determined by the amount of light absorbed by the canopy. The different model versions are, therefore, evaluated for a realistic range of daily irradiance and canopy leaf area index.

To illustrate its order of magnitude, daily crop assimilation is plotted in Fig. 2 in relation to radiation level and leaf area index (LAI). A canopy with  $\text{LAI} = 5$  can be considered to be completely closed. During the growing season, the mean atmospheric transmission in the Netherlands is 0.42. A day without sunshine has on the average a transmission of 0.20, while for a cloudless day the transmission amounts to 0.76.

The different model versions are evaluated by expressing their computed daily canopy assimilation relative to that of the reference (Fig. 3). Random variation in irradiance around the diurnal sine wave was expressed in relation to the radiation level (eq. 11 in Spitters et al., 1986). For each of the canopy layers and 15-min time intervals the assimilation rate was integrated numerically over the assumed normal distribution with 5% intervals. Neglecting this random variation introduced an overestimation of canopy assimilation of only 2–3% (reference compared to curve a in Fig. 3). This constancy was promoted by the decrease of relative variation in irradiance with radiation level. This random variation is neglected in the reference version because of its small influence and the preliminary character of its quantification.

Neglecting the variation in irradiance of the sunlit leaf area, i.e. substitution of eq. 14 into 15 rather than using eq. 17, overestimated canopy assimilation with 0.8, 2 and 5% at atmospheric transmissions of 0.4, 0.5 and 0.7, respectively. LAI had only a minor effect on these percentages.

The diurnal course in atmospheric transmission was accounted for in eq. 6 and 7 in Spitters et al. (1986). Neglecting this source of variation overestimated daily assimilation of a canopy of  $\text{LAI} = 5$  with 1.0, 1.6 and 3.8% at transmissions of 0.4, 0.5 and 0.7, respectively.

Treating all the incident light as diffuse discards the differences between the diffuse and direct flux. The resulting overestimation of canopy assimilation increases sharply with the share of the direct flux and therefore with an increase in atmospheric transmission (curve b in Fig. 3). Assimilation of canopies of very low LAI is, on the other hand, underestimated because  $k_{df}$  is smaller than  $k_{bl}$  at low and moderate solar heights (eq. 8). The resulting underestimation of total light absorption of the canopy becomes significant at very low LAI, the more as mutual shading of leaves is then nearly absent.

Using a light intensity averaged over the day or over the canopy layers

greatly overestimates canopy assimilation (curves c and d in Fig. 3). The bias increases sharply with atmospheric transmission. For closed canopies the bias introduced by averaging over canopy layers is larger than the bias from averaging over the day. For canopies of lower LAI, the reverse is true.

The usual way to discriminate between direct and diffuse light in crop growth simulation is by defining a standard clear and a standard overcast day and computing daily canopy assimilation for both. Actual canopy assimilation is obtained as the sum of the assimilation rates during the clear and overcast periods with both weighted to their share in the daylight period (de Wit, 1965). In Fig. 3 of Spitters et al. (1986), it was demonstrated that this approach is incorrect: the share of the direct flux and the random variation in irradiance are overestimated at intermediate sky conditions. An underestimation of canopy assimilation up to 20% at intermediate sky conditions results (curve e in Fig. 3).

The overestimation introduced by using averaged light intensities may be partly avoided by applying a hyperbolic light response function as this function proceeds more gradually than the asymptotic exponential. Use of the absorbed amount of light averaged over daylight period and canopy layers (eq. 25) gave, also with the hyperbola, a serious overestimation of assimilation of closed canopies. The bias was strongly affected by the LAI of the crop (curve f in Fig. 3). Because of its mediocre performance, this approach is only suitable for very simple growth models. To restrict overestimation, an upper bound of about 4 has to be introduced for LAI in the calculations.

Taking account of the light profile within the canopy and averaging the absorption over the daylight period only (eq. 26), resulted in only a slight underestimation of canopy assimilation (curve g in Fig. 3). That approach therefore looks very attractive as a concise model, especially for closed crop surfaces.

Daily canopy assimilation was approximated very closely by a weighted average of the assimilation rates at three selected canopy depths at three selected moments of the daylight period (curve h in Fig. 3; Goudriaan, 1986). This approach, which uses only  $3 \times 3$  discrete points, selected by Gaussian integration, to calculate daily canopy assimilation is very suitable for use in crop growth models.

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