A sensitivity analysis of the radiation use efficiency for gross photosynthesis and net carbon accumulation by wheat

Bhaskar J. Choudhury *

Hydrological Sciences Branch, Laboratory for Hydrospheric Processes, NASA Goddard Space Flight Center, Greenbelt, MD 20771, USA

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Abstract

Radiation use efficiency (RUE) provides a useful diagnostic approach for estimating carbon accumulation by terrestrial plant communities. A model for instantaneous gross photosynthesis by a canopy, considering sunlit and shaded leaves, variation of maximum rate of leaf photosynthesis within the canopy and a solution of the radiative transfer equation for propagation of direct and diffuse photosynthetically active radiation within the canopy, is numerically integrated in space (angular variation of radiances and depth within the canopy) and time (diurnal variation) to obtain daily total gross photosynthesis. Then, to obtain net carbon accumulation, growth and maintenance respiration at a prescribed temperature are calculated from nitrogen content of foliage, stem and root using field measurements for 27 canopies representing two cultivars of winter wheat and average data for five cultivars of spring wheat. The leaf area index ($L_o$) of these canopies varies between 0.5 and 5.2. The results show that for any given irradiance, the coefficient of variation of RUE for gross photosynthesis and net carbon accumulation due to changes in $L_o$ is generally less than 10%. Strongly linear relationships are found between the RUE and diffuse fraction of the incident radiation, with slope varying with $L_o$. Temperature appears as an important factor determining RUE under predominantly cloudy conditions. The calculated RUE values are compared with observations. ©2000 Published by Elsevier Science B.V.

Keywords: Photosynthesis; Respiration; Radiation use efficiency; Wheat

1. Introduction

The daily rate of net carbon accumulation by terrestrial vegetation per unit land area ($dC/dt$) is the difference of daily gross photosynthesis ($A_g$) and autotrophic respiration ($R$):

$$\frac{dC}{dt} = A_g - R$$

(1)

When respiration of heterotrophs is also considered, Eq. (1) will give net carbon accumulation per unit land area or net ecosystem exchange.

Seasonal variation of photosynthetically active radiation (PAR) intercepted by a canopy (IPAR) is an important determinant of seasonal variation of $A_g$, while seasonal variation of $R$ is determined by ontogenic changes in foliage, stem and root biomass and their growth and maintenance respiration coefficients. Considering field observations of accumulation of dry matter and intercepted solar radiation (which are considered here to be equivalent to, respectively, $dC/dr$ and IPAR integrated over time) for several crops, Monteith (1977) proposed the following equation:

$$\frac{dC}{dt} = e \times \text{IPAR}$$

(2)
where $e$ is commonly referred to as the radiation use efficiency.

By taking $R$ to be a constant fraction of $A_g$ ($R/A_g = 0.4$), Monteith (1977) showed that $e$ increases as the maximum rate of leaf photosynthesis ($A_{\text{max}}$) increases. The dependence of $e$ on biophysical factors has been further clarified by Sinclair and Horie (1989), Sinclair et al. (1992), Sinclair and Shiraiwa (1993) and Leuning et al. (1995). These studies confirmed the dependence of $e$ on $A_{\text{max}}$, and also showed that $e$ increases with increasing fraction of diffuse radiation incident on the canopy, and when leaf nitrogen content within the canopy changes with height (non-uniform distribution). Leuning et al. (1995) calculated leaf respiration that continues in the light in terms of nitrogen concentration, while Sinclair and his colleagues determined respiration separately for growth and maintenance. The growth respiration was estimated from biochemical composition of plant, while maintenance respiration was assumed to consume 15–20% of the hexose produced by photosynthesis. Although it was recognized that the magnitude of growth and maintenance respiration changes with plant age, temperature, among other factors (Amthor, 1989), the effect of these changes on $e$ was not evaluated.

Considering light response function for leaf photosynthesis to be a non-rectangular hyperbola and respiration to be proportional to $A_{\text{max}}$, Haxeltine and Prentice (1996) showed analytically that optimized (with respect to $A_{\text{max}}$) daily canopy net photosynthesis is proportional to absorbed PAR (APAR), and obtained a general model for radiation use efficiency (RUE). Then, by relating the light response function to a biochemical model of photosynthesis, they showed that the optimization can provide an understanding of a number of observed physiological responses to temperature and ambient CO$_2$, among them being increase in leaf nitrogen concentration with decreasing growing season temperature. Dewar (1996) derived an analytic model for RUE based on the hypothesis that there would an optimal plant nitrogen content at which net primary productivity will be maximum. Using a mechanistic model, Dewar et al. (1998) found that time-averaged net primary productivity is proportional to the time-averaged canopy absorbed irradiance, and to gross canopy photosynthesis when fast turnover pools of carbon, starch and protein follow a moving steady state, tracking the average environmental conditions. This study showed that not only RUE but carbon use efficiency (the ratio of net and gross photosynthesis) is also approximately constant.

Eq. (2) has formed the basis for a number of studies addressing carbon accumulation by terrestrial plant communities at regional and global scale using satellite data (for example, Malmstrom et al., 1997). While Eq. (2) provides a diagnostic approach to estimating carbon accumulation, a diagnostic approach would be to apply Eq. (1) by calculating $A_g$ and $R$ separately. A diagnostic approach has the appeal that impact of different biophysical factors on $A_g$ and $R$ could be addressed (Ryan, 1991), which could provide a better understanding of the factors determining $e$. Such an understanding would be helpful in extrapolating experimentally determined values of $e$ to different locations and/or environmental conditions.

Following a thorough evaluation of CO$_2$ flux measurements at different temporal resolution over wheat and many other ecosystems (Ruimy et al., 1995), a global scale application of the diagnostic approach has been presented by Ruimy et al. (1996). For this global study, $A_g$ (mol CO$_2$ m$^{-2}$ per day) was calculated from the following equation, based on chamber measurements and modeling of CO$_2$ flux for the growing season of wheat near Manhattan (KS) by Wall and Kanemasu (1990) and Wall et al. (1990):

$$A_g = e_{a,g} \times \text{APAR} \tag{3}$$

where $e_{a,g}$ is radiation use efficiency for gross photosynthesis, taken to be 0.02 mol CO$_2$ mol$^{-1}$ photon. Then, maintenance respiration was determined from biomass of leaf, stem and root, together with their respiration coefficients. And, growth respiration was calculated as a constant fraction of assimilated CO$_2$ remained after accounting for maintenance respiration.

It is pertinent to note that, complementing Eq. (3), Wall and Kanemasu (1990) also obtained the efficiency for net carbon accumulation ($e$) as 0.012 mol$^{-1}$ CO$_2$ mol$^{-1}$ photon. However, from measurements of biomass and radiation at two locations in UK, Gallagher and Biscoe (1978) obtained an efficiency of 3.0 g (dry matter produced) MJ$^{-1}$ (APAR) for growth of wheat and barley until anthesis. Taking carbon content of the dry matter as 41% (van den Boogaard et al., 1996) and 1 MJ (PAR) to be equal to 4.6 mol
photon (Wall and Kanemasu, 1990), an efficiency of 3.0 g MJ$^{-1}$ would correspond to $e = 0.022 \text{ mol CO}_2 \text{ mol}^{-1}$ photon. Factors contributing to these differences in $e$ of wheat have not been fully analyzed.

The objective of the present study is to assess the sensitivity of $e_g$ and $e$ to biophysical parameters of wheat during its vegetative period for unstressed conditions through a diagnostic approach. A model for instantaneous gross photosynthesis by a canopy, considering sunlit and shaded leaves, a solution of the radiative transfer equation for propagation of direct and diffuse PAR, and variation of maximum rate of leaf photosynthesis within the canopy, is numerically integrated in space (angular variation of radiances and depth within the canopy) and time (diurnal variation) to obtain $A_g$. Growth and maintenance respiration at a prescribed temperature are determined from nitrogen content of foliage, stem, and root. Calculations of $A$ and $R$ have been done using field data for 27 canopies representing two cultivars of winter wheat and average data for five cultivars of spring wheat. The leaf area index of these canopies ranged between 0.5 and 5.2.

The model and the data used are described further, followed by results and comparison with observations. Since all input data needed to run the model were not known equally well corresponding to the measured RUE, a sensitivity analysis has been done to assess the impact of uncertainties in these data before comparing with the observed RUE.

2. Description of the model

2.1. Gross photosynthesis ($A_g$)

A biochemical model coupled to an energy balance model can provide a basis for understanding leaf photosynthesis in terms of thermodynamic and biochemical parameters (Leuning et al., 1995). The present study follows Hirose and Werger (1987), Sinclair and Horie (1989), Kull and Jarvis (1995), among others, in that an empirical equation for light response function for leaf photosynthesis has been integrated to obtain canopy photosynthesis. The empirical equation has been chosen to be a non-rectangular hyperbola, and, in a biochemical model, such an equation is considered to describe the relationship between electron transport rate and photon absorbed by Photosystem II. Photosynthesis is rate limited by electron transport and Rubisco activity. Since limitation due to Rubisco activity is not addressed, the empirical equation is a descriptor rather than a predictor of leaf photosynthesis. The model formulated by Leuning et al. (1995) can provide photosynthesis and respiration of leaves, but a model of comparable sophistication for respiration of stem and roots has not yet been formulated and tested. In the present study both canopy photosynthesis and plant respiration are obtained from organ-level data rather than biochemical data.

2.1.1. Leaf photosynthesis

The dependence of leaf photosynthesis ($A_l; \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$) on irradiance on leaf surface ($F_l; \mu\text{mol photon m}^{-2} \text{s}^{-1}$) is represented by a non-rectangular hyperbola (Boote and Loomis, 1991; Hirose et al., 1997):

$$A_l(F_l) = \frac{A_m[(1 + \eta) - [(1 + \eta)^2 - 4\eta\eta]^{0.5}}{(2\eta)}$$

where,

$$\eta = \frac{e\alpha F_l}{A_m}$$

$A_m$ is the maximum rate of gross photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$), $\varepsilon$ is quantum efficiency ($\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon absorbed), $\alpha$ is the PAR absorbance of a leaf, and $\theta$ is an empirical curvature factor.

The quantum efficiency ($\varepsilon$) varies with temperature, which has been prescribed according to the data given in Leverenz and Oquist (1987) and Ehleringer et al. (1997). The curvature factor ($\theta$) is often found to be between 0.7 and 0.9 (Boote and Loomis, 1991). A base value of 0.8 has been taken for $\theta$ (Hirose et al., 1997), while sensitivity results are given for 0.7 and 0.9.

The variation of $A_m$ within the canopy is assumed to be governed by the dependence of $A_m$ on specific leaf nitrogen ($n_l$, mmol N m$^{-2}$), which varies within the canopy (Hirose and Werger, 1987; Sinclair and Shiraia, 1993). For winter wheat plants (cv. Aoba) grown in solution culture, Makino et al. (1988) observed the following linear relation between $A_m$ and $n_l$ ($n_l$ varied from ca. 30 to 180 mmol m$^{-2}$):

$$A_m = 0.28(n_l - 23)$$

de Pury and Farquhar (1997) estimate that $A_m$ becomes zero when $n_l$ is 25 mmol m$^{-2}$ or lower, which
substantially agrees with Eq. (6). However, values of $A_m$ in the range 40–44 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ found for these water culture plants at high values of $n_l$ are somewhat higher than those observed in field studies (see further).

It is now necessary to prescribe variation of $n_l$ within the canopy. A synthesis of data quantifying changes of $n_l$ within the canopy by Sadras et al. (1993) gave $n_l$ as:

$$n_l = n_0 \exp(-k'L)$$

(7)

where

$$k' = \frac{(0.43 + 0.11L_0)}{L_0}$$

(8)

$L$ is the leaf area index increasing downward within the canopy starting at $L = 0$ at the top, $L_0$ is the total leaf area index and $n_0$ is the value of $n_l$ at the top of the canopy. de Pury and Farquhar (1997) obtained $k = 0.3$ for a wheat canopy having $L_0 = 2.4$, which is consistent with Eq. (8).

The value of $n_0$ in Eq. (7) is constrained by the total nitrogen content of the foliage ($n_l$ mmol N m$^{-2}$) since by integrating Eq. (7) one obtains $n_l$ as:

$$n_l = \frac{n_0}{k'} \left[1 - \exp(-k'L_0)\right]$$

(9)

Thus, data for $L_0$ and $n_l$ (Table 1, elaborated later) can be used to calculate $n_0$ from Eqs. (8) and (9).

**Table 1** Summary of wheat canopy characteristics used in the calculation$^a$

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>$n$</th>
<th>$L_0$</th>
<th>Nitrogen content (mmol m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Foliage</td>
</tr>
<tr>
<td>Coker</td>
<td>14</td>
<td>3.4</td>
<td>364</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.2)</td>
<td>(84)</td>
</tr>
<tr>
<td>MH</td>
<td>9</td>
<td>1.9</td>
<td>191</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.2)</td>
<td>(93)</td>
</tr>
<tr>
<td>SW</td>
<td>4</td>
<td>3.4</td>
<td>469</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.7)</td>
<td>(189)</td>
</tr>
<tr>
<td>All</td>
<td>27</td>
<td>2.9</td>
<td>322</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.4)</td>
<td>(143)</td>
</tr>
</tbody>
</table>

$^a$ The data given are: cultivar name (MH for Maris Huntsman, and SW for the average data for five cultivars of spring wheat), number of data values ($n$), mean leaf area index ($L_0$), and nitrogen content of foliage, stem and root (standard deviations are given in parenthesis). The summary of all data is also given.

Since $n_l$ is maximum at the top of the canopy ($n_l = n_0$), Eq. (6) would give the maximum value of $A_m$ ($A_m = A_{\text{max}}$) also at the top of the canopy as:

$$A_{\text{max}} = 0.28(n_0 - 23)$$

(10)

From Eqs. (6), (7) and (10), one can explicitly express variation of $A_m$ within the canopy in terms of $A_{\text{max}}$ and $n_0$ as:

$$A_m = \frac{A_{\text{max}} \left[n_0 \exp(-k'L) - 23\right]}{(n_0 - 23)}$$

(11)

Measurements of maximum net photosynthesis reported by Austin et al. (1982) for five cultivars of field grown winter wheat give mean and range, respectively, as 17.7 and 16.4–19.6 $\mu$mol m$^{-2}$ s$^{-1}$, and such measurements by Morgan et al. (1993) for eight cultivars give mean and range, respectively, as 19.3 and 17.8–20.7 $\mu$mol m$^{-2}$ s$^{-1}$. The overall mean and standard deviation of these field measurements for winter wheat are, respectively, 18.7 and 1.4 $\mu$mol m$^{-2}$ s$^{-1}$ ($n = 13$). Similar values might also apply to spring wheat (Blum, 1990). A previous compilation of maximum net photosynthesis by Angus and Wilson (1976) gave mean and standard deviation, respectively, as 19.0 and 1.7 $\mu$mol m$^{-2}$ s$^{-1}$ ($n = 7$).

The above measurements of maximum net photosynthesis need to be adjusted for dark respiration to obtain $A_{\text{max}}$. Angus and Wilson (1976) found dark respiration to be 5% of the maximum net photosynthesis for two cultivars of wheat (cvs. Chile IB and Olympic), while Marshall and Biscoe (1980) found this fraction to be 7% for cv. Maris Huntsman. If mean maximum net photosynthesis is taken to be either 18.7 or 19 $\mu$mol m$^{-2}$ s$^{-1}$ (as discussed earlier), then 6% adjustment would give $A_{\text{max}} = 20 \mu$mol m$^{-2}$ s$^{-1}$. Sensitivity to $A_{\text{max}}$ has been presented by taking $A_{\text{max}}$ to be either 18 or 22 $\mu$mol m$^{-2}$ s$^{-1}$, based on standard deviation of the measurements quoted earlier.

The PAR absorptance ($\alpha$) is strongly determined by the chlorophyll content of a leaf ($c_1$; mmol m$^{-2}$) although other factors like wax and hair also affect the absorptance. For four species grown under different irradiances and nutrients, Evans (1996) found the following relation between $\alpha$ and $c_1$:

$$\alpha = \frac{c_1}{(c_1 + 0.076)}$$

(12)
By taking the ratio \( (c_1/n_1) \) as 0.0045 for leaves at the top of the canopy exposed to high irradiances (Pons et al., 1994; Evans, 1996), \( \alpha \) was calculated from the following equation (obtained by substituting \( c_1 = 0.0045 \) \( n_0 \) in Eq. (12),

\[
\alpha = \frac{n_0}{(n_0 + 17)}
\]  

(13)

2.1.2. Irradiances within the canopy and interception

Because of nonlinear dependence of \( A_m \) on \( F_1 \), leaves within the canopy have been separated into sunlit and shaded components for calculating \( A_g \). Calculation of irradiances within the canopy is summarized further; details could be found in Choudhury (1987) and Chandrasekhar (1960) (pp. 216–218).

The starting point is Eqs. (A12)–(A13) of Choudhury (1987), which describe the propagation of scattered radiation within the canopy (idealized to be a plane parallel homogeneous medium) and the boundary condition for the radiance at the top of the canopy. The equation for scattered radiance \( I(L, \mu) \) propagating in the direction \( \mu \) (cosine of zenith angle) at leaf area index equivalent of depth \( L \) is:

\[
\frac{\mu}{G} \left( \frac{dI}{dL} \right) = -I + \frac{\omega}{2} \int_{-1}^{1} I(\mu')d\mu' + \frac{\omega S_0}{4} \exp \left( -\frac{L G_0}{\mu_0} \right)
\]  

(14)

and the boundary condition is:

\[
I(0, \mu) = S_d
\]  

(15)

where \( G \) and \( G_0 \) are, respectively, the projection of unit foliage along the radiance \( I \) and the direction of incident direct PAR (Choudhury, 1987), \( \omega \) is the single scattering albedo of a leaf (\( \omega = 1 - \alpha \); Eq. (13)), \( S_0 \) is the direct PAR on a perpendicular surface at the top of the canopy, \( \mu_0 \) is cosine of solar zenith angle of incident direct PAR, and \( S_d \) is diffuse PAR irradiance on top of the canopy. The total PAR incident on the canopy is equal to \( (S_0 \mu_0 + S_d) \).

For a purely absorptive medium (\( \omega = 0 \)) the solution of Eq. (14) gives an exponentially damped radiance. Since \( \omega \) of leaves for PAR is small (ca. 0.1–0.2), an improvement over the radiance for a purely absorptive medium would be to consider single scattering within the canopy (i.e., photons being absorbed after one scattering). In the single scattering approximation, Eq. (14) reduces to,

\[
\frac{\mu}{G} \left( \frac{dI}{dL} \right) = -I + \frac{\omega S_0}{4} \exp \left( -\frac{L G_0}{\mu_0} \right)
\]  

(16)

The solution of Eq. (16) for radiance propagating in the direction of soil surface satisfying Eq. (15) is given by (Chandrasekhar, 1960) (p. 12):

\[
I(L, \mu) = \frac{S_0 \exp(-L G_0/\mu) + (\omega S_0 G \mu_0 / 4)}{[\exp(-L G_0/\mu) - \exp(-L G_0/\mu_0)]} \left( G_0 \mu - G \mu_0 \right)
\]  

(17)

The diffuse irradiance on a horizontal surface at depth \( L \) is obtained by integrating \( I(L, \mu) \) over the angle as:

\[
F_{\text{diff}}(L) = 2 \int_0^1 I(L, \mu) \mu \; d\mu
\]  

(18)

The integration in Eq. (18) has been done using the Gauss quadrature of eight points.

An integration similar to Eq. (18) gives diffuse irradiance on the shaded leaves at depth \( L \), \( F_{\text{I,shade}}(L) \). Then, the irradiances on the sunlit leaves at depth \( L \) is obtained as:

\[
F_{\text{I, sun}}(L) = F_{\text{I, shade}}(L) + G_0 S_0
\]  

(19)

where the second term is direct radiation on the leaf surface.

The irradiance intercepted by the canopy is given by:

\[
F_{\text{int}} = (S_0 \mu_0 + S_d) - (S_0 \mu_0 \exp(-L_0 G_0/\mu_0) + F_{\text{diff}}(L_0))
\]  

(20)

Calculation of \( G \) and \( G_0 \) from leaf inclination index (\( \chi \)) has been discussed in Choudhury (1987). A base value of \( \chi = 0 \) (representing randomly oriented leaves) has been taken, while sensitivity results are given for \( \chi = -0.2 \) (erectophile canopy) and \( \chi = +0.2 \) (planophile canopy). Differences in leaf orientation among varieties of wheat has been noted by Yunusa et al. (1993), among others.

2.1.3. Daily gross photosynthesis and radiation use efficiency

The instantaneous canopy photosynthesis (\( A_c; \mu \text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \)) is obtained by weighting photosynthesis by sunlit and shaded leaves (respectively, \( A_{1, \text{sun}} \) and
The integration in Eq. (21) has been done using Gauss quadrature (eight points) after replacing $L$ by a normalized variable $y (= L/L_0)$.

The daily total interception (IPAR; mol photon m$^{-2}$ per day) and gross photosynthesis ($A_g$: mol CO$_2$ m$^{-2}$ per day) has been obtained by integrating the instantaneous values (Eqs. (20) and (21)) at 15 min interval throughout a day. Then, $e_g$ (mol CO$_2$ mol$^{-1}$ photon intercepted) is obtained as:

$$e_g = \frac{A_g}{\text{IPAR}}$$

(26)

2.2. Respiration ($R$)

Respiration has been calculated separately for growth ($R_g$) and maintenance ($R_m$) components. Considering that much of maintenance respiration is to support turnover of protein (Amthor, 1989, p. 15), $R_m$ (mol CO$_2$ m$^{-2}$ per day) has been calculated in terms of nitrogen content of foliage, stem, and roots. Observations for six crop species (alfalfa, chick pea, field bean, kidney bean, pea, and tobacco) by Irving and Silsbury (1987) gave the following relation between $R_m$ at 20°C and organic nitrogen content, N (mmol m$^{-2}$):

$$R_m = 2.5 \times 10^{-4} N$$

(28)

Root respiration is generally observed to be higher than shoot respiration possibly due to energy required for ion uptake from the soil (Amthor, 1989) (pp. 96–97). The data for maintenance coefficients of Italian ryegrass, sunflower, and alfalfa given in Amthor (1989) (pp. 78–80) show the ratio of root to shoot respiration to be in the range 1.17–2.80, with a mean and standard deviation as, respectively, 1.95 and 0.69 ($n = 4$; two sets of measurements for ryegrass).

Assuming that difference between N and N$_0$ is small (Lafitte and Loomis, 1988), an average value of the coefficients in Eqs. (27) and (28) has been used to calculate $R_m$ for foliage and stem, while this coefficient has been doubled to calculate $R_m$ for roots. Specifically, the following equation has been used to calculate $R_m$ at 20°C:

$$R_m = 2.1 \times 10^{-4} (n_f + n_s + 2n_r)$$

(29)

where $n_f$, $n_s$, and $n_r$ are, respectively, nitrogen content of foliage, stem, and roots (mmol N m$^{-2}$).

Although the mentioned discussion has pointed to variabilities in the coefficient relating $R_m$ to N, some of these variabilities are associated with the method of determining $R_m$ (Irving and Silsbury, 1987). The results of Ryan et al. (1996) for pine foliage at 15°C, when corrected to 20°C (see further), give the coefficient as $2.1 \times 10^{-4}$, which is the value appearing in Eq. (29).

The variation of $R_m$ with temperature has been considered to be governed by $Q_{10} = 2$ (Amthor, 1989) (p. 77). Thus, at temperature $T$, different from 20°C, $R_m$ has been calculated from the following equation:

$$R_m(T) = R_m(T = 20) 2^{(T−20)/10}$$

(30)

where $R_m (T = 20)$ is given by Eq. (29). Since sunlit and shaded leaves differ in temperature and so also stem and roots, an improvement over Eq. (30) would be to calculate maintenance respiration of these components separately. This will require supplementing Eq. (30) with energy balance equation for these components (see Leuning et al. (1995) for sunlit and shaded leaves).
The following equation is used to calculate $R_g$ (mol CO$_2$ m$^{-2}$ per day) (Amthor, 1989) (pp. 11–12):
\[
R_g = (1 - Y_G) \left[ A_g - R_m(T) \right] \tag{31}
\]
where $Y_G$ is the growth conversion efficiency, taken to be 0.74 as the average of three values for wheat given in Amthor (1989) (p. 79). For estimating net carbon accumulation over the global land surface, Ruimy et al. (1996) had taken $Y_G$ to be 0.72. According to Johnson and Thornley (1983), $Y_G$ is typically about 0.75. While it is recognized that $Y_G$ may not be constant during growth due to changes in biochemical composition of plant (Lafitte and Loomis, 1988; Amthor, 1989) (pp. 41–43), there is insufficient measurement for wheat to prescribe such changes. Nevertheless, possible effect of changes in $Y_G$ during growth is assessed while presenting the results.

Respiration ($R$) is obtained as the sum of the values from Eqs. (30) and (31), viz.,
\[
R = (1 - Y_G) A_g + Y_G R_m(T) \tag{32}
\]

2.3. Net carbon accumulation and radiation use efficiency

Daily gross photosynthesis ($A_g$) and respiration ($R$) values are used in Eq. (1) to obtain net carbon accumulation (dC/dt). Using Eq. (32) one obtains,
\[
\frac{dC}{dt} = Y_G \left[ A_g - R_m(T) \right] \tag{33}
\]

Note that use of a constant $Y_G$ in Eq. (33) implies that plant is in a steady state with respect to nonstructural carbohydrate pool. For sorghum, McCree (1988) shows that $Y_G$ increases with plant growth (see Section 4.3.4, Eq. (35)).

Then, the corresponding radiation use efficiency ($e$; mol CO$_2$ mol$^{-1}$ photon intercepted) is calculated as the ratio of (dC/dt) and IPAR.

3. Input data and methods

3.1. Canopy characteristics

The canopy characteristics (leaf area index and nitrogen content) used in the present calculations are summarized in Table 1 and elaborated further.

Harper et al. (1987) present measurements of leaf area index, and nitrogen content of live foliage, stem and roots for winter wheat (cv. Coker) planted at Southern Piedmont Conservation Research Center near Watkinsville (GA). The planting density was 25 plants m$^{-2}$. The crop was fertilized with 112 kg N ha$^{-1}$ as ammonium nitrate in split application at planting in November 1982 (39.2 kg N ha$^{-1}$) and in March 1983 (72.8 kg N ha$^{-1}$). These data are presented as best-fit curves to the measurements. The canopy characteristics for 14 days have been extracted from these curves covering the period from middle of March to middle of May.

Gregory et al. (1979) and Monteith (private communication, 1986) present biomass and nitrogen concentration of foliage, stem and roots of winter wheat (cv. Mans Huntsman) grown on a field of University of Nottigham Farm at Sutton Bonington (Leics.). The plant density of the established crop was 250 plants m$^{-2}$. No fertilizer was applied at planting (October 1974), but 97 kg N ha$^{-1}$ was applied in May 1975. The leaf area index has been determined from the foliage biomass and specific leaf weight of 525 mg dm$^{-2}$ for this cultivar given by Austin et al. (1982). The canopy characteristics for 9 days have been used, covering the period from middle of March to middle of June. The data after anthesis have not been considered to minimize inclusion of senescing leaves.

McNeal et al. (1966) present biomass and nitrogen content of foliage, stem and roots as average values for five cultivars of spring wheat (cvs. Thatcher, Min- dum, Chinook, P. I. 266148, and C.I. 13636) grown at Bozeman (MT) without fertilizer. The leaf area index has been determined from foliage biomass and specific leaf area of 18.5 m$^2$ kg$^{-1}$ obtained by van den Boogaard et al. (1997) as the average value for 10 spring wheat cultivars. The canopy characteristics for 4 days covering the period from middle of June (tillering stage) to middle of July (flowering stage), have been used.

The data presented in Table 1 show considerable differences in partitioning of total plant nitrogen into foliage, stem and roots for winter and spring wheat. The average fraction of total nitrogen in foliage, stem and roots for winter wheat is, respectively, about 48, 38 and 14%, while it is 70, 26 and 4% for spring wheat. Factors contributing to this difference are not known, although we note that spring wheat was not
3.2. Air temperature and incident radiation

Both air temperature and incident radiation change during the growing season of wheat, and they also vary with location. On a monthly basis, these two environmental variables are not totally uncorrelated. To have some guidance in specifying air temperature and radiation for model calculations, weather conditions corresponding to the data given in Table 1 was considered, as summarized further.

From March to May at Watkinsville (GA), mean daily air temperature increased from 5 to 20°C (Sharpe et al., 1988), while irradiance increases from about 32 to 45 mol m\(^{-2}\) per day (Lof et al., 1966; 1 J solar radiation has been taken to be equal to 2 µmol photon). At Sutton Bonington (UK), mean daily air temperature and irradiance increased, respectively, from 3.5 to 15.5°C and from 15 to 34 mol m\(^{-2}\) per day during the period, March to June (Gregory et al., 1981). The mean air temperature and radiation at Bozeman (MT) during June–July period are, respectively, about 16.7°C and 50 mol m\(^{-2}\) per day.

Near Manhattan (KS), where chamber measurements and calculations were done to obtain gross photosynthesis and net carbon accumulation by winter wheat (cv. Newton) (Wall and Kanemasu, 1990), air temperature ranged between 13 and 25°C and from 15 to 34 mol m\(^{-2}\) per day (Wall et al., 1990). From these measurements, the mean daily irradiance is estimated to be about 48 mol m\(^{-2}\) per day.

Considering the above environmental conditions, calculations have been done for a base value of temperature as 15°C, while sensitivity results are presented for 10 and 20°C.

Incident direct and diffuse irradiances were calculated at 15 min interval for 34°N (Watkinsville, GA) by prescribing atmospheric conditions and time periods of a day being cloudy (Choudhury, 1982, 1987). A sample of 13 realizations of daily total irradiance and its diffuse fraction, obtained by varying the time periods of a day being cloudy, used in the present calculations are given in Table 2. Cloud cover varies from zero (Realization #1) to 100% (Realization #13). It is commonly observed that the diffuse fraction does not change significantly at high irradiances, but then it increases as the total irradiance decreases (Collares-Pereira and Rabl, 1979), as seen in Table 2. These irradiances will be considered to provide possible realizations of day-to-day fluctuations. While it was desirable to use an ensemble of measured diurnal values of direct and diffuse PAR, such measurements were not available to me for the present calculations.

### 3.3. Summary of parameters and sensitivity

Calculation of the efficiency values for the 27 canopies (Table 1) has been done for all realizations of the incident irradiance (Table 2) assuming the base values of maximum leaf photosynthesis (\(A_{\text{max}}\)) as 20 µmol m\(^{-2}\) s\(^{-1}\), curvature factor (\(\theta\)) in the light response function for leaf photosynthesis as 0.8, leaf

<table>
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<th>#</th>
<th>(I_{\text{sat}})</th>
<th>(e_{g,10})</th>
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<td>0.027(7)</td>
</tr>
</tbody>
</table>

Table 2

Possible realizations (#) of incident total irradiance used in the calculations (\(I, \text{ mol m}^{-2} \text{ per day}\)) and the fraction of this irradiance which is diffuse (\(f_{\text{diff}}\))^\(a\)

---

^a Totally clear and cloudy sky conditions are presented here as, respectively, Realization #1 and #13. Also given are calculated mean radiation use efficiency (mol CO₂ mol\(^{-1}\) photon intercepted) for gross photosynthesis (\(e_{g,10}\) and \(e_{g,20}\)) and for net carbon accumulation (\(e_{10}\) and \(e_{20}\)) when air temperature is 10 and 20°C for the 27 canopies in Table 1. The coefficient of variation (in percent) of the efficiency values for the 27 canopies are given in parenthesis.

---

^b The last line gives the mean irradiance and diffuse fraction, together with the summary of efficiency values for all realization. These efficiency values are for randomly oriented leaves and \(A_{\text{max}} = 20 \mu\text{mol m}^{-2} \text{s}^{-1}\).
inclination index ($\chi$) as 0 and temperature ($T$) as 15°C (Base Case). Sensitivity analysis considers $A_{max}$ to be either 18 or 22 $\mu$mol m$^{-2}$ s$^{-1}$, $\theta$ being either 0.7 or 0.9, $\chi$ being either −0.2 or +0.2, and $T$ being either 10 or 20°C (Sensitivity results). The sensitivity results are presented in terms of relative change (in %). Thus, for example, sensitivity of $e_g$ to $A_{max}$ has been calculated as: $100 \left[ e_g(A_{max} = 22 \text{ or } 18) - e_g(A_{max} = 20) \right] / e_g(A_{max} = 20)$.

4. Results and discussion

4.1. Base case

The efficiencies for gross photosynthesis ($e_g$) and net carbon accumulation ($e$) for the 27 canopies at four irradiances ($I$) are shown in Fig. 1. It is seen that $e_g$ increases with leaf area index ($L_0$) towards saturation, which is less evident for $e$. Quantitatively, the coeffi-

![Fig. 1. Variation of the radiation use efficiency (mol CO$_2$ mol$^{-1}$ photon intercepted) for, (a) gross photosynthesis, and (b) net carbon accumulation, with leaf area index of the 27 canopies at four irradiances, as annotated within the figure.](image-url)
Fig. 2. Variation of the radiation use efficiency (mol CO$_2$ mol$^{-1}$ photon intercepted) for, (a) gross photosynthesis, and (b) net carbon accumulation, with the diffuse fraction of the incident irradiance for three canopies, as annotated within the figure by leaf area index ($L_0$).

cients of variation (cv) for $e_g$ at $I = 65$ and 14 mol m$^{-2}$ per day are, respectively, 4.5 and 5.9% ($n = 27$), while those for $e$ are, respectively, 3.3 and 4.3% ($n = 27$). It is also seen in Fig. 1 that both $e$ and $e_g$ increase with decreasing irradiance. The results for three canopies ($L_0 = 0.5$, 2.0, and 5.2) plotted in Fig. 2 show that both efficiencies increase systematically with the diffuse fraction ($f_{\text{dif}}$). These relationships with the diffuse fraction are strongly linear ($r^2 > 0.994$, $n = 13$), although with somewhat different slopes. For $L_0 = 0.5$, the slopes for $f_{\text{dif}}$ versus $e_g$ and $f_{\text{dif}}$ versus $e$ are, respectively, 0.031 and 0.021, while the corresponding values for $L_0 = 5.2$ are, respectively, 0.043 and 0.024. Thus, the slope for $f_{\text{dif}}$ versus $e_g$ changes more with $L_0$ compared to that for $f_{\text{dif}}$ versus $e$ (the slope varies, respectively, by 32 and 13% in going from $L_0 = 0.5$ to 5.2). For four realizations of the irradiance which have the same $f_{\text{dif}}$ (#1 to #4 in Table 2), the cv for $e_g$ is less than 3.5%, and that for $e$ is less than 2%. These results suggest that $f_{\text{dif}}$ is a significant determinant of both efficiencies. While diffuse radiation is utilized better for photosynthesis due to penetration within the canopy, at any given $L_0$ there would be scatter in the relation between RUE and $f_{\text{dif}}$ when ensemble of irradiances other than those in Table 2 are used. This is because the same $f_{\text{dif}}$ can result from varied combination of the magnitudes of diffuse and direct irradiances, and the magnitude of these irradiances affect canopy photosynthesis through the light response function for leaf photosynthesis (Eqs. (24) and (25)). Thus, $f_{\text{dif}}$ and total irradiance determine the efficiencies. For CO$_2$ assimilation by soybean and maize canopies, Sinclair et al.
(1992) found a somewhat non-linear relation between RUE and $f_{dfr}$ which varied in the range 0.15–0.50.

The results presented earlier demonstrate a weak dependence of $e_g$ and $e$ on $L_0$, but a strong dependence on $f_{dfr}$.

4.2. Sensitivity results

For brevity, the sensitivity results are presented for four incident irradiances and as average values for all 27 canopies (Table 3).

Changes in $A_{max}$ affect $e_g$ and $e$ in a very similar fashion; higher $A_{max}$ gives higher efficiencies. The absolute values of the change decrease from 7% for clear sky ($I = 65$ mol m$^{-2}$ per day) to about 4% for cloudy sky ($I = 14$ mol m$^{-2}$ per day). This happens because at lower irradiances, photosynthesis depends more upon the quantum efficiency than on $A_{max}$.

The effect of changes in the empirical curvature factor ($\theta$) in the light response function for leaf photosynthesis is found to be similar for $e_g$ and $e$. Both the efficiency values increase (decrease) when $\theta$ is increased (decreased). The absolute values of the change increase as irradiance decreases. When $\theta$ is increased, a higher value of leaf photosynthesis is realized at a lower irradiance, and thus increasing the efficiencies. The effect of increasing or decreasing $\theta$ on $e_g$ and $e$ is not totally symmetric because of non-linear dependence of photosynthesis on $\theta$ (Eq. (4)).

Changes in leaf inclination index ($\chi$) also affect $e_g$ and $e$ in a very similar fashion. The efficiencies are lower when leaves are oriented preferentially in the horizontal direction ($\chi > 0$) as compared to being randomly oriented ($\chi = 0$). This happens because radiation decreases more strongly inside planophile canopies ($\chi > 0$), which results in lower photosynthesis. The absolute values of the change in the efficiencies decrease from 6% for clear sky ($I = 65$ mol m$^{-2}$ per day) to about 1% for cloudy sky ($I = 14$ mol m$^{-2}$ per day). Thus, the impact of leaf orientation on the efficiencies decreases as the diffuse fraction increases.

Changes in temperature affect $e_g$ and $e$ differently. Changes in $e_g$ occur due to its dependence on quantum efficiency, while $e$ is affected by both $e_g$ and dependence of respiration on temperature. The quantum efficiency is higher at lower temperature, but respiration is lower. The quantum efficiency becomes progressively important determinant of photosynthesis as irradiance decreases, and thus, sensitivity of $e_g$ to temperature increases with decreasing irradiance. In Table 3, the absolute changes in $e_g$ are seen to increase from 3 to 6% in going from clear to cloudy sky. And, these changes get doubled when $e$ is considered.

The results in Table 3 show that, of the four parameters considered here for sensitivity analysis, temperature and the empirical curvature factor can have noticeable effect on the efficiencies for cloudy conditions. These sensitivities are elaborated further.

4.3. Comparison with observations

The base value of parameters has been used for these comparisons, unless stated otherwise.
4.3.1. Observations near Manhattan

Based on chamber measurements of CO$_2$ fluxes near Manhattan (KS) and estimation of respiration during the growing season of winter wheat (cv. Newton), Wall and Kanemasu (1990) found mean $e_g$ and $e$, respectively, as 0.018 and 0.012 mol mol$^{-1}$ ($n = 92$). As noted earlier, air temperature varied from 13 to 25°C, while daily incident PAR fluctuated between 10 and 70 mol m$^{-2}$ per day without clearly discernible seasonal trend. The mean daily PAR is estimated to be about 48 mol m$^{-2}$ per day. The magnitude of diffuse radiation is not given.

The following assumptions are made to compare with the efficiency values: (a) the mean temperature is 20°C, and (b) the irradiance conditions can be represented by realizations #1 to #11 (Table 2), which have the range 17–65 mol m$^{-2}$ per day and an average value 47 mol m$^{-2}$ per day. The mean efficiency values for the 27 canopies at these irradiances are given in Table 2. The overall mean and standard deviation (in parenthesis) of $e_g$ and $e$ are calculated to be, respectively, 0.024 (0.008) and 0.0 15 (0.005) mol mol$^{-1}$ ($n = 297$; 11 irradiances × 27 canopies). While the calculated mean $e_g$ and $e$ are higher than the observed values by, respectively, 33 and 25%, the differences are within one standard deviation. It should, however, be noted that the present calculations are for the vegetative period, while the efficiency values determined by Wall and Kanemasu (1990) are for the growing season. The present calculations do not consider respiration associated with flowering and seed growth, and $A_{max}$ generally decreases after anthesis (Gregory et al., 1981). Also, while senescing leaves intercept radiation, they contribute less to gross photosynthesis. A lower $A_{max}$ and interception by senescing foliage will decrease $e_g$, and higher respiration will further decrease $e$.

4.3.2. Observations at Sutton Bonington and Rothamsted

Gallagher and Biscoe (1978) obtained an efficiency of 3.0 g (dry matter produced) MJ$^{-1}$ (APAR) for growth up to anthesis, and 2.2 g (dry matter produced) MJ$^{-1}$ (APAR) for the growing season for wheat and barley at Sutton Bonington (Leics., UK) and Rothamsted (Herts., UK). Assuming carbon content of the dry matter to be 41% (van den Boogaard et al., 1996), and 1 MJ (PAR) to be equal to 4.6 mol photon (Wall and Kanemasu, 1990), the efficiency for net carbon accumulation ($e$) would be 0.022 mol mol$^{-1}$ for growth up to anthesis and 0.016 mol mol$^{-1}$ for the growing season.

As noted earlier, mean daily air temperature increased from 3.5 to 15.5°C (average 9.8°C), while mean incident radiation increased from about 14 to 34 mol m$^{-2}$ per day (average 24 mol m$^{-2}$ per day) during the vegetative period of winter wheat (March–June). The mean air temperature and incident radiation for the growing season (March–August) are, respectively, 11.3°C and 25 mol m$^{-2}$ per day. Additionally, measurements of radiation reported by Manley (1970) suggest that the diffuse fraction of the incident radiation ($f_{diff}$) could be about 0.6.

For comparison with these efficiency values, mean air temperature has been taken to be 10°C. Possible realizations of incident irradiance was considered to be #8–#13 in Table 2, which give mean irradiance as 24 mol m$^{-2}$ per day and has a diffuse fraction of 0.63. The efficiency values for individual irradiances are given in Table 2. The overall mean and standard deviation (in parenthesis) of $e_g$ and $e$ are, respectively, 0.042 (0.011) and 0.028 (0.007) mol mol$^{-1}$ ($n = 162$). The calculated mean $e$ is 27% higher than the estimated value (0.022 mol mol$^{-1}$) for growing period up to anthesis, but significantly higher (75%) than that estimated for the growing season (0.016 mol CO$_2$ mol$^{-1}$ photon). Since mean air temperature and incident radiation are very similar for both growth periods, it is unlikely that environmental factors are causing this difference in efficiency. As noted earlier, interception of radiation by senescing foliage and physiological changes occurring after anthesis can decrease the efficiency corresponding to growing season.

Gregory et al. (1981) show light response function for leaf photosynthesis of wheat (cv. Maris Huntsman) at anthesis from an unfertilized and a fertilized (with nitrogen) plots at Sutton Bonington. For these measurements, $A_{max}$ values are, respectively, 17.2 and 12.9 μmol m$^{-2}$ s$^{-1}$ for unfertilized and fertilized plots. (Note that $A_{max}$ for fertilized plot is lower than that for unfertilized plot, although fertilized plot had higher nitrogen concentration in the leaf.) The curvature factor (θ) for the light response function for this wheat cultivar has been estimated to be 0.996 (Marshall and Biscoe, 1980). With these changes in the leaf photosynthesis parameters, the overall mean and standard
deviation (in parenthesis) of $e_g$ and $e$ are found to be, respectively, (a) 0.046 (0.013) and 0.032 (0.009) mol mol$^{-1}$ ($n = 162$) for the unfertilized plot, and (b) 0.040 (0.013) and 0.027 (0.008) mol mol$^{-1}$ ($n = 162$) for the fertilized plot. The calculated mean $e$ is 23% higher for the fertilized plot, and 46% higher for the unfertilized plot, compared to the observed value of 0.022 mol mol$^{-1}$.

The mentioned results are obtained for a temperature of 10°C, being the average value for the vegetative period. Observations at Sutton Bonington show that, with progression of the growing season, as biomass (and nitrogen content) is increasing, temperature is also increasing. Thus, increasing respiration load (through nitrogen; Eq. (29)) gets coupled with increasing respiration demand (through temperature; Eq. (30)). To quantify the impact of this correlation between respiration load and temperature on the efficiency, calculations were done using nine data sets (as mentioned earlier, for cv. Maris Huntsman); $\theta = 0.996$, $A_{\text{max}} = 17.2$ and 12.9 $\mu$mol m$^{-2}$ s$^{-1}$, and possible realizations of incident irradiance are #8–#13 in Table 2 (as noted earlier). The results for individual irradiances obtained with these changes are summarized in Table 4. The overall mean and standard deviation (in parenthesis) of $e_g$ and $e$ are found to be, respectively, (a) 0.043 (0.012) and 0.030 (0.008) mol mol$^{-1}$ ($n = 54$; nine canopies × six irradiances) when $A_{\text{max}} = 17.2$ $\mu$mol m$^{-2}$ s$^{-1}$, and (b) 0.036 (0.011) and 0.025 (0.007) mol mol$^{-1}$ ($n = 54$) when $A_{\text{max}} = 12.9$ $\mu$mol m$^{-2}$ s$^{-1}$. The calculated mean $e$ is overestimated by 36% when $A_{\text{max}} = 17.2$ (unfertilized plot) and by 14% when $A_{\text{max}} = 12.9$ (fertilized plot), compared to the observation (0.022 mol mol$^{-1}$).

For the data analyzed by Gallagher and Biscoe (1978) to determine $e$, five of the seven plots at Sutton Bonington, and two of the five plots at Rothamsted were fertilized with nitrogen. Thus, the weighted mean calculated $e$ (0.027 mol mol$^{-1}$) exceeds the measurement by 23%.

The above comparison is based on leaf photosynthetic parameters specific to cv. Maris Huntsman and changes in temperature during growth. What would have been the discrepancy if the base values of leaf photosynthetic parameters ($A_{\text{max}} = 20$ $\mu$mol m$^{-2}$ s$^{-1}$, and $\theta = 0.8$) are used, but variation of temperature is considered? The overall mean (standard deviation, $n = 54$) of $e_g$ and $e$ are found to be, respectively, 0.039 (0.010) and 0.026 (0.006) mol mol$^{-1}$. The calculated mean exceeds the measurement by 18%, which is substantially less than that found for constant temperature of 10°C, viz., 27% (noted earlier).

The results thus presented suggest that interaction between growth and environment can have a noticeable impact on the efficiency.

### Table 4

<table>
<thead>
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<th>I</th>
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<th>$A_{\text{max}} = 17.2$</th>
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<tr>
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</table>

$e_g$ and $e$ are calculated for varied incident irradiances ($I$, mol m$^{-2}$ per day) and for maximum leaf photosynthesis ($A_{\text{max}}$) of 17.2 and 12.9 $\mu$mol m$^{-2}$ s$^{-1}$, and possible realizations of incident irradiance are #8–#13 in Table 2 (as noted earlier). The results for individual irradiances obtained with these changes are summarized in Table 4. The overall mean and standard deviation (in parenthesis) of $e_g$ and $e$ are found to be, respectively, (a) 0.043 (0.012) and 0.030 (0.008) mol mol$^{-1}$ ($n = 54$; nine canopies × six irradiances) when $A_{\text{max}} = 17.2$ $\mu$mol m$^{-2}$ s$^{-1}$, and (b) 0.036 (0.011) and 0.025 (0.007) mol mol$^{-1}$ ($n = 54$) when $A_{\text{max}} = 12.9$ $\mu$mol m$^{-2}$ s$^{-1}$. The calculated mean $e$ is overestimated by 36% when $A_{\text{max}} = 17.2$ (unfertilized plot) and by 14% when $A_{\text{max}} = 12.9$ (fertilized plot), compared to the observation (0.022 mol mol$^{-1}$).

### 4.3.3. Observations at Perth

Yunusa et al. (1993) obtained efficiency values of 1.48, 1.98, and 2.35 g (above ground dry matter produced) MJ$^{-1}$ (IPAR) for growth up to anthesis for three varieties of spring wheat, respectively, Bencubbin, Gamenya, and Kulin from measurements of biomass and radiation at Field Station of the University of Western Australia in Perth. From root and shoot biomass data given in Siddique et al. (1990), the mean root to shoot ratio up to anthesis is found to be 0.83 and 0.67, respectively, for Gamenya and Kulin (root biomass data for Bencubbin is not given). Adjustment of the efficiency values for root biomass would give the efficiency for total biomass production as, 3.62 arid 3.93 g (dry matter produced) MJ$^{-1}$ (IPAR), respectively, for Gamenya and Kulin. Conversion of these dry matter values into carbon, and energy into photon (as mentioned earlier), would give $e$ for
growth up to anthesis as, 0.027 and 0.029 mol mol\(^{-1}\) for, respectively, Gamenya and Kulin.

Weather data at Perth (Yunusa et al., 1990) show that mean daily temperature remained relatively constant at about 14°C, while incident radiation increased from about 15 to 34 mol m\(^{-2}\) per day (average ca. 22 mol m\(^{-2}\) per day) during the measurement period, June–September. The magnitude of the diffuse fraction is not given. However, radiation data at Perth presented by McCormick and Suehrcke (1991) suggest that the diffuse fraction could be between 0.4 and 0.9, and a comparable range of the fraction can also be derived from the data presented by Collares-Pereira and Rabl (1979) for five locations within the US. A high fraction of diffuse radiation would be consistent with the rainfall data presented by Yunusa et al. (1990), which show that rainfall occurred on almost every 10-day period during the measurement (for the 2 years of study, total rainfall during the measurement period were 424 and 680 mm).

For comparison with the efficiency values, air temperature has been taken to be 14°C. Possible realizations of incident irradiance was considered to be #8 to #13 in Table 2, which give mean irradiance as 23 mol m\(^{-2}\) per day and has a diffuse fraction of 0.64. The overall mean and standard deviation (in parenthesis) of \(e_g\) and \(e\) are, respectively, 0.040 (0.0 10) and 0.026 (0.006) mol mol\(^{-1}\) (\(n = 162\)). The calculated mean \(e\) is underestimated by 7% compared to the measured mean (0.028 mol mol\(^{-1}\)).

Yunusa et al. (1993) have noted that leaves of Kulin are more erect than those for Gamenya. When calculations were done by assigning leaf inclination index of \(-0.2\) to Kulin and 0.2 to Gamenya, the results differed by ca. 2% from those quoted earlier. As can be seen in Table 3, moderate changes in the leaf inclination index have little impact on the efficiencies under predominantly cloudy conditions.

4.3.4. Carbon use efficiency

Since different biophysical factors affect gross photosynthesis and net carbon accumulation, and considering the uncertainties in the comparison presented earlier between the calculated and the observed \(e_g\) near Manhattan, an attempt is made to assess the calculated carbon use efficiency, CUE, which is the ratio of net carbon accumulation and gross photosynthesis (McCree, 1988). From Eq. (33) one can write,

\[
\text{CUE} = Y_G \left\{ 1 - \frac{R_m(T)}{A_g} \right\}
\]

(Yamaguchi (1978) quotes CUE as 0.85 for the initial growth period, while 0.73 around anthesis for wheat. Field measurements at Hokkaido (Japan) of \(^{14}\)C depletion in spring wheat (cv. Haruhikari) for about 55 days, starting 43 days after planting, by Tanaka and Oasaki (1983) gave CUE of 0.62. From \(^{14}\)C and chamber measurements of CO\(_2\) flux for four winter wheat cultivars ( cvs. Honor, Houser, Purcell, and Ticonderoga) grown in the field at Hamden (CT), Gent (1994) found CUE to be 0.67 during the period of maximum assimilation (around anthesis), while the average CUE for the vegetative period appears to be about 0.6 (estimated from data in Fig. 2 of Gent (1994)). A growth room study of 22-day old plants of four spring wheat cultivars ( cvs. Debeira, Katya, Maya Sap, and Mexipak) by van den Boogaard et al. (1996) gave CUE in the range 0.69–0.72, with a mean of 0.70. Growth room study by Gifford (1994) gave CUE of 0.6, and by Monje and Bugbee (1998) for cv. Veery-10 gave CUE of 0.53 for seedlings (0–8 days after emergence, DAE), 0.60 for early vegetative state (9–15 DAE) and 0.61 for late vegetative state (16–33 DAE). The above studies give CUE in the range 0.53–0.85 for wheat at various stages and duration within the vegetative period. Some of the uncertainties associated with measurement techniques are discussed by Amthor (1989) (pp. 113–115), where some additional values of CUE for periods other than the vegetative period could be found (p. 116).

The calculated CUE values (Base Case, described earlier) for the 27 canopies at three irradiances (65, 39, and 14 mol m\(^{-2}\) per day) are shown in Fig. 3. The CUE decreases from about 0.7 to 0.6 as leaf area index increases from 0.5 to 5.2. Also, CUE values are generally lower for lower irradiance.

The mean CUE corresponding to the comparisons presented above are: 0.63 (Manhattan), 0.69 (Sutton Bonington), and 0.65 (Perth).

These calculated CUE values appear reasonable in the context of the measurements reported earlier.

One can see in Fig. 3 that CUE decreases as \(L_0\) increases. This variation appears because \(R_m\) (Eq. (29)) increases with plant growth due to increasing nitrogen content, which, in turn, decreases dC/dt (Eq. (33)).
Fig. 3. Variation of the carbon use efficiency (ratio of net carbon accumulation and gross photosynthesis) with leaf area index of the 27 canopies at three irradiances, as annotated within the figure.

or CUE (Eq. (34)). There are, however, observations (e.g., Cock and Yoshida, 1973; Yamaguchi, 1978; Koshkin et al., 1987; McCree, 1988; Bunce, 1989) which show that CUE is less variable during growth. The earlier mentioned results are obtained assuming a constant value of growth conversion efficiency, $Y_G$ (see Section 2.2; after Eq. (31)). Clearly, if $Y_G$ increases during growth, as has been determined for sorghum (McCree, 1988; Lafitte and Loomis, 1988), the CUE could change less with $L_0$ because $Y_G$ appears as a multiplier in Eq. (33) or (34). Thus, based on the data of Lafitte and Loomis (1988), $Y_G$ was expressed in terms of plant nitrogen concentration $N$ (percent of dry biomass) as:

$$Y_G = 0.814 - 0.051 N$$  \hspace{1cm} (35)

Fig. 4. Same as Fig. 3, except that the growth conversion efficiency ($Y_G$) varies with nitrogen concentration, as discussed in the text.

With this change in $Y_G$, the CUE values corresponding to Fig. 3 are shown in Fig. 4. Linear regression analysis of $L_0$ versus CUE for the irradiance of 65 mol m$^{-2}$ per day gave $r^2$ and slope ($n = 27$) as, respectively, 0.71 and $-0.011$ when $Y_G$ is constant (Fig. 3), but as 0.03 and 0.003 when $Y_G$ is variable (Fig. 4). Similarly, at the irradiance of 14 mol m$^{-2}$ per day, $r^2$ and slope ($n = 27$) are, respectively, 0.77 and $-0.020$ when $Y_G$ is constant (Fig. 3), but are 0.10 and $-0.006$ when $Y_G$ is variable (Fig. 4). Thus, use of Eq. (35) considerably reduces variation of CUE with $L_0$ and conforms with Bunce (1989). The simulated range of CUE, ca. 0.55–0.65, is much smaller than the range of measurements, but agrees well with the range suggested by Monteith (1981).
The behavior of CUE during growth of wheat will become better clarified when further measurements of $Y_G$ become available.

Previous modeling by McCree (1988) has given an approximately constant CUE during growth of sorghum, while modeling by Dewar et al. (1998) suggests that an approximately constant CUE could occur for other species.

5. Summary and conclusions

The objective of the present study was to assess sensitivity of RUE of wheat during its vegetative period of growth under well-watered conditions to biophysical parameters. A diagnostic approach was used for this objective, so that net carbon accumulation was calculated as the difference of daily gross photosynthesis ($A_g$) and respiration ($R$). A model for instantaneous gross photosynthesis, considering variation of maximum rate of leaf photosynthesis within the canopy due to changes in leaf nitrogen content, sunlit and shaded leaves, a solution of the radiative transfer equation for propagation of direct and diffuse photosynthetically active radiation (PAR) within the canopy, was numerically integrated in space (angular variation of radiances and depth within the canopy) and time (diurnal variation) to obtain $A_g$. A non-rectangular hyperbola was used to describe the light response function for leaf photosynthesis. $R$, at a prescribed temperature, was calculated separately for growth and maintenance; the latter being determined by nitrogen content of foliage, stem, and root.

Calculations were done using field data for 27 canopies, representing two cultivars of winter wheat and average data for five cultivars of spring wheat. The leaf area index ranged between 0.5 and 5.2. Possible realizations of diurnal and day-to-day fluctuations of incident direct and diffuse PAR due to varied cloud cover were obtained by running a model at 15 min interval. Base values of maximum rate of leaf photosynthesis ($A_{max}$), empirical curvature factor ($\theta$) for non-rectangular hyperbola, leaf inclination index ($\chi$), and temperature ($T$) were prescribed, and the impact of changes in the base values on RUE for gross photosynthesis ($e_g$) and net carbon accumulation ($e$) based on intercepted PAR were assessed by sensitivity analysis.

The results showed that $e_g$ and $e$ are strongly determined by the diffuse fraction of incident irradiance (both efficiencies increase with increasing diffuse fraction), while changes in leaf area index introduce 10% variability in $e_g$ and $e$. A change in $A_{max}$ of 10% (absolute change of 2 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$) affected both $e_g$ and $e$ by 7% for clear sky and by 4% for cloudy sky. A change in $\theta$ of 13% (absolute change by 0.1) affected $e_g$ and $e$ by 4% for clear sky and by 7% for cloudy sky. When $\chi$ was changed from 0 (i.e., a canopy of randomly oriented leaves) to 0.2 (leaves are more horizontal, i.e., planophile) or −0.2 (erectophile), $e_g$ and $e$ changed by 6% for clear sky and 1% for cloudy sky. A change in temperature of 33% from the base value (absolute change of 5°C) affected $e_g$ by 3% for clear sky and 7% for cloudy sky, and these changes were doubled for $e$. These results suggest that extrapolation of measured RUE from one location to another should consider changes occurring in the magnitude and fraction of diffuse radiation, and temperature. Consideration of these meteorologic conditions is also relevant in crop growth modeling using RUE, and could provide an understanding of interannual variation of RUE for same cultivar and husbandry at a location.

The RUE values calculated for the vegetative period were compared with observations at several locations without adjusting model parameters. The calculated $e_g$ and $e$ were found to be higher than those observed for the growing season near Manhattan (KS) by, respectively, 33 and 25%. Comparison with measurements of $e$ for the vegetative period at Sutton Bonington and Rothamsted (UK) showed 20% overestimation, while it was 7% underestimation compared to measurements at Perth (Australia). Correlated increase of plant nitrogen content and temperature was found to have a noticeable impact on the RUE. The calculated carbon use efficiency, CUE (ratio of net carbon accumulation and gross photosynthesis) values were within the observed range (ca. 0.53–0.85) determined at various stages of vegetative period and for varied duration within this period. When growth conversion efficiency was considered to depend upon the plant nitrogen concentration, the simulated carbon use efficiency was found to be in the range, ca. 0.55–0.65, and was essentially independent of the leaf area index.

The present study has focused on RUE during the vegetative state of wheat in the absence of any stress. Extension of this study would be to consider the effect...
of stress during the vegetative phase, and the period beginning anthesis with and without stress. The effect of soil water stress during the vegetative phase might be addressed by modifying $A_{\text{max}}$ (Ritchie, 1981) and maintenance coefficient (Wilson et al., 1980), and changes in tissue temperature would have to be considered through an energy balance model. The CUE might not change significantly under soil water stress which occur under field conditions (McCree, 1986). Modeling of RUE starting anthesis would require much additional effort because of major physiological changes which occur in this period.

References


