A model of canopy photosynthesis incorporating protein distribution through the canopy and its acclimation to light, temperature and CO_2

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• *Background and Aims* The distribution of photosynthetic enzymes, or nitrogen, through the canopy affects canopy photosynthesis, as well as plant quality and nitrogen demand. Most canopy photosynthesis models assume an exponential distribution of nitrogen, or protein, through the canopy, although this is rarely consistent with experimental observation. Previous optimization schemes to derive the nitrogen distribution through the canopy generally focus on the distribution of a fixed amount of total nitrogen, which fails to account for the variation in both the actual quantity of nitrogen in response to environmental conditions and the interaction of photosynthesis and respiration at similar levels of complexity.
• *Model* A model of canopy photosynthesis is presented for C_3 and C_4 canopies that considers a balanced approach between photosynthesis and respiration as well as plant carbon partitioning. Protein distribution is related to irradiance in the canopy by a flexible equation for which the exponential distribution is a special case. The model is designed to be simple to parameterize for crop, pasture and ecosystem studies. The amount and distribution of protein that maximizes canopy net photosynthesis is calculated.
• *Key Results* The optimum protein distribution is not exponential, but is quite linear near the top of the canopy, which is consistent with experimental observations. The overall concentration within the canopy is dependent on environmental conditions, including the distribution of direct and diffuse components of irradiance.
• *Conclusions* The widely used exponential distribution of nitrogen or protein through the canopy is generally inappropriate. The model derives the optimum distribution with characteristics that are consistent with observation, so overcoming limitations of using the exponential distribution. Although canopies may not always operate at an optimum, optimization analysis provides valuable insight into plant acclimation to environmental conditions. Protein distribution has implications for the prediction of carbon assimilation, plant quality and nitrogen demand.

Key words: Canopy photosynthesis, respiration, protein distribution, acclimation, optimization, model.

INTRODUCTION

The description of canopy photosynthesis and respiration lies at the core of most biophysical crop and pasture simulation models. These models need to include the acclimatory responses of protein, including photosynthetic enzymes, to environmental conditions of light, temperature and CO_2 during growth, as this will affect the rate of photosynthesis and also nitrogen demand and, in the case of pastures, plant quality. Models of canopy gross photosynthesis generally incorporate a description of light interception and attenuation through the canopy and of single leaf gross photosynthesis in response to irradiance, or photon flux density. These are then combined to give the rate of canopy gross photosynthesis. Models were presented by Thornley (1976) and there have been several developments since then with different degrees of complexity (e.g. Campbell, 1977; Johnson and Thornley, 1984; Johnson *et al.*, 1989, 1995; Sands, 1995; Anten *et al.*, 1995; Anten, 1997; Cannell and Thornley, 1998; Thornley and Johnson, 2000; Thornley, 2002; Thornley and France, 2007). The first models considered homogeneous light distribution through the canopy, while later developments separate it into direct and diffuse beams, and include other factors such as the movement of the sun across the sky. For leaf photosynthesis, early models had a fixed light response curve for photosynthesis while later models include variation in leaf nitrogen through the canopy. Most descriptions of leaf photosynthesis in canopy photosynthesis models are based on the non-rectangular hyperbola (as described later), which is a versatile semi-empirical approach for describing the light response for leaf photosynthesis. Whereas the initial focus was to explore the influence of light interception and attenuation on leaf photosynthesis as it influences canopy photosynthesis, later models addressed issues such as the importance of diurnal variation in irradiance and temperature (e.g. Johnson and Thornley, 1984; Thornley and Johnson, 2000).

It is well established that the photosynthetic potential of leaves is influenced by the environment in which they are grown, including irradiance, temperature, nitrogen availability and CO_2 concentration (for a review, see Kull, 2002). The inclusion of acclimation into canopy photosynthesis models

has generally focused on the acclimation of photosynthetic potential to light and its subsequent variation through the depth of the canopy. Charles-Edwards (1981, p. 70) assumed that the light-saturated leaf photosynthetic potential for leaves within the canopy was proportional to the attenuation of light at that position in the canopy. This has been applied widely and is discussed in further detail later. Anten *et al.* (1995) and Sands (1995) considered a fixed quantity of nitrogen (N) within the canopy and, by seeking an optimum distribution such that canopy photosynthesis was maximized, derived a similar expression to Charles-Edwards' assumption theoretically.

Respiration, in particular maintenance respiration, is also related to protein content through its role in the synthesis and recycling of proteins, and so increasing the photosynthetic enzymes (and protein concentration in general) will not only increase photosynthetic potential, but also maintenance respiratory costs. Johnson *et al.* (1995) considered optimized N concentration through the balance between photosynthesis and respiration, so that increases in N influenced both photosynthetic potential and maintenance respiration losses. The direct and diffuse light components were incorporated and then the mean light incident on the leaves was used to calculate canopy photosynthesis. The light-saturated rate of leaf gross photosynthesis and maintenance respiration rate were assumed to be proportional to the leaf N concentration and the mean N concentration within the canopy was then evaluated such that daily canopy net photosynthesis was maximized for a prescribed set of environmental conditions.

The present study extends the analysis of Johnson *et al.* (1995) by using protein distribution through the canopy rather than the mean value, and looks at the acclimation to light, temperature, CO_2 and canopy leaf area index. We consider protein concentration, mol protein carbon (mol leaf carbon)$^{-1}$, rather than N, although both of these have been used in the literature. Leaf N is often expressed as N per unit leaf area or N per unit plant mass, and is related to protein concentration through the specific leaf area (leaf mass per unit area). Protein concentration is preferred for the present analysis, as our discussions about plant metabolism refer to protein, or photosynthetic enzymes, directly, and also consider cell-wall and sugar components of plant mass.

Our objective is to give a complete description of modelling photosynthesis and respiration components as influenced by the environment and to analyse the overall amount and distribution of protein through the canopy. The model does not use the widely applied assumption that N is exponentially distributed through the canopy. As stated by Kull (2002), the nitrogen gradient through the canopy is never proportional to the light gradient. Rather, the distribution is fairly linear in the upper canopy and then curves at depth through the canopy. Examples of such observations can be found in Yin *et al.* (2003). Kull (2002) further argues that optimization models fail to treat acclimation as a whole-plant phenomenon. We attempt to overcome this limitation by treating respiration at similar detail as carbon assimilation.

MODEL STRUCTURE

An overview of the model is presented here – for more detail see Johnson (2010). Variables and parameters, with default values,

are listed in Tables 1–3. Clearly, the environmental variables vary with location and time of year. For example, at Logan, UT, using standard equations for potential total daily global radiation (Johnson, 2010), assuming half the total daily global radiation is photosynthetically active radiation (PAR), and taking 1 μmol PAR photons = 0·218 J PAR (Clear Sky Calculator, 2010) the potential clear-sky mean daily photosynthetic photon flux (PPF) ranges from 720 to 1416 μmol m^{-2} s^{-1}. Actual values are lower due to cloud cover, and our choice of 750 μmol m^{-2} s^{-1} is representative of growth conditions, although there is value in exploring different climates.

Light attenuation and interception

The treatment of light interception and attenuation follows Johnson *et al.* (1995), which combines Beer's law for light attenuation (Monsi and Saeki, 1953) with Campbell's (1977) treatment of direct and diffuse irradiance components. The PPF, or irradiance, I (μmol m^{-2} s^{-1}), is given by

$$I(\ell) = I_0 e^{-k\ell} \tag{1}$$

where I_0 is the PPF at the surface of the canopy, ℓ (m^2 leaf m^{-2} ground) is the cumulative leaf area index (LAI) through the canopy and k (m^2 ground m^{-2} leaf) is the canopy extinction coefficient. If the direct fraction of PPF incident on the canopy is f_s, then

$$I_{0,s} = f_s I_0 \text{ and } I_{0,d} = (1 - f_s)I_0. \tag{2}$$

Let subscripts 's' and 'd' denote the direct solar and diffuse components of the PPF, so that at the top of the canopy and within the canopy

$$I_0 = I_{0,s} + I_{0,d} \text{ and } I = I_s + I_d. \tag{3}$$

Now, assuming both the direct and the diffuse components of PPF decline through the canopy according to eqn (1), which can be derived under simplifying assumptions discussed by Thornley and France (2007), it follows that

$$I_s = f_s I_0 e^{-k\ell} \text{ and } I_d = (1 - f_s)I_0 e^{-k\ell}. \tag{4}$$

Note that I_s is expressed per unit ground area and hence declines through the canopy as fewer leaves are in direct

TABLE 1. *Environmental variables*

Variable	Definition	Units
C, C_{amb}	Actual and current ambient atmospheric CO_2 concentration	380 μmol CO_2 (mol air)$^{-1}$
f_{day}	Daylength as fraction of 24 h	14/24
f_s	Direct solar fraction of PPF	0·7
I_0	Photon flux density, PPF, incident on the canopy	750 μmol photons m^{-2} s^{-1}
T	Temperature	22 °C
T_d, T_n	Day and night temperature	22, 12 °C
τ	Daylength	14 × 3600 s d^{-1}

The values given here are used in the figures unless stated otherwise. Symbols are listed alphabetically with English first and then Greek.

TABLE 2. *Model variables, definitions and units*

Variable	Definition	Units
Canopy structure		
ℓ, ℓ_s, ℓ_d	Total cumulative leaf area index (LAI) within the canopy, and the components in direct (sun) and diffuse PPF	m^2 leaf (m^{-2} ground)
η	Fraction of gross photosynthesis allocated to shoot processes	–
ρ	Leaf fraction of shoot mass	–
σ	Specific leaf area	m^2 leaf (kg d. wt)$^{-1}$
Light attenuation and interception		
$I(\ell)$, $I_s(\ell)$, $I_d(\ell)$	Total, direct and diffuse components of PPF on a horizontal plane within the canopy	μmol photons (m^{-2} ground) s^{-1}
$I_\ell(\ell)$, $I_{\ell,s}(\ell)$, $I_{\ell,d}(\ell)$	Total, direct and diffuse components of PPF incident on leaves within the canopy	μmol photons (m^{-2} leaf) s^{-1}
Leaf photosynthesis		
f_p	Leaf protein concentration. For canopy calculations, f_p is a function of ℓ	mol protein C (mol leaf C)$^{-1}$
$\bar{f}_p$	Mean protein concentration in the canopy	mol protein C (mol canopy C)$^{-1}$
$P_{\ell,g}$	Leaf rate of gross photosynthesis	μmol CO$_2$ (m^{-2} leaf) s^{-1}
P_m	$P_{\ell,g}$ at saturating PPF	μmol CO$_2$ (m^{-2} leaf) s^{-1}
$T_{opt,Pm}(C)$	Optimum temperature for P_m as a function of C	°C
$T_{opt,\alpha}(C)$	Temperature at which α starts to decline	°C
α	Leaf photosynthetic efficiency	mol CO$_2$ (mol photons)$^{-1}$
Canopy photosynthesis		
CQY	Canopy quantum yield	mol CO$_2$ (mol photons)$^{-1}$
CUE	Carbon use efficiency	–
m	Maintenance respiration coefficient	d^{-1}
P_g	Instantaneous rate of canopy gross photosynthesis	μmol CO$_2$ (m^{-2} ground) s^{-1}
$P_{g,day}$	Daily rate of canopy gross photosynthesis	mol CO$_2$ (m^{-2} ground) d^{-1}
$P_{n,day}$	Daily rate of canopy net photosynthesis	mol CO$_2$ (m^{-2} ground) d^{-1}
PPF$_{day,abs}$	PPF for the day absorbed by the canopy	mol photons (m^{-2} ground) d^{-1}
R_{day}, $R_{g,day}$, $R_{m,day}$	Total respiration, and growth and maintenance components	mol CO$_2$ (m^{-2} ground) d^{-1}
Y	Growth respiration efficiency	–

PPF, photon flux density (μmol m^{-2} s^{-1}). Environmental parameters and model parameters are defined in Tables 1 and 3, respectively. Symbols are grouped for canopy structure, light attenuation and interception, leaf and canopy photosynthesis. They are also listed alphabetically with English first and then Greek.

TABLE 3. *Model parameters, definitions, units and default values*

Parameter	Definition	Default value
Leaf photosynthesis		
$f_{C,m}$	$P_m/P_{m,ref}$ at T_{ref}, $f_{p,ref}$, saturating C	C$_3$: 2·0; C$_4$: 1·15
$f_{p,mx}$	Maximum f_p value for $P_{\ell,g}$	C$_3$: 0·30; C$_4$: 0·25 mol protein C (mol protein C)$^{-1}$
$f_{p,ref}$	Reference f_p value for leaves	C$_3$: 0·20; C$_4$: 0·15 mol protein C (mol leaf C)$^{-1}$
$P_{m,ref}$	P_m at C_{amb}, T_{ref}, $f_{p,ref}$	C$_3$: 20; C$_4$: 35 μmol CO$_2$ (m^{-2} leaf) s^{-1}
q	Curvature parameter for P_m temperature response	2
T_{mn}	Minimum temperature for P_m	C$_3$: 5 °C; C$_4$: 10 °C
$T_{opt,Pm,amb}$	Optimum temperature for P_m at C_{amb}	C$_3$: 20 °C; C$_4$: 25 °C
T_{ref}	Reference temperature for P_m	C$_3$: 20 °C; C$_4$: 25 °C
$\alpha_{amb,15}$	Photosynthetic efficiency at C_{amb} and 15 °C	80 mmol CO$_2$ (mol photons)$^{-1}$
γ_α	Temperature scale parameter for the optimum temperature for the photosynthetic efficiency	6 °C
γ_{Pm}	$T_{opt,Pm}$ parameter	10 °C
θ	$P_{\ell,g}$ curvature parameter	0·8
λ	$P_m/P_{m,ref}$ at T_{ref}, $f_{p,ref}$, 2 × C_{amb}	C$_3$: 1·5; C$_4$: 1·1
λ_α	Temperature parameter for the optimum temperature for the photosynthetic efficiency	0·02 °C^{-1}
Canopy respiration		
Q_{10}	Q_{10} value for maintenance respiration	1·5
Y_p	Growth efficiency for protein synthesis	0·55
Y_w	Growth efficiency for cell-wall synthesis	0·9
m_{ref}	Maintenance respiration coefficient at T_{ref}, $f_{p,ref}$	0·03 d^{-1}
Canopy structure		
$f_{p,0}$	Value of f_p at the top of the canopy	0·3 mol protein C (mol leaf C)$^{-1}$
$f_{p,b}$	Minimum value of f_p for a leaf	0·05 mol protein C (mol leaf C)$^{-1}$
k	Canopy extinction coefficient	0·5 m^2 ground (m^{-2} leaf)
L	Total canopy LAI	5 m^2 leaf (m^{-2} ground)
γ_p	Protein variation coefficient	5
η_{amb}	Carbon fraction allocated for shoot growth at C_{amb}	0·9
ρ_{amb}	Leaf fraction of shoot mass at C_{amb}	0·7
σ_{amb}	Specific leaf area at C_{amb}	15 m^2 leaf (kg d. wt)$^{-1}$
ζ	Conversion factor for d. wt to mole units	37 mol C (kg d. wt)$^{-1}$

Environmental parameters and model variables are defined in Tables 1 and 2 respectively. Symbols are grouped for leaf photosynthesis, canopy respiration and canopy structure. They are also listed alphabetically with English first and then Greek.

sunlight. It is readily shown that the PPFs incident on both diffusely lit and sunlit leaves in the canopy are

$$I_{\ell,d} = kI_0(1 - f_s)e^{-k\ell} \text{ and } I_{\ell,s} = kI_0[f_s + (1 - f_s)e^{-k\ell}]. \quad (5)$$

Note that the sunlit leaves also receive diffuse light. Finally, the total LAI components in direct and diffuse irradiance are

$$\ell_s = (1 - e^{-k\ell})/k \text{ and } \ell_d = \ell - \ell_s. \quad (6)$$

The direct irradiance term incident on leaves, kI_0f_s, in the second of eqns (5) is the same for all leaves in direct sunlight, but the leaf area in direct sunlight declines through the canopy.

Leaf gross photosynthesis

The rate of single leaf gross photosynthesis, $P_{\ell,g}$ μmol CO$_2$ (m^{-2} leaf) s^{-1}, is described as a function of the PPF incident

on the leaves, I_ℓ μmol photons (m^{-2} leaf) s^{-1}, by the non-rectangular hyperbola:

$$\theta P_{\ell,g}^2 - (\alpha I_\ell + P_m) P_{\ell,g} + \alpha I_\ell P_m = 0 \qquad (7)$$

where P_m, μmol CO$_2$ (m^{-2} leaf) s^{-1}, is the value of $P_{\ell,g}$ at saturating I_ℓ; θ, mol CO$_2$ (mol photons)$^{-1}$, is the photosynthetic efficiency, and θ ($0 \le \theta \le 1$) is a dimensionless curvature parameter. For more discussion of the non-rectangular hyperbola see Thornley and Johnson (2000), Thornley and France (2007) and Johnson (2010). $P_{\ell,g}$ is given by the lower root of eqn (7), which is

$$P_{\ell,g} = (1/2\theta)[\alpha I_\ell + P_m - \{(\alpha I_\ell + P_m)^2 - 4\theta\alpha I_\ell P_m\}^{1/2}]. \quad (8)$$

When $\theta = 0$ it becomes the rectangular hyperbola and with $\theta = 1$ it reduces to two straight lines.

Our approach is to use the non-rectangular hyperbola, and then incorporate the influence of temperature, CO$_2$ and protein on the three model parameters. This is preferable to using a more detailed biochemical leaf photosynthesis model such as Farquhar *et al.* (1980), Collatz *et al.* (1991) or Thornley and Johnson (2000) because the complexity of biochemical models poses considerable practical challenges owing to the greater number of parameters and their various responses to the environmental factors (e.g. Grace and Zhang, 2006). Our objective is to be able to define characteristic responses to temperature and CO$_2$ in a simple manner for a wide range of species.

The influence of temperature, CO$_2$ and N supply, or protein concentration, on leaf gross photosynthesis is dominated by the effect on the parameter P_m in eqn (8). The photosynthetic efficiency α also depends on temperature, CO$_2$ and N. There is less evidence that the curvature parameter θ responds to these factors (Sands, 1995; Cannell and Thornley, 1998; Peri *et al.*, 2005) and it is treated as constant. The methods used here follow, or are adapted from, Cannell and Thornley (1998), Thornley (1998), and Thornley and France (2007). Mathematical details are given in the Appendix. The overall leaf photosynthetic response to the interaction between PPF, temperature and CO$_2$ is consistent with general observations in the literature. Note that atmospheric CO$_2$ has units μmol mol^{-1}, which is a fractional concentration. For brevity, this is referred to simply as 'concentration'.

The general characteristics of the response of the light-saturated leaf gross photosynthesis, P_m, to temperature ($T\,°C$), CO$_2$ concentration (C μmol mol^{-1}) and protein concentration [f_p mol protein C (mol leaf C)$^{-1}$] are:

P_m increases from zero as temperature increases from some low value;

there is an optimum temperature above which there is no further increase;

the temperature optimum increases in response to atmospheric CO$_2$ concentration, C, which is due to the fall in photorespiration;

as temperature continues to rise there is a decline in P_m for C$_3$ species, due to the increase in photorespiration;

for C$_4$ species, P_m may remain stable or may decline slightly as temperature increases past the optimum;

for C$_3$ species, P_m increases in response to increasing C in an asymptotic manner, approaching a maximum value at saturating C;

C$_4$ species show little photosynthetic response to increasing C above ambient, C_{amb};

P_m increases as the protein concentration increases.

These factors are incorporated as described in the Appendix. The response of P_m to temperature at three C concentrations is shown in Fig. 1. The temperature response is defined in terms of the minimum, optimum and maximum temperatures, so that parameterization is quite straightforward.

The photosynthetic efficiency, α, increases in response to CO$_2$. α also increases in response to protein concentration, f_p, through the influence on proteins that bind the light-absorbing pigments. In addition, for C$_3$ plants at C_{amb}, α declines as temperature increases above 15 °C due to a shift from carboxylation (carbon fixation) to oxygenation (photorespiration) in the photosynthesis reactions. The critical temperature above which α starts to decline increases as the CO$_2$ concentration rises. These factors are incorporated as described in the Appendix, and the response of α to temperature at three CO$_2$ concentrations is shown in Fig. 1.

Protein distribution through the canopy

Calculating canopy photosynthesis and respiration requires the amount and distribution of protein through the canopy to
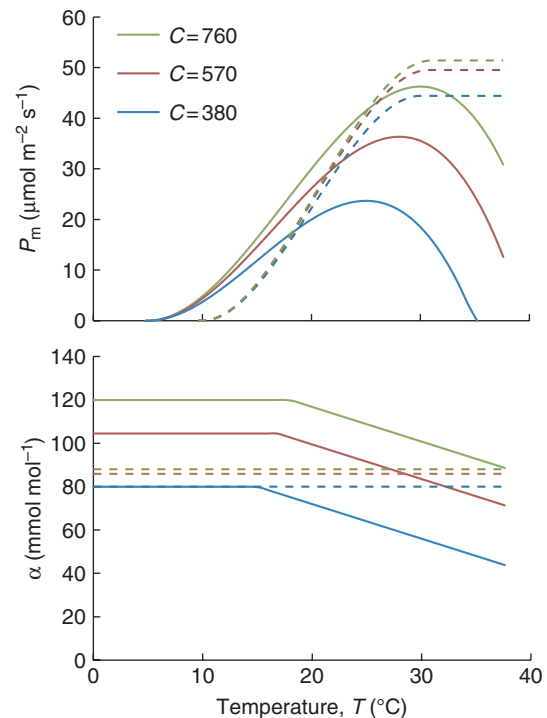

FIG. 1. Top: light-saturated leaf gross photosynthetic rate, P_m (μmol m^{-2} s^{-1}), in response to temperature and CO$_2$ concentration, C, with the parameters in Tables 1 and 3, and C (μmol mol^{-1}) as indicated. C$_3$, solid lines; C$_4$, broken lines. Bottom: photosynthetic efficiency, α, as a function of temperature for CO$_2$ concentrations of 380 (current ambient), 570 (50 % increase) and 760 (doubling) μmol mol^{-1}. C$_3$, solid lines; C$_4$, broken lines.

be defined. P_m in eqn (7) declines through the canopy, which can be interpreted as a response of protein, or photosynthetic enzymes, to the growth light environment. In practice, photosynthetic enzymes will acclimate to environmental conditions over periods of approx. 2–8 d (Thornley, 2004). To incorporate this effect, Charles-Edwards (1981, p. 70) assumed that P_m is proportional to light intensity, so that

$$P_m = P_{m,0}e^{-k\ell} \qquad (9)$$

where $P_{m,0}$ is the value at the top of the canopy ($\ell = 0$). This approach has been widely used (Thornley, 2004), and is simple to implement.

As it is assumed that P_m is proportional to the protein concentration, f_p [Appendix eqns (A1) and (A7)], using eqn (9) for P_m implies that $f_p(\ell)$, the leaf protein concentration at depth ℓ in the canopy, is given by

$$f_p(\ell) = f_{p,0}e^{-k\ell} \qquad (10)$$

where $f_{p,0} = f_p(\ell = 0)$ is the value of f_p for leaves in full sunlight at the top of the canopy. This equation does not account for fluctuations in light incident on the canopy, but this will be discussed later. Thornley (2004) derived eqn (10) from a model of leaf photosynthetic acclimation to light that incorporates the synthesis and degradation of the photosynthetic enzyme. However, this model assumes that synthesis of photosynthetic N from non-photosynthetic N is proportional to irradiance and if this is relaxed then other relationships for the distribution will be derived.

Several authors have extended eqn (10) to include a basal N, or protein, concentration, so that

$$f_p(\ell) = (f_{p,0} - f_{p,b})e^{-k\ell} + f_{p,b} \qquad (11)$$

where $f_{p,b}$ is a basal protein concentration that is not involved in photosynthesis. When $f_{p,b} = 0$ this is identical to eqn (10). This type of response has been derived by Sands (1995) by optimizing a prescribed amount of N in order to maximize canopy gross photosynthesis. Anten *et al.* (1995) also derived a similar equation that incorporated a simple treatment of respiration and then optimized the distribution of a prescribed quantity of N in order to maximize canopy net photosynthesis. Other authors have used equations of this type (e.g. Kull and Jarvis, 1995; Dewar, 1996). In spite of the appeal of eqn (11), experimental observations rarely follow this pattern (Yin *et al.*, 2003). Furthermore, as mentioned earlier, Kull (2002) notes that the N gradient through the canopy is never proportional to the light gradient, but that it is fairly linear in the upper canopy and then curves at depth through the canopy.

Equation (11) can be generalized as

$$f_p(\ell) = f_{p,0} - (f_{p,0} - f_{p,b})(1 - e^{-k\ell})^{\gamma_p} \qquad (12)$$

where $\gamma_p \geq 0$ is a dimensionless empirical coefficient. With $\gamma_p = 0$, eqn (12) simplifies to a constant protein distribution defined by $f_{p,b}$; with $\gamma_p = 1$ it becomes eqn (11); with $\gamma_p = 1$ and $f_{p,b} = 0$ it reduces to eqn (10); and as $\gamma_p \to \infty$ it simplifies to a constant protein distribution defined by $f_{p,0}$. The starting values $f_{p,0} = 0.3$, $f_{p,b} = 0.05$ mol protein C (mol

leaf C)$^{-1}$ and $\gamma_p = 8$ are used here, although variation in $f_{p,0}$ and γ_p is considered later. Equation (12), illustrated in Fig. 2, is a versatile equation for describing the possible protein decline through the canopy. Note that although eqn (12) is defined in terms of cumulative LAI, ℓ, this is really a surrogate for the irradiance within the canopy relative to that at the top, eqn (1), so that the protein distribution is responding to variation in light within the canopy.

The mean protein concentration in the canopy is

$$\bar{f}_p(L) = \frac{1}{L} \int_{\ell=0}^{L} f_p(\ell)\,d\ell \qquad (13)$$

which can be integrated with eqn (12), provided γ_p is a rational number; however, it is straightforward to solve numerically.

Instantaneous and daily canopy gross photosynthesis

The rate of canopy gross photosynthesis, P_g μmol CO_2 (m^{-2} ground) s^{-1}, is calculated by summing the leaf photosynthetic rate over all leaves in the canopy. Separating the leaves into direct and diffuse components of PPF and using eqn (6) gives

$$P_g = \int_0^L P_{\ell,g}(I_{\ell,s})\,e^{-k\ell}d\ell + \int_0^L P_{\ell,g}(I_{\ell,d})(1 - e^{-k\ell})\,d\ell. \qquad (14)$$

Equation (14) is the key equation for calculating the rate of canopy gross photosynthesis and, subject to eqn (9), can be solved analytically (Thornley, 2002), although the analysis is complex. In the present work, eqn (12) is used, and the integral is solved numerically.

The daily canopy gross photosynthesis, $P_{g,day}$ mol CO_2 (m^{-2} ground) day^{-1} is defined as the integral of P_g throughout the day:
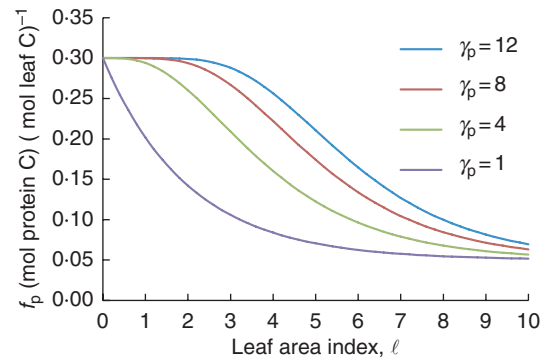
$$P_{g,day} = 10^{-6}\int_0^\tau P_g dt \qquad (15)$$

FIG. 2. Decline in protein concentration through the depth of the canopy as defined by eqn (12). $f_{p,0}$ and $f_{p,b}$ are 0.3 and 0.05 mol protein C (mol leaf C)$^{-1}$, respectively, $k = 0.5$, and $\gamma_p = 12$, 8, 4 and 1 as indicated.

where t is time (s), τ (s) is the daylight period in seconds and the factor 10^{-6} converts from μmol CO_2 to mol CO_2. Diurnal variation in both light and temperature can be incorporated in eqn (15).

Canopy structure and carbon partitioning

To calculate canopy net photosynthesis, it is necessary to evaluate canopy respiration, which requires values for LAI as a function of plant mass and the carbon allocation between the shoot and root.

Defining the shoot mass as W mol C (m^{-2} ground), it follows that

$$L = \sigma \rho W / \zeta \qquad (16)$$

where σ, m^2 leaf (kg leaf d. wt)$^{-1}$ is the specific leaf area, ρ is the leaf fraction of the shoot d. wt., and ζ converts from d. wt to mole units and is taken to be 37 mol C (kg d. wt)$^{-1}$ (which corresponds to 45 % plant carbon content – for more discussion, see Johnson, 2010). While σ could be defined with mole units and the need for the ζ coefficient avoided, dry weight (d. wt) units are used to be consistent with the common definition of specific leaf area. It is also observed that ρ and σ generally decline as the CO_2 concentration increases, corresponding to thicker leaves and a smaller leaf fraction in the shoot. There is some variation in these responses, and a discussion can be found in Pritchard and Amthor (2005), and different responses could be readily incorporated in the model. It is therefore assumed that

$$\sigma = \frac{\sigma_{amb}}{\sqrt{f_C(C)}} \quad \text{and} \quad \rho = \frac{\rho_{amb}}{\sqrt{f_C(C)}} \qquad (17)$$

where ρ_{amb} and σ_{amb} are the values of ρ and σ at ambient CO_2 and $f_C(C)$ is a general CO_2 response function (Appendix eqn A3). According to this function, which is a non-rectangular hyperbola,

$$\left.\begin{array}{l} f_C(C = C_{amb}) = 1 \\ f_C(C = 2C_{amb}) = \lambda \\ f_C(C \to \infty) = f_{C,m} \end{array}\right\} \qquad (18)$$

which takes the value unity at ambient CO_2, λ at double ambient, and $f_{C,m}$ at saturating CO_2. This equation requires the two parameters (λ, $f_{C,m}$) to be defined, and default values are (1·5, 2) for C$_3$ and (1·1, 1·15) for C$_4$. The square root term is introduced to moderate the response. With these values for C$_3$ plants, $1/\sqrt{[f_C(C)]}$ takes the values 0·87 and 0·82 at 50 % increase and doubling of CO_2, respectively. These values are consistent with general observations in the literature – for a further discussion, see Hikosaka et al. (2005). Equation (16) now becomes

$$L = \frac{\sigma_{amb}\rho_{amb}}{f_C(C)}\frac{W}{\zeta} \qquad (19)$$

which is used to relate LAI and plant mass. The default values for ρ_{amb} and σ_{amb} are taken to be 15 m^2 leaf (kg d. wt)$^{-1}$ and 0·7 kg leaf d. wt (kg shoot d. wt)$^{-1}$, respectively.

This treatment of specific leaf area, σ, gives a relatively simple description of the likely response to atmospheric CO_2 concentration but, in practice, σ responds to internal plant variables, particularly carbohydrate and possibly substrate nitrogen. There are other observed responses, such as thinner leaves at higher temperatures, lower light and higher nitrogen nutrition. However, although these factors are likely to vary during plant growth, the ambient CO_2 will remain relatively fixed. Thus, short-term variation in σ for new leaf growth should be captured through the parameter σ_{amb}.

The carbon partitioned to the root is also required for the analysis. Shoot : root partitioning has been addressed in a variety of ways, from the transport-resistance model of Thornley (1972) to simpler schemes based on the functional hypotheses of White (1937), Brouwer (1962) and Davidson (1969), which assume that carbon allocation between the shoot and root is such that the acquisition of resources from those organs is in some form of equilibrium (e.g. Johnson and Thornley, 1987). There is considerable variation in the observed carbon allocation between the shoot and root as CO_2 increases, although the general trend is for a shift towards root growth (Rogers et al., 1996), which is consistent with the functional hypothesis. We therefore adopt the same approach as for σ and ρ, by assuming that the fraction of gross photosynthesis that is allocated for shoot processes, η, is

$$\eta = \frac{\eta_{amb}}{\sqrt{f_C(C)}} \qquad (20)$$

which again incorporates a moderate decline in η as CO_2 increases. In the present model the value $\eta_{amb} = 0·9$ is used. Again, a range of factors influence shoot : root partitioning, but eqn (20) allows for the influence of atmospheric CO_2, which will be relatively stable during plant growth.

Canopy respiration

Respiration, excluding photorespiration, is calculated with the widely used McCree–Thornley approach (McCree, 1970; Thornley, 1970), which identifies the growth and maintenance components of respiration. In its standard form, the McCree–Thornley equation can be written:

$$R_{day} = \left(\frac{1-Y}{Y}\right)\frac{dW}{dt} + mW \qquad (21)$$

where R_{day}, mol C m^{-2} d^{-1}, is the daily canopy respiration rate, t (day) is time, Y (dimensionless) is the growth efficiency, so that for 1 mole of C utilized for growth, there are Y moles of structural C produced and $(1 - Y)$ respired, and m (d^{-1}) is the maintenance coefficient, with maintenance costs being a fraction m of plant mass. The terms on the right-hand side of eqn (21) are the growth and maintenance components of respiration, respectively, denoted by $R_{g,day}$ and $R_{m,day}$, so that

$$R_{day} = R_{g,day} + R_{m,day}. \qquad (22)$$

There has been some debate regarding the concepts of growth and maintenance respiration (see, for example, van Iersel, 2006, for a brief discussion), as there is no obvious difference

in the underlying physiological process for either component. However, in terms of plant function and overall carbon dynamics, these components can be of considerable benefit. For example, van Iersel (2006) accurately described the long-term temperature response of respiration by separating into growth and maintenance components, highlighting the different temperature responses for the components. van Iersel (2003) also found this approach to be effective in studying carbon use efficiency in plants, which is the ratio of net to gross photosynthesis. The separation of respiration into growth and maintenance components is a practical method for many applications and is ideally suited to modelling carbon assimilation by plant canopies. These components are now considered in turn.

Growth respiration. The respiratory costs of synthesizing plant cell wall and protein are different, and growth respiration is now defined in terms of plant structural components (Johnson, 1990). Consider the plant structure comprising cell wall, protein and sugars, with molar concentrations f_w, f_p, f_s, respectively, and where these factors sum to unity. If the growth efficiencies for cell wall and protein are Y_w and Y_p, then these are related to the overall growth efficiency, Y, by

$$Y = \frac{1}{1 + \left(\frac{1 - Y_w}{Y_w}\right)f_w + \left(\frac{1 - Y_p}{Y_p}\right)f_p}. \tag{23}$$

This allows for the direct influence of plant structure on the overall growth efficiency.

The growth respiration is therefore

$$R_{g,day} = \left(\frac{1 - Y}{Y}\right)\frac{dW}{dt}. \tag{24}$$

For example, with 10 % sugars, 30 % protein and 60 % cell wall, $Y = 0.79$, whereas if protein content is reduced to 20 % and cell wall increased to 70 %, this becomes $Y = 0.83$. Values for Y that are observed experimentally are generally in the range 0·75–0·85.

Maintenance respiration. The maintenance respiration coefficient is often related to live plant mass as in eqn (21). However, as plant protein is subject to continual degradation and resynthesis, maintenance respiration is primarily related to the energy costs associated with the resynthesis of degraded proteins and, as a rate process, is strongly temperature-dependent. Maintenance respiration is assumed to be given by

$$R_{m,day} = m_{ref}f_m(T)W\frac{\bar{f}_p}{f_{p,ref}} \tag{25}$$

where $f_m(T)$ is a maintenance temperature response function taking the value unity at the reference temperature T_{ref}, W (mol C m^{-2}) is shoot mass which is related to L by eqn (19), $\bar{f}_p$ is the mean canopy protein concentration, eqn (13), $f_{p,ref}$ is the reference protein composition and m_{ref} (d^{-1}) is the maintenance coefficient at the reference temperature and protein concentration, with default value 0·03 d^{-1}. There are other maintenance costs, such as the energy required for

phloem loading, but these are not considered explicitly, so that it is assumed that the protein concentration is an indicator of overall maintenance costs. Note that the maintenance coefficient in eqn (21) is now

$$m = m_{ref}f_m(T)\frac{\bar{f}_p}{f_{p,ref}}. \tag{26}$$

Common equations for the temperature response function are either the Arrhenius equation or simpler Q_{10}. These can both be shown to give virtually identical behaviour over practical temperature ranges (Johnson, 2010), and so the latter is used as it is simpler to work with. Thus

$$f_m(T) = Q_{10}^{(T-T_{ref})/10} \tag{27}$$

which is unity at $T = T_{ref}$, as required. The default value is $Q_{10} = 1.5$. Note that different day and night temperatures are required to calculate $f_m(T)$ and, denoting these with obvious subscripts,

$$f_m(T) = f_m(T_{day})f_{day} + f_m(T_{night})(1 - f_{day}) \tag{28}$$

where f_{day} is the daytime fraction of the 24-h period. In this equation, T represents the daily temperature in some form, although it is not evaluated explicitly. Rather, the day and night values are prescribed.

Using eqns (16)–(19), eqn (25) can now be written

$$R_{m,day} = m_{ref}f_m(T)\frac{\zeta f(C)L}{\sigma_{amb}\rho_{amb}}\frac{\bar{f}_p}{f_{p,ref}} \tag{29}$$

which completely defines the canopy maintenance respiration rate, as a function of L, in response to temperature, CO_2, canopy structure and protein distribution through the canopy. Note that the influence of CO_2 on $R_{m,day}$ is through its effect on the relationship between L and W.

Daily growth rate and net canopy photosynthesis

Photosynthesis and respiration are now combined to calculate the daily growth rate and net canopy photosynthesis rate. Carbon partitioned to the root is included, but the analysis focuses on the shoot, which is consistent with most practical applications. Daily net canopy photosynthesis is

$$P_{n,day} = P_{g,day} - R_{day} \tag{30}$$

and the shoot growth rate is

$$dW/dt = \eta P_{g,day} - R_{day} \tag{31}$$

where $P_{g,day}$ is given by eqn (15), η by eqn (20) and R_{day} as defined above. Note that R_{day} is the canopy respiration rate and does not include root respiration, which is included in the carbon partitioned to the roots. Combining eqn (31) with eqns (22) and (24) leads to

$$R_{day} = (1 - Y)\eta P_{g,day} + YR_{m,day} \tag{32}$$

which can be used in eqns (30) and (31) to calculate $P_{n,day}$ and dW/dt. dW/dt is readily derived as

$$dW/dt = P_{n.day} - P_{g,day}(1 - \eta) \qquad (33)$$

which is consistent with the definitions of the growth rate and net and gross photosynthetic rates – i.e. the growth rate is the daily net shoot carbon assimilation minus the carbon partitioned to the roots. This completely defines the shoot growth rate, net and gross canopy photosynthetic rates, along with the growth and maintenance respiration rates. Note that the canopy net photosynthesis, as defined here, is the shoot carbon exchange that would be measured without accounting for root respiration. Of this carbon, some is partitioned to the roots, which will be used for root growth and respiration. Thus, the canopy growth rate is less than the canopy net photosynthetic rate.

Figure 3 shows dW/dt, $P_{g,day}$, $P_{n,day}$, R_{day}, $R_{g,day}$ and $R_{m,day}$ as functions of PPF and temperature with the environmental and physiological parameters given in Tables 1 and 3. These responses are consistent with general observations. The growth and maintenance respiration components have quite different temperature responses, highlighting their independent characteristics.

Two derived quantities that are often of value are the canopy quantum yield, CQY, and carbon use efficiency, CUE. These are defined as:

$$CUE = P_{n,day}/P_{g,day} \qquad (34)$$

and

$$CQY = P_{n,day}/PPF_{day,abs} \qquad (35)$$

respectively, where $PPF_{day,abs}$ (mol photons m^{-2} d^{-1}) is the total PPF for the day absorbed by the canopy. These terms are defined in relation to the shoot carbon balance and do not include root respiration, and can be related to field measurements. CUE and CQY are shown in Fig. 4, and the responses are consistent with observations (Monje and Bugbee, 1998; Frantz and Bugbee, 2005).

OPTIMUM PROTEIN DISTRIBUTION

The analysis presented so far defines daily growth rate as well as photosynthesis and respiration components in response to plant and canopy characteristics, environmental conditions, and protein distribution through the canopy as given by eqn (12), which relates the protein concentration to the value at the top of the canopy, $f_{p,0}$, and light attenuation through the canopy. Just as protein distribution within the canopy will depend on irradiance, so will $f_{p,0}$. As both canopy gross photosynthesis and maintenance respiration increase in response to $f_{p,0}$, the optimum value for $f_{p,0}$ can be calculated for which daily net photosynthesis is maximized. Although optimization, or goal-seeking, models are attractive, they must be applied with caution, as they depend on the actual goal being defined. The optimization criterion applied here is simply to maximize the daily net photosynthesis, $P_{n,day}$ (eqn 30), for specified growth conditions by varying both the absolute concentration and distribution of protein through the canopy. This accounts for the effects on both carbon assimilation and respiratory losses from increasing protein concentration. This differs from other approaches where it is generally assumed either that there is a fixed total canopy N, or that the value at the top of the canopy is prescribed and the subsequent decay is estimated. By looking at both the amount and the distribution, we can explore possible acclimatory responses to environmental conditions. Dewar (1996) calculated the optimum N concentration in the canopy by balancing photosynthesis and respiration, and this analysis gave insight into the notion that net primary production is often proportional to total light intercepted. However, Dewar's analysis includes several simplifications in the description of canopy photosynthesis and also uses the exponential distribution of N through the canopy, similar to eqn (9), which, as discussed earlier, does not agree with general observations. Other optimization schemes have been explored, although they do not examine the balance between photosynthesis and the growth and maintenance components of respiration, and they all use some form of the Charles-Edwards assumption. For example, Schieving and Poorter (1999), using game theory, considered variation in specific leaf area in multi-species stands for allocation of nitrogen, while Franklin and Ågren (2002) and Boonman
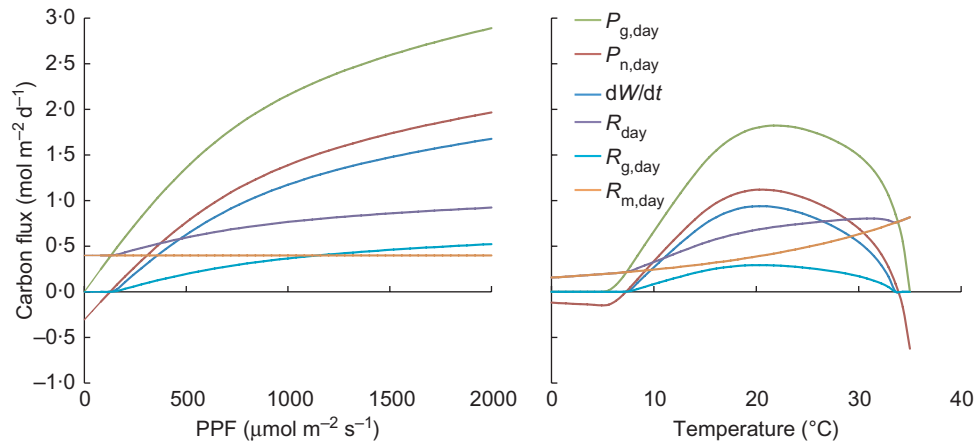

FIG. 3. dW/dt, $P_{n,day}$, $P_{g,day}$, R_{day}, $R_{g,day}$ and $R_{m,day}$ as indicated. Left: PPF response. Right: temperature response. Temperature denotes the average of day and night temperature with a 10 °C difference. Environmental and physiological parameters are defined in Tables 1 and 3.
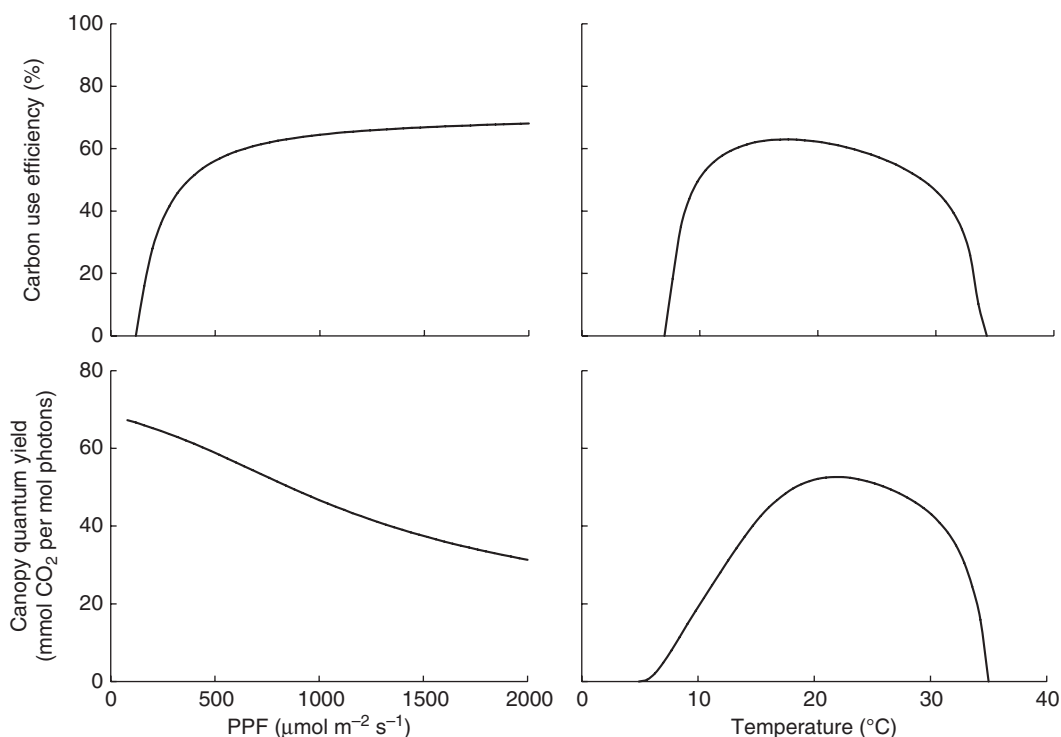
FIG. 4. Carbon use efficiency, CUE (top), and canopy quantum yield, CQY (bottom), for the default environmental and physiological parameters (Tables 1 and 3). Left: PPF response. Right: temperature response. Temperature denotes the average of day and night temperature with a 10 °C difference.

et al. (2006) consider the redistribution of nitrogen through leaf senescence. The present analysis does not impose the Charles-Edwards assumption, does not assume a fixed quantity of nitrogen (or protein) in the canopy, and includes both growth and maintenance respiration, which respond differently to environmental conditions and plant protein.

The parameters to be varied are the protein concentration at the top of the canopy, $f_{p,0}$, and γ_p in eqn (12). (Recall that $\gamma_p = 1$ corresponds to exponential decline.) The basal protein concentration, $f_{p,b}$, is fixed at the value 0·05 mol protein C (mol total leaf C)$^{-1}$. The optimum parameters are calculated using a search procedure. LAI could also be optimized, but we regard it as a variable that is influence by other factors. For example, in pastures, it will be affected by grazing pressure, and for crops it generally increases during vegetative growth. The values for the environmental parameters and LAI that are given in Tables 1 and 3 are used unless mentioned otherwise.

The role of direct and diffuse light components is considered first. Optimum protein distribution is shown in the top set of graphs in Fig. 5 with either 70 % direct or all diffuse PPF (I_0), and the corresponding $P_{g,day}$, $P_{n,day}$ and R_{day} vs. I_0 responses are also shown. For these illustrations, total canopy LAI is fixed at 5 m^2 leaf (m^{-2} ground) and instantaneous PPF at 750 μmol photons m^{-2} s^{-1}, so that the graph on the left shows the variation in f_p through the depth of the canopy while the graph on the right shows the response for the carbon flux components to PPF for canopies that have acclimated to 750 μmol photons m^{-2} s^{-1}. The derived parameter values are $f_p = 27$ and 30 mol protein C (mol total leaf C)$^{-1}$ and $\gamma_p = 8·7$ and 7·9 for the solid and dashed lines, respectively. With diffuse irradiance, f_p is lower although the photosynthesis components are greater than when the direct beam is included. For the diffuse PPF there will be fewer leaves in high irradiance and less benefit associated with high protein. However, even with this smaller f_p value, diffuse irradiance results in greater carbon fixation, owing to the more homogeneous distribution of irradiance through the canopy. There is little effect on respiration. These results demonstrate the potential importance of incorporating direct and diffuse components of I_0.

Acclimation to growth irradiance (I_0) is now considered. For these illustrations, I_0 includes the 70 % direct component. Whereas the top set of graphs in Fig. 5 show the response for $I_0 = 750$ μmol photons m^{-2} s^{-1} incident on the canopy, by contrast the corresponding optimum f_p distribution and carbon flux components are illustrated in the middle set for canopies that have acclimated to either 500 or 1000 μmol photons m^{-2} s^{-1}. The derived parameter values are $f_p = 26$ and 30 mol protein C (mol total leaf C)$^{-1}$ and $\gamma_p = 6·7$ and 12·6 for the solid and dashed lines, respectively. The influence of growing plants in the higher PPF is quite marked, with substantially greater f_p, both at the top and through the depth of the canopy. Consequently, the short-term irradiance responses of both gross and net canopy photosynthesis are greater for the canopy that has acclimated to the higher growth irradiance. However, it can be seen that there is negligible difference in $P_{n,day}$ at the low I_0, suggesting that plants grown in low irradiance can have a wide range of protein concentrations with relatively little impact on net photosynthesis.
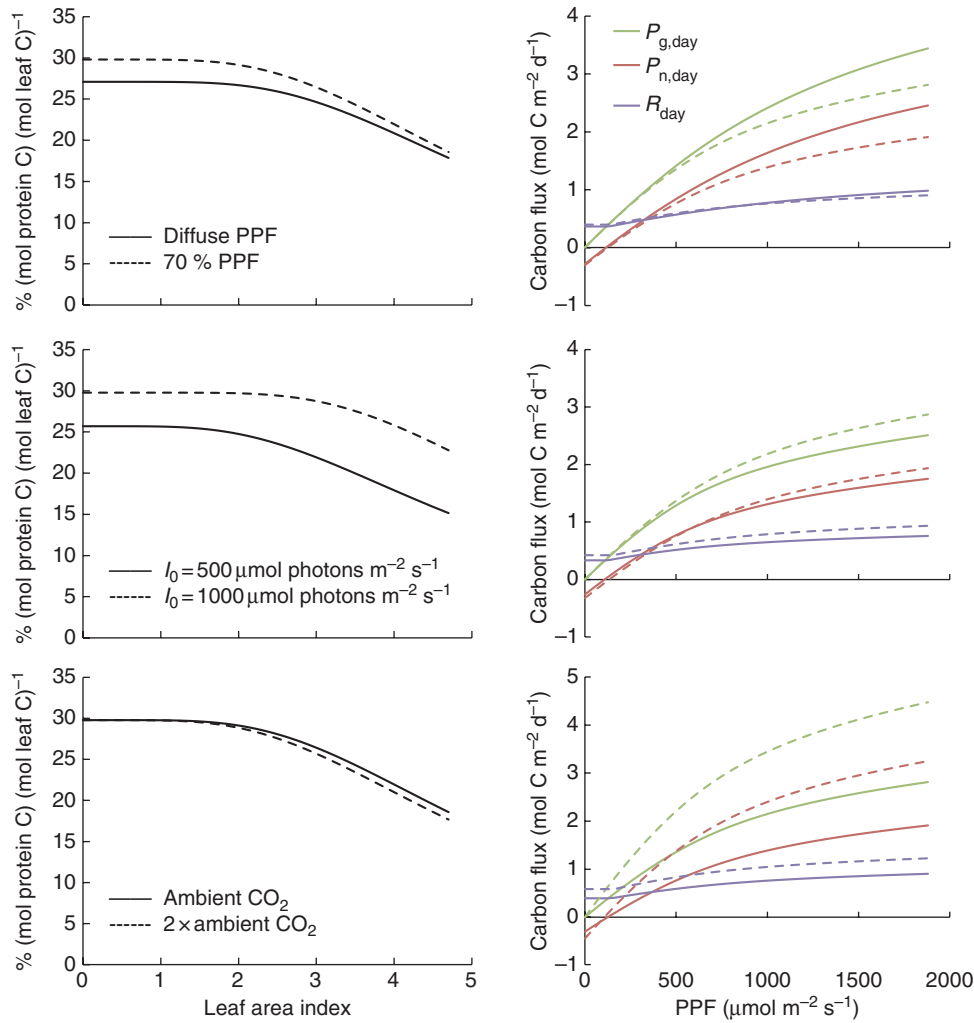
FIG. 5. The graphs on the left show the protein concentration distribution through the canopy [% mol protein C (mol total leaf C)$^{-1}$ (eqn (12)], as a function of leaf area index, optimizing daily net photosynthesis [eqn (30), $P_{n,day}$] with respect to $f_{p,0}$ and γ_p for the environmental conditions in Table 1 and parameters in Table 3 [$L = 5$ m^2 leaf (m^2 ground)$^{-1}$ and $I_0 = 750$ µmol photons m^{-2} s^{-1}]. The graphs on the right are the corresponding daily rates of gross photosynthesis [$P_{g,day}$, eqn (15)], net photosynthesis [$P_{n,day}$, eqn (30)] and respiration [R_{day}, eqn (22)] vs. instantaneous photosynthetic photon flux (PPF) density, I_0. Top: PPF all diffuse (solid lines); 70 % PPF in the direct beam (dashed lines). Middle: PPF incident on the canopy $I_0 = 500$ (solid) or 1000 µmol photons m^{-2} s^{-1} (dashed). Bottom: canopies grown in ambient (solid) or double ambient (dashed) CO$_2$. Note the different scale for the carbon flux graph.

Acclimation to the atmospheric CO$_2$ concentration during growth, C, is now considered. All other environmental parameters are as prescribed in Table 1. The bottom set of graphs in Fig. 5 show the optimum f_p distribution and carbon flux components for canopies at ambient and double ambient C. The derived parameter values are $f_p = 30$ and 30 mol protein C (mol total leaf C)$^{-1}$ and $\gamma_p = 7.9$ and 7.1 for the solid and dashed lines, respectively. There is negligible decline in protein concentration at elevated CO$_2$, so that the observed increases in daily rates of gross and net photosynthesis, $P_{g,day}$, $P_{n,day}$ and R_{day}, are primarily due to the direct effect of elevated CO$_2$. Note that the response of R_{day} to increased C is due to the greater growth respiration that accompanies the greater growth rate. Experimental indications of a small reduction in N at elevated CO$_2$ are fairly modest and may well be explained through a dilution effect due to increases in water-soluble carbohydrates (Pritchard and Amthor, 2005), which are not considered directly in the present model.

We have not used the widely applied exponentially declining protein concentration, but have generalized this according to eqn (12) where, as noted earlier, an exponential distribution is a special case. In Fig. 6, the optimized f_p distribution and carbon flux components are shown for ambient CO$_2$ for eqn (12), so that both $f_{p,0}$ and γ_p are optimized, and the exponential distribution, which is eqn (12) with $\gamma_p = 1$, so that only $f_{p,0}$ is optimized. The derived parameter values with both $f_{p,0}$ and γ_p being optimized (solid line) are 30 mol protein C (mol total leaf C)$^{-1}$ and 7.9, respectively, while for the exponential distribution with $\gamma_p = 1$, (dashed line), $f_{p,0} = 42$ mol protein C (mol total leaf C)$^{-1}$. As expected, the f_p distribution is quite different. Furthermore, the exponential distribution results in lower photosynthetic rates, particularly at high PPF, due to the fact that the exponential distribution reduces the
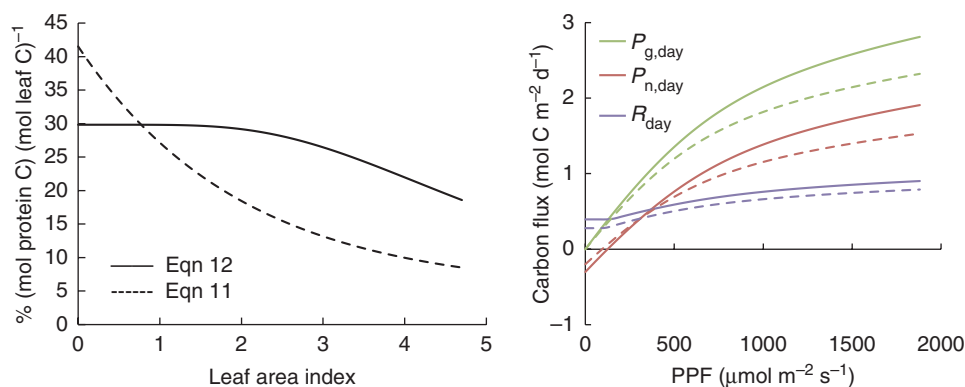
FIG. 6. As for Fig. 5 but the solid lines correspond to the protein distribution through the canopy described by eqn (12) with both $f_{p,0}$ and γ_p being varied while the broken line is for the exponential distribution, corresponding to eqn (11), in which case $\gamma_p = 1$ and only $f_{p,0}$ is adjusted.
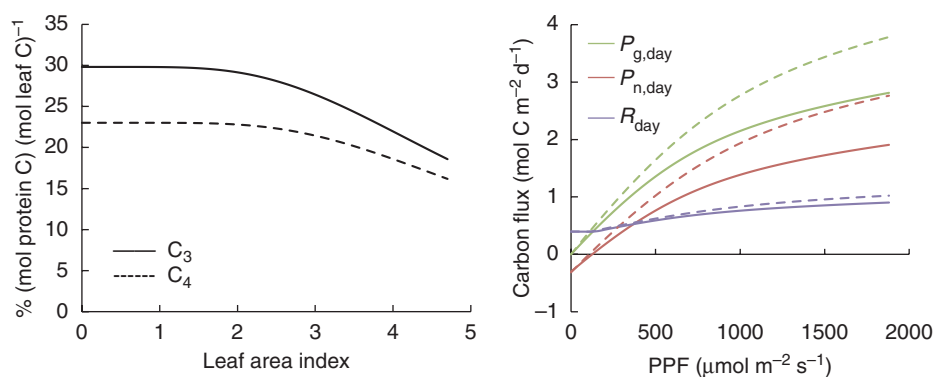

FIG. 7. As for Fig. 5 but the solid and broken lines are for the C_3 and C_4 canopy, respectively.

photosynthetic capacity of leaves near the top of the canopy quite substantially even though they are at irradiances that could benefit from greater f_p.

C_4 CANOPIES

The optimum protein distribution for a C_4 canopy, with $L = 5$, and corresponding carbon flux components are illustrated in Fig. 7, as compared with the C_3 canopy, but with the day and night temperatures increased by $5\,^{\circ}C$ for the C_4 canopy to reflect the generally higher temperatures that suit C_4 plants. The derived parameter values are $f_p = 30$ and 23 mol protein C (mol total leaf C)$^{-1}$ and $\gamma_p = 7 \cdot 9$ and $9 \cdot 7$ for the solid (C_3) and dashed (C_4) lines, respectively. Elevated CO_2 is not considered as the C_4 response is generally small, although it can be incorporated by implementing different parameter values for the CO_2 response if required. It can be seen that f_p is noticeably lower through the depth of the C_4 canopy, while the rates of gross and net photosynthesis are considerably higher.

DISCUSSION

Protein concentration and distribution through the canopy have been examined using a detailed model of canopy photosynthesis that incorporates direct and diffuse irradiance components, leaf photosynthesis in response to

light, temperature, CO_2 and protein, as well as canopy growth and maintenance respiration. Both C_3 and C_4 canopies have been considered. Although we have only considered monocultures, the model can also be applied to mixtures. The model differs from other approaches in that the canopy is treated as a whole system and a balanced approach of carbon assimilation is given based on both gross photosynthesis and respiratory losses, which are treated at similar levels of complexity, as well as partitioning of carbon within the plant. Rather than using the commonly applied model of exponential decline in protein, or N, through the canopy, a more general approach is used in which the distribution follows the widely observed pattern of being fairly linear near the top of the canopy with a subsequent decline through the canopy depth (Kull, 2002). The photosynthesis model is robust and gives expected behaviour for the photosynthesis and respiration components as well as the derived quantities of CUE and CQY. Acclimation of amount and distribution of protein through the canopy was derived by maximizing the daily net canopy photosynthetic rate. Acclimation of the overall protein concentration is as important as its distribution through the canopy. For example, with PPF incident on the canopy changing from 500 to 1000 μmol photons m^{-2} s^{-1}, and with environmental and physiological parameters given in Tables 1 and 3, the protein concentration at the top of the canopy, $f_{p,0}$, increases from 26 to 30 mol protein C (mol leaf C)$^{-1}$ and the total canopy concentration from 22 to 28 mol

protein C (mol leaf C)$^{-1}$. Furthermore, although our approach includes the exponential distribution of protein (or N) through the canopy as a special case [$\gamma_p = 1$ in eqn (12)] none of our optimization calculations derived this value. Rather, the optimized distributions are all consistent with general observations, with the protein distribution varying for different growth conditions. The optimization analysis has focused on steady-state conditions whereas, in practice, plant canopies respond to varying conditions. Given that acclimation is known to occur over periods of a few days (e.g. Kull, 2002; Thornley, 2004), the model can be incorporated into crop and pasture models using rolling averages of environmental conditions, particularly PPF and temperature.

The model is straightforward to implement and uses easily interpreted photosynthesis parameters, such as minimum, optimum and maximum temperatures for light-saturated leaf gross photosynthesis. It is therefore simple to prescribe parameters for different species such as perennial ryegrass or cotton that have markedly different temperature responses. Apart from the variation in protein concentration being important for the calculation of canopy photosynthesis, it also has implications for plant quality and nitrogen demand. Although the simulations presented here are for non-limited N supply, the system is equally applicable to canopies that are growing under N-limited conditions. The model gives a clear view of the role and possible importance of photosynthetic acclimation in contributing to net canopy photosynthesis, the primary driver of the plant ecosystem.

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APPENDIX

The effects of temperature (T, °C), atmospheric CO_2 concentration [C, μmol CO_2 (mol air)$^{-1}$] and protein concentration [f_p, mol protein C (mol leaf C)$^{-1}$] on the light-saturated leaf photosynthetic rate [P_m, μmol CO_2 (m^{-2} leaf) s^{-1}] and leaf photosynthetic efficiency [α, mol CO_2 (mol photons)$^{-1}$] were described qualitatively in the main text. The mathematical implementations are briefly presented here, but for more discussion see Johnson (2010).

P_m is defined by

$$P_m = P_{m,ref} f_C(C) f_{P_m,TC}(T, C) f_{P_m,fp}(f_p) \qquad (A\,1)$$

where $f_C(C)$ is a CO_2 response function, $f_{P_m,TC}(T,C)$ is a combined response to temperature and CO_2, $f_{P_m,fp}$ is the response to protein concentration, f_p mol protein C (mol leaf C)$^{-1}$, and $P_{m,ref}$ is a reference value for P_m, and is the value of P_m at a reference temperature, T_{ref}, ambient CO_2 concentration, C_{amb}, and reference protein concentration, as discussed below. The functions are constrained by

$$f_C(C_{amb}) = f_{P_m,TC}(T_{ref}, C_{amb}) = f_{P_m,fp}(f_{p,ref}) = 1. \qquad (A\,2)$$

Default values for $P_{m,ref}$ are 20 and 35 μmol CO_2 (m^{-2} leaf) s^{-1} for C_3 and C_4 species, respectively, reflecting the greater photosynthetic potential of C_4 plants. However, it must be noted that leaf photosynthetic potential is subject to considerable variation.

The CO_2 response function, $f_C(C)$, will be used for other processes in the model. It is given by the non-rectangular hyperbola:

$$f_C(C) = (1/2\phi)[\beta C + f_{C,m} - \{(\beta C + f_{C,m})^2 - 4\phi\beta f_{C,m} C\}^{1/2}] \qquad (A\,3)$$

where C is atmospheric CO_2 concentration, β is the initial slope, ϕ ($0 \le \phi \le 1$) the curvature, and $f_{C,m}$ the asymptote. Rather than prescribe β and ϕ, the function is defined to

take the value unity at ambient CO_2 and λ at double ambient, so that

$$\left. \begin{array}{l} f_C(C = C_{amb}) = 1 \\ f_C(C = 2C_{amb}) = \lambda \end{array} \right\}. \qquad (A\,4)$$

The default values for C_3 species are $\lambda = 1.5$ and $f_{C,m} = 2$ so that f_C increases by 50 % at $2 \times C_{amb}$ and doubles at saturating C. C_4 plants have a more limited response to CO_2 due to the lack of photorespiration (as discussed below) and, in this case, the values are $\lambda = 1.1$ and $f_{C,m} = 1.15$.

The parameters ϕ and β in eqn (A3) with (A4) can be shown to be

$$\phi = \frac{f_{C,m}[\lambda(f_{C,m} - 1) - 2(f_{C,m} - \lambda)]}{\lambda^2(f_{C,m} - 1) - 2(f_{C,m} - \lambda)} \qquad (A\,5)$$

and

$$\beta = \frac{\lambda(f_{C,m} - \phi\lambda)}{2C_{amb}(f_{C,m} - \lambda)} \qquad (A\,6)$$

Although this has involved some algebra, it allows the simple parameterization of eqn (A3). Note that constraints apply to ensure that $\beta > 0$ and $0 \le \phi \le 1$ (for more detail, see Johnson, 2010).

The protein response function is the same for both C_3 and C_4 species and is defined as a simple ramp function, so that

$$f_{Pm,fp}(f_p) = \begin{cases} f_p/f_{p,ref}, & f_p \le f_{p,ref} \\ f_{p,mx}/f_{p,ref}, & f_p > f_{p,mx} \end{cases}. \qquad (A\,7)$$

According to this function, $f_{Pm,fp}$ increases linearly as the protein concentration increases to the maximum value, above which there is no further increase in the rate of photosynthesis. The default parameter values for ($f_{p,ref}, f_{p,mx}$) are (0·2, 0·3) and (0·15, 0·25) for C_3 and C_4 species, respectively. The lower values for C_4 plants reflect the fact that these species generally have lower nitrogen levels (see Fig. 7 and the text). Equation (A7) is then used to relate the light-saturated leaf photosynthetic rate distribution through the canopy as given by eqn (12).

The approach to temperature responses used here is developed from Cannell and Thornley (1998) and Thornley (1998). Temperature functions based on activation energy of chemical reactions are sometimes used, but these are quite complex and difficult to apply routinely to species with different temperature characteristics. Also, it is debatable as to whether the detailed physical–chemistry descriptions of individual reactions are applicable to the enzyme-catalysed reactions involved in photosynthesis. Thus, a general temperature response function is defined as

$$f(T) = \begin{cases} \left(\frac{T - T_{mn}}{T_{ref} - T_{mn}}\right)^q \left(\frac{T_{mx} - T}{T_{mx} - T_{ref}}\right), & T_{mn} \le T \le T_{mx} \\ 0, & \text{otherwise} \end{cases} \qquad (A\,8)$$

where $q > 0$ is a curvature coefficient. Note that Cannell and Thornley (1998) used $q = 2$. The parameters in this equation

are defined so that

$$f(T_{mn}) = f(T_{mx}) = 0; \; f(T_{ref}) = 1 \qquad (A9)$$

and there is a maximum at

$$T_{opt} = (T_{mn} + qT_{mx})/(1+q) \qquad (A10)$$

which can be used to eliminate T_{mx}, so that eqn (A8) can be rewritten in terms of T_{ref}, T_{mn} and T_{opt} as

$$f(T) = \left(\frac{T - T_{mn}}{T_{ref} - T_{mn}}\right)^q \left(\frac{(1+q)T_{opt} - T_{mn} - qT}{(1+q)T_{opt} - T_{mn} - qT_{ref}}\right) \qquad (A11)$$

This is the general form of the temperature response function used here and has parameters with simple interpretation. Equation (A11) is illustrated in Fig. A1 at ambient CO_2 for a range of q values, and it can be seen that it is a versatile, flexible function for describing the temperature response.

The combined temperature and CO_2 response function in eqn (A1) is defined by eqn (A11), but with

$$T_{opt,Pm} = T_{opt,Pm,amb} + \gamma_{Pm}[f_C(C) - 1] \qquad (A12)$$

where $f_C(C)$ is again defined by the CO_2 function, eqns (A3)–(A6). The default value

$$\gamma_{P_m} = 10\,^{\circ}C \qquad (A13)$$

is used.

C_3 and C_4 species are treated in the same way, with the exception that for C_4 species the constraint

$$C_4 : f_{P_m,TC}(C, T) = f_{P_m,TC}(C, T_{opt,Pm}), \; \text{for} \, T > T_{opt,Pm} \qquad (A14)$$

applies, so that the temperature response does not fall when temperatures exceed the optimum. In practice, photosynthesis may decline at high temperatures due to water stress or enzyme damage. However, the analysis here aims to capture only the decline due to a shift towards photorespiration and, because this is assumed to be eliminated in C_4 plants, the
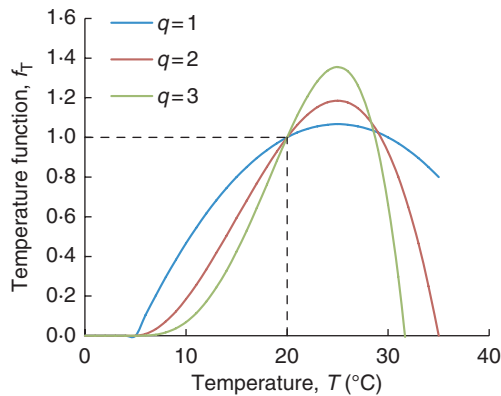

FIG. A1. Temperature function, eqn (A11), at C_{amb}. Parameters are: $T_{ref} = 20\,^{\circ}C$, $T_{m,n} = 5\,^{\circ}C$, $T_{opt} = 25\,^{\circ}C$, q as indicated. Note that $f(T = T_{ref}) = 1$.

constraint in eqn (A14) is reasonable. Note that although P_m may not decline at high temperatures, there can be a fall in net photosynthesis due to increases in respiration rate. Equations (A11)–(A14) completely define the function $f_{Pm,TC}$ for C_3 and C_4 species. P_m is illustrated in Fig. 1 in the main text for both C_3 and C_4 species.

Now consider leaf photosynthetic efficiency, α, defined by

$$\begin{aligned} C_{3:\,\alpha} &= \alpha_{amb,15}f_{\alpha,C}(C)f_{\alpha,TC}(T, C)f_{\alpha,f\,p}(f_p) \\ C_{4:\,\alpha} &= \alpha_{amb,15}f_{\alpha,C}(C)f_{\alpha,f\,p}(f_p) \end{aligned} \qquad (A15)$$

where $\alpha_{amb,15}$, mol CO_2 (mol photons)$^{-1}$, is the value of α at ambient CO_2 concentration, C_{amb}, and $15\,^{\circ}C$, with default value $\alpha_{amb,15} = 50$ mmol CO_2 (mol photons)$^{-1}$.

The function $f_{\alpha,C}(C)$ in eqn (A15) captures the direct influence of C on α, and is given by the CO_2 function that was used above, eqns (A3)–(A6).

The function $f_{\alpha,TC}(T,C)$ in eqn (A15) defines the temperature response on α and the influence of C on this temperature response, as given by

$$f_{\alpha,TC}(T, C) = \begin{cases} \left\{1 - \lambda_\alpha \frac{C_{amb}}{C}(T - T_{opt,\alpha})\right\}, & T \geq T_{opt,\alpha} \\ 1, & T < T_{opt,\alpha} \end{cases} \qquad (A16)$$

where λ_α is a constant and

$$T_{opt,\alpha} = 15 + \gamma_\alpha[f_C(C) - 1] \qquad (A17)$$

and again the CO_2 response function, eqns (A3)–(A6), is used. Note that eqn (A17) will not be valid for very small values of C, as the term C_{amb}/C will become infinitely large. Rather than address this issue to deal with unrealistic CO_2 concentrations, the theory is restricted to CO_2 concentrations greater than $100\,\mu$mol mol^{-1}, and subject to

$$f_{\alpha,C}(T, C) \geq 0 \; \text{for all } T \text{ and } C. \qquad (A18)$$

Default parameter values are $\lambda_\alpha = 0.02\,^{\circ}C^{-1}$ and $\gamma_\alpha = 6\,^{\circ}C$. With these parameter values, $T_{opt,\alpha}$ increases from its ambient value of $15\,^{\circ}C$ by $3\,^{\circ}C$ for a doubling of CO_2 from ambient.

The function f_{α,f_p} defines the protein response for α and is assumed to be a simple ramp function (Peri *et al.*, 2005), and is taken to be

$$f_{\alpha,f\,p}(f_p) = \begin{cases} 0.5 + 0.5f_p/f_{p,ref}, & f_p \leq f_{p,ref} \\ 1, & f_p > f_{p,ref} \end{cases} \qquad (A19)$$

This equation will not be valid for very low f_p, but, for that situation, photosynthesis will be primarily restricted by the influence on P_m.

According to these equations, photosynthetic efficiency α increases with increasing C for both C_3 and C_4 species, but for C_3 plants there is also a decline for temperatures above $15\,^{\circ}C$. The increase in α in response to C reflects the greater availability of CO_2, while the decline in response to temperature for C_3 species indicates a shift towards photorespiration as temperature increases, while this shift is reduced at increasing C. The lack of temperature response for C_4 species is due to

the lack of photorespiration in those plants. The response of α to temperature at three CO_2 concentrations, with parameter values given in Table 3, is illustrated in Fig. 1 in the main text, for both C_3 and C_4 species. Photosynthetic efficiency α also increases with protein content.

These equations for P_m and α are simple in structure and easy to program, while capturing the key features of the response of α to CO_2 concentration and temperature. Furthermore, they use parameters that are readily connected to experimental data.