Dynamic Model of Leaf Photosynthesis with Acclimation to Light and Nitrogen

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Received: 26 August 1997 Accepted: 19 November 1997

A simple model of photosynthesis in a mature C₃ leaf is described, based on a non-rectangular hyperbola: the model allows the high-light asymptote of that equation ($P_{\text{max}}$) to respond dynamically to light and nitrogen. This causes the leaf light response equation to acclimate continuously to the current conditions of light and N nutrition, which can vary greatly within a crop canopy, and through a growing season, with important consequences for gross production. Predictions are presented for the dynamics of acclimation, acclimated and non-acclimated photosynthetic rates are compared, and the dependence of leaf properties on light and N availability is explored. There is good correspondence of predictions with experimental results at the leaf level. The model also provides a mechanism for a down regulation of photosynthesis in response to increased carbon dioxide concentrations, whose magnitude will depend on conditions, particularly of nitrogen nutrition.

Key words: Leaf, photosynthesis, hyperbola, model, C₃, acclimation, light, nitrogen.

INTRODUCTION

Photosynthesis is the initial process driving the growth of crops and of plant ecosystems. It is affected by the past environment as well as the current environment and thus its prediction is a dynamic problem. Thus, we are used to thinking in terms of an immediate response (within minutes) of photosynthetic rate to current conditions of light, carbon dioxide and temperature, summarized by a response function with certain parameters. Acclimation is a slower process (taking several days) by which the plant adjusts the parameters of the photosynthetic response function by making changes to metabolic pools and possibly morphology. The acclimated photosynthetic response function has parameters whose values depend on an average of environmental conditions over the past week or two. Acclimation of photosynthesis to light (Prioul, Brangeon and Reyss, 1980; see Robson, Ryle and Woleadge, 1988, for a review) and to nitrogen (N) supply can be substantial (Hirose and Werger, 1987b; Evans and Terashima, 1988; Evans, 1989; Hollinger, 1996). Furthermore, the effects of irradiance and N nutrition on photosynthetic capacity are related (Hirose and Werger, 1987b; Evans and Terashima, 1988; Zhang and Allen, 1996; Murthy, Zarnoch and Dougherty, 1997). Light and N supply vary greatly over a growing season in temperate climates. Acclimation of photosynthetic characteristics to these seasonal changes is seldom taken into account when calculating photosynthesis. Also, within a canopy of moderate to high leaf area index (LAI), there may be a wide range of light environments and foliage N contents (Hikosaka and Terashima, 1996). It is therefore desirable that leaf photosynthesis models should represent acclimation to light and nitrogen supply, so that both within-canopy and seasonal effects can be considered.

The objective of the present study is to describe a model where acclimation to light and to N availability of leaf N content and photosynthetic response arise from a single mechanism, embedded in a leaf-level phenomenology which is easily tested and parameterized at the leaf level and is moreover suitable for calculations of canopy photosynthesis in crop and plant ecosystem models.

Many models of leaf photosynthesis are static. That is, given values of say irradiance, ambient CO₂ concentration and temperature, the model predicts photosynthetic rate, but not its time course. It is assumed that a steady state is achieved instantaneously. Any temporal variations in irradiance, ambient CO₂ concentration and temperature are followed immediately, without a time lag. Any pools appearing in such static models are assumed to be small, so that, given a change in conditions, the pool concentration moves very rapidly to its new steady-state value. This approach, which leads to a diminishing-returns photosynthetic response, was pioneered by Maskell (1928) who constructed an ordinary rectangular hyperbola response equation, developed further by Rabinowitch (1951) who introduced CO₂ diffusion resistance and obtained a non-rectangular hyperbolic equation, and also by Chartier (1966). The method has since been pursued by many authors with numerous variations.

The non-rectangular hyperbola (NRH) gives an excellent phenomenological description of leaf photosynthesis (e.g. Hirose and Werger, 1987b), and as such, we use it as the basis of our acclimation model. We could have used, equally easily, the simpler rectangular hyperbola (RH), and followed an exactly analogous method. We chose to use the NRH rather than the RH because empirically it is far superior and theoretically it has some modest advantages.

Arguably, a view which is gaining ground is that the NRH is a suitable equation for use in higher-level models of crops and plant ecosystems, whereas the problems of understanding the parameters of the NRH in terms of underlying biochemistry and molecular biology, can be
regarded as a separate, although important, project. This position agrees with views expressed by de Wit (1970); that it is important not to try to encompass too many levels of description when modelling complex systems, and that sharply focused modules should be used within large models where possible. A module such as is provided by the NRH can integrate and support two research communities by serving as a common component: (1) for those working towards an understanding of crop and plant ecosystems, these modules constitute the bottom level of their system; and (2) for those working on improving our understanding of say leaf photosynthesis, the module with its well-characterized phenomenology and parameterization can constitute the top level of their own researches (Thornley, 1980).

THE MODEL

Symbols, definitions, parameter values and units are listed in the Appendix. The abbreviations DM = dry mass and XDM = structural dry mass are used in equations.

Leaf photosynthesis

Leaf gross photosynthetic rate, \( P_{\text{leaf}} \) (kg CO\(_2\) \( m^{-2} \text{s}^{-1} \)), depends on the light incident on the upper leaf surface, \( I_{\text{leaf}} \) (J PAR \( m^{-2} \text{s}^{-1} \)), according to a non-rectangular hyperbola (NRH)

\[
0 = \xi \bar{P}^2_{\text{leaf}} - P_{\text{leaf}}(\alpha I_{\text{leaf}} + P_{\text{max}}) + \alpha I_{\text{leaf}} P_{\text{max}},
\]

\( \xi = 0.5 \), \( \alpha = 1 \times 10^{-8} \text{ kg CO}_2 \text{ (J PAR)}^{-1} \text{ [ = 0.0494 mol CO}_2 \text{ (mol PAR)}^{-1} \].

This equation has three parameters: \( \xi \), \( \alpha \) and \( P_{\text{max}} \). It is illustrated in Fig. 1 for four values of \( \xi \). \( \xi \) determines the sharpness of the knee of the curve. Although there is some evidence that \( \xi \) varies with growth light environment and with tissue N content (Hirose and Werger, 1987b), it is assumed constant in our analysis. \( \alpha \text{ [kg CO}_2 \text{ (J PAR)}^{-1} \] is the initial slope of the light response curve, and is often called the photosynthetic efficiency. The value used in eqn (1) and Fig. 1 is rounded, but is typical of \( C_3 \) leaves (e.g. Hirose and Werger, 1987b). \( \alpha \) does not depend on growth irradiance or N content to a significant degree (Prioul et al., 1980; Hirose and Werger, 1987b; Gastal and Bélanger, 1993). \( P_{\text{max}} \) is the instantaneous high-light asymptote of eqn (1): \( I_{\text{leaf}} \to \infty, P_{\text{leaf}} \to P_{\text{max}} \). \( P_{\text{max}} \) is determined by the concentration of photosynthetic N according to eqn (10). This allows acclimation to light and N supply to occur.

The NRH of eqn (1) and Fig. 1 is quadratic in \( P_{\text{leaf}} \), with the solution

\[
P_{\text{leaf}} = \frac{\alpha I_{\text{leaf}} + P_{\text{max}} - \sqrt{(\alpha I_{\text{leaf}} + P_{\text{max}})^2 - 4\xi \alpha I_{\text{leaf}} P_{\text{max}}}}{2\xi}.
\]

The properties of the NRH have been discussed by many authors (e.g. Thornley and Johnson, 1990). The rectangular hyperbola (RH) is a special case of the NRH (Fig. 1). The RH is still preferred to the NRH by some workers on the grounds of simplicity. The acclimation model presented below works equally well with either the RH or the NRH. I have chosen to use the NRH because it is empirically superior to the RH: it is able to fit a much wider range of leaf photosynthetic response data. The RH can be obtained from the NRH by putting \( \xi = 0 \) in eqn (2); this involves taking the limit as \( \xi \to 0 \) and is rather tedious. It is easier to put \( \xi = 0 \) in eqn (1) which immediately gives the RH: \( P_{\text{leaf}} = \alpha I_{\text{leaf}} P_{\text{min}}/(\alpha I_{\text{leaf}} + P_{\text{max}}) \).

Leaf variables

The scheme assumed for the acclimation model is given in Fig. 2, for a single mature leaf connected to a root. Processes such as the utilization of C and N substrates for growth, and the utilization of C substrate for maintenance, are omitted. It is formulated so that the extension of the approach to a multi-leaf plant or canopy is straightforward.

There are three state variables: the masses of C substrate, N substrate, and photosynthetic N, in the leaf (Appendix). These three state-variable pools represent aggregated biochemical species whose definition is inevitably imprecise. It is envisaged that C substrates consist of water soluble carbohydrates and any other fairly easily metabolizable carbohydrates; N substrates are mostly amino acids and other mobile forms of N; photosynthetic N is largely rubisco. The three state variables are dynamic quantities whose temporal behaviour gives rise to photosynthetic acclimation. However, the acclimation model as presented here for a non-growing leaf in a non-growing plant is independent of C substrate dynamics, although this would not be the case when these simplifying assumptions are relaxed.

A constant leaf area of \( A_{\text{leaf}} = 0.001 \text m^2 (10 \text cm \times 1 \text cm) \) is assumed. Leaf mass comprises the three metabolic state-variable pools just introduced, plus a "structural" mass component, envisaged as being principally cellulose. In a
With a constant concentration of structural N of the leaf, the total leaf nitrogen content (kg N) is (Fig. 1), giving photosynthetic acclimation to light and N supply. The model has three state variables, shown in the upper three boxes. The concentrations of substrate C, substrate N and photosynthetic N are per unit leaf area is given by
\[ C_{\text{leaf},X} = \frac{M_{\text{CS,leaf}}}{M_{\text{X,leaf}}}, \quad N_{\text{leaf},X} = \frac{M_{\text{NS,leaf}}}{M_{\text{X,leaf}}}, \quad N_{\text{ph,leaf},X} = \frac{M_{\text{NS,ph,leaf}}}{M_{\text{X,leaf}}}, \]

With a constant concentration of structural N of 0.08 kg structural N (kg structural dry mass\(^{-1}\)), the total leaf nitrogen content (kg N) is
\[ M_{\text{X,leaf}} = M_{\text{X,leaf}}(N_{\text{X,leaf},X} + N_{\text{leaf},X} + N_{\text{ph,leaf},X}). \]

Thus, while the structural N concentration of the leaf is constant, the substrate N and photosynthetic N concentrations are variables [eqn (4)]. The value of 0.8% for \(N_{\text{X,leaf}}\) provides a floor for the leaf N content, and is chosen to be compatible with observed values, and also to be satisfactory in the present context. A wide range of total leaf N concentrations has been observed, ranging from 0.7 to 5% (e.g. Fig. 1.2 of Field and Mooney, 1986). Total N content per unit leaf area is
\[ N_{\text{leaf},A} = \frac{M_{\text{X,leaf}}}{A_{\text{leaf}}} = \frac{N_{\text{X,leaf},X} + N_{\text{leaf},X} + N_{\text{ph,leaf},X}}{S_{\text{LA}}}. \]

Equations (5) and (3) have been substituted to give the second expression. An N concentration of 1% of structural dry mass corresponds to a superficial N concentration of 0.4 \(\times\) 10\(^{-3}\) kg N m\(^{-2}\).

### Root parameters

Root structural dry mass (XDM), substrate C and substrate N concentrations are assumed to be constant at
\[ M_{\text{X,root}} = M_{\text{X,leaf}}, \quad C_{\text{S,root}X} = 0.02 \text{ kg C substrate (kg XDM)}^{-1}, \quad N_{\text{S,root}X} = 0.011 \text{ kg N substrate (kg XDM)}^{-1}. \]

The structural dry mass root:shoot ratio is constant and equal to unity. In a plant growth model all these quantities would vary.

### Transport resistances

Resistances to substrate C and N transport are associated with the leaf and root separately (Fig. 2), and summed to give overall resistances between leaf and root, with (Thornley, 1997)
\[ r_{\text{C,leaf}} = \frac{\rho_c}{M_{\text{X,leaf}}}, r_{\text{C,root}} = \frac{\rho_c}{M_{\text{X,root}}}, r_{\text{C,leaf-root}} = r_{\text{C,leaf}} + r_{\text{C,root}}, \]
\[ r_{\text{N,leaf}} = \frac{\rho_n}{M_{\text{X,leaf}}}, r_{\text{N,root}} = \frac{\rho_n}{M_{\text{X,root}}}, r_{\text{N,root-leaf}} = r_{\text{N,root}} + r_{\text{N,leaf}}, \]
\[ \rho_c = 0.2 \text{ d}, \rho_n = 2 \text{ d}. \]

All resistances have units of d (kg structural dry mass\(^{-1}\)). \(\rho_c\) and \(\rho_n\) are resistivity parameters.
\[ P_{\text{max}, \text{of the photosynthesis light response}} \]

Photosynthetic N per unit leaf area is (kg photosynthetic N m\(^{-2}\))

\[ N_{\text{ph, leaf}} = \frac{M_{\text{ph, leaf}}}{A_{\text{leaf}}} \]  \(\text{(9)}\)

It is assumed that \( P_{\text{max}} \) of eqn (1) is proportional to \( N_{\text{ph, leaf}} \), with

\[ P_{\text{max}} = c_{\text{Pmax}, N} N_{\text{ph, leaf}} \]  \(\text{(10)}\)

The standard value of photosynthetic N content is 0.0042 kg CO\(_2\) s\(^{-1}\) (kg photosynthetic N)\(^{-1}\).

\[ c_{\text{Pmax}, N} = 0.001 \text{ kg CO}_2 \text{ s}^{-1} \text{ (kg photosynthetic N)}^{-1}. \]

\[ \text{The input to this pool (Fig. 2) is by light-driven synthesis, and is given by} \]

\[ I_{\text{ph, leaf}} = k_{G, \text{ph}} M_{X, \text{leaf}} \frac{N_{\text{leaf}}}{N_{\text{leaf}} + K_{\text{S,leaf}} I_{\text{leaf}} + K_{I,\text{leaf}}} \]

\[ k_{G, \text{ph}} = 0.008 \text{ kg photosynthetic N (kg XDM)}^{-1} \text{ d}^{-1}, \]

\[ K_{\text{S,leaf}} = 0.01 \text{ kg substrate N (kg XDM)}^{-1}, \]

\[ K_{I, \text{leaf}} = 100 \text{ J PAR m}^{2} \text{ s}^{-1}. \]

The units of \( I_{\text{ph, leaf}} \) are kg photosynthetic N d\(^{-1}\). Michaelis-Menten dependence on N substrate concentration and on irradiance is assumed. Any C substrate requirement, either for building blocks or energy, is ignored. Essentially, in constructing eqn (11) it is assumed that the synthesis of photosynthetic N (rubisco) is co-limited by the supply of N substrate (amino acids) and energy (ATP); the energy supply is proportional to light level; substrate C level is irrelevant in this approximation. This effect of light in driving eqn (11) is over and above its effect in driving eqn (1). Equation (11) is also tentatively supported by many observations concerning the direct involvement of light energy in leaf N metabolism (nitrate reductase), and the fact that there appears to be energy available for this purpose additional to the requirements of the photosynthetic carbon reduction cycle for energy (e.g. Lawlor, 1987).

Output from the pool is due to degradation

\[ O_{\text{ph, leaf}} = k_{D, \text{ph}} M_{\text{ph, leaf}} \cdot k_{D, \text{ph}} = 0.2 \text{ d}^{-1}. \]  \(\text{(12)}\)

This decay rate of 0.2 d\(^{-1}\) corresponds to a half-life of 3.5 d. Peterson, Kleinkopf and Huffaker (1973) measured turnover rates for rubisco in the range 0.06 to 0.38 d\(^{-1}\).

The differential equation for the rate of change of the photosynthetic N pool is

\[ \frac{dM_{\text{ph, leaf}}}{dt} = I_{\text{ph, leaf}} - O_{\text{ph, leaf}} \]  \(\text{(13)}\)

\[ M_{\text{ph, leaf}}(t = 0) = 0.42 \times 10^{-6} \text{ kg photosynthetic N}. \]

The initial concentration of photosynthetic N is \( N_{\text{ph, leaf}} \) \((t = 0) = 0.0105 \text{ kg N (kg structural dry mass)}^{-1}\) [eqns (3) and (4)].

\[ C \text{ substrate pool, } M_{C, \text{leaf}} \]

The only input to this pool is from photosynthesis [eqn (2), Fig. 2]. Any contribution from the degradation of photosynthetic N is ignored.

The only output is to the root by transport, with

\[ O_{\text{C, leaf}} = \frac{C_{\text{leaf}} - C_{\text{root}}}{r_{\text{C, leaf}} - r_{\text{root}}}. \]  \(\text{(14)}\)

The transport resistance is calculated in eqn (8). The differential equation is

\[ \frac{dM_{C, \text{leaf}}}{dt} = \frac{12}{44} \times 86400 A_{\text{leaf}} P_{\text{leaf}} - O_{\text{C, leaf}} \]  \(\text{(15)}\)

\[ M_{C, \text{leaf}}(t = 0) = 4.073 \times 10^{-6} \text{ kg substrate C}. \]

The factor of 12/44 is to convert kg CO\(_2\) to kg C. 86400 converts per second to per day. The initial concentration of substrate C is \( C_{\text{leaf}}(t = 0) = 0.102 \text{ kg substrate C (kg structural dry mass)}^{-1}\) [eqns (3) and (4)]. This is the steady-state standard value. Note that in the simplified model presented here, C substrate does not have a functional role.

In the class of plant models where this acclimation submodel may be used (e.g. Fig. A1 of Thornley and Cannell, 1997), C substrate is used for growth, maintenance, is recycled from senescing plant material, and will interact with N substrate levels, protein synthesis and \( P_{\text{max}} \) of the photosynthetic response equation (Fig. 1).

\[ N \text{ substrate pool, } M_{N, \text{leaf}} \]

\[ N \text{ inputs are from the decay of photosynthetic N, with eqn (12), and from the root by transport [with eqn (8)],} \]

\[ I_{\text{N, leaf}} = O_{\text{N, leaf}} + I_{\text{NS, root}} - \frac{N_{\text{leaf}} - N_{\text{root}}}{r_{\text{N, root}}} \]  \(\text{(16)}\)

The sole output is to photosynthetic N synthesis, with eqn (11)

\[ O_{\text{N, leaf}} = I_{\text{N, leaf}}. \]  \(\text{(17)}\)

The differential equation for the N substrate pool is

\[ \frac{dM_{\text{N, leaf}}}{dt} = I_{\text{N, leaf}} + I_{\text{NS, root}} - O_{\text{N, leaf}} \]  \(\text{(18)}\)

\[ M_{\text{N, leaf}}(t = 0) = 0.44 \times 10^{-6} \text{ kg substrate N}. \]

The initial N substrate concentration is \( N_{\text{leaf}}(t = 0) = 0.011 \text{ kg substrate N (kg structural dry mass)}^{-1}\) [eqns (3) and (4)]. This is the steady-state standard value.

**SIMULATIONS**

The model was programmed in ACSL (Mitchell and Gauthier, 1993). Euler’s method of integration was employed (e.g. Thornley and Johnson, 1990) with an integration interval of 0.1 d.
**Dynamics of photosynthetic acclimation**

The model (Fig. 2) provides for acclimation to leaf irradiance $I_{leaf}$, eqn (1) and to N supply, represented in the model by the root N substrate concentration. This is illustrated in Fig. 3 where the irradiance (Fig. 3A and C) and the root N substrate concentration have been doubled (Fig. 3B and D).

An increase in irradiance (Fig. 3A) causes an immediate shift along the current photosynthesis-light response curve [eqn (2), Fig. 1] which increases photosynthetic rate $P_{leaf}$, followed by further gradual change as the asymptote of that curve ($P_{max}$, Fig. 1) adjusts to the new light level. The time constant for this latter gradual change depends on the rate of degradation of photosynthetic N [eqn (12), Fig. 2]. Successive increases in the asymptote $P_{max}$ have decreasing influence on the actual photosynthetic rate $P_{leaf}$ because at high $P_{max}$ the photosynthetic efficiency $\alpha$ is increasingly important [with $P_{max}$ very large in eqn (1) the solution is $P_{leaf} = \alpha I_{leaf}$]. N content per unit leaf area, $N_{leaf,A}$ [eqn (6)], increases in parallel with $P_{max}$ [eqn (10)]. The immediate effect on leaf substrate N (Fig. 3C) is a decrease, resulting from leaf substrate N being converted to photosynthetic N (Fig. 2) faster than it can be replenished from the root N substrate pool, followed by a return of leaf substrate N to its former level. Working with grass leaves, *Lolium multiflorum*, Prioul *et al.* (1980) transferred leaves between irradiances of 16 and 110 W PAR m$^{-2}$, and found that acclimation was substantially complete after about 6 d, a time scale consistent with Fig. 3A.

In Fig. 3B and D acclimation to increased N availability is shown. The photosynthetic response is similar to, but smaller than, the acclimation response to light (Fig. 3A) where, as explained above, the latter response is a result of two mechanisms. There are now two dynamic components to the increase in total leaf N (Fig. 3B). First leaf N substrate increases rapidly in response to the doubling of root N substrate as N substrate moves in from the root (Fig. 3D); within-plant substrate transport is a relatively rapid process so this initial transient is substantially complete after about 6 d, a time scale consistent with Fig. 3A.

In Fig. 3C the phase is the same as in Fig. 3C under doubled leaf substrate N concentrations are given by eqn (4): leaf structural N concentration, $N_{leaf,S}$ [eqn (5), Appendix] is constant. An integration interval of 0.01 d was used, not for reasons of stability but to obtain better graphs.
obtained by running the dynamic model until a steady state is reached, with a delay in acclimation that means the actual rate
\[ P_{\text{leaf}} \] is below the asymptote. The rate of change in acclimation of \( P_{\text{leaf}} \) to irradiance,
\[ I \], is given by eqn (2).

The dynamics of acclimation of \( P_{\text{leaf}} \) to irradiance,
\[ I \], respond to changes in \( N \) availability. Leaf age is an important factor in the ability of a leaf to respond to changes in \( N \) availability. Thornley (1977) has shown that the substrate \( N \) concentration equilibrates to a value equal to the root \( N \) substrate concentration (Fig. 2). In a steady-state, non-growing leaf, the \( N \) substrate concentration in root and leaf is equal. This is a consequence of the model: in the steady state there are no sinks for \( N \) in the leaf; there is therefore no transport of \( N \) into the leaf and the \( N \) concentrations in leaf and root are equal [eqn (16)]. Leaf \( N \) substrate concentration influences the irradiance-dependent synthesis of leaf photosynthetic \( N \) according to eqn (11). Figure 5 illustrates some properties of the leaf, fully acclimated to light and to \( N \) availability. The responses given were generated by varying leaf irradiance at each value of the root \( N \) concentration (\( N_{\text{root}} \)).

**Effect of \( N \) supply on acclimated photosynthetic rate**

Nitrogen supply has been varied by assigning different constant values to the root \( N \) substrate concentration (Fig. 2). In a steady-state, non-growing leaf, the \( N \) substrate concentration in root and leaf is equal. This is a consequence of the model: in the steady state there are no sinks for \( N \) in the leaf; there is therefore no transport of \( N \) into the leaf and the \( N \) concentrations in leaf and root are equal [eqn (16)]. Leaf \( N \) substrate concentration influences the irradiance-dependent synthesis of leaf photosynthetic \( N \) according to eqn (11). Figure 5 illustrates some properties of the leaf, fully acclimated to light and to \( N \) availability. The responses given were generated by varying leaf irradiance at each value of the root \( N \) concentration (\( N_{\text{root}} \)).

**Light-response curves for acclimated and non-acclimated leaves**

In Fig. 4A, responses of leaf photosynthetic rate, \( P_{\text{leaf}} \) [eqn (2)], to irradiance, \( I_{\text{leaf}} \), are illustrated. The solid curves are for a leaf that is fully acclimated at each irradiance level: the upper solid curve depicts \( P_{\text{max}} \) [Fig. 1, eqns (1) and (10)], the asymptote of the light response curve, and the lower solid curve is the actual leaf photosynthetic rate \( P_{\text{leaf}} \) at that irradiance. The ratio of these two quantities is given in the upper solid curve of Fig. 4B: although the asymptote \( P_{\text{max}} \) increases with irradiance, the actual photosynthetic rate \( P_{\text{leaf}} \) approaches the asymptote more closely at higher irradiances. The instantaneous light response of leaf photosynthesis \( P_{\text{leaf}} \) [eqn (2)] for high-light (200 W PAR m\(^{-2}\)) acclimated leaves is drawn in the upper dashed curve and asymptote in Fig. 4A, and similarly the response for a low-light acclimated leaf is given in the lower dashed curve and asymptote. The leaf total \( N \) content [Fig. 4B] responds positively to irradiance, due to an increasing photosynthetic \( N \) component. In this application, the substrate and structural components of leaf \( N \) are constant, as shown. In Fig. 4A, we can compare the photosynthetic rate \( P_{\text{leaf}} \) of leaves fully acclimated to leaf irradiance, with that of leaves at the same irradiance but which have been acclimated to 200 W m\(^{-2}\). These two curves cross over at about 200 W m\(^{-2}\). At light levels lower than 200 W m\(^{-2}\), leaves acclimated to 200 W m\(^{-2}\) outperform fully acclimated leaves; at light levels higher than 200 W m\(^{-2}\), fully acclimated leaves outperform leaves acclimated to 200 W m\(^{-2}\).

The results in Fig. 4 compare well with Fig. 1 of Hikosaka and Terashima (1996), Fig. 2 of Prioul et al. (1980) and Fig. 7 of Hirose and Werger (1987b).

**Fig. 4.** A, Photosynthetic light responses, with and without acclimation. Solid lines, fully acclimated asymptote \( P_{\text{max}} \) [Fig. 1 and eqn (10)] and leaf photosynthetic rate \( P_{\text{leaf}} \) [eqn (2)]; dashed lines, leaf photosynthetic rate \( P_{\text{leaf}} \) of leaves acclimated to 20 W m\(^{-2}\) (92 \( \mu \)mol m\(^{-2}\) s\(^{-1}\)) and to 200 W m\(^{-2}\) (820 \( \mu \)mol m\(^{-2}\) s\(^{-1}\)); the asymptotes \( P_{\text{max}} \) are also shown. B, Ratio of the actual acclimated leaf photosynthetic rate \( P_{\text{leaf}} \) at a given irradiance \( I_{\text{leaf}} \) to the \( P_{\text{max}} \) for that irradiance; the total leaf \( N \) content \( N_{\text{leaf}} \) and its three components [eqn (6)]. Acclimated values are obtained by running the dynamic model until a steady state is achieved (see Fig. 3), typically 100 d. 10 \(^{-6}\) kg CO\(_2\) = 23 \( \mu \)mol CO\(_2\) /PAR.

1 J PAR = 4.6 \( \mu \)mol PAR.

irradiance and is discussed above. I have not found data on the dynamics of acclimation of \( P_{\text{max}} \) to \( N \) availability. The model predicts that acclimation to \( N \) availability is a little slower than acclimation to light, due to the root-leaf resistance causing an extra delay. The dynamics of photosynthetic acclimation in Fig. 3 are such that there will be only a minor adjustment to diurnal variation in the environment, but the seasonal changes in environment can be tracked quite closely, with a time lag of about 5 d. A more realistic model could include other pathways for \( N \) supply (Dewar, 1993), and other sources of \( N \) such as degradable (non-photosynthetic) structure (Thornley, 1977). Investigation by Woleodge and Pearse (1985) suggest that leaf age is an important factor in the ability of a leaf to respond to changes in \( N \) availability.
where the measured CO₂ exchange rate is probably a reasonable approximation to $P_{max}$. There is also satisfactory qualitative agreement for a montane tropical forest tree, *Tetrorchidium rubri*, and the leaf N content

**DISCUSSION AND CONCLUSIONS**

The non-rectangular hyperbola provides a convenient and accurate summary of leaf photosynthetic response to irradiance, and it has been much used for this purpose (Marshall and Biscoe, 1980; Hirose and Werger, 1987b; Pachepsky, Haskett and Acock, 1996). It has also been widely employed for calculating canopy photosynthesis (Johnson and Thornley, 1984; Jarvis, Miranda and McMurtrie, 1990; Topp and Doyle, 1996).

The most transparent way of calculating instantaneous canopyp photosynthesis from leaf photosynthesis is to sum...
over the elements of the canopy (but see De Pury and Farquhar, 1997). This calculational method can be directly compared with experimental data (e.g. Acock et al., 1978). However, difficulties of using this approach are: (1) acclimation of leaf parameters to seasonal changes in N supply and irradiance (acclimation to temperature is much weaker, e.g. Robson et al., 1988); and (2) acclimation of leaf parameters to changing position within the canopy, since position in the canopy affects the local N supply and leaf irradiance. The first problem is often ignored by simulation models. The second problem means that analytical integration through the canopy assuming constant leaf photosynthesis parameters (e.g. Johnson and Thornley, 1984) may be unacceptably inaccurate. Until recently, the computational costs of numerically integrating through the canopy have been substantial, especially for high leaf area index canopies, and this has given rise to many algebraic schemes for calculating canopy photosynthesis directly (e.g. see Sands, 1995, who gives references to earlier work). However, this is no longer the case, and it seems mistaken to use complex algebraic schemes with possibly dubious approximations when direct calculations are feasible.

For instance, it is sometimes assumed that nitrogen is distributed within the canopy so as to optimize canopy photosynthesis (e.g. Hirose and Werger, 1987b). However, Hollinger (1996) has shown that at least some observed canopy N allocation patterns do not give maximum canopy assimilation. Furthermore, in terms of scientific methodology, it is preferable to use a ‘free’ or ‘objective’ set of equations and assumptions (Monod, 1974), rather than what are often highly subjective ‘optimality’ or ‘goal-seeking’ assumptions. Since ‘goal-seeking’ controls can always be represented within an objective framework (e.g. as factors influencing fluxes), it is methodologically preferable to begin with an objective framework, and to refine that framework systematically as its failures are identified.

My first aim has been to present a mechanistic approach to the acclimation problem which modifies the current very successful leaf-level phenomenology encapsulated in the non-rectangular hyperbola, and also permits extension to the evaluation of canopy photosynthesis while avoiding the use of optimization schemes. A second aim has been to develop a method which is compatible with the class of crop growth and plant ecosystem models where (a) plant dry matter is divided into aggregated biochemical categories (e.g. ‘structure’ and ‘storage’; Warren Wilson, 1972), and (b) the process by which dry matter is partitioned between the different parts of the plant is achieved by the transport of substrates within the plant, and their utilization (conversion into other components) in those different parts (e.g. Thornley, 1997). A future investigation will attempt to combine the acclimation model presented here with the transport-resistance approach to allocation (Thornley, 1997), in order to examine the distribution of N and photosynthetic parameters within the crop canopy.

Note that the present model extended to a growing plant provides a simple mechanism for ‘down regulation’ for leaves exposed to enhanced atmospheric CO$_2$ concentrations over long periods. The decrease in $P_{\text{max}}$ is in addition to any decrease in $P_{\text{max}}$ produced by decreasing stomatal conductance. The model of Fig. 2 can predict down regulation of $P_{\text{max}}$ by the following route. Increased CO$_2$ raises sugar levels (C substrates) and decreases N substrate concentrations because growth depends on the product of C and N substrates, and the sink for N substrates is increased. The synthetic rate of photosynthetic N is thereby decreased [eqn (11)], and thus there are decreases in the concentration of photosynthetic N [eqn (13)] and $P_{\text{max}}$ [eqn (10), Figs 1 and 5A]. The extent to which this effect occurs will depend on the conditions, agreeing with the fact that observations of down regulation have been very variable: Jones, Jongen and Doyle (1996) and Casella, Soussana and Loiseau (1996) observed little down regulation, in contrast to the findings of Korner and Miglietta (1994) and Schappi and Korner (1996). In a more general context, Cannell and Thornley (1998) discuss the dependence of CO$_2$ responses on other factors and in particular N nutrition, which can lead to apparently inconsistent findings. Their findings will apply equally to down regulation.

Acclimation to temperature has not explicitly been considered here. All the fluxes in Fig. 2 depend on rate parameters which are functions of temperature. In principal, a different temperature function can apply to each rate parameter although in practice the temperature functions for the different rate parameters may be similar. If the temperature functions are explicitly represented in the model, then the model could be used to make analogous predictions to those presented above about the instantaneous and acclimatory responses of the system, including photosynthesis, to temperature. Plant responses to temperature are highly important, and a significant, perhaps major, component of the plant’s response to temperature is due to the instantaneous response to temperature of some of the parameters of the photosynthetic response function [eqn (2), Fig. 1]. However, the evidence is that the acclimatory response to temperature of photosynthesis is small compared to that to light and nitrogen (e.g. Robson et al., 1988). It has therefore been ignored in this investigation.

ACKNOWLEDGEMENTS

I thank Roddy Dewar and an anonymous referee for many helpful suggestions and comments. The work has been supported by NERC through its TIGER programme, Department of the Environment contracts on carbon sequestration, European Community Epoch and Espace Projects, and the AFRC Institute of Grassland & Environmental Research (North Wyke).

LITERATURE CITED


### Symbols, definitions, units and values

Abbreviations: DM, dry matter; XDM, structural dry matter; phN, photosynthetic N; PAR, photosynthetically active radiation. Numbers in parentheses refer to the equation where the symbol is introduced. Initial values of the state variables cause the system to be in a steady state when the ‘driving’ variables, leaf irradiance $I_{\text{leaf}}$ and root N substrate concentration $N_{\text{S, rootX}}$, have their standard values.

#### State variables

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Initial value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M_{\text{CS, leaf}}$</td>
<td>Mass of C substrate in leaf (15)</td>
<td>$4.0729 \times 10^{-6}$ kg substrate C</td>
</tr>
<tr>
<td>$M_{\text{Nph, leaf}}$</td>
<td>Mass of photosynthetic N in leaf (13)</td>
<td>$0.41905 \times 10^{-6}$ kg phN</td>
</tr>
<tr>
<td>$M_{\text{NS, leaf}}$</td>
<td>Mass of N substrate in leaf (18)</td>
<td>$0.44 \times 10^{-6}$ kg substrate N</td>
</tr>
</tbody>
</table>

#### Parameters

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_{\text{leaf}}$</td>
<td>Leaf area (3)</td>
<td>$0.001$ m²</td>
</tr>
<tr>
<td>$C_{\text{S, rootX}}$</td>
<td>C substrate concentration in root (7)</td>
<td>$0.02$ kg substrate C (kg XDM)$^{-1}$</td>
</tr>
<tr>
<td>$c_{\text{phN}}$</td>
<td>Parameter relating $P_{\text{max}}$ to leaf N (10)</td>
<td>$0.001$ kg CO$_2$ s$^{-1}$ (kg phN)$^{-1}$</td>
</tr>
<tr>
<td>$I_{\text{leaf}}$</td>
<td>Leaf irradiance (1) (standard value)</td>
<td>$100$ J PAR m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$K_{\text{LeafM}}$, $K_{\text{NS, leaf}}$</td>
<td>Michaelis-Menten constants in photosynthetic N synthesis (11)</td>
<td>$100$ J PAR m$^{-2}$ s$^{-1}$, $0.01$ kg substrate N (kg XDM)$^{-1}$</td>
</tr>
<tr>
<td>$k_{\text{DPH}}$</td>
<td>Degradation rate constant of photosynthetic N (12)</td>
<td>$0.2$ d$^{-1}$</td>
</tr>
<tr>
<td>$k_{\text{GPH}}$</td>
<td>Synthesis rate constant for photosynthetic N (11)</td>
<td>$0.008$ kg phN (kg XDM)$^{-1}$ d$^{-1}$</td>
</tr>
<tr>
<td>$M_{\text{X, leaf}}$</td>
<td>Leaf structural dry mass (3)</td>
<td>$0.04$ kg XDM</td>
</tr>
<tr>
<td>$M_{\text{X, root}}$</td>
<td>Root structural dry mass (7)</td>
<td>$0.04$ kg XDM</td>
</tr>
<tr>
<td>$N_{\text{S, rootX}}$</td>
<td>N substrate concentration in root (7) (standard value)</td>
<td>$0.011$ kg substrate N (kg XDM)$^{-1}$</td>
</tr>
<tr>
<td>$N_{\text{X, leafX}}$</td>
<td>N concentration in leaf structure (5)</td>
<td>$0.01$ kg structural N (kg XDM)$^{-1}$</td>
</tr>
<tr>
<td>$r_{\text{C, leaf}}$, $r_{\text{N, leaf}}$, $r_{\text{C, root}}$, $r_{\text{N, root}}$</td>
<td>Resistances to C, N substrate transport associated with leaf, root (8)</td>
<td>$5000$ (C), $50000$ (N) d (kg XDM)$^{-1}$</td>
</tr>
<tr>
<td>$r_{\text{C, leaf-root}}$, $r_{\text{N, root-leaf}}$</td>
<td>Resistances to C, N substrate transport between leaf and root (8)</td>
<td>$10000$ (C), $100000$ (N) d (kg XDM)$^{-1}$</td>
</tr>
<tr>
<td>$S_{\text{LA}}$</td>
<td>Structural specific leaf area (3)</td>
<td>$25$ m² (kg XDM)$^{-1}$</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Photosynthetic efficiency (1)</td>
<td>$1 \times 10^{-8}$ kg CO$_2$ (J PAR)$^{-1}$</td>
</tr>
<tr>
<td>$\xi$</td>
<td>Sharpness parameter of photosynthetic response (1)</td>
<td>$0.5$</td>
</tr>
<tr>
<td>$\rho_{\text{C, phN}}$</td>
<td>Resistivity parameters for C, N substrates (8)</td>
<td>$0.2$, $2$ d</td>
</tr>
</tbody>
</table>

#### Other variables

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C_{\text{S, leafX}}$</td>
<td>C substrate concentration (4)</td>
<td>kg substrate C (kg XDM)$^{-1}$</td>
</tr>
<tr>
<td>$I_{\text{Nph, leaf}}$</td>
<td>Input to photosynthetic N pool (11)</td>
<td>kg phN d$^{-1}$</td>
</tr>
<tr>
<td>$I_{\text{NS, leaf, NphD}}$</td>
<td>Input to leaf N substrate from photosynthetic N by degradation (16)</td>
<td>kg substrate N d$^{-1}$</td>
</tr>
<tr>
<td>$I_{\text{NS, root-leaf}}$</td>
<td>Input to leaf N substrate from root by transport (16)</td>
<td>kg substrate N d$^{-1}$</td>
</tr>
<tr>
<td>$M_{\text{N, leaf}}$</td>
<td>Total leaf nitrogen (5)</td>
<td>kg N</td>
</tr>
<tr>
<td>$N_{\text{leafA}}$</td>
<td>Total N content per unit leaf area (6)</td>
<td>kg N m$^{-2}$</td>
</tr>
<tr>
<td>$N_{\text{S, leafX}}$</td>
<td>N substrate concentration in leaf (4)</td>
<td>kg substrate N (kg XDM)$^{-1}$</td>
</tr>
<tr>
<td>$N_{\text{ph, leafA}}$</td>
<td>Photosynthetic N per unit leaf area (9)</td>
<td>kg phN m$^{-2}$</td>
</tr>
<tr>
<td>$N_{\text{ph, N}}$</td>
<td>Photosynthetic N concentration (4)</td>
<td>kg phN (kg XDM)$^{-1}$</td>
</tr>
<tr>
<td>$O_{\text{C, leaf-to-root}}$</td>
<td>Output of C substrate from leaf to root (14)</td>
<td>kg substrate C d$^{-1}$</td>
</tr>
<tr>
<td>$O_{\text{ph, leaf}}$</td>
<td>Output from photosynthetic N pool (12)</td>
<td>kg phN d$^{-1}$</td>
</tr>
<tr>
<td>$O_{\text{NS, leaf}}$</td>
<td>Output from leaf N substrate pool (17)</td>
<td>kg substrate N d$^{-1}$</td>
</tr>
<tr>
<td>$P_{\text{leaf}}$</td>
<td>Leaf gross photosynthetic rate (2)</td>
<td>kg CO$_2$ m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$P_{\text{max}}$</td>
<td>Light-saturated photosynthetic rate (1)</td>
<td>kg CO$_2$ m$^{-2}$ s$^{-1}$</td>
</tr>
</tbody>
</table>