ABSTRACT

A new analytical model for the response of whole-leaf potential electron transport rate \( J \) to light is presented. The model treats inconstant irradiance at the upper and lower leaf surfaces independently, describes transdermal profiles of light absorption and electron transport capacity explicitly, and calculates \( J \) by integrating the minimum of light- and capacity-limited rates among paradermal chloroplast layers. The capacity profile is assumed to be a weighted average of two opposed exponential profiles, each of which corresponds to the profile of light-limited rate when only one surface is illuminated; the weights may take on any values provided they sum to unity, so the model can describe leaves with a wide range of 'preferred' illumination regimes. By inverting irradiance at either surface independently and assuming the capacity profile is fixed on short time scales, the model predicts observed effects of leaf inversion on light-response curves and their apparent convexity. By assuming the capacity profile can adapt on developmental time scales the model can predict the observed dependence of inversion effects on the growth lighting regime. It is suggested that the new model, which is mathematically compact and formally similar to the standard non-rectangular hyperbola model for \( J \), be used in place of the standard model in studies in which the effects of leaf angle or diffuse light fraction on gas exchange are of interest.

Key-words: electron transport; gas exchange; light response; photosynthesis.

INTRODUCTION

Many gas exchange models predict net \( \text{CO}_2 \) assimilation rate using the biochemical model of Farquhar, von Caemmerer and Berry (1980), which is based on steady-state Rubisco kinetics and on the linked stoichiometries of the Calvin cycle, photosynthetic electron transport and photorespiration. In that model, the actual rate of thylakoid electron transport per unit of chlorophyll \( j_i \) may be limited by the sink strength of the Calvin cycle for NADPH and ATP, and hence by \( \text{CO}_2 \) availability, by the supply of energized electrons, and hence by the rate of light absorption; or by the electron transport capacity of thylakoids themselves. Various labels are used to denote electron transport rate in the limiting cases where one of more of these constraints is imagined to be negligible. For example, the 'potential electron transport rate', denoted \( J \) (or \( J_l \) at the leaf scale), is the actual rate in the presence of saturating \( \text{NADP}^+ \) and ATP.

The potential electron transport rate \( J \), like the actual rate, can also be described in terms of limiting values; in this case there are two limiting values, the rate at which electrons are supplied by photo-oxidation of water at PSII, and \( j_o \), the electron transport capacity or 'maximum potential electron transport rate'. \( j_o \) is proportional to the rate of light absorption, so it approaches zero at low light, but may exceed \( J_l \) at high light; \( J_l \) can not exceed either of these limiting values, so it behaves roughly as the minimum of \( j_o \) and \( J_l \). In practice, however, \( J_l \) may be lower than either \( j_o \) or \( J_l \) and is thus calculated as a hyperbolic minimum of \( j_o \) and \( J_l \) (Farquhar & Wong 1984): \( j = \min(j_o, J_l) \cdot (j_o + J_l - (j_o + J_l)^2 - 4j_o J_l)^{0.5} / 2j_o J_l \). When the parameter \( \theta \) equals 1, this expression degenerates to a simple minimum (i.e. \( \min(j_o, J_l) \)), but for \( \theta < 1 \) \( j \) is always lower than \( \min(j_o, J_l) \). Hence, \( \theta \) is a measure of 'co-limitation' of electron transport by light and capacity.

A problem arises when this model is applied to whole leaves. Because light absorption and electron transport capacity generally vary among paradermal layers in intact leaves, \( j \cdot \text{min}(j_o, J_l) \) does not generally imply \( J = \min(j_o, J_l) \cdot (\text{integals of } j_o \text{ and } J_l \text{ over the leaf}) \). This problem is conventionally evaded by assuming that the ratio \( j_o / J_l \) is constant among paradermal layers in a leaf at a given incident irradiance (physiologically, this means electron transport capacity is allocated in proportion to light absorption). This assumption renders the min function 'scale-invariant' (Farquhar 1989), which means that the same formal relationship holds between integrals of the independent variables over any scale. Hence, whole-leaf potential electron transport rate, \( J \), is conventionally modelled as...
Equation 1 (Fig. 1) is used in many models of leaf and canopy gas exchange. Typically, $J$ is assumed proportional to incident irradiance, $J_0$ is either estimated from the value of $J$ at saturating light or assumed proportional to carbon assimilation capacity, and $O_j$ is either fitted to light-response curves or treated as a constant and taken from the literature.

The assumption underlying Eqn 1—that $j_{\text{m}}$ is proportional to $j_{\text{i}}$ among paradermal layers—would appear to be supported by the observed similarity between transdermal profiles of photosynthetic capacity and light absorption under controlled conditions (Evans 1995; Evans & Vogelmann 2003). However, the transdermal light profile is controlled by the irradiances at both the upper and lower leaf surfaces, and these irradiances can vary independently as leaves flutter in the wind, as the sun moves through the sky, and as atmospheric conditions fluctuate, varying the proportions of collimated and isotropic (direct and diffuse) light. As a result, the transdermal profile of light absorption can also change very quickly, and probably too quickly for the capacity profile to adapt. This causes the light and capacity profiles to differ, violating the assumption of scale-invariance and rendering $J$ sensitive to changes in the fraction of light incident on the upper surface.

Experiments have in fact shown that $J$ is sensitive to the direction of incident light. In horizontally grown leaves, $J$ is higher at a given irradiance when the upper surface alone is illuminated (Moss 1964; Leverenz 1988; DeLucia et al. 1991; Evans, Jakobsen & Ogren 1993). This can be explained by the presence of a fixed capacity profile that is biased in favour of the upper surface: when light arrives at the lower surface, light absorption is high in layers with low capacity, and low in layers with high capacity. Similarly, in vertically grown leaves, $J$ is maximal when a given irradiance is evenly divided between the two surfaces (Evans et al. 1993). Furthermore, these acclimations to growth lighting regime can be overcome by applying a new lighting regime, which causes re-acclimation on time scales of several days to weeks. For instance, if a horizontally grown leaf is inverted, and then kept in that position indefinitely, it eventually 'prefers' light from what was formerly the lower surface (Ogren & Evans 1993).

These results all suggest that leaves can adapt their transdermal capacity profiles to the prevailing illumination regime on long time scales, but that on short time scales of a day or less, the capacity profile is fixed. Hence, the scale invariance assumption, and consequently Eqn 1, fails when the illumination regime differs from that to which the capacity profile is adapted. A more flexible model is required to predict the light response of potential electron transport rate and gas exchange to naturally varying light conditions.

In this study, we present a model that predicts the response of $J$ to variable illumination of each leaf surface. The model is based on explicit transdermal profiles of light absorption and electron transport capacity, it can accommodate capacity profiles that are adapted to a range of

\[ J = \min\{J_l, J_m, \theta_J\} \]  

where $J$ is the whole-leaf potential electron transport rate, $J_l$ is the light-limited potential rate, $J_m$ is the capacity-limited potential rate, and $\theta_J$ is the convexity parameter.

Figure 1. Diagram of the standard model for the response of whole-leaf potential electron transport rate, $J$, to incident irradiance, $I$, for different values of the convexity parameter, $\theta$. When $\theta_J = 1$ (solid line), $J$ is simply the minimum of the light-limited and capacity-limited potential rates $J_l$ and $J_m$, respectively, (left-dashed line). For $\theta_J < 1$, $J$ is always smaller than either $J_l$ or $J_m$, reflecting some degree of co-limitation between light and capacity.

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illumination regimes, and it is simple enough to incorporate into existing models of leaf and canopy gas exchange without great difficulty.

THE MODEL

This section presents a few key equations chosen from the detailed derivation of our model, which is given in the Appendix. We imagine the leaf to consist of many infinitely thin paradermal layers, each with a fixed amount of chlorophyll per unit leaf area, \( dc \) (Table 1 gives a list of symbols with descriptions and units). This defines a transdermal axis of cumulative chlorophyll content, \( c \), ranging from 0 at the upper surface to \( C \), the whole-leaf chlorophyll content, at the lower surface. We show in the Appendix that the transdermal profile of the rate of light absorption, \( i(c) \), can be approximated by

\[ I(c) = \frac{I_U}{p} \exp(-kc) \]

where \( I_U \) and \( I_L \) are the incident irradiances at the upper and lower surfaces, respectively; \( p > 1 \) is a factor that accounts for back-scattered light flux through the uppermost layer, which increases the space irradiance in upper layers; \( p \) is surface reflectance; \( k_c \) is the absorption coefficient for white light; \( k_c \) is the sum of absorption and scattering coefficients; and \( p \exp(-k_c C) \) is leaf transmittance to non-reflected light, or \( 1 - \alpha \) where \( \alpha \) is absorbance. Equation 2 is Eqn 16 in the Appendix.

The rate at which photo-oxidation of water yields energized electrons, or equivalently, the light-limited potential electron transport rate, \( J \), is proportional to the rate of photon absorption by the maximum quantum yield of electrons, \( \Phi_m \), and by a factor \( 1 - f' \) that accounts for the intrinsic inefficiency of photon utilization (i.e., \( f' \) is the limiting

<table>
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<td>Term in expression for ( \Phi_\text{m} ) that accounts for ( W_u ) and ( \tau )</td>
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<td>Pooled parameter, ( \alpha \cdot (1 - f') \cdot \rho ) to ( \text{photon generation} )</td>
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Finally, the capacity profiles created by this compromise rarely match the light profile exactly, so light and capacity settings for the upper and lower surfaces are denoted \( w_u \) and \( w_l \), respectively, and they sum to unity (\( w_u + w_l = 1 \)).

Formally, we hypothesize \( j(c) \) is a weighted average of two files, each of which results when a single leaf surface is illuminated at some 'preferred' irradiance, \( I^* \). The weightings are spatially decoupled under most conditions (e.g. Fig. 2c).

Because the light absorption profile may fluctuate diurnally, that the transdermal profile of electron transport capacity \( j(c) \) is adaptive in situations where the ratio between \( I_u \) and \( I_l \) varies on time scales shorter than the time constant for adaptive adjustment of \( j_u \) (on the order of days to weeks; Green 1993). We propose a different assumption, namely that the photosynthetic transduction profile of electron transport capacity reflects a compromise between perfect adaptation to illumination at the upper and lower surfaces. Formally, we hypothesize \( j(c) \) is a weighted average of two \( j \) profiles, each of which results when a single leaf surface is illuminated at some preferred irradiance, \( I_u \). The weightings for the upper and lower surfaces are denoted \( w_u \) and \( w_l \), respectively, and they sum to unity (\( w_u + w_l = 1 \)), so the hypothesized \( j(c) \) distribution is

\[
\begin{align*}
\int j(c) dc = w_u j_u(c) + w_l j_l(c) = k_F I_u e^{-k_u c} + k_F I_l e^{-k_l c} + w_u j_u(c) + w_l j_l(c) \\
\end{align*}
\]

(Eqn 10 in the Appendix). For example, a leaf that is equally well adapted to illumination from either surface would have a symmetrical capacity profile, with \( w_u = w_l = 0.5 \), \( j_u = k_F I_u e^{-k_u c} \), and \( j_l = k_F I_l e^{-k_l c} \); the profile for a leaf adapted to illumination only at the upper surface would be a simple exponential function, highest at the upper surface, that is, \( w_u = 1 \) and \( w_l = 0 \): \( j_u = k_F I_u e^{-k_u c} \). Because the light absorption profile may fluctuate diurnally, the capacity profiles created by this compromise rarely match the light profile exactly, so light and capacity are spatially decoupled under most conditions (e.g. Fig. 2c & d).

Integrating to the leaf scale

When the hyperbolic minimum model for \( j \) (Eqn 4) is applied to the expressions for \( j_u \) and \( j_l \) (Eqns 3 and 5, respectively), the resulting expression for \( j \) can not be integrated analytically to the whole leaf (see Appendix). After investigating many options for dealing with this problem, we concluded that the best approach was to assume, initially, that \( \theta = 1 \) (i.e., \( j = \min(j_u, j_l) \)), then to integrate the model to the whole leaf (Eqn 6 below), and finally to modify the integrated model to account for \( \theta < 1 \) (Eqn 11 below). This article yields a whole-leaf model that does not represent Eqns 3 and 5 perfectly, but is tractable and empirically adequate. The simple minimum of \( j_u \) and \( j_l \) (given by Eqns 3 and 5) can be integrated over \( c \) (as shown in the Appendix) to yield whole-leaf expressions:

\[
\int \min(j_u(c), j_l(c)) dc = \min(J, -I_u, -I_l) \\
\int J_u dc = \int J_l dc = \theta \int J dc \\
\]

(Eqns 6-11 are Eqs 40, 21, 22, 39, 25 and 41, respectively, in the Appendix.)

What is \( J \)?

Our model is similar in form to the standard model (cf. Eqs 1 and 11), except that our model contains a new term, \( J \), defined as

\[
J = \min(I_u - J_u, J_l - I_l) \\
\]

(Note the minus sign in Eqn 10. Finally, the integral of \( \min(j_u, j_l) \) in Eqn 6 overestimates the integral of \( \min(j_u, j_l) \) if \( \theta < 1 \). One way to correct for this is to modify Eqn 6 as follows:

\[
\int \min(J_u - J, J_l - J) \\
\]

Equations 7-11 comprise our model. (Eqs 6-11 are Eqs 40, 21, 22, 39, 25 and 41, respectively, in the Appendix.)
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The meaning of $J_s$ can be understood from various perspectives. First, $J_s$ is only non-zero when the transdermal profiles of light absorption and electron transport capacity cross one another within the leaf (e.g., Figs 2c & d, 3, & 5a). When the profiles do cross over, portions of them ‘overlap’ (e.g., shaded region in Fig. 3f). Graphically, $J_s$ is the portion of the area under the light absorption profile $C_j(c)$ that does not overlap the capacity profile $(J_s(C))$ (Fig. 3d).

Mathematically, $J_s$ is the integral of the difference $O_{2604}^{Blackwell Publishing Ltd, Plant, Cell and Environment}

Figure 2. (a) A hypothetical transdermal profile of electron transport capacity, $J_s$ (thick line), equal to a weighted sum of two exponential profiles (dashed lines), each of which matches the absorption profile for illumination at either surface. (b–d) Three profiles of light-limited potential electron transport rate, $j_i$ (dotted lines), overlaid on the $J_s$ profile (dashed lines) from (a) and showing the resultant profile of potential electron rate, $J_s$ (solid lines) for $\gamma = 0.93$. In (b), the illumination regime is optimal (65% to the upper surface, because $\sigma_w = 0.65$), whereas in (c) and (d) only one surface (upper or lower, respectively) is lit. (e) Whole-leaf light-response curves for the leaf shown in (a), but using the lighting proportions from (b–d). $J_i$ and $J_s$, the integrals of the $j_i$ and $J_s$ profiles shown in (a–d), are shown with dashed lines in (e).
quantities is simply the integral of the layer-wise minima of \( j_i \) and \( j_p \), given by Eqn 6, whereas the larger of these two quantities is the integral of the layerwise maxima of \( j_i \) and \( j_p \), given by Eqn 6. The layerwise maxima and minima are shown graphically in Fig. 3e and f, respectively.

(Note that, despite the minus sign, \( J_i - J_s \) is not necessarily the smaller of \( J_i \) and \( J_p \), for example, when \( J_i > 0 \) and \( J_s > 0 \), as in Fig. 4b).

Figure 3. Geometric interpretation of integrated terms in the model. (a) Hypothetical transdermal profiles of \( j_i \) and \( j_p \) (capacity- and light-limited potential electron transport rates), taken from Fig. 2d (the upper surface is at the left side of each panel; \( w_u = 0.65, I_u = 0 \) and \( I_s = *) \). (b) \( J_i \) and \( J_p \) are simply the areas under the \( j_i \) and \( j_p \) profiles, respectively. (c) \( J \) is the portion of the area under the \( j_i \) profile that does not overlap the \( j_p \) profile: \( J = J_i + J_p \) and \( J = j_i \) are the areas under the layerwise maxima and minima, respectively, of \( j_i \) and \( j_p \). Our model incorporates layerwise convexity by taking the hyperbolic minimum of (e) and (f).

Figure 4. Illustration of four different cases for the integral of the layer-wise minimum of transdermal profiles of light absorption \( j_i (z) \) and electron transport capacity \( j_p (z) \). (a) Case 1: all layers are light-limited, so the minimum is \( j_i \) everywhere. (b) Case 2: all layers are light-saturated, so the minimum is \( j_i \) for all layers. (c), (d) Cases 3 and 4: the profiles cross over somewhere within the leaf, creating distinct light-limited and light-saturated regions that must be integrated separately. In case 3 (c), the upper surface is light-saturated, whereas in case 4 (d), the lower surface is light-saturated. [Values of \( w_u \) and \( w_s \) used to create these sample profiles are shown on the figure; the total irradiance, \( I \), was 0.88* for (a), 1.21* for (b), and 1.0 I* for both (c) and (d).]
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Figure 5. Comparison between two leaves whose capacity profiles have the same adaptive weighting \( w_a = 0.7 \), whose upper and lower surfaces are illuminated in the same proportion \( W_\text{uo} = 0.3 \), and for which \( I = I_\text{c} \), but which have different values of \( r = 0.015 \)
and \( s = 0.3 \).

(a) Transdermal profiles of electron transport capacity \( J_c \) and light-limited potential electron transport rate \( J_\text{c} \), expressed relative to the value of \( J_\text{c} \) at the upper surface, and plotted against the ratio of cumulative chlorophyll content \( c \) to whole-leaf Chl content \( C \). (b) Whole-leaf light-response curves for potential electron transport rate for the leaves depicted in (a), with \( J \) expressed relative to whole-leaf capacity, \( J_\text{c} \), and total incident irradiance, \( I \), expressed relative to \( I_* \). (Both curves) The leaf with lower transmittance captures a greater fraction of incident light than the other leaf, but has a greater relative deficit in potential electron transport rate (i.e. \( J_c/J_\text{c} \) is lower) when the illumination regime does not match the capacity profile.

Parameters

Our model contains seven degrees of freedom \( (J_\text{c}, I_\text{c}, I_\text{c}, 4, 5, w_a, 0) \) — three more than the standard model’s four \( (J_\text{c}, I_\text{c}, 4, 0) \). One of the new degrees of freedom comes from separating irradiance into \( I_\text{ho} \) and \( I_\text{uo} \), but this is properly considered an additional independent variable, rather than a parameter. The other two new degrees of freedom are required to capture salient aspects of the hypothesized transdermal capacity profiles. \( w_a \) describes the extent to which the capacity profile is skewed towards either surface. \( r \) measures light attenuation; however, this could be described without reference to the capacity profile, and in fact \( r \) also appears in the standard model, embedded in \( 4 \). The reason \( w_a \) must be considered independently of \( 4 \) in our model is that \( r \) describes the ‘depth’, and thus the degree of curvature, in the exponential-based profiles of light absorption and capacity; that curvature, in turn, affects the magnitude of the deficit in whole-leaf \( J \) caused by mismatch between the two profiles. This is illustrated in Fig. 5. These curvature effects are not explicit in the standard model, so \( r \) runs, in principle, remain embedded in \( 4 \) in that model.

The value of \( 4 \) can be estimated for both models from the initial slope of \( J \) versus \( I \) (total incident irradiance). In the standard model, \( 4 \) and \( 0 \) can then be estimated by fitting Eqn 1 to \( J \) versus \( 4 \). In our model, \( J_\text{c}, 0, r, \) and \( w_a \) can be estimated by fitting Eqn 11 to two light-response curves simultaneously, each obtained with a different measurement lighting regime. It may also be possible to estimate \( w_a \) by varying the proportions of light supplied to either surface while keeping the total constant, because the ratio of \( I_\text{uo} \) to \( I \) that maximizes \( J \) should equal \( w_a \). However, we did not attempt to test that approach.

RESULTS AND DISCUSSION

The general behaviour of our model is illustrated in Fig. 6, which shows light-response curves for leaves with different degrees of preference for illumination at the upper surface (i.e., different values for the adaptive weighting parameter, \( w_a \)), varying proportions of total irradiance supplied to the upper surface \( (W_\text{uo}/I) \), and two different values for the convexity parameter, \( 0 \). Three major features of these response curves stand out. First, the value of \( 0 \) predicted for any given total irradiance \( I \) is greatest when the fraction of \( I \) supplied to the upper surface equals the adaptive weighting of the capacity profile towards that surface (that is, \( I_\text{uo} = W_\text{uo} \) solid lines in Fig. 6). This is because, in such cases, the ratio between light absorption rate and electron transport capacity is the same in all paradermal layers (e.g. Fig. 2c), so that neither light nor capacity is more limiting in one layer than in another. When any fraction of \( I \) other than \( W_\text{uo} = w_a \) is supplied to the upper surface, however, \( J \) may be lower than for \( W_\text{uo} = w_a \), because in that case some layers may be light saturated at the same time that other layers are light-limited (e.g. Fig. 3b).

Second, the magnitude of the effects of lighting regime
Figure 6. Light-response curves (J versus I) predicted by the model for different values of \( \tau \), \( \omega \), \( I_{UL} \) and \( I_{LU} \). (a), (b), (c): \( \tau = 0.2, \omega = 0.86 \). (d), (e), (f): \( \tau = 0.02, \omega = 0.99 \). (g), (h), (i): \( \tau = 0.02, \omega = 0.86 \). (a), (d), (g): \( \omega = 0.5 \) (a perfectly isobilateral leaf). (b), (e), (h): \( \omega = 0.75 \) (a leaf with transdermal capacity gradient partially biased towards the upper surface). (c), (f), (i): \( \omega = 1.0 \) (a perfectly bifacial leaf). Within each plot, each different line represents the response curve for a different proportion of light supplied to the upper surface \( (W, \omega) \), as indicated by the inset legends in a-c; where line styles indicated in the legends are not visible in a plot, it is because they overlap with other lines. \( J_u \) and \( J_l \) are shown by dashed lines, as labelled in (a).

Depends on the 'steepness' or curvature of the transdermal profiles of light absorption and electron transport capacity. The profiles are steeper when the total chlorophyll content (C) is high, and thus when the transmittance to non-reflected light (\( \tau \)) is low (e.g. Fig. 5a); hence the difference between the light-response curves for optimal and suboptimal lighting regimes is larger in leaves with low \( \tau \) (cf. the two curves in Fig. 5b and Fig. 6a-c versus 6d-f). The effects of lighting regime may be experimentally negligible in some cases (e.g. for \( \tau = 0.2 \) and \( \omega = 0.5 \), Fig. 6a), but very large in other cases (e.g. for \( \tau = 0.02 \) and \( \omega = 1.0 \), Fig. 6f). Third, in leaves whose capacity profiles are partially but not totally biased toward the upper surface (e.g. \( \omega = 0.75 \), Fig. 6b, e & h), illumination of the upper surface alone yields equal or greater \( J \) than illumination of the lower surface alone (cf. curves for \( W = 1.0 \) and \( W = 0 \)).

These predictions are consistent with observed effects of leaf inversion and growth lighting regime on light-response curves. Evans et al. (1993) performed a comprehensive study of these effects for four species. They constrained growing leaves to horizontal or vertical positions to induce adaptation to illumination from one surface or both surfaces, respectively, measured light-response curves for these leaves while supplying light to one or both surfaces, and fitted the standard \( J \) model (Eqn 1) to the measured response curves. For horizontally restrained leaves, the fitted convexity parameter \( \theta \) was substantially higher (and thus \( J \) was higher at all irradiances) when the upper surface
was illuminated than when the lower surface was illuminated, but in vertically restrained leaves \( \Phi \) was independent of which surface was illuminated. DeLucia et al. (1991) also reported that vertical leaves responded identically to light supplied at either surface, whereas horizontal leaves responded more strongly to light at the upper surface.

To demonstrate the performance of our model more directly, we fitted it to 12 of the light-response curves measured by Evans et al. (1993), corresponding to three lighting regimes (upper, lower, or both surfaces illuminated) for each of four plant treatments (horizontally and vertically restrained leaves of each of two species: *Eucalyptus maculata* and *E. pauciflora*). DeLucia et al. (1991) also reported that vertical leaves responded identically to light supplied at either surface, whereas horizontal leaves responded more strongly to light at the upper surface. To demonstrate the performance of our model more directly, we fitted it to 12 of the light-response curves measured by Evans et al. (1993), corresponding to three lighting regimes (upper, lower, or both surfaces illuminated) for each of four plant treatments (horizontally and vertically restrained leaves of each of two species: *Eucalyptus maculata* and *E. pauciflora*).

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There are two essential differences between our model and the standard model for $J_e$. One is the fixed, non-uniform stomatal surface. It is lit, layers with more light will have less stomata. Therefore, when the non-reflected light is increased, the resulting rise in Rubisco capacity per unit of chlorophyll near the lower surface of a sun leaf, but leaf surfaces may influence the extent to which CO$_2$ diffusion to non-reflected light is constrained. This was suggested by Sun, Nishio, and Vogelmann (1996) found that extremely high light (4000 μE m$^{-2}$ s$^{-1}$ for 4 h) caused the greatest damage to mesophyll tissues, suggesting that the upper leaf surface for horizontally restrained leaves and roughly symmetrical for vertically restrained leaves. However, because our model applies continuum to the transdermal profile of electron transport capacity (Nm), the second corollary is that capacity should be higher at the upper surface for horizontally restrained leaves and roughly symmetrical for vertically restrained leaves. Consistent with this, Sun, Nishio & Vogelmann (1996) observed that extremely high light (4000 μE m$^{-2}$ s$^{-1}$ for 4 h) caused the greatest damage to mesophyll tissues, suggesting that the upper leaf surface for horizontally restrained leaves and roughly symmetrical for vertically restrained leaves. However, because our model applies continuum to the transdermal profile of electron transport capacity (Nm), the second corollary is that capacity should be higher at the upper surface for horizontally restrained leaves and roughly symmetrical for vertically restrained leaves. 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However, because our model applies continuum to the transdermal profile of electron transport capacity (Nm), the second corollary is that capacity should be higher at the upper surface for horizontally restrained leaves and roughly symmetrical for vertically restrained leaves. Consistent with this, Sun, Nishio & Vogelmann (1963), who used the numerical model of Terashima & Sack (1985) to interpret their data, allowing the photosynthetic capacity of each paradermal layer to vary independently to produce a best fit to the observed whole-leaf responses. The fits can be transduced capacity profiles (Nm) were physiologically adapted to higher space irradiances than medial tissues. More direct evidence on either lighting regime or the leaf's optical geometry. In particular, the standard model minimizes co-limitation between a different pair of quantities (J$_m$, J$_{i+}$, and J$_i$, J$_{i+}$, respectively). In the standard model, Ω$_h$ must capture not only decoupling between light absorption and electron transport capacity within each layer, but also decoupling between the transdermal gradients of light and capacity. In our model, the term Ω$_h$ captures most of the effect of the measurement lighting regime, thus allowing Ω$_h$ to be treated as a constant for a given leaf. However, because our model applies convexity after integrating over the leaf it imprints Ω$_h$, with the information about the shape of the capacity profile (encoded in ω$_h$ and τ), with the result that Ω$_h$ must vary among leaves to account for variation in stone properties. The layer-scale convexity parameter (Ω$_h$) needs only to capture decoupling within each layer, so it has no direct dependence on either lighting regime or the leaf’s optical geometry.

The relationship between Ω$_h$ and Ω$_h$ has a convenient and useful mathematical formulation. In particular, the standard model matches our model at I = I$_*$ when the former uses a special value of Ω$_h$ given by:

Table 2. Parameter values for the model (Eqn 11) fitted to light responses of E. maculosa and E. pauciflora (data of Evans et al. (1993), see above). The coefficients of determination ranged from 0.991 to 0.999

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Units</th>
<th>Horizontal</th>
<th>Vertical</th>
<th>Horizontal</th>
<th>Vertical</th>
</tr>
</thead>
<tbody>
<tr>
<td>Electron transport capacity</td>
<td>J$_e$</td>
<td>μmol e$^{-}$ m$^{-2}$ s$^{-1}$</td>
<td>139</td>
<td>123</td>
<td>184</td>
<td>182</td>
</tr>
<tr>
<td>Max. quantum yield of electrons</td>
<td>θ</td>
<td>μelectron</td>
<td>0.162</td>
<td>0.145</td>
<td>0.162</td>
<td>0.165</td>
</tr>
<tr>
<td>Adaptive weighting for upper surface</td>
<td>w$_u$</td>
<td>unitless</td>
<td>0.870</td>
<td>0.554</td>
<td>0.600</td>
<td>0.512</td>
</tr>
<tr>
<td>Transmittance to non-reflected light</td>
<td>τ</td>
<td>unitless</td>
<td>0.058</td>
<td>0.062</td>
<td>0.077</td>
<td>0.022</td>
</tr>
<tr>
<td>Convexity parameter relevant to Eqn 11</td>
<td>Ω$_h$</td>
<td>unitless</td>
<td>0.836</td>
<td>0.864</td>
<td>0.824</td>
<td>0.906</td>
</tr>
<tr>
<td>Modal irradiance (I at which J$<em>i=J</em>{i+}$)</td>
<td>I$_*$</td>
<td>μE m$^{-2}$ s$^{-1}$</td>
<td>854</td>
<td>852</td>
<td>1140</td>
<td>1102</td>
</tr>
</tbody>
</table>

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This expression (plotted in Fig. 8, and derived as Eqs 42 and 44 in the appendix) shows how the apparent convexity of light-response curves depends on both the lighting regime (W) and the leaf's optical geometry (w, and r). Equation 12 provides a tool for interpreting the variation in \( w \) reported for upper and lower leaf surfaces, and for expressing in succinct form the model's predictions about the effects of leaf inversion on convexity. We compared the predictions of Eqn 12 with values of \( w \), fitted to light-response curves by Evans et al. (1993) under various growth and measurement lighting regimes, and found reasonable qualitative agreement (Fig. 8).

**Other models**

Several other transdermally explicit models for photosynthesis or potential electron transport rate exist in the literature. We are aware of two analytical models (Badeck 1995; Kull & Kruijt 1998), both of which assume that electron transport capacity is uniform among paradermal chlorophyll layers (i.e., \( w \) is a constant over \( c \)). This precludes the ability to predict different responses to illumination at either surface, and it contrasts with most experiments, which have found that the transdermal profiles of light absorption, carbon fixation, Rubisco activity, photosynthetic activity, and photo-inhibitory sensitivity are strongly non-uniform (Terashima & Inoue 1984, 1985a, b; Nishio et al. 1993; Sun et al. 1996; Evans & Vogelmann 2003). Our model prescribes an explicitly non-uniform capacity profile, so it is a step towards accommodating those results.

Other transdermally explicit models permit non-uniform transdermal capacity profiles but require numerical integration over paradermal layers. Terashima & Saeki (1985) presented a numerical model with 10 paradermal layers, of which the upper four layers (representing the 'palisade' mesophyll) had one value for photosynthetic capacity, while the lower six ('spongy') layers had a different capacity, and all layers had distinct optical properties measured by experiment. That model predicted that light-use efficiency should increase with the ratio of palisade to spongy photosynthetic capacity when the upper surface is illuminated. Ustun, Jacquemoud & Govaerts (2001) reached a similar conclusion, using a highly sophisticated three-dimensional numerical model of transdermal light propagation coupled to a simple photosynthesis model. Ustun et al. (2001) also commented that the profiles of carbon fixation and light were decoupled, as earlier reported by Nishio et al. (1993). However, the decoupling in their simulations was a consequence of the bimodal capacity profile that they assumed; instead, they had assumed a capacity profile that matched their predicted light absorption profiles, the decoupling would necessarily have disappeared. Evans (1995) showed that the apparent decoupling observed by Nishio et al. (1993) was in fact caused by incongruence of the spatial profiles of space irradiance and light absorption, which resulted, in turn, from spatial inhomogeneity in absorption characteristics. When the data were re-ordinated to the light-absorbing axis of...
cumulative chlorophyll content, and the fixation profile was compared with the profile of absorption, rather than that of space irradiance, the two profiles matched very well (as later confirmed experimentally by Evans & Vogelmann 2003). Our model codifies those insights by optimizing the transdermal axis by cumulative chlorophyll content rather than by spatial position. Therefore, while the 'layers' in our model may represent paradermal layers of different thickness or cell type (e.g. palisade versus spongy), each layer has equal absorptance by definition. Because of this abstraction, to make our model directly commensurate with spatially ordinated measurements (e.g. Niinemets et al. 1993) or models (e.g. Ustin et al. 2001), the spatial distribution of chlorophyll must be known.

SUMMARY

A new analytical model is presented for whole-leaf potential electron transport rate (J). The model predicts different responses to illumination at either leaf surface, it can accommodate varying degrees of preference for lighting at each leaf surface, and it is consistent with observed transdermal profiles of photosynthetic capacity, and with observed effects of leaf inversion, during both growth and measurement, on whole-leaf light responses. Our model captures these features with a fairly small mathematical cost of two additional parameters (the adaptive weighting of the capacity profile, \( w_a \), and the transmittance to non-reflected light, \( T_0 \)) and one independent variable (the irradiance \( I \) at the upper or lower surface, \( I_a \) or \( I_b \)) and its parameters are readily estimated from light-response curves. We suggest this model as a replacement for the more commonly used expression (Eqn 1) in cases where one wishes to account for variation in the proportions of irradiance arriving at either leaf surface, and/or variation in the adaptive preferences of leaves for illumination of either leaf surface.

ACKNOWLEDGMENTS

T.N.B thanks John Evans for many suggestions and insights that led to the present development and for providing the data in Figs 7 and I, and Belinda Barnes for verifying the facility of attempting to integrate Eqn 19.

REFERENCES


Kubelka V.P. & Munk F. (1931) Ein Beitrag zur optik der farbhaften.


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APPENDIX

We divide the leaf into infinitesimal paradermal layers, each having the same amount of chlorophyll per unit of leaf area, \( dc \). This defines an axis of cumulative chlorophyll content, \( c \), ranging from 0 at the upper surface to \( C \), the whole-leaf chlorophyll content, at the ‘lower’ surface (units for all terms are given in Table 1). The upper surface is arbitrarily defined as the one whose normal vector points above the horizon (regardless of its ontogenetic status as adaxial or abaxial), and we denote the upper and lower surfaces with subscripts ‘\( u \)’ and ‘\( l \)’, respectively.

Transdermal light propagation and capture

Kubelka & Munk (1931) developed equations to describe light propagation within leaves. Their theory accounts for reflection among paradermal chlorophyll layers, which can increase the total flux of photons passing through each layer (the ‘space irradiance’; Vogelmann & Bjorn 1984), and can cause some light that has entered the leaf to be reflected back out of the same surface. Kirschbaum (1984) extended the Kubelka-Munk theory to account for the angular dependence of absorptance and reflectance among paradermal layers, and found that the predicted profiles of space irradiance and light absorption can be described adequately by exponential functions. However, the space irradiance in layers near the illuminated surface is predicted to be higher than the incident irradiance, due to internal reflection among paradermal layers, and found that the predicted profiles of space irradiance can be described adequately by exponential functions. However, the space irradiance in layers near the illuminated surface is predicted to be higher than the incident irradiance, due to internal reflection among paradermal layers, and found that the predicted profiles of space irradiance can be described adequately by exponential functions.

\[ \phi'(x) = \phi_{0}(x) e^{-k_{c}x} \]

where \( \phi'_{0}(x) \) is the space irradiance due to illumination of the upper leaf surface, \( \phi_{0} \), incident irradiance at the upper surface, and \( k_{c} \) is the sum of absorption and scattering coefficients.

Kirschbaum's simplifications also suggested that the angle of incidence of incoming radiation strongly affects the fraction of light reflected from the upper leaf surface (the surface reflectance, \( p \)), but that, of light not reflected at the surface, the fraction that is transmitted (\( w \)) varied little with angle of incidence. Hence, we may approximate \( p \to p(\theta) \), where \( p \) accounts strictly for internal reflection and may be considered independent of the angle of incidence, whereas \( p \), the surface reflectance, depends on the angle of incidence. If the angular distribution of photons making within the leaf does not vary among paradermal chlorophyll layers, then the absorptance of each layer will also be conserved among layers, in which case the rate of absorption of photons that entered the upper leaf surface, \( \omega_{l}(x) \), is simply proportional to the surface irradiance by an absorption coefficient, \( k_{l} \):

\[ \omega_{l}(x) = \phi_{0} \cdot p \cdot k_{l} \]

The absorption coefficient, \( k_{l} \), differs from the apparent extinction coefficient for the space irradiance profile, \( k_{c} \), because the latter is the sum of absorption and scattering coefficients (Kirschbaum 1984). Most leaves will also receive some light at their lower surface for at least some part of a typical day, and the profile of light absorption for photons coming from that surface can be modelled in the same fashion as the upper surface, except that the direction of transmission across \( \Delta k \), for some distance from incident) light. Note that this \( \tau \) differs from the conventional transmission; the latter is defined as the complement of absorptance and reflectance (\( 1 - \tau \), where \( r \) here is related to absorptance by the relation \( \tau = 1 - \tau (1 - \rho) \), or equivalently, \( \tau = (1 - \rho)/(1 - \rho) \) (Fig. 9).

The main reason for choosing this convention was mathematical expediency—it makes the resulting model formulation simpler.

The total rate of photon capture by layer \( l \) is the sum of Eqs 14 and 15:

\[ \omega_{l} = \phi_{l} \cdot \rho \cdot k_{l} \]

Components of potential electron transport rate in each paradermal layer

We assume that the potential electron transport rate of a single paradermal chlorophyll layer, \( \phi_{l}(c) \), can be accurately modelled as a hyperbolic minimum of two limiting rates: a light-limited rate (\( \phi_{l}(c) \)) and a rate limited by local electron transport capacity (\( \phi_{t}(c) \)). To calculate the light-limited rate, we assume that a fraction \( f \) of the absorbed photons do not contribute to photochemistry, and that the other free electrons from water with as efficiency \( \alpha_{n} \), hence, \( \phi_{l} \) may be written

\[ \phi_{l}(c) = \phi_{l} \cdot \rho \cdot k_{l} \cdot f \cdot \mathbf{e}^{-k_{l} \cdot x} \]

Figure 9. Diagram explaining the relationship among surface reflectivity (\( \rho \)) and absorptance (\( \omega \)) and transmittance to non-reflected (as distinct from incident) light. Note that this \( \tau \) differs from the conventional transmission; the latter is defined as the complement of absorptance and reflectance (\( 1 - \tau \)).
\[ F = \sum_{k=1}^{N} \int_{0}^{\infty} f(t) e^{-kt} dt \]  
(17)

where \( F \) is a weighted average of electron transport capacity, \( f(t) \) is a weighted average of a set of model parameters, each of which corresponds to a different leaf surface. \( f(t) \) is defined as a function of the effective leaf temperature, \( T_e \), and the ratio of leaf-to-air temperature, \( T_a \).

\[ f(t) = \frac{1}{2} \left( 1 + \frac{T_e}{T_a} \right) \]
(18)

The adaptive weightings towards the upper and lower surfaces, \( w_\ell \) and \( w_s \), respectively, sum to unity (\( w_\ell + w_s = 1 \)) by definition. The potential electron transport rate for a single leaf is then given by

\[ P(E) = \int_{0}^{\infty} f(t) e^{-kt} dt \]
(19)

Integrating to the leaf

Whole-leaf potential electron transport rate, \( P \), is the integral of Eqn 19 over \( c \):

\[ P = \int_{0}^{\infty} f(t) e^{-kt} dt \]
(20)

The first two integrals in Eqn 20 are easily computed. The first is simply the whole-leaf light-limited rate, mathematically identical to the term \( j_0 \) in the standard model (Eqn 1):

\[ j_0 = \int_{0}^{\infty} f(t) e^{-kt} dt = \frac{1}{2} \left( 1 + \frac{T_e}{T_a} \right) \]
(21)

The third integral in Eqn 20 is identical to the maximum potential electron transport rate, \( j_m \) in the standard model (Eqn 1):

\[ j_m = \int_{0}^{\infty} f(t) e^{-kt} dt = \frac{1}{2} \left( 1 + \frac{T_e}{T_a} \right) \]
(22)

We will proceed to develop an approximate solution for the third integral in Eqn 20, which represents the effect of the intercept term in the response of \( j_0 \) to \( T_e \) and \( T_a \) within individual chlorophyll layers. The integral of the simple minimum of \( j_0 \) and \( j_m \) is then given by

\[ P = \int_{0}^{\infty} f(t) e^{-kt} dt \]
(23)

where \( f(t) \) is defined as a function of the effective leaf temperature, \( T_e \), and the ratio of leaf-to-air temperature, \( T_a \), and \( \alpha \) is defined as a function of the light intensity, \( I_0 \), and the leaf area, \( A \).

The first step is to generate a test to determine whether the profiles cross over within the leaf. Cross-over points are found by equating \( j_\ell \) with \( j_m \) and solving for \( c \):

\[ c^\ell(c) = \frac{1}{2} \left( 1 + \frac{T_e}{T_a} \right) \ln \left( \frac{c^\ell_0}{c^\ell_0 - \frac{1}{2}} \right) \]
(24)

Integrating \( j_\ell(c) \) over the leaf

Integrating \( j_\ell(c) \) over the leaf

\[ \int_{c^\ell_0}^{c^\ell_0} j_\ell(c) dc = \frac{1}{2} \left( 1 + \frac{T_e}{T_a} \right) \ln \left( \frac{c^\ell_0}{c^\ell_0 - \frac{1}{2}} \right) \]
(25)

Equation 27 covers cases 1 and 2 for the integral. Instead of \( j_\ell \), we must decide between the third and fourth cases; this requires a test to determine which surface (upper or lower) is light-limited. The upper surface is light-limited if \( j_\ell(c) > j_m(c) \) and \( J_m(c) \) < 0.

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\[ c^\ell(c) = \frac{1}{2} \left( 1 + \frac{T_e}{T_a} \right) \ln \left( \frac{c^\ell_0}{c^\ell_0 - \frac{1}{2}} \right) \]
(26)

where \( c^\ell_0 \) is a sufficient condition to ensure \( j_\ell(c) \) < \( j_m(c) \) for \( c \leq c^\ell_0 \). We will proceed to develop an approximate solution for \( j_\ell(c) \) by integrating the simple minimum of \( j_\ell(c) \) and \( j_m(c) \):
Modelling whole-leaf potential electron transport rate

\[ \text{We add these to give} \]
\[ J_a = \left( \frac{I_s}{1 - \frac{I_s}{I_s + I_{\text{not}}}} \right)^{t} \]  
(39) 
\[ \text{where } \tau(\theta) \text{ refers to the light-saturated surface (the upper surface if } I_s > I_{\text{not}}, \text{or the lower surface if } I_s < I_{\text{not}}).\]  
(Note that to generalize and simplify the notation, we have replaced \( s_i \) in Eqn 34 with \( \Upsilon_s \), as defined in Eqn 25, replaced \( F \) with \( 4/(1 - \zeta) \), and replaced \( I* \) with \( J, I_q \).) This is Eqn 9 in the main text, where it is expressed without the conditional notation.

To summarize the four cases for the integral of \( \min\{j_i, j_x\} \):
- When \( I_s \) is not between \( \zeta \) and \( I_{\text{not}} \), the integral is \( \min\{J_i, J_x\} \) (this covers cases 1 and 2). When \( I_s \) is between \( \zeta \) and \( I_{\text{not}} \), the integral is \( \min\{J_i - J, J_x\}; \) this covers cases 3 and 4, which are distinguished using the conditional notation \( \Upsilon(s) \) in Eqn 38. Furthermore, because \( J, \theta = 0 \) in cases 1 and 2 by definition, \( \min\{J_i, J_x\} \) covers those cases as well.

Therefore, we may write a single expression for all four cases:

\[ \int \min\{j_i, j_x\}(\theta) d\theta = \min\{J_i, J_x\} \]  
(40)

**Accounting for convexity**

Equation 40 is equal to the integral of Eqn 20 only if \( \theta = 1 \). Although Eqn 20 can not be integrated analytically for \( \theta < 1 \), the effects of layer-scale convexity may be accounted for, in part, by calculating the hyperbolic minimum of \( J_i - J_x \) and \( J_{\text{not}} + J_x \), which are the integrals of the layerwise minima and the layerwise maxima of \( j_i \) and \( j_x \) (as illustrated in Fig.3f & e), namely \( \min\{j_i, j_x\} \) and \( \max\{j_i, j_x\}: \)

\[ J = \min\left\{ J_i, J_x \right\} = J_{\text{not}}\]  
(41) 
\[ J > J_{\text{not}} \text{ in which case } J_i = J_x \text{ is the integral of the layerwise maxima, and } J_{\text{not}} = J \text{ is the integral of the minima.} \]
Relationship between $\theta_1$ and $\theta_2$

The shape of the whole-leaf light-response curve is affected by the lighting regime both during measurement and during growth. In the standard model, the curvature parameter $\theta_2$ must vary to capture both of these effects, whereas in our model, the convexity parameter $\theta_1$ is independent of measurement lighting regime. It is possible, however, to predict how $\theta_1$ would need to vary to mimic the qualitative dependence of the light responses predicted by our model on growth and measurement lighting regimes.

We make use of a convenient feature of the hyperbolic minimum function: when $J = J_m$, in the standard model, $J = J_m(1 - \frac{1}{1 + \theta_2})$, which is readily verified by substituting $J$ for $J_m$ in Eqn 11. This can be simplified by writing $\theta_2$ as $(1 - \frac{1}{1 + \theta_2})$, factoring to give $(1 - \frac{1}{1 + \theta_2})$, and cancelling terms to yield $J = J_m(1 - \frac{1}{1 + \theta_2})$. Similarly, our model (Eqn 41) reduces to $J = J_m(1 - \frac{1}{1 + \theta_2})$, when $J = J_m$ (to see this, replace $J$ with $J_m$ in Eqn 11 and rearrange). Then define $\theta_1 = \frac{1}{1 - \frac{1}{1 + \theta_2}}$, write $\theta_2$ in the denominator as $(1 - \theta_1)\theta_1$, and, as for $\theta_2$, above, write $\theta_1$ as $1 - (1 - \theta_1)$, factor to $(1 - \theta_1)^2$, and cancel terms to give $J = J_m(1 - \frac{1}{1 + \theta_2})$. Hence the two models coincide when $\theta_1 = \frac{1}{1 - \frac{1}{1 + \theta_2}}$, or $\theta_1 = \frac{1}{1 - \frac{1}{1 + \theta_2}}$.

To express $\theta_1$ in terms of $\theta_2$, $\theta_1$, and the distribution of light between leaf surfaces, note that, because of the complementarity relations inherent in the identities $I + I_w = I$ and $w_c + w_t = 1$, Eqn (25) can be written as $\frac{(1 - w_c)}{I} = \frac{(1 - \theta_1)}{I_w}$.

Then, since $J = J_m$ implies $I = I_w$, $I - I_w$ vanishes in the denominator and $\theta_1 = 1$. By a similar argument, $J = J_m$ implies $\theta_1 = 1$, so $\theta_1$ is simply $\frac{1}{1 - \theta_1}$. From Eqs 39. Now we factor the quantity $(1 - \tau)$ in Eqn 22 to write $J_m$ as $(1 - \tau) \frac{1}{1 + \theta_2}F_n$, and compute the ratio of $J_1$ to $J_m$ as

$$J_1 = \frac{1 - \theta_1}{1 + \theta_2}F_n \frac{(1 - \theta_2)}{(1 + \theta_2)} = \frac{1 - \theta_1}{1 + \theta_2}F_n \frac{(1 - \theta_2)}{(1 + \theta_2)} = \frac{1 - \theta_1}{1 + \theta_2}F_n \frac{(1 - \theta_2)}{(1 + \theta_2)}$$

The last step uses $I = I_w$ at $J = J_m$ and defines the weighting of the lighting regime towards the upper surface $(\theta_1)$ as $W_c$. Finally, since $(W_c + \theta_2) = 1 - (1 - \theta_1)$, and $W_c = \frac{(1 - \theta_1)}{1 + \theta_2}$, and Eqn 42 takes the square of this quantity, the result is the same whether $\theta_1 = 1$ or not, and we can arbitrarily replace $\theta_1$ with $\theta_1$ and write

$$\epsilon = \frac{1}{(1 + \theta_1)}W_c - \frac{1}{\theta_1}W_t$$

Equations 42 and 44 provide a tool for interpreting or predicting the qualitative effects of $W_c$, $W_t$, and $\epsilon$ on the apparent convexity of whole-leaf light-response curves.

Model fitting procedure

We fitted our model (Eqs 7-11) to the light-response curves published by Evans et al. (1993) as follows. First, we multiplied their measurements of oxygen evolution (gross photosynthesis rate) by 4 to estimate whole-leaf potential electron transport rate ($J$) (assuming saturating intercellular CO$_2$ on the grounds that ambient CO$_2$ was 5.0 kPa). Second, we calculated the initial slope of $J$ versus absorbed irradiance by fitting lines forced through the origin ($n = 7-8$ and $z = 0.97$ in all cases) to measurements at low light ($I < 300 \, \mu$E m$^{-2}$ s$^{-1}$), averaged the resulting slopes over three light-response curves for each plant treatment (species $\times$ growth orientation), and estimated $J_1$ as the product of this slope and absorbed irradiance. Third, we fitted all three complete light responses for each plant treatment to our model (Eqn 11) by least-squares, treating $J$ and $J_1$ as independent and dependent variables, respectively, and allowing $J_1$, $\theta_1$, $w_c$, and $\epsilon$ to vary as free parameters.

$J_1 = \frac{1 - \theta_1}{1 + \theta_2}F_n \frac{(1 - \theta_2)}{(1 + \theta_2)} = \frac{1 - \theta_1}{1 + \theta_2}F_n \frac{(1 - \theta_2)}{(1 + \theta_2)} = \frac{1 - \theta_1}{1 + \theta_2}F_n \frac{(1 - \theta_2)}{(1 + \theta_2)}$