Contributions of leaf photosynthetic capacity, leaf angle and self-shading to the maximization of net photosynthesis in Acer saccharum: a modelling assessment

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INTRODUCTION

Since net available carbohydrates can be allocated to key fitness components that improve growth, survival and reproduction (Givnish, 1988; Reich et al., 2003), maximizing plant net photosynthetic gain is expected to be favoured by natural selection. Although plants exploit light, photosynthetic photon flux density (PPFD), as their source of energy, they also require ancillary resources (e.g. water, nitrogen, phosphorus, etc.) to build and maintain their photosynthetic machinery. Acquiring and retaining these additional resources comes at a cost, and to maximize their net gain in principle plants should minimize these costs while maximizing their gross photosynthetic gains. Various studies suggest net photosynthetic gain can be maximized if plants maximize the efficiency with which they use available resources (Toomina, 1970; Mooney and Gulmon, 1979; Field, 1983; Bloom et al., 1985; Chapin et al., 1987; Nikinmaa, 1992), but there are discrepancies between theoretical predictions and observed resource-use efficiencies (reviews by Kull, 2002; Niinemets and Anten, 2009).

Since nitrogen (N) is a key component of both chlorophyll and photosynthetic enzymes (Evans, 1989) and N frequently limits productivity at higher latitudes (Chapin et al., 1987; Martinelli et al., 1999), attention has focused especially on optimizing photosynthetic N-use efficiency (PNUE), the ratio of photosynthesis to leaf N content. Yet, observed N allocation to leaves typically deviates from theoretical expectations (Field, 1983; Hirose and Werger, 1987; Evans, 1993; Hollinger, 1996; Kull, 2002; Meir et al., 2002; Wright et al., 2006; Niinemets and Anten, 2009), based on the idea that PNUE should be maximal and the same for all leaves independently of their position in the canopy (Mooney and Gulmon, 1979; Field, 1983). These discrepancies can arise because there is...
co-limitation between multiple resources (Chapin et al., 1987; Wright et al., 2006; Kaspari et al., 2008), incomplete estimates of costs (Field, 1983; Hollinger, 1996), competitive interactions among neighbouring plants (Anten, 2005), and trade-offs in the efficient use of different resources (Hikosaka et al., 1999). This latter point is particularly relevant since it suggests that plants may not be able to optimize the use of several resources simultaneously. For instance, it has been shown that leaves that maximize PNUE should have lower N content than leaves that maximize PPFD-use efficiency (Hikosaka et al., 1999). Given the importance of PPFD for plant fitness, an alternative to the PNUE hypothesis would be that plants have evolved to optimize PPFD use instead.

In theory, a plant could maximize its net photosynthetic gains if all its leaves attain maximal net photosynthetic PPFD use efficiency (\( e_{\text{max}} \), i.e. the ratio of net photosynthesis to PPFD) independently of their position in the canopy (Fig. 1; e.g. Tooming, 1970). Instantaneous \( e_{\text{max}} \) occurs on the ascending part of a leaf photosynthetic light-response curve, at the point where a tangent drawn from the origin intercepts the curve (Tooming, 1970; Kadaja and Tooming, 2004). Typically, \( e_{\text{max}} \) occurs at low to medium PPFD and well below photosynthetic saturation (\( A_{\text{max}} \)) (Fig. 1). Note that the apparent quantum yield (\( \phi \)) on a photosynthetic light-response curve is a different measure of efficiency because \( \phi \) occurs on the initial section of the curve where net carbon gain is negative. In contrast, \( e_{\text{max}} \) is the point of maximum net positive photosynthetic PPFD-use efficiency, i.e. the point where the marginal net gain in PPFD is highest. Despite its potentially important role in the evolution of plant form and function, the functional basis for attaining \( e_{\text{max}} \) remains poorly studied.

To reach \( e_{\text{max}} \) at the whole-plant level, the PPFD incident on each leaf (\( I \)) should be equal to \( I_{\text{max}} \) (cf. Fig. 1), which suggests \( e_{\text{max}} \) could be attained either by changing \( I \) incident on a leaf or by changing the value of \( I_{\text{max}} \) through physiological adjustments (e.g. by increasing \( A_{\text{max}} \)). Plants can readily change PPFD on leaves within their canopy through changes in leaf inclination (Monsi and Saeki, 1953; Ehleringer and Forseth, 1980; Kao and Forseth, 1992; Terashima and Hikosaka, 1995; Terashima et al., 2005). Similarly, leaves acclimate their physiology to the availability of PPFD (Boardman, 1977; Björkman, 1981), which rescale the photosynthetic light-response curve (Koyama and Kikuzawa, 2010), affecting the value of \( I_{\text{max}} \). Furthermore, several studies suggest that leaves concentrate their photosynthetic activity on the ascending part of the photosynthetic PPFD-response curve (Rosati and DeJong, 2003; Rosati et al., 2004; Posada et al., 2009; Koyama and Kikuzawa, 2010). Since \( e_{\text{max}} \) is about half way on the ascending portion of the curves (Fig. 1), this indirectly support the idea that plants are attaining \( e_{\text{max}} \) in nature.

Posada et al. (2009) showed that leaves of tropical canopy trees maintained constant light-use efficiency along PPFD gradients and proposed that this efficiency was maintained by simultaneous acclimation in leaf angle (\( L_A \)) and leaf \( A_{\text{max}} \). Here we investigated through a model, using some simple plasticity rules acting at the scale of individual leaves, whether distributions of \( L_A \) and \( A_{\text{max}} \) within crowns exist that maximize whole-plant net carbon gain. We tested the hypothesis that maximization of plant net carbon gain occurred when all individual leaves attained \( e_{\text{max}} \). We approached the problem of maximizing plant net photosynthesis computationally using the spatially explicit functional–structural tree model LIGNUM (Perttunen et al., 2001) to generate simulated saplings of Acer saccharum. Plants had the capacity to change both the \( A_{\text{max}} \) and \( L_A \) of individual leaves within their crown as a function of PPFD availability, but no optimization criteria was imposed \( a \text{ priori} \) at the leaf level, i.e. any optimal leaf-level resource use would be a consequence of plants maximizing their net photosynthesis. Simulations were carried out for saplings of four different sizes (Table 1) that were either in an open field or in a large forest gap, with leaf \( A_{\text{max}} \) either unconstrained or constrained to a maximum upper value.

**MATERIALS AND METHODS**

**Functional–structural tree model**

LIGNUM (Perttunen et al., 1998, 2001; Sievänen et al., 2008) is a spatially explicit tree growth model that iteratively utilizes a few basic structural units as a framework to integrate both physiology and architecture. Accurate methods are used
to calculate radiation conditions (Perttunen et al., 1998, 2001) and the photosynthetic rate in the crown depends on local light conditions. To account for incoming radiation the upper sky hemisphere is divided into sectors and their number and brightness are given as input to the model. LIGNUM has successfully simulated both coniferous and deciduous trees (Perttunen et al., 2001; Sievänen et al., 2008).

**Template saplings**

We first simulated open-grown Acer saccharum saplings aged between 1 and 4 years (Table 1), and used each one of them as architectural ‘templates’ for the optimization calculations (see below). The simulation was carried out with a version of LIGNUM that has been adapted to A. saccharum (Perttunen et al., 2001). In the simulation, the incoming photosynthetic active radiation (PAR) during the entire growing season was kept constant at a 1450 MJ m$^{-2}$ with a hemispherical distribution of radiation corresponding to that of standard overcast conditions (Ross, 1981). The area of individual leaves varied between 30 cm$^2$ and 97 cm$^2$ in relation to light availability and relative position on a branch. Template saplings varied in size between 0.51 m and 2.23 m, with large differences in individual leaf area index (LAI$_{ind}$) and in the degree of potential self-shading (Table 1). Sapling LAI$_{ind}$ was calculated as plant total leaf area divided by the area of the sapling crown silhouette projected on a horizontal plane.

**OptimalTree**

We then developed a modified version of LIGNUM called ‘OptimalTree’ that used the four sapling architectural templates to find the distributions of $L_A$ and $A_{max}$ in the crown that maximized instantaneous whole-plant net photosynthesis. OptimalTree used the tridimensional information of each template sapling (e.g. trunk and branch dimension, position and angle, individual leaf areas and bud positions), changing only $L_A$ and $A_{max}$ of individual leaves along gradients of PPFD in the crown. Calculations were done from top to bottom. First, the program calculated PPFD incident on a horizontal plane ($I_h$; see Table 2 for a list of abbreviations) next to the point of emergence of the uppermost leaf and assigned values of $A_{max}$ and leaf angle ($L_A$) using eqns (1) and (2), below. Second, $I_h$, $A_{max}$ and $L_A$ were determined for the second highest leaf considering the shade cast by the uppermost leaf, which was influenced by its leaf angle. This calculation was repeated down to the lowest leaf considering the shading caused by leaves above. In addition, leaves that would produce negative net photosynthetic rate were excluded from the calculations (i.e. areas were set equal to zero).

Leaf $A_{max}$ and $L_A$ were a function of $I_h$ next to the point of emergence of leaves. Leaf $A_{max}$ was subject to a simple hyperbolic function given by

\[ A_{max} = \frac{ah}{b + I_h} \]  

where $a$ is the asymptote and $b$ is a parameter that determines the ‘rate’ of change of $A_{max}$ along gradients of $I_h$ in the sapling canopies. Various studies have shown that leaf $A_{max}$, or other traits functionally related to $A_{max}$, are distributed non-linearly along PPFD gradients in the canopy (e.g. Evans, 1993; Hollinger, 1996; Dang et al., 1997; Kull, 2002; Posada et al., 2009). Variation in $A_{max}$ with PPFD regime has also been described with simple linear equations (for a review, see Kull, 2002) but non-linear functions appear to be more appropriate to describe changes in leaf functional traits when gradients of PPFD in the canopy of plants are pronounced (e.g. Evans, 1993; Hollinger, 1996; Posada et al., 2009). Leaf angle (degrees) was set by a linear equation

\[ L_A = c I_h + d \]  

where $c$ is the slope and $d$ the intercept. An angle of 90° corresponded to a horizontal leaf and 0° to a vertical-up leaf. Leaf azimuth, i.e. the compass direction of the leaf lamina, was assigned according to the morphological rules of the A. saccharum version of LIGNUM (Perttunen et al., 2001) in the generation of the template saplings; leaf blade rotational angle was equal to 0°.

The rate of leaf dark respiration ($R_d$, μmol m$^{-2}$ s$^{-1}$) was related to $A_{max}$ using the simple relationship

\[ R_d = 0.1 A_{max} \]  

This function defined the respiratory cost of increasing $A_{max}$.

Leaf $A_{max}$ and $R_d$ are generally strongly correlated (Niinemets and Tenhunen, 1997) and $R_d$ is approx. 10% of $A_{max}$ (Zotz and Winter, 1993; Hollinger, 1996; Posada et al., 2009). For simplicity, we assumed a zero intercept due to statistical uncertainty in estimates of the intercept of $R_d$–$A_{max}$ regressions for A. saccharum (Ellsworth and Reich, 1993; Raulier et al., 1999).

Leaf net assimilation ($A$; μmol m$^{-2}$ s$^{-1}$) was subject to a photosynthetic light-response curve given by a non-rectangular equation (Thornley, 1976)

\[ A = \frac{\phi I + A_{max} - \sqrt{(\phi I + A_{max})^2 - 4\phi I A_{max}}}{2\theta} - R_d \]  

**Table 1. General characteristics of A. saccharum saplings used in the simulations**

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>LAI$_{ind}$</th>
<th>Height (m)</th>
<th>No. of leaves</th>
<th>Total leaf surface area (m$^2$)</th>
<th>Self shading (% max reduction)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.443</td>
<td>0.506</td>
<td>8</td>
<td>0.063</td>
<td>7.6</td>
</tr>
<tr>
<td>2</td>
<td>0.837</td>
<td>1.054</td>
<td>38</td>
<td>0.314</td>
<td>42.3</td>
</tr>
<tr>
<td>3</td>
<td>0.973</td>
<td>1.559</td>
<td>72</td>
<td>0.574</td>
<td>51.8</td>
</tr>
<tr>
<td>4</td>
<td>2.562</td>
<td>2.232</td>
<td>481</td>
<td>3.337</td>
<td>96.8</td>
</tr>
</tbody>
</table>

The data are for saplings in an open environment with all leaves horizontal. Potential self-shading was calculated as the ratio between PPFD incident on the least-exposed leaf to PPFD incident on the most-exposed leaf in the plant.
where \( I \) is instantaneous PPFD (\( \mu mol \cdot m^{-2} \cdot s^{-1} \)) incident on the adaxial surface of the leaf, \( \phi \) is apparent quantum yield (unitless) and \( \theta \) is the curvature parameter (unitless). We assumed that both \( \phi \) and \( \theta \) were constant and equal to 0.05 and 0.75, respectively. These constant values of \( \phi \) and \( \theta \) result in photosynthetic light-response curves with the same shape irrespective of the value of \( A_{\text{max}} \) (Koyama and Kikuzawa, 2010). This assumption was supported by studies that have indicated that these two parameters are commonly not related to PPFD gradients in the canopy (e.g. Posada et al., 2009) and, even in cases where they are, their effect on the shape of the photosynthetic light curve is small (Koyama and Kikuzawa, 2010).

Other theoretical studies have taken similar approaches to simulate leaf and canopy photosynthesis (e.g. Sands, 1995; Niinemets and Tenhunen, 1997).

Leaf mass per area (LMA; g m\(^{-2}\)) generally varies with PPFD regime and \( A_{\text{max}} \) within plant canopies (Gutschick and Wiegel, 1988; Reich et al., 1991; Ellsworth and Reich, 1993; Niinemets and Tenhunen, 1997). In our initial simulations we used a linear relationship between LMA and \( A_{\text{max}} \) based on empirical parameters for \( A. \) saccharum, which allowed us to increase leaf size with decreasing \( A_{\text{max}} \) (assuming constant leaf mass). However, there was uncertainty in the intercepts of the LMA–\( A_{\text{max}} \) regression for \( A. \) saccharum (Reich et al., 1991), which caused some of our initial ‘optimal’ saplings to have biologically unrealistic leaf sizes (e.g. 16 m\(^2\)). Thus, we took a more conservative approach and used the leaf sizes of the template saplings in the calculations.

Instantaneous plant net photosynthesis (\( A_{\text{plant}} \); \( \mu mol \cdot s^{-1} \)) was calculated as the sum of the leaf area-weighted net photosynthetic rate of individual leaves, 1, …, \( N \)

\[
A_{\text{plant}} = \sum_{i=1}^{N} A_{i}S_{i} \quad (5)
\]

where \( A \) (\( \mu mol \cdot m^{-2} \cdot s^{-1} \)) is leaf net photosynthesis and \( S \) is leaf area (m\(^2\)).

Light environments

Optimal distributions of \( A_{\text{max}} \) and \( L_{A} \) were estimated with a light distribution for an open site and for a site equivalent to a large forest gap. In the open environment the distribution of PPFD in the hemisphere followed that of a standard overcast sky (Ross, 1981). The brightest PPFD was at the zenith but a large fraction of radiation still came from lateral sectors of the sky. Saplings in the open were exposed to a constant PPFD of 500 \( \mu mol \cdot m^{-2} \cdot s^{-1} \) on a horizontal surface, corresponding to a daily (12 h) exposure of 21.6 \( \mu mol \cdot m^{-2} \cdot d^{-1} \). The gap environment was created by blocking 95\% of the PPFD between 90\% (the horizon) and 20\%, leaving a circular opening of 40\% centred at the zenith. PPFD incident on a horizontal plane in the gap was 83.3 \( \mu mol \cdot m^{-2} \cdot s^{-1} \), which corresponded to a daily exposure of 3.6 mol m\(^{-2} \cdot d^{-1} \). In each light environment, we subdivided the sky into 100 sectors of equal area and obtained an integral value of PPFD per sector. LIGNUM traced PPFD rays coming from the centre of each sky sector and determined if leaves intercepted them and assumed that PPFD transmission was equal to 0.06 (Ross, 1981); reflection of light was not considered. Light incident on an individual leaf was ultimately obtained by summing PPFD rays coming from all 100 sectors. For computational efficiency in radiation calculations leaves were simplified as ellipses with an eccentricity of 0.42 and it was assumed that 80\% of the area was covered by the leaf blade (see eqn 4 in Perttunen et al., 2001).

Genetic algorithm

We used a genetic algorithm (GA) to explore the search space of the four parameters \( a, b, c \) and \( d \) (eqns (1) and (2)) and find the combination(s) of \( A_{\text{max}} \) and \( L_{A} \) distributions along \( h \) gradient in the sapling canopies that maximized \( A_{\text{plant}} \) (e.g. Fig 2). A GA is a search heuristic based on principles inspired from evolutionary biology that is commonly used to find solutions to optimization problems (Lucasius and Kateman, 1993, 1994). We utilized a GA with floating point chromosome in the package genalg and the function rbga in R (R Development Core Team, 2008).

We ran detailed preliminary tests to tune the GA conditions to find reasonable limits for the optimization search space. The \( A_{\text{max}} \) distribution given by parameters \( a \) and \( b \) (eqn 1) varied within a broad search space of positive numbers. Parameters \( c \) and \( d \) varied in both positive and negative values, although we limited the range of \( L_{A} \) to between 180\% (leaf vertically down) and 0\% (leaf vertically up). The search space for parameters \( a \) and \( b \) was relatively ‘smooth’ while parameters \( c \) and \( d \) had a rugged space with several local optima, which required a more detailed search. We ran the GA for 400–600 generations with a constant population size of 2000 saplings; given the small number of parameters relatively few generations were necessary to converge to a solution. During the optimization, 20\% of the saplings with the best \( A_{\text{plant}} \) values were allowed to pass unchanged to the next generation; the mutation rate (random changes in the parameter values) was set to a constant value of 10\%. The largest saplings (Table 1) required considerable computational time and, to increase efficiency, we ran the GA a first time to determine the overall structure of the search space and then reran the GA within a narrower parameter space (i.e. local optimization) for 200 generations.

Analyses

We evaluated how the optimal distributions of \( A_{\text{max}} \) and \( L_{A} \) changed depending on whether saplings were in an open environment or in a gap. We also determined the effect of constraining leaf \( A_{\text{max}} \) to an upper value or letting it be unconstrained. Constrained \( A_{\text{max}} \) was set to a maximum value of 12.0 \( \mu mol \cdot m^{-2} \cdot s^{-1} \), which is within the upper range of naturally occurring \( A_{\text{max}} \) values reported for \( A. \) saccharum (Ellsworth and Reich, 1993; Raulier et al., 1999; Jones and Thomas, 2007). For each sapling size (Table 1), we evaluated four conditions: open/unconstrained (OU), open/constrained (OC), gap/unconstrained (GU) and gap/constrained (GC). Note that given the positive relationship between \( A_{\text{max}} \) and leaf \( N_{\text{area}} \) in \( A. \) saccharum (Ellsworth and Reich, 1993;
Niinemets and Tenhunen, 1997), the two cases where $A_{\text{max}}$ was unconstrained were equivalent to assuming that soil N availability relative to other resources was unlimited for a given leaf area and $N_{\text{area}}$ could potentially take any value. Our constrained maximum leaf $A_{\text{max}}$ was equivalent to limiting individual leaf $N_{\text{area}}$ to a maximum and allowing optimal plants to have a lower total N than the maximum potential total N. Yet, both constrained and unconstrained cases differed from studies that have looked at the optimal allocation of a fixed amount of N in the canopy (e.g. Field, 1983; Hirose and Werger, 1987).

Leaf photosynthetic PPFD-use efficiency ($\varepsilon$), the efficiency of CO$_2$ assimilation per unit PPFD, was calculated as

$$\varepsilon = \frac{A}{I}$$

For any photosynthetic light-response curve (eqn 4) the value of $I$ that maximized $\varepsilon$ ($I_{\varepsilon_{\text{max}}}$) was calculated as

$$I_{\varepsilon_{\text{max}}} = \frac{1}{A_{\text{max}}} \left[ (2\theta - 1) - (2\theta r_d - A_{\text{max}}) \sqrt{\frac{\theta - 1}{r_d(\theta r_d - A_{\text{max}})}} \right]$$

We calculated maximal $\varepsilon$ ($\varepsilon_{\text{max}}$) as $A(I_{\varepsilon_{\text{max}}})/I_{\varepsilon_{\text{max}}}$ using eqns (4) and (6).

**RESULTS**

**Optimal solutions**

We identified two key functional characteristics in the genetic algorithm search that were simultaneously optimized. To maximize net photosynthesis, plants had to maximize both instantaneous leaf $\varepsilon$ across gradients of PPFD in their crowns and PPFD absorption by the whole plant (Fig. 2). In Fig. 2 each point corresponds to one simulated plant with a particular combination of parameters $a$, $b$, $c$ and $d$, which define the distribution of leaf $A_{\text{max}}$ and $L_A$ along PPFD gradients in the plant (eqns 1 and 2). The genetic algorithm generated many saplings in which average $\varepsilon$ or PPFD absorption were maximal but with $A_{\text{plant}}$ below the maximum. Only when both $\varepsilon$ and PPFD absorption where maximized did the plants attain maximum $A_{\text{plant}}$.

This response was observed for plants in the open with an unconstrained $A_{\text{max}}$ (OU) and for plants in a gap with either constrained (GC) or unconstrained $A_{\text{max}}$ (GU). Small OU seedlings ($L_{\text{AI_{ind}}} = 0.4$) had an average $\varepsilon$ that reached the maximum $\varepsilon_{\text{max}}$ of 0.0323 (i.e. when average $\varepsilon$ was exactly equal to maximum $\varepsilon_{\text{max}}$ in all leaves; Fig. 3A). Yet, average $\varepsilon$ declined slightly with increasing $L_{\text{AI_{ind}}}$ and was 99.8, 99.6 and 97.5% of maximum $\varepsilon_{\text{max}}$ for 2-, 3- and 4-year-old individuals, respectively; there was some variability in $\varepsilon$ between leaves in the 4-year-old saplings, albeit small. In contrast, OC plants had significantly lower average $\varepsilon$ than OU or GC/GU individuals (Fig. 3B). In OC seedlings, average $\varepsilon$ was only 56.9% of $\varepsilon_{\text{max}}$, although $\varepsilon$ increased with $L_{\text{AI_{ind}}}$ reaching 77.1% of $\varepsilon_{\text{max}}$ in the largest individuals. Plants in a gap (GC and GU) behaved similarly to the OU individuals, yet their decline in average $\varepsilon$ at the highest $L_{\text{AI_{ind}}}$ was more pronounced than for OU individuals (average $\varepsilon$ for 4-year-old saplings was 90.8% of $\varepsilon_{\text{max}}$) and between leaves variability in $\varepsilon$ increased with size (Fig. 3C).

Not surprisingly, plant PPFD absorption increased with $L_{\text{AI_{ind}}}$ and was higher in the open than in a gap (Fig. 4A). Interestingly, however, and, in contrast, with average leaf $\varepsilon$, there were no marked differences in PPFD absorption when comparing OC and OU plants. This suggests that the
optimal solution prioritized the maximization of PPFD absorption over the maximization of leaf $e$ when $A_{\text{max}}$ was constrained. There was no difference between PPFD absorption in GC and GU saplings. Values of $A_{\text{plant}}$ mirrored PPFD absorption in OU, GC and GU plants, yet carbon gain was lower in OC individuals (Fig. 4B). Since OU and OC plants had the same PPFD absorption, lower photosynthesis of OC plants was attributed to their lower average leaf $e$.

In addition, we found strong linear relationships between plant photosynthesis and PPFD absorption in all plants (Fig. 4C). These relationships for OU and GU/GC had comparable slopes, with values close to the maximum $e_{\text{max}}$ of 0.0323 (slopes: OU = 0.0317; GU/GC = 0.0304), and fell along one line. In contrast, OC plants had lower photosynthesis than OU individuals and a considerably lower slope (0.0247). All regression lines had intercepts close to zero (not shown).

Role of leaf $A_{\text{max}}$ and $L_A$ in the optimization

Since individual leaf area and plant architecture did not change during the GA parameter-search, PPFD absorption...
was almost exclusively determined by $L_A$. The leaves that were excluded due to their negative carbon gain played a minor role as only two out of 481 leaves in the 4-year-old GC and GU saplings (0.37% of the total leaf surface) were such; all other plants maintained the maximum number of leaves independently of age, light environment or constraints on $A_{\text{max}}$. While plant PPFD absorption was determined by $L_A$, maximization of $\epsilon$ was more complex and required co-ordinated adjustments in both $A_{\text{max}}$ and $L_A$.

In order to attain $\epsilon_{\text{max}}$, $I$ (PPFD incident on a leaf) should be equal to $I_{\text{max}}$ (Fig. 1), a condition which could be satisfied in two ways. Since leaf $A_{\text{max}}$ and $I_{\text{max}}$ were linearly related, a leaf could change its $I_{\text{max}}$ by changing $A_{\text{max}}$ (Fig. 5A) or a leaf could modulate $I$ through changes in its angle of inclination to attain $I_{\text{max}}$ (Fig. 5B). The change in $I$ with angle was small in the open environment, reflecting the relatively homogeneous PPFD distribution for a standard overcast sky but was more pronounced in the gap. A completely upward oriented leaf in the open environment received 77% of PPFD incident on a horizontal plane because there was considerable PPFD available in lower positions in the sky hemisphere. In the gap environment, most PPFD came from the upper part of the sky and, as a result, PPFD declined more steeply with increasing leaf inclination than in the open (Fig 5B). For reference, we also plotted changes in $I$ predicted by the cosine law, which corresponded to the case where all PPFD would come from a single point source of beam radiation in the zenith. These curves show that the role of $L_A$ in the optimization of $\epsilon$ is modest under cloudy conditions, but can be significant in gaps or under clear sunny skies.

The distributions of $L_A$ and $A_{\text{max}}$ (Fig. 3D–I) were a consequence of the simultaneous maximization of plant PPFD absorption and $\epsilon$. Seedlings had leaves with mostly horizontal orientation (90°), but as $LAI_{\text{ind}}$ increased self-shading also increased, suggesting that larger individuals increased leaf inclination to better distribute PPFD to more shaded leaves (Fig. 3D, E). The OU plants decreased average $L_A$ from 91° to 42°, while OC individuals showed a more pronounced decrease from 86° to 30°, particularly in the transition between an $LAI_{\text{ind}}$ of 0.85 and 0.97 (Fig. 3E). Similar to previous results, there were no differences between GU and GC plants, yet plants in the gap maintained their leaves more horizontally than plants in the open, even when $LAI_{\text{ind}}$ was at its highest. Except for seedlings that had mostly horizontal leaves, average $L_A$ of saplings was below 90°, and most leaf blades were pointing upward despite having a potential range of variation between 0° and 180°.

Average leaf $A_{\text{max}}$ of OU seedlings was 46.3 μmol m$^{-2}$ s$^{-1}$ which illustrated how $A_{\text{max}}$ and $L_A$ were ‘co-ordinated’ to maximize $\epsilon$ (Fig. 3G). If PPFD incident on a leaf would be 500 μmol m$^{-2}$ s$^{-1}$ (which was the PPFD incident on a horizontal plane in the open environments) then leaf $A_{\text{max}}$ had to be equal to 47.4 μmol m$^{-2}$ s$^{-1}$ to have $I_{\text{max}}$ at 500 μmol m$^{-2}$ s$^{-1}$ (Fig. 5A). The OU seedlings had a maximum $A_{\text{max}}$ of 47.1 μmol m$^{-2}$ s$^{-1}$ and mostly horizontal leaves, meaning that these plants basically attained $\epsilon_{\text{max}}$ by increasing $A_{\text{max}}$ and $I_{\text{max}}$ to very high values (Fig. 3D, G). Similarly, the greatest $A_{\text{max}}$ of GC/GU seedlings was 7.9 μmol m$^{-2}$ s$^{-1}$, which corresponded to an $I_{\text{max}}$ of 83.3 μmol m$^{-2}$ s$^{-1}$ = exactly equal to the PPFD of 83.3 μmol m$^{-2}$ s$^{-1}$ incident on a horizontal plane in the gap. The $A_{\text{max}}$ of OC seedling attained the maximum of 12.0 μmol m$^{-2}$ s$^{-1}$ but was particular in that the plant maintained its leaves horizontal, suggesting that the benefits of maximizing PPFD absorption outweighed the cost of having an $\epsilon$ well below $\epsilon_{\text{max}}$.

**Fig. 5.** (A) Relationship between PPFD at which a leaf attains maximum photosynthetic light-use efficiency ($I_{\text{max}}$; eqn 7) and leaf $A_{\text{max}}$. (B) Relative change in PPFD incident on a leaf ($I$) as a function of leaf angle in the open and gap environments simulated in this study. For comparison, relative changes in $I$ that would follow the cosine law (Campbell and Norman, 1998) are also plotted as a dotted line.

**Role of self-shading and $LAI_{\text{ind}}$ in the optimization**

As $LAI_{\text{ind}}$ increased, the proportion of leaves in the sapling crowns exposed to low PPFD also increased (Fig. 3J–L). Average PPFD incident on leaves declined from 488 to 296 μmol m$^{-2}$ s$^{-1}$ in OU plants and from 487 to 295 in μmol m$^{-2}$ s$^{-1}$ in OC plants. The largest difference between OU and OC plants was for 3-year-old saplings, which had an average PPFD of 411 and 372 μmol m$^{-2}$ s$^{-1}$, respectively. This difference was due to the more erect leaves in OC plants (Fig. 3D, E). Average PPFD for GC/GU changed from 83 to 39 μmol m$^{-2}$ s$^{-1}$ (Fig. 3K). This general increase in self-shading helped explain the decrease in $A_{\text{max}}$ with $LAI_{\text{ind}}$. In OU plants, average $A_{\text{max}}$ declined from 46.3 to 28.7 μmol m$^{-2}$ s$^{-1}$ with increasing $LAI_{\text{ind}}$, and in GC/GU plants $A_{\text{max}}$ declined from 7.9 to 4.0 μmol m$^{-2}$ s$^{-1}$.
(Fig. 3G–I). Since $A_{\text{max}}$ is linearly related to $I_{\text{e max}}$, the decline in $A_{\text{max}}$ can be attributed to the decrease in average $I$, i.e. leaves exposed to a lower PPFD attain $\varepsilon_{\text{max}}$ with a lower $A_{\text{max}}$ than leaves exposed to a higher PPFD. Average $A_{\text{max}}$ of OC saplings also declined slightly (12.0 to 11.3 $\mu$mol m$^{-2}$ s$^{-1}$), reflecting the increase in the proportion of leaves that were exposed to low $I$ with increasing LAI$_{\text{ind}}$.

**DISCUSSION**

Our results showed that whole-plant net photosynthesis was maximal when average leaf $\varepsilon$ and whole-plant PPFD absorption were maximized. This suggests that there are selection pressures to simultaneously absorb the maximum amount of PPFD available and use it as efficiently as possible. Many observations show that vegetation commonly absorbs almost all incident radiation. For instance, average PPFD transmittance measured below the crown of mature trees in temperate forest biomes varies between 2.5 % and 7.7 % (Messier et al., 2009) and, in the case of forest canopies dominated by *A. saccharum*, transmittance is 7.7 % (Beaudet et al., 2004). Understory tropical species also converge towards high PPFD capture ratios (Valladares et al., 2002), suggesting selection favouring maximal PPFD capture. These results are consistent with the self-limiting development of plant canopies to the point where shade leaves can maintain a positive carbon balance, provided no other resources than PPFD are limiting (Saeki, 1960; Oikawa et al., 2006). If the availability of resources other than light allows, we can expect that plants have evolved to maximize absorption of available PPFD.

By comparison to PPFD capture, maximization of leaf $\varepsilon$ remains poorly studied. Theoretical analyses suggest that plant photosynthesis is maximized if all leaves in a plant are exposed to their $I_{\text{e max}}$ (Tooming, 1970; Kadaja and Tooming, 2004) which is indirectly supported by field studies indicating that leaves concentrate their photosynthetic activity on the ascending part of their photosynthetic light-response curves (Monteith, 1994; Rosati and DeJong, 2003; Rosati et al., 2004; Posada et al., 2009; Koyama and Kikuzawa, 2010) where $\varepsilon$ is highest. Our results further support this prediction, showing that there should be selection pressure for both maximizing $\varepsilon$ and for leaf acclimatory responses to PPFD availability that lead to PPFD incident on a leaf coincident with $I_{\text{e max}}$.

We found, however, that there are limits to maximizing $\varepsilon$ because of trade-offs associated with a decrease in PPFD absorption at the leaf level. This occurred in individuals with a constrained $A_{\text{max}}$ growing in the open, which had an average $\varepsilon$ well below $\varepsilon_{\text{max}}$ but still maintained maximum PPFD absorption at the whole-plant level (i.e. absorption was nearly equal to that of saplings growing in the open with an unconstrained $A_{\text{max}}$). This hierarchical response suggests that the benefits of maximizing absorption were higher than the costs of a decrease in average leaf $\varepsilon$; plants could have improved $\varepsilon$ to some extent by increasing their angle of inclination, but the costs in terms of a decrease in PPFD absorption by the whole plant were higher than the benefits. In contrast, however, constrained saplings in a gap attained $\varepsilon_{\text{max}}$, indicating that optimization of $\varepsilon$ was possible in environments with lower PPFD availability. Thus, the prediction that plants should maximize $\varepsilon$ was supported in our study, although when $A_{\text{max}}$ was constrained to an upper value and PPFD availability was high optimization of $\varepsilon$ was not possible.

In addition to showing that plants are under selection pressure to simultaneously maximize both $\varepsilon$ and PPFD absorption, our simulations illustrated that maximization of net photosynthesis required strongly integrated adjustments between the angle and $A_{\text{max}}$ of leaves, and LAI$_{\text{ind}}$. Maximization of plant PPFD absorption was basically controlled in concert by LAI$_{\text{ind}}$ and the distribution of leaf angles because sapling branch architecture and leaf size could not change. Attaining $\varepsilon_{\text{max}}$ involved co-ordinated leaf-level adjustments between leaf angle and $A_{\text{max}}$, but also plant-level adjustments in the PPFD gradients within the crowns related to leaf angle and LAI$_{\text{ind}}$. LAI$_{\text{ind}}$ played an important role in the optimization because it influenced PPFD absorption, the degree of self-shading and the optimal distribution of leaf angle and $A_{\text{max}}$.

When saplings were small, maximizing PPFD absorption was attained by placing leaves horizontally and matching PPFD incident on leaves with $I_{\text{e max}}$ which, in the case of open-unconstrained plants, required a very high $A_{\text{max}}$. With increasing LAI$_{\text{ind}}$, self-shading increased, leaves became more inclined and average $A_{\text{max}}$ declined due to a lower average PPFD incident on leaves. Thus, our results suggest that the well-documented relationships among leaf angle, leaf $A_{\text{max}}$, LAI and PPFD gradients in the canopy (Monsi and Saeki, 1953; Terashima and Hikosaka, 1995; Kul, 2002; Kitajima et al., 2005; Terashima et al., 2005) are an emergent property of the co-ordinated maximization of canopy PPFD absorption and maximization of $\varepsilon$ at the leaf level.

An important aspect of our study was to evaluate how constraining maximum $A_{\text{max}}$ to an upper value consistent with field measurements for *A. saccharum* trees (Ellsworth and Reich, 1993; Raulier et al., 1999; Jones and Thomas, 2007) influenced this dual maximization. At an $A_{\text{max}}$ of 12.0 $\mu$mol m$^{-2}$ s$^{-1}$, the PPFD at which photosynthetic efficiency was maximal (i.e. $I_{\text{e max}}$) was only 126-5 $\mu$mol m$^{-2}$ s$^{-1}$; leaves will have lower efficiency if PPFD incident on their surface is above this value. There were two noteworthy effects of constraining $A_{\text{max}}$ in the simulations. First, there was a decrease in average $\varepsilon$ in the open environment where the PPFD on a horizontal plane of 500 $\mu$mol m$^{-2}$ s$^{-1}$ was well above the maximum $I_{\text{e max}}$. An increase in leaf inclination in these constrained individuals could have brought the PPFD incident on leaves closer to $I_{\text{e max}}$, but the potential role of leaf inclination was limited by the relatively homogenous distribution of PPFD in the open and costs associated with a reduction in PPFD absorption. A second important aspect of constraining $A_{\text{max}}$ was that, despite limitations in $I_{\text{e max}}$, average $\varepsilon$ improved considerably with LAI$_{\text{ind}}$. Self-shading increased with increasing LAI$_{\text{ind}}$; hence the constraint on $A_{\text{max}}$ was gradually released because more leaves were exposed to $I$ values closer to $I_{\text{e max}}$. This suggests that in large *A. saccharum* individuals with an LAI of 5.7–6.1 (Ellsworth and Reich, 1993), most leaves in the crown should attain $\varepsilon_{\text{max}}$ because self-shading will be higher. Several studies have reported that self-shading can favour plants because it can reduce photoinhibition (e.g. Howell et al., 2002; Kern et al., 2004). Our results show that, in addition, self-shading can be crucial for plants because it improves average marginal returns in PPFD (i.e. $\varepsilon$).
Despite the consequences of a constrained $A_{\text{max}}$ on $\varepsilon$, our results appear consistent with the evolution of $A.\ saccharum$ as a shade-tolerant species and suggest that optimization of $\varepsilon$ should take place during most life stages in $A.\ saccharum$. In gap conditions, seedlings were not influenced by constraints on $A_{\text{max}}$ because the PPFD incident above the plants was $83.3 \mu\text{mol m}^{-2}\text{s}^{-1}$ and the maximum $A_{\text{max}}$ of the most exposed leaves was optimized at $7.9 \mu\text{mol m}^{-2}\text{s}^{-1}$, which is below the maximum $A_{\text{max}}$ of $12.0 \mu\text{mol m}^{-2}\text{s}^{-1}$ reported for $A.\ saccharum$. In forests were $A.\ saccharum$ grows, PPFD in gaps varies between approx. 5.6 and 6.5 mol m$^{-2}\text{d}^{-1}$ with an average instantaneous PPFD of only $122 \mu\text{mol m}^{-2}\text{s}^{-1}$ (Ellsworth and Reich, 1992; Beaudet et al., 2004). Thus, under gap conditions, or in understory conditions with lower PPFD availability, $A.\ saccharum$ saplings should be able to maximize leaf $\varepsilon$. However, under the relatively high PPFD of open environments simulated in this study ($500 \mu\text{mol m}^{-2}\text{s}^{-1}$) or measured in the field ($932 \mu\text{mol m}^{-2}\text{s}^{-1}$; Ellsworth and Reich, 1992), seedlings and saplings of $A.\ saccharum$ will not attain $\varepsilon_{\text{max}}$ in all leaves. Nonetheless, since the LAI$_{\text{ind}}$ of 2-6 for the largest individuals that we simulated was well below the 5-7-6-1 LAI in mature $A.\ saccharum$ (Ellsworth and Reich, 1993), adult trees should be able to maximize $\varepsilon$ in leaves under high PPFD conditions because most leaves in the trees will be exposed to a lower PPFD due to self-shading. Thus, we suppose that $A.\ saccharum$ spends most of its juvenile stages in the shade or in small to medium gaps and only reaches the sunlit canopy as an adult with a large LAI$_{\text{ind}}$, then maximization of $\varepsilon$ should occur during most life stages.

Another consideration is that optimization of $\varepsilon$ will also be influenced by the temporal distribution of PPFD. In this study, we applied two static distributions of incoming light (standard overcast distribution in the open and within a forest gap). Yet, under natural conditions, instantaneous PPFD will often be highly variable in time due to both broken cloud cover and the effects of fine-scale canopy heterogeneity on insolation regime (e.g. sunflecks). Consequently leaves should have a lower $\varepsilon$ than the one we estimated. Acclimation of the photosynthetic apparatus to PPFD availability is also a relatively slow process that can take days or weeks (Turnbull et al., 1993; Oguchi et al., 2003, 2006; Niinemets and Anten, 2009). Therefore, under natural conditions leaves will not be able to adjust to rapid changes in instantaneous PPFD.

An important outcome of the maximization of PPFD absorption and $\varepsilon$ was the linear relationship observed between plant net photosynthesis and PPFD absorbed by the saplings (Fig 5). In all but open-constrained plants, leaf $\varepsilon$ did not vary to a large extent: leaves used PPFD with similar efficiency regardless of their position in the plant crown. If all leaves converted PPFD into photosynthesize with similar efficiency then, by extension, plant photosynthesis was proportional to the amount of PPFD absorbed by the crown. These results agree with studies that have shown that leaf $\varepsilon$ stays constant along canopy PPFD gradients and could be used to scale photosynthesis from leaves to canopy (Rosati and DeJong, 2003; Rosati et al., 2004; Posada et al., 2009; Koyama and Kikuzawa, 2010). Our results are also consistent with the general observation that plant biomass production is linearly related to PAR absorbed by the canopy (Monteith, 1977). Thus, these biomass-absorbed PAR relationships should be functionally related to leaves concentrating their photosynthetic activity on the ascending portion of the photosynthetic light-response curves, where $\varepsilon$ is highest (Monteith, 1994).

In summary, to maximize net photosynthesis, plants had to simultaneously maximize PPFD absorption at the plant level and maximize $\varepsilon$ at the leaf level. Given the importance of net carbon gain for plant fitness (Givnish, 1988; Reich et al., 2003) we expect that plants have been under continuous selection pressure to attain these two conditions through adjustments in leaf angle, $A_{\text{max}}$ and LAI$_{\text{ind}}$. Optimization of $\varepsilon$ required adjustments at the level of individual leaves, which suggests that plants should have evolved a co-ordinating a mechanism between leaf angle and $A_{\text{max}}$ that exposes a leaf to $I_{\text{E,max}}$. The existence of such mechanism, however, remains hypothetical and will have to be demonstrated experimentally. We also found that imposing constraints on $A_{\text{max}}$ limited the range of PPFD environments where saplings could maximize their marginal returns on PPFD. Nevertheless, $A_{\text{max}}$ of $A.\ saccharum$ was relatively low compared with other species (Wright et al., 2004), suggesting that species with higher $A_{\text{max}}$ could attain $\varepsilon_{\text{max}}$ in a broader range of light environments. Lastly, our results support previous findings that have indicated that leaf $\varepsilon$ should be a key functional trait behind the linear relationship between canopy photosynthesis and absorbed PPFD (Rosati and DeJong, 2003; Posada et al., 2009). We note, however, that our

### Table 2. Summary of abbreviations used in the study

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>$I_{\text{PPFD}}$</td>
<td>Photosynthetic photon flux density ($\mu\text{mol m}^{-2}\text{s}^{-1}$)</td>
</tr>
<tr>
<td>$I_{\text{LAI}}$</td>
<td>PPFD incident on a leaf surface ($\mu\text{mol m}^{-2}\text{s}^{-1}$)</td>
</tr>
<tr>
<td>$I_{\text{H}}$</td>
<td>PPFD incident on a horizontal plane ($\mu\text{mol m}^{-2}\text{s}^{-1}$)</td>
</tr>
<tr>
<td>$A_{\text{CO}_2}$</td>
<td>Leaf net CO$_2$ assimilation ($\mu\text{mol m}^{-2}\text{s}^{-1}$)</td>
</tr>
<tr>
<td>$A_{\text{plant}}$</td>
<td>Plant net photosynthesis ($\mu\text{mol s}^{-1}$)</td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>Leaf maximum gross CO$_2$ assimilation ($\mu\text{mol m}^{-2}\text{s}^{-1}$)</td>
</tr>
<tr>
<td>$R_{\text{d}}$</td>
<td>Leaf dark respiration ($\mu\text{mol m}^{-2}\text{s}^{-1}$)</td>
</tr>
<tr>
<td>$\phi$</td>
<td>Apparent quantum yield (unitless)</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Convexity (unitless)</td>
</tr>
<tr>
<td>$\varepsilon$</td>
<td>Photosynthetic light-use efficiency (unitless)</td>
</tr>
<tr>
<td>$\varepsilon_{\text{max}}$</td>
<td>Maximum photosynthetic light-use efficiency (unitless)</td>
</tr>
<tr>
<td>$I_{\text{E,max}}$</td>
<td>$I$ at which $\varepsilon_{\text{max}}$ is attained ($\mu\text{mol m}^{-2}\text{s}^{-1}$)</td>
</tr>
<tr>
<td>$L_{\alpha}$</td>
<td>Leaf angle (°)</td>
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</table>
model was static (Anten and During, 2011) and mostly applicable to deciduous tree species that flush their leaves once in the season. Further studies should explore the extent to which these results will be influenced by changes in edaphic resource availability and nutrient resorption from senescent leaves (Anten, 2005; Hikosaka, 2003). It will also be important to evaluate the effect of covariation between leaf mass per area along PPFD gradients, interspecific interactions (e.g., Anten, 2005) and variability in spatial and temporal availability of PPFD on the optimal functional organization of plants at leaf and crown levels. These modelling exercises, combined with field experiments, will keep strengthening our understanding of the key functional traits that determine the functional organization of plants.

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LITERATURE CITED


