

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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• **Background and Aims** Plants are expected to maximize their net photosynthetic gains and efficiently use available resources, but the fundamental principles governing trade-offs in suites of traits related to resource-use optimization remain uncertain. This study investigated whether *Acer saccharum* (sugar maple) saplings could maximize their net photosynthetic gains through a combination of crown structure and foliar characteristics that let all leaves maximize their photosynthetic light-use efficiency (ϵ).

• **Methods** A functional–structural model, LIGNUM, was used to simulate individuals of different leaf area index (LAI_{ind}) together with a genetic algorithm to find distributions of leaf angle (L_A) and leaf photosynthetic capacity (A_{max}) that maximized net carbon gain at the whole-plant level. Saplings grown in either the open or in a forest gap were simulated with A_{max} either unconstrained or constrained to an upper value consistent with reported values for A_{max} in *A. saccharum*.

• **Key Results** It was found that total net photosynthetic gain was highest when whole-plant PPFD absorption and leaf ϵ were simultaneously maximized. Maximization of ϵ required simultaneous adjustments in L_A and A_{max} along gradients of PPFD in the plants. When A_{max} was constrained to a maximum, plants growing in the open maximized their PPFD absorption but not ϵ because PPFD incident on leaves was higher than the PPFD at which ϵ_{max} was attainable. Average leaf ϵ in constrained plants nonetheless improved with increasing LAI_{ind} because of an increase in self-shading.

• **Conclusions** It is concluded that there are selective pressures for plants to simultaneously maximize both PPFD absorption at the scale of the whole individual and ϵ at the scale of leaves, which requires a highly integrated response between L_A , A_{max} and LAI_{ind} . The results also suggest that to maximize ϵ plants have evolved mechanisms that co-ordinate the L_A and A_{max} of individual leaves with PPFD availability.

Key words: *Acer saccharum*, sugar maple, canopy architecture, functional–structural modelling, LIGNUM, scaling, photosynthetic light-use efficiency, leaf A_{max} , leaf angle, nitrogen, resource use, optimization, plant evolution, plasticity, acclimation.

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 (Tooming, 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 (Hirose and Bazzaz, 1998; 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 (ϵ_{\max} ; i.e. the ratio of net photosynthesis to PPFD) independently of their position in the canopy (Fig. 1; e.g. Tooming, 1970). Instantaneous ϵ_{\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, ϵ_{\max} occurs at low to medium PPFD and well below photosynthetic

saturation (A_{\max}) (Fig. 1). Note that the apparent quantum yield (ϕ) on a photosynthetic light-response curve is a different measure of efficiency because ϕ occurs on the initial section of the curve where net carbon gain is negative. In contrast, ϵ_{\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 ϵ_{\max} remains poorly studied.

To reach ϵ_{\max} at the whole-plant level, the PPFD incident on each leaf (I) should be equal to $I\epsilon_{\max}$ (cf. Fig. 1), which suggests ϵ_{\max} could be attained either by changing I incident on a leaf or by changing the value of $I\epsilon_{\max}$ through physiological adjustments (e.g. by increasing A_{\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 $I\epsilon_{\max}$. 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 ϵ_{\max} is about half way on the ascending portion of the curves (Fig. 1), this indirectly support the idea that plants are attaining ϵ_{\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_{\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_{\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 ϵ_{\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_{\max} and L_A of individual leaves within their crown as a function of PPFD availability, but no optimization criteria was imposed *a 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_{\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 reiteratively utilizes a few basic structural units as a framework to integrate both physiology and architecture. Accurate methods are used

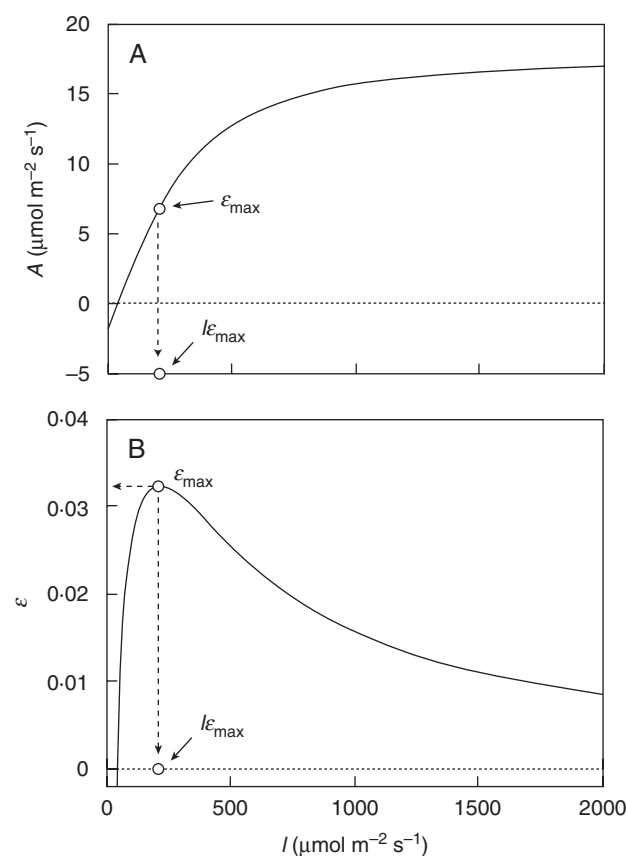


FIG. 1. (A) Representative photosynthetic PPFD-response curve of a leaf; I is PPFD incident on the leaf surface. The curve was obtained using the equation for a non rectangular hyperbola (Thornley, 1976) with parameter values $A_{\max} = 20.0 \mu\text{mol m}^{-2} \text{s}^{-1}$, $\phi = 0.05$, $\theta = 0.75$ and $R_d = 2.0 \mu\text{mol m}^{-2} \text{s}^{-1}$. (B) Corresponding photosynthetic light-use efficiency (ϵ) curve where $\epsilon = A/I$. Instantaneous ϵ_{\max} is the point of maximum ϵ while $I\epsilon_{\max}$ is the PPFD at which ϵ_{\max} was attained.

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

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

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.

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 cm² and 97 cm² 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

$$A_{\max} = \frac{aI_h}{b + I_h} \quad (1)$$

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

$$L_A = cI_h + d \quad (2)$$

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 , $\mu\text{mol m}^{-2} \text{s}^{-1}$) was related to A_{\max} using the simple relationship

$$R_d = 0.1 A_{\max} \quad (3)$$

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 ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) was subject to a photosynthetic light-response curve given by a non-rectangular equation (Thornley, 1976)

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

where I is instantaneous PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) incident on the adaxial surface of the leaf, ϕ is apparent quantum yield (unitless) and θ is the curvature parameter (unitless). We assumed that both ϕ and θ were constant and equal to 0.05 and 0.75, respectively. These constant values of ϕ and θ result in photosynthetic light-response curves with the same shape irrespective of the value of A_{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 curves 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_{max} within plant canopies (Gutschick and Wiegand, 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_{max} based on empirical parameters for *A. saccharum*, which allowed us to increase leaf size with decreasing A_{max} (assuming constant leaf mass). However, there was uncertainty in the intercepts of the LMA– A_{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_{plant} ; $\mu\text{mol s}^{-1}$) 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 ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is leaf net photosynthesis and S is leaf area (m^2).

Light environments

Optimal distributions of A_{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 $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ on a horizontal surface, corresponding to a daily (12 h) exposure of $21.6 \text{ mol m}^{-2} \text{d}^{-1}$. 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 $83.3 \mu\text{mol m}^{-2} \text{s}^{-1}$, which corresponded to a daily exposure of $3.6 \text{ mol m}^{-2} \text{d}^{-1}$. 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_{max} and L_A distributions along I_h gradient in the sapling canopies that maximized A_{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_{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_{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_{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_{max} to an upper value or letting it be unconstrained. Constrained A_{max} was set to a maximum value of $12.0 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is within the upper range of naturally occurring $A_{\text{max, net}}$ 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_{max} and leaf N_{area} in *A. saccharum* (Ellsworth and Reich, 1993;

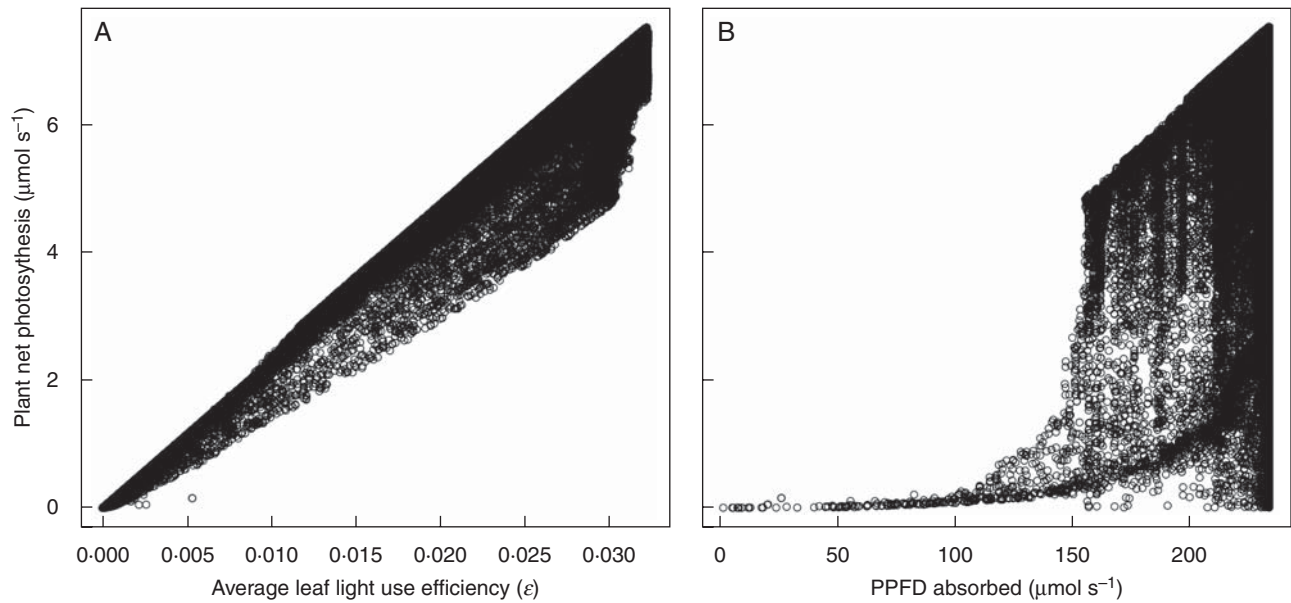


FIG. 2. (A) Net plant photosynthesis (A_{plant}) versus average photosynthetic PPFD-use efficiency (ϵ) and (B) net plant photosynthesis versus PPFD absorbed by the plant for a 3-year-old sapling growing in the open with an unconstrained A_{max} (OU condition). In these figures, each point represents an individual plant with a certain combinations of parameters a , b , c and d generated during the genetic algorithm search ($n = 165467$; see Materials and Methods).

Niinemets and Tenhunen, 1997), the two cases where A_{max} was unconstrained were equivalent to assuming that soil N availability relative to other resources was unlimited for a given leaf area and N_{area} could potentially take any value. Our constrained maximum leaf A_{max} was equivalent to limiting individual leaf N_{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 fix amount of N in the canopy (e.g. Field, 1983; Hirose and Werger, 1987).

Leaf photosynthetic PPFD-use efficiency (ϵ), the efficiency of CO_2 assimilation per unit PPFD, was calculated as

$$\epsilon = A/I \quad (6)$$

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

$$I\epsilon_{\text{max}} = \frac{1}{\frac{\phi}{A_{\text{max}}} \left[(2\theta - 1) - (2\theta R_d - A_{\text{max}}) \sqrt{\frac{\theta - 1}{R_d(\theta R_d - A_{\text{max}})}} \right]} \quad (7)$$

We calculated maximal ϵ (ϵ_{max}) as $A(I\epsilon_{\text{max}})/I\epsilon_{\text{max}}$ 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 ϵ 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_{max} and L_A along PPFD gradients in the plant (eqns 1 and 2). The genetic algorithm generated many saplings in which average ϵ or PPFD absorption were maximal but with A_{plant} below the maximum. Only when both ϵ and PPFD absorption were maximized did the plants attain maximum A_{plant} .

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

Not surprisingly, plant PPFD absorption increased with LAI_{ind} and was higher in the open than in a gap (Fig. 4A). Interestingly, however, and, in contrast, with average leaf ϵ , there were no marked differences in PPFD absorption when comparing OC and OU plants. This suggests that the

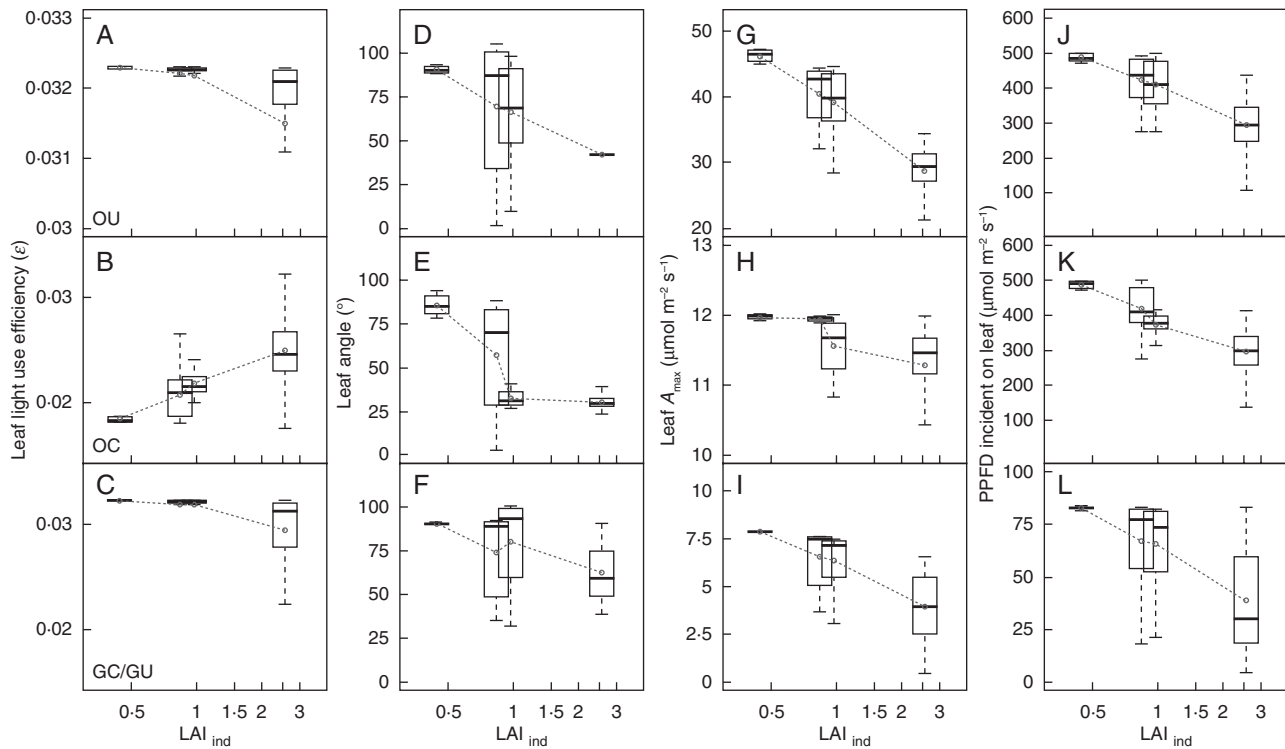


FIG. 3. (A–C) Box plots showing the distribution of leaf photosynthetic light-use efficiency (ϵ) as a function of plant leaf area index (LAI_{ind}). All upper panels correspond to plants in the open with unconstrained A_{max} (OU), middle panels correspond to plants in the open with constrained maximum A_{max} (OC), and lower panels to plants in a gap with constrained A_{max} (GC) and unconstrained A_{max} (GU); since there were no differences between GC and GU plants, only GC individuals were plotted in the bottom panels. (D–F) Distributions of leaf angle ($^{\circ}$; where 90° corresponds to a horizontal leaf) as a function of LAI_{ind} for OU (D), OC (E) and GC/GU plants (F). (G–I) Box plots of leaf A_{max} as a function of LAI_{ind} for OU (G), OC (H) and GC/GU plants (I). (J–L) Box plots of PPFD incident on individual leaves as a function of LAI_{ind} for OU (J), OC (K) and GC/GU plants (L). The dashed lines connect the means of each variable. The horizontal line in each box plot correspond to the median while the boxes are the upper and lower quartile (50 % of the data) and the whiskers encompass the data with values that extend to 1.5 times the interquartile range.

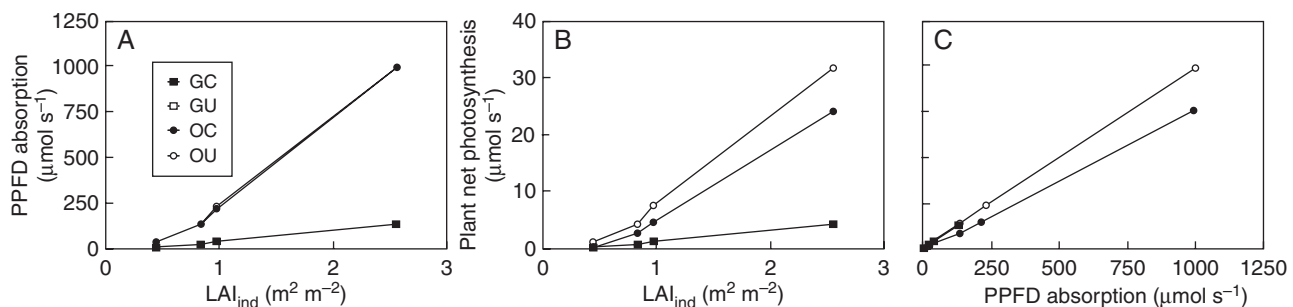


FIG. 4. (A) Relationship between PPFD absorbed by the plants and LAI_{ind} , (B) between plant net photosynthesis and LAI_{ind} and (C) between plant net photosynthesis and PPFD absorption. In each plot, the relationships for plants in the open with unconstrained (OU) and constrained A_{max} (OC) and for plants in gaps with constrained (GC) and unconstrained A_{max} (GU) are shown. The results for GC and GU plants were identical and only the points for GC are visible.

optimal solution prioritized the maximization of PPFD absorption over the maximization of leaf ϵ when A_{max} was constrained. There was no difference between PPFD absorption in GC and GU saplings. Values of A_{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 ϵ . 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 ϵ_{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_{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_{\max} . While plant PPFD absorption was determined by L_A , maximization of ε was more complex and required co-ordinated adjustments in both A_{\max} and L_A .

In order to attain ε_{\max} , I (PPFD incident on a leaf) should be equal to $I_{\varepsilon_{\max}}$ (Fig. 1), a condition which could be satisfied in two ways. Since leaf A_{\max} and $I_{\varepsilon_{\max}}$ were linearly related, a leaf could change its $I_{\varepsilon_{\max}}$ by changing A_{\max} (Fig. 5A) or a leaf could modulate I through changes in its angle of inclination to attain $I_{\varepsilon_{\max}}$ (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 ε is modest under cloudy conditions, but can be significant in gaps or under clear sunny skies.

The distributions of L_A and A_{\max} (Fig. 3D–I) were a consequence of the simultaneous maximization of plant PPFD absorption and ε . Seedlings had leaves with mostly horizontal orientation (90°), but as LAI_{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_{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 horizontal than plants in the open, even when LAI_{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_{\max} of OU seedlings was $46.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ which illustrated how A_{\max} and L_A were ‘co-ordinated’ to maximize ε (Fig. 3G). If PPFD incident on a leaf would be $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ (which was the PPFD incident on a horizontal plane in the open environments) then leaf A_{\max} had to be equal to $47.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ to have $I_{\varepsilon_{\max}}$ at $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 5A). The OU seedlings had a maximum A_{\max} of $47.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ and mostly horizontal leaves, meaning that these plants basically attained ε_{\max} by increasing A_{\max} and $I_{\varepsilon_{\max}}$ to very high values (Fig. 3D, G). Similarly, the greatest A_{\max} of GC/GU seedlings was $7.9 \mu\text{mol m}^{-2} \text{s}^{-1}$, which corresponded to an $I_{\varepsilon_{\max}}$ of $83.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ – exactly equal to the PPFD of $83.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ incident on a horizontal plane in the gap. The A_{\max} of OC seedling attained the maximum of $12.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ 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 ε well below ε_{\max} .

Role of self-shading and LAI_{ind} in the optimization

As LAI_{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 $296 \mu\text{mol m}^{-2} \text{s}^{-1}$ in OU plants and from 487 to 295 in $\mu\text{mol m}^{-2} \text{s}^{-1}$ 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 $372 \mu\text{mol m}^{-2} \text{s}^{-1}$, 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 $39 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3K). This general increase in self-shading helped explain the decrease in A_{\max} with LAI_{ind} . In OU plants, average A_{\max} declined from 46.3 to $28.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ with increasing LAI_{ind} , and in GC/GU plants A_{\max} declined from 7.9 to $4.0 \mu\text{mol m}^{-2} \text{s}^{-1}$

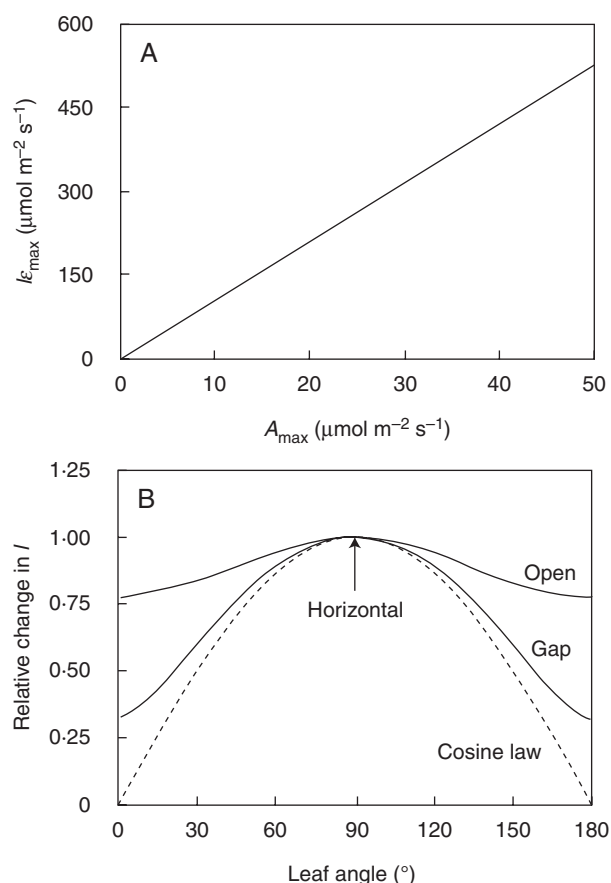


FIG. 5. (A) Relationship between PPFD at which a leaf attains maximum photosynthetic light-use efficiency ($I_{\varepsilon_{\max}}$; eqn 7) and leaf A_{\max} . (B) Relative change in PPFD incident on a leaf (I) as a function of leaf angle in the open and gap environments simulated in this study. For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

(Fig. 3G–I). Since A_{\max} is linearly related to $I_{\epsilon_{\max}}$, the decline in A_{\max} can be attributed to the decrease in average I , i.e. leaves exposed to a lower PPFD attain ϵ_{\max} with a lower A_{\max} than leaves exposed to a higher PPFD. Average A_{\max} of OC saplings also declined slightly (12.0 to 11.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$), reflecting the increase in the proportion of leaves that were exposed to low I with increasing LAI_{ind} .

DISCUSSION

Our results showed that whole-plant net photosynthesis was maximal when average leaf ϵ 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). Understorey 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 ϵ remains poorly studied. Theoretical analyses suggest that plant photosynthesis is maximized if all leaves in a plant are exposed to their $I_{\epsilon_{\max}}$ (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 ϵ is highest. Our results further support this prediction, showing that there should be selection pressure for both maximizing ϵ and for leaf acclimatory responses to PPFD availability that lead to PPFD incident on a leaf coincident with $I_{\epsilon_{\max}}$.

We found, however, that there are limits to maximizing ϵ because of trade-offs associated with a decrease in PPFD absorption at the leaf level. This occurred in individuals with a constrained A_{\max} growing in the open, which had an average ϵ well below ϵ_{\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_{\max}). This hierarchical response suggests that the benefits of maximizing absorption were higher than the costs of a decrease in average leaf ϵ ; plants could have improved ϵ 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 ϵ_{\max} , indicating that optimization of ϵ was possible in environments with lower PPFD availability. Thus, the prediction that

plants should maximize ϵ was supported in our study, although when A_{\max} was constrained to an upper value and PPFD availability was high optimization of ϵ was not possible.

In addition to showing that plants are under selection pressure to simultaneously maximize both ϵ and PPFD absorption, our simulations illustrated that maximization of net photosynthesis required strongly integrated adjustments between the angle and A_{\max} of leaves, and LAI_{ind} . Maximization of plant PPFD absorption was basically controlled in concert by LAI_{ind} and the distribution of leaf angles because sapling branch architecture and leaf size could not change. Attaining ϵ_{\max} involved co-ordinated leaf-level adjustments between leaf angle and A_{\max} , but also plant-level adjustments in the PPFD gradients within the crowns related to leaf angle and LAI_{ind} . LAI_{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_{\max} . When saplings were small, maximizing PPFD absorption was attained by placing leaves horizontally and matching PPFD incident on leaves with $I_{\epsilon_{\max}}$, which, in the case of open-unconstrained plants, required a very high A_{\max} . With increasing LAI_{ind} , self-shading increased, leaves became more inclined and average A_{\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_{\max} , LAI and PPFD gradients in the canopy (Monsi and Saeki, 1953; Terashima and Hikosaka, 1995; Kull, 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 ϵ at the leaf level.

An important aspect of our study was to evaluate how constraining maximum A_{\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_{\max} of 12.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$, the PPFD at which photosynthetic efficiency was maximal (i.e. $I_{\epsilon_{\max}}$) was only 126.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$; leaves will have lower efficiency if PPFD incident on their surface is above this value. There were two noteworthy effects of constraining A_{\max} in the simulations. First, there was a decrease in average ϵ in the open environment where the PPFD on a horizontal plane of 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was well above the maximum $I_{\epsilon_{\max}}$. An increase in leaf inclination in these constrained individuals could have brought the PPFD incident on leaves closer to $I_{\epsilon_{\max}}$, 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_{\max} was that, despite limitations in $I_{\epsilon_{\max}}$, average ϵ improved considerably with LAI_{ind} . Self-shading increased with increasing LAI_{ind} ; hence the constraint on A_{\max} was gradually released because more leaves were exposed to I values closer to $I_{\epsilon_{\max}}$. 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 ϵ_{\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. ϵ).

Despite the consequences of a constrained A_{\max} on ε , our results appear consistent with the evolution of *A. saccharum* as a shade-tolerant species and suggest that optimization of ε should take place during most life stages in *A. saccharum*. In gap conditions, seedlings were not influenced by constraints on A_{\max} because the PPFD incident above the plants was $83.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ and the maximum A_{\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_{\max} of $12.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ reported for *A. saccharum*. In forests where *A. saccharum* grows, PPFD in gaps varies between approx. 5.6 and $6.5 \text{ mol m}^{-2} \text{d}^{-1}$ 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 understorey conditions with lower PPFD availability, *A. saccharum* saplings should be able to maximize leaf ε . 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 ε_{\max} in all leaves. Nonetheless, since the LAI_{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 ε in leaves under high PPFD conditions because most leaves in the trees will be exposed to a lower PPFD due to self-shading. Thus, if 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_{ind} , then maximization of ε should occur during most life stages.

Another consideration is that optimization of ε 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 ε 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 (minutes/hours) changes in instantaneous PPFD and will only attain $I\varepsilon_{\max}$ during a fraction of the day. Here, average instantaneous leaf ε estimates were close to the maximum possible value ($\varepsilon_{\max} = 0.032$) except for open-constrained plants which had values that varied between 0.018 and 0.025 (Fig. 2A). In contrast, field measurements of leaf ε measured over a time scale of days/weeks vary between approx. 0.07 and 0.026 depending on light conditions (e.g. cloudy/sunny) and the time scale (day/weeks) over which ε is integrated (Rosati and DeJong, 2003; Rosati et al., 2004; Posada et al., 2009; Koyama and Kikuzawa, 2010). These results suggest that in natural conditions leaves should acclimate so that PPFD incident on their surface remains as close as possible to $I\varepsilon_{\max}$, but that deviations from $I\varepsilon_{\max}$ are unavoidable during parts of the day due to rapid changes in instantaneous PPFD.

An important outcome of the maximization of PPFD absorption and ε was the linear relationship observed between plant net photosynthesis and PPFD absorbed by the saplings (Fig 5). In all but open-constrained plants, leaf ε 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 photosynthate 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 ε 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 ε is highest (Monteith, 1994).

In summary, to maximize net photosynthesis, plants had to simultaneously maximize PPFD absorption at the plant level and maximize ε 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_{\max} and LAI_{ind} . Optimization of ε 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_{\max} that exposes a leaf to $I\varepsilon_{\max}$. The existence of such mechanism, however, remains hypothetical and will have to be demonstrated experimentally. We also found that imposing constraints on A_{\max} limited the range of PPFD environments where saplings could maximize their marginal returns on PPFD. Nevertheless, A_{\max} of *A. saccharum* was relatively low compared with other species (Wright et al., 2004), suggesting that species with higher A_{\max} could attain ε_{\max} in a broader range of light environments. Lastly, our results support previous findings that have indicated that leaf ε 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

Abbreviation	Description
PPFD	Photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
I	PPFD incident on a leaf surface ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
I_h	PPFD incident on a horizontal plane ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
A	Leaf net CO_2 assimilation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
A_{plant}	Plant net photosynthesis ($\mu\text{mol s}^{-1}$)
A_{\max}	Leaf maximum gross CO_2 assimilation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
R_d	Leaf dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
ϕ	Apparent quantum yield (unitless)
θ	Convexity (unitless)
ε	Photosynthetic light-use efficiency (unitless)
ε_{\max}	Maximum photosynthetic light-use efficiency (unitless)
$I\varepsilon_{\max}$	I at which ε_{\max} is attained ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
L_A	Leaf angle ($^\circ$)

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 (Franklin and Ågren, 2002; 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 experimentations, will keep strengthening our understanding of the key functional traits that determine the functional organization of plants.

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