Evolutionarily Stable Leaf Area Production in Plant Populations

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Using an analytical model, it was shown that for a given amount of nitrogen in the canopy of a stand (NT), there exists an evolutionarily stable leaf area index (ES-LAI), and therefore an evolutionarily stable average leaf nitrogen content (nESav; nESav = NT/ES − LAI), at which no individual plant in the stand can increase its photosynthesis by changing its leaf area. It was also shown that this ES-LAI is always greater than the optimal LAI that maximizes photosynthesis per unit NT of the stand. This illustrates that the canopy structure that maximizes photosynthesis of a population is not the same as the canopy structure that maximizes photosynthesis of individuals within a population. It was further derived that the ES-LAI at given NT increases with the ratio between the light-saturated photosynthesis and the N content per unit leaf area (leaf-PPNUE) and that it decreases with the canopy extinction coefficient for light (KL), the light availability and the apparent quantum yield (Φ). These hypotheses were tested by comparing calculated ES-LAI and nESav values to actual LAIs and leaf N contents measured for stands of a large variety of herbaceous plants. There was a close correspondence between the calculated and measured values. As predicted by the model, plants with high leaf-PPNUEs produced more leaf area per unit nitrogen than those with low leaf-PPNUEs while plants with horizontal leaves, forming stands with higher KL values, produced less leaf area than those with more vertically inclined leaves. These results suggest that maximization of individual plant photosynthesis per unit of nitrogen plays an important role in determining leaf area production of plants and the resulting canopy structure of stands of vegetation. They further suggest this optimization to be a mechanism by which leaf traits such as leaf-PPNUE and leaf inclination angle are causally related to structural characteristics of the population, i.e. the leaf area index of the stand. © 2002 Elsevier Science Ltd. All rights reserved.

Introduction

Photosynthesis provides the structural substrates for growth and reproduction that are important determinants of plant fitness. In view of this relationship, many authors (e.g. Monsi & Saeki, 1953; Saeki, 1960; Hirose & Werger, 1987; Anten et al., 1995a,b; Anten & Hirose, 2001) have argued that maximization of photosynthesis has been an important driving force determining the evolution of leaf and canopy characteristics in plants. The photosynthetic rate of a plant, in turn, is largely determined by its total leaf area (Monsi & Saeki, 1953; Saeki, 1960).
Plants often grow closely together in stands of vegetation. Such stands typically form dense canopies with large amounts of leaf area per unit ground area (the latter is generally denoted as the leaf area index, LAI) and as a result there is much mutual shading between plants. It is important to note that an LAI can be defined both for stands of vegetation and for individual plants. A number of studies (e.g. Saeki, 1960; Oikawa, 1987; Schieving et al., 1992; Anten et al., 1995b, 1998; Goudriaan, 1995; Schieving & Poorter, 1999) have addressed the problem of whether there exists an optimal LAI that maximizes canopy photosynthesis and how this optimum is determined. Saeki (1960) derived that the LAI of a canopy is optimal when the lowest most shaded leaves in the canopy receive an amount of light that is equal to their light compensation point. Light intensity (photon flux density, PFD) decreases with increasing cumulative LAI above a given point in the canopy (Monsi & Saeki, 1953). Consequently, increasing the LAI beyond the optimum implies that the incident PFD on the lowest leaf will become lower than the light compensation point and canopy photosynthesis is reduced, because the lowest leaf will have negative carbon gain.

The analysis of Saeki (1960) assumes that there are no constraints on leaf area production other than light availability. However, many factors may limit leaf area production, one of the most important of these being nitrogen availability (Lambers et al., 1990). On a worldwide scale, nitrogen is one of the mineral nutrients most limiting to plant growth (Lee et al., 1983), while its acquisition involves a considerable part of a plant’s carbon budget (Lambers et al., 1990). Plants are, therefore, restricted in the amount of nitrogen that they can allocate to their leaves and there are generally very strong positive correlations between the total leaf area of stands of vegetation and the availability of nitrogen in the ecosystem (Lambers et al., 1990; Hirose et al., 1997).

To understand how nitrogen might be important in determining the relationship between leaf area and photosynthesis it is essential to know that a large proportion of the nitrogen in leaves is incorporated into proteins associated with the photosynthetic process and that there is, therefore, generally a strong positive correlation between photosynthesis and nitrogen content per unit leaf area (Natr, 1975; Field & Mooney, 1986) and this relationship can be expressed both on an area and on a mass basis. Assume that the total amount of leaf nitrogen in a canopy (NT) is fixed. A greater amount of leaf area will then not only enable plants to intercept more light, but will also imply that leaf N contents per unit area (nL) and associated rates of leaf photosynthesis are lower. Theoretical studies (Anten et al., 1995b; Goudriaan, 1995) have consequently shown that there exists an optimal leaf area index (optimal LAI) and thus an optimal average nL (nLopt; nLopt = NT/optimal LAI), at which canopy photosynthesis for a given NT (i.e. canopy photosynthetic nitrogen-use efficiency, canopy-PNUE) is maximized. Using an analytical model, Anten et al. (1995b) analysed the question whether optimal LAIs and leaf N contents differ between plants with different leaf or canopy characteristics. For example, they hypothesized that the optimal LAI increases with increasing potential leaf photosynthetic nitrogen-use efficiency (leaf-PPNUE; i.e. light-saturated leaf photosynthesis per unit nL) and that it should be lower for plants with horizontally projected leaves forming stands with high extinction coefficients for light than for plants with vertical leaves. Both of these predicted trends were confirmed with experimental data (Anten et al., 1995b, 1998). Surprisingly, however, all studies comparing optimal LAIs for maximization of canopy-PNUE to LAIs measured for actual stands of vegetation have found that the measured LAIs were considerably (30–60%) greater than the optimal values while canopy photosynthesis for actual LAIs were 2–12% lower than the predicted values (Gutschik & Wiegel, 1988; Werger & Hirose, 1991; Schieving et al., 1992; Anten et al., 1995b, 1998; Hirose et al., 1997).

Why are real leaf area indices of stands of vegetation larger and the associated N contents lower than the optimal values for maximization of carbon gain? So far the optimal LAI has consistently been defined as the LAI that maximizes canopy photosynthesis of a stand of vegetation. Stands of vegetation consist of various plants and this definition therefore
implicitly assumes that the optimal characteristics that maximize fitness of the individuals in a stand are manifest as optimal properties at the stand level. This, in turn, is subject to the condition that the optimum for an individual is not affected by the characteristics of its neighbors (i.e. simple optimization, Parker & Maynard Smith, 1990). It is unlikely that this holds true for leaf area production of individuals in stands because the leaf area of an individual affects the light climate and thus the photosynthetic performance of its neighbors (Werger & Hirose, 1991; Schieving, 1998). It is, therefore, more appropriate to analyse leaf areas in terms of competitive optimization or evolutionarily stable strategies (ESS) (Schieving & Poorter, 1999). By means of sensitivity analysis, Anten & Hirose (2001) showed that in stands with optimal LAI, an increase in leaf area of individuals increased their photosynthesis, which indicates that the optimal LAI was not evolutionarily stable. Moreover, it indicated that a possible evolutionarily stable LAI (ES-LAI) would be greater than the optimal LAI.

In this paper I analyse whether (1) for a given amount of nitrogen in a stand of vegetation \( N_T \), there exists an ES-LAI at which no individual plant in the stand can increase its photosynthesis by changing its leaf area, (2) the ES-LAI is a better predictor of actual LAIs than the optimal LAI that maximizes whole-stand canopy-PNUE and (3) the relationship between the ES-LAI and a number of leaf and canopy characteristics of plants. To this end, I developed an analytical model for photosynthesis of individual plants as a function of their leaf area. This model was used to analyse both the ES- and optimal LAI of stands of vegetation. A more elaborate and realistic numerical model was then developed to determine ES-LAIs that could be compared to actually measured values.

**Analytical Model**

**PLANT PHOTOSYNTHESIS**

Consider an area, \( A \), which is the total horizontal area in which an individual has leaves (Table 1). The individual has a total leaf area \( L_i \), which is equal to the product of its amount of leaf area per unit ground area, i.e. the leaf area index \( \text{LAI}_i \) and \( A \):

\[
L_i = A \text{LAI}_i
\]

with \( \text{LAI}_i \) being constant throughout \( A \). For simplicity, I assume that \( A \) equals 1 m\(^2\) so that \( L_i = \text{LAI}_i \), i.e. leaf area and photosynthesis are expressed on a ground area basis. Apart from the individual plant, there are \( n \) neighbor plants that have a fraction \( x \) of their leaf area within \( A \) such that the total LAI of neighbors within \( A \) equals \( nxL_0 \), with \( L_0 \) the LAI of an individual neighbor plant. The total LAI within \( A \) \( (L_T) \) is thus equal to

\[
L_T = L_i + nxL_0.
\]

Stands are considered to consist of identical individuals with the same leaf area such that \( L_i = L_0 \). The leaf area of the individual and that of its neighbors is assumed to be uniformly distributed, both horizontally and vertically. The ratio of the individual’s leaf area to the total leaf area \( (\beta_i) \) is therefore also constant

\[
\beta_i = \frac{L_i}{L_T} = \frac{L_i}{(L_i + nxL_0)}.
\]

The value of \( \beta_i \) denotes the degree to which canopies of plants are mixed. \( \beta_i = 1 \) means that canopies of plants are not mixed and that the light climate of a plant is only affected by its own leaves. Very low \( \beta_i \) values, on the other hand, indicate that the canopies of plants are strongly mixed and that the light climate of a plant is strongly determined by the leaf area of its neighbors.

The photon flux density (PFD) incident on a leaf of an individual at a certain depth in the canopy \( (I_L) \) is given by

\[
I_{L,i} = I_0K_L\exp(-K_L(l_i + nxL_0))
\]

\[
= I_0K_L\exp(-K_Ll_i/\beta_i),
\]

where \( I_0 \) is the PFD at the top of the canopy, \( K_L \) the canopy extinction coefficient of the stand, and \( l_i \) and \( L_0 \) the cumulative leaf area indices of the individual and its neighbors above that depth in the canopy (Saeki, 1960). Note that \( l_i + nxL_0 \) is equivalent to the total cumulative LAI \( (l_T, l_T = l_i + nxL_0) \) and is therefore also equal to \( l_i/\beta_i \) [see eqn (3)].
Following Thornley (1976) we use a rectangular hyperbola to describe the relationship between net leaf photosynthesis \( p_{L,i} \) and \( I_{L,i} \):

\[
p_{L,i} = p_{\text{max},i} \Phi I_{L,i} / \left( p_{\text{max},i} + \Phi I_{L,i} \right) - r_{d,i} \tag{5}
\]

with \( p_{\text{max},i} \) the gross photosynthesis of a leaf when photosynthesis is completely light saturated, \( r_{d,i} \) dark respiration and \( \Phi I_{L,i} \)—the product of the apparent quantum yield (\( \Phi \)) and incident PFD—the gross photosynthesis of a leaf at infinitely low PFD when photosynthesis is completely light limited. \( p_{\text{max},i} \) and \( r_{d,i} \) are assumed to be linearly increasing functions of the leaf nitrogen content per unit area \( (n_{L,i}) \):

\[
p_{\text{max},i} = a_p (n_{L,i} - n_b), \tag{6a}
\]

\[
r_{d,i} = a_r (n_{L,i} - n_b) + b_r, \tag{6b}
\]
where $a_p$ and $n_b$ are the slope and $x$-intercept of the $p_{\text{max}} - n_L$ relationship, $a_r$ the slope of the $r_d - n_L$ relationship and $b_r$ the $r_d$ for a leaf with $n_L$ equal to $n_b$ (Hirose & Werger, 1987; Schieving et al., 1992; Anten et al., 1995a, b). The value of $\Phi$ is assumed to be constant (Schieving et al., 1992; Anten et al., 1995a, b).

To find an analytical expression for whole plant photosynthesis ($P_i$), I assume that $n_i$ is optimally distributed within the canopy such that canopy photosynthesis for given $L_i$ and total canopy N ($N_i$) is maximized. Anten et al., (1995b) showed that under this assumption and with leaf photosynthesis given by eqn (5), the following rectangular hyperbolic expression can be found for $P_i$:

$$P_i = \frac{P_{\text{max},i}P_{\text{lim},i}}{(P_{\text{max},i} + P_{\text{lim},i})} - R_{d,i},$$

(7)

where $P_{\text{max},i}$ is the photosynthetic rate of a plant when all its leaves are light saturated, $P_{\text{lim},i}$ its photosynthetic rate when all leaves are completely light limited and $R_{d,i}$ whole plant dark respiration. Expressions for $P_{\text{max},i}, P_{\text{lim},i}$ and $R_{d,i}$ can be found by integration of $p_{\text{max},i}$ [eqn (6a)], $\Phi L_i$ with $I_{L,i}$ [given by eqn (4)] and $r_d$ [eqn (6b)], respectively, over canopy depth from 0 to $L_i$:

$$P_{\text{max},i} = a_p(N_i - n_bL_i),$$

(8a)

$$P_{\text{lim},i} = \beta_i \Phi I_0[1 - \exp(-K_i(L_i + n_zL_0))],$$

(8b)

$$R_{d,i} = a_r(N_i - n_bL_i) + b_rL_i.$$  

(8c)

Note that $P_{\text{lim},i}$ of an individual is the product of the total light intercepted by the canopy, the apparent quantum yield and its fractional contribution to the total LAI of the canopy ($\beta_i$).

**Evolutionarily Stable Leaf Area**

The theory of evolutionarily stable strategies assumes that no change in a characteristic can increase an individual’s fitness over that of other individuals with the same strategy (Maynard Smith, 1974; Givnish, 1982; Sakai, 1991). If whole plant carbon gain ($P_i$) is assumed to be a measure for a plant’s fitness, the total LAI of the stand will be evolutionarily stable if no individual can increase its photosynthesis by changing its leaf area:

$$P_i(L_i, L_i^*) < P_i(L_i, L_i^*) \neq L_i^*.$$  

(9a)

This is equivalent to the condition that the partial derivative of $P_i$ to its leaf area ($L_i$) equals zero:

$$\frac{\partial P_i(L_i, L_i^*)}{\partial L_i} \bigg|_{L_i=L_i^*} = 0,$$  

(9b)

where $L_i^*$ would then be equal to the evolutionarily stable leaf area of an individual plant. The total ES-LAI will be equal to

$$L_i^* = L_i^*/\beta_i.$$  

(9c)

As noted above, I assume that the total amount of nitrogen in the canopy of a plant ($N_i$) is constant and that leaf N contents ($n_b$) cannot be lower than the minimal $n_L$ which is assumed to be equal to the $x$-intercept of the $p_{\text{max}} - n_L$ relationship ($n_b$, Charles-Edwards et al., 1987; Anten et al., 1995a). Thus, the constraint on $L_i^*$ is

$$0 \leq L_i^* \leq N_i/n_b.$$  

(9d)

I further assume that by increasing its leaf area, an individual does not increase the area ($A$) in which it has its leaves but only its LAI and the associated ratio of its leaf area to the total leaf area within $A$ ($\beta_i$). For plant photosynthesis given by eqn (7), eqn (9b) can be solved following Anten et al. (1995b):

$$\frac{\delta P_i}{\delta L_i} = \left[ \frac{(\delta P_{\text{max},i}/\delta L_i)P_{\text{lim},i}^2 + (\delta P_{\text{lim},i}/\delta L_i)P_{\text{max},i}^2}{(P_{\text{max},i} + P_{\text{lim},i})^2} - \frac{\delta R_{d,i}}{\delta L_i} \right] = 0.$$  

(10)

The expressions for $\delta P_{\text{max},i}/\delta L_i$ and $\delta R_{d,i}/\delta L_i$ can be found from eqns (8a) and (8c):

$$\frac{\delta P_{\text{max},i}}{\delta L_i} = -a_p n_b < 0,$$  

(11a)

$$\frac{\delta R_{d,i}}{\delta L_i} = -a_r n_b + b_r \approx 0.$$  

(11b)
\( \frac{\delta P_{\text{max},i}}{\delta L_i} \) is smaller than zero. This is because with increasing leaf area more leaves require a minimum amount of non-photosynthetic nitrogen \((n_h)\) and relatively less nitrogen can therefore be invested in photosynthetic enzymes. The term \((-a_h n_h + b_h)\) in the expression for \(\delta R_{d,i}/\delta L_i\) [eqn (11b)] is equivalent to the x-intercept of the relationship between leaf dark respiration and leaf N content [eqn (6b)] that is generally found to be close to zero (Hirose & Werger, 1987; Schieving et al., 1992; Anten et al., 1995a,b). In this analysis \(\delta R_{d,i}/\delta L_i\) is therefore assumed to be zero. The partial derivative of completely light-limited plant photosynthesis \((P_{\text{lim},i})\) to \(L_i\) can be found from eqn (8b):

\[
\frac{\delta P_{\text{lim},i}}{\delta L_i} = \Phi I_0 \left[ \frac{(1 - \beta_i)}{\left(L_i^* + n_i L_i^*\right)} \right] \left(1 - \exp(-K_L(L_i^* + n_i L_i^*))\right) + K_L \exp(-K_L(L_i^* + n_i L_i^*)) \right] > 0. \quad (11c)
\]

\(L_0\) has been replaced by \(L_i^*\) since in the ES condition \(L_0 = L_i^*\). From eqn (11c) it can be seen that when an individual in a stand increases its leaf area this will not only increase the total light capture and associated light-limited photosynthesis of the stand (right-hand expression between the brackets) but also the fraction of the total available light that is captured by the individual (left-hand expression between the brackets).

The denominator in eqn (10) \([(P_{\text{lim},i} + P_{\text{max},i})^2]\) is always greater than zero so that the evolutionarily stable leaf area can be found by solving

\[
\frac{\delta P_{\text{lim},i} P_{\text{max},i}^2}{\delta L_i} = -\frac{\delta P_{\text{max},i} P_{\text{lim},i}^2}{\delta L_i}. \quad (12a)
\]

Dividing both sides of this equation by \(P_{\text{max},i} P_{\text{lim},i}\) yields

\[
\frac{\delta P_{\text{lim},i}}{\delta L_i} / P_{\text{lim},i} = -\frac{\delta P_{\text{max},i}}{\delta L_i} / P_{\text{lim},i}. \quad (12b)
\]

For simplicity, we denote the expressions on the left- and right-hand side of the equal sign in eqn (12b) \(V_1\) and \(V_2\), respectively. Expressions for \(V_1\) and \(V_2\) can be found by substituting for \(P_{\text{max},i} P_{\text{lim},i}\), \(\delta P_{\text{max},i}/\delta L_i\), and \(\delta P_{\text{lim},i}/\delta L_i\) from eqns (8a), (8b), (11a) and (11c), respectively:

\[
V_1 = \frac{a_h (N_i - n_h L_i^*)}{[1 - \exp(-K_L(L_i^* + n_i L_i^*))]} \times \left[ \frac{(1 - \beta_i)}{(L_i^* + n_i L_i^*)} \right] \left(1 - \exp(-K_L(L_i^* + n_i L_i^*))\right) + \frac{1}{\beta_i} K_L \exp(-K_L(L_i^* + n_i L_i^*)) \right], \quad (13a)
\]

\[
V_2 = n_h \beta_i \Phi I_0 (1 - \exp(-K_L(L_i^* + n_i L_i^*)) / (N_i - n_h L_i^*). \quad (13b)
\]

From eqn (13a) and (13b) the limits of \(V_1\) and \(V_2\) [i.e. with the constraint imposed by eqn (9d)] can be found as

\[
\lim_{V_1} = \infty \quad \lim_{V_2} = 0 \quad \text{if } L_i^* < L_i^* \quad \lim_{V_1} = 0 \quad \lim_{V_2} = \infty \quad \text{if } L_i^* > N_i / n_h. \quad (14)
\]

This shows that for some value of \(L_i^*(0 < L_i^* < N_i / n_h)\), \(V_1\) equals \(V_2\), that eqn (12b) can be solved and that an evolutionarily stable leaf area therefore exists (see Fig. 1).

**RELATIONSHIP BETWEEN EVOLUTIONARILY STABLE LAI AND PLANT AND ENVIRONMENTAL CHARACTERISTICS**

Plant photosynthesis \((P_i)\) is a smooth concave function of its leaf area \(L_i\) \((\delta^2 P_i/\delta L_i^2 < 0\) for all values of \(L_i\)). It, therefore, holds that if \(\delta P_i / \delta L_i > 0\), then \(L_i\) is smaller than the optimal value \((L_i^*)\) and if \(\delta P_i / \delta L_i < 0\), it will be larger. From eqns. (12)–(14) it can be thus derived that

\[
V_1 = V_2 \Rightarrow \delta P_i / \delta L_i = 0 \Rightarrow L_i = L_i^*, \quad (15a)
\]

\[
V_1 > V_2 \Rightarrow \delta P_i / \delta L_i > 0 \Rightarrow L_i < L_i^* \Rightarrow L_i^*, \quad (15b)
\]

\[
V_1 < V_2 \Rightarrow \delta P_i / \delta L_i < 0 \Rightarrow L_i > L_i^* \Rightarrow L_i^*. \quad (15c)
\]
Assume the situation in which \( L_t = L_t^* \) [\( V_1 = V_2; \text{eqn (15a)} \)]. If \( V_1 \) is a positive function and \( V_2 \) a negative function of some parameter \( z \), an increase in \( z \) (keeping all other parameters including \( L_t \) constant) will create the situation described by eqn (15b), the evolutionarily stable leaf area \( (L_t^*) \) will have increased (i.e. it holds that \( L_i < L_t^* \)) and \( L_t^* \) is therefore a positive function of \( z \) [see Fig. 1(B)]. Conversely, if \( V_1 \) is a negative function of \( z \) and \( V_2 \) is a positive function, an increase in \( z \) will create the situation described by eqn (15c). \( L_t^* \) will have decreased and is therefore a negative function of \( z \) [Fig. 1(C)]. From eqn (13) it can be seen directly that \( V_1 \) increases with \( a_p \) and \( N_t \) and decreases with \( \beta_i \) and \( n_b \). The relationship between \( V_1 \) and \( K_L \) is less apparent. However, solving \( \delta V_1 / \delta K_L \) yields

\[
\delta V_1 = \frac{a_p (1/\beta_i) (N_t - n_b L_t^*) \exp(-K_L L_t^*)}{(1 - \exp(-K_L L_t^*))^2}
\]

showing that \( V_1 \) is a negative function of \( K_L \). It can also be seen directly from eqn (13) that \( V_2 \) is an increasing function of \( n_b \), \( \beta_i \), \( I_0 \), \( K_L \) and \( \Phi \) and a negative function of \( N_t \). It can thus be concluded that the ES-LAI \( (L_t^*) \) is a positive function of the total canopy nitrogen \( (N_t) \) and the slope of the relationship between light-saturated photosynthesis and nitrogen \( (a_p) \) and that it is a negative function of the ratio of an individual’s photosynthesis and nitrogen \( (a_p) \) and the extinction coefficient for light \( (K_L) \), light availability \( (I_0) \), the apparent quantum yield \( (\Phi) \) and the minimum leaf nitrogen content \( (n_b) \).

These predictions are summarized in Table 2.

As noted above, \( \beta_i = 1 \) means that the canopies of plants are not mixed. Thus, the \( L_t^* \) for \( \beta_i = 1 \) is equivalent to the optimal LAI that maximizes whole-stand canopy photosynthesis. A reduction in \( \beta_i \), from one towards zero, means that plants increasingly influence each other’s light climate. Thus, the negative relationship between \( L_t^* \) and \( \beta_i \) implies that the ES-LAI is greater than the optimal LAI and that the ES-LAI increases with the degree in which canopies of plants are mixed.
The analytical model described above made it possible to determine the formal relationships between the ES-LAI \((L_n^\text{ES})\) of a stand and a number of leaf and canopy characteristics and allowed me to show that \(L_n^\text{ES}\) should always be greater than the optimal LAI which maximizes photosynthesis of a stand. However, the complexity of canopy structure and photosynthesis make it impossible to make accurate estimates of canopy photosynthesis by means of analytical models. Here, canopy photosynthesis is therefore calculated with a more realistic numerical model. This model is based on previously presented models (Spitters, 1986; Anten, 1997; De Pury & Farquhar, 1997) with modifications that allow for the calculation of photosynthesis of individual plants within a stand. It calculates net daily rates of canopy carbon gain for individuals or populations of close to identical plants expressed per m² soil area. These rates are obtained by integrating instantaneous leaf photosynthetic rates (per second and per m² leaf area) over the day and over canopy depth.

### LIGHT DISTRIBUTION IN THE CANOPY

Most previous models for optimal LAI (Saeki, 1960; Schieving et al., 1992; Anten et al., 1995b, 1998; Hirose et al., 1997) used Beer’s law [eqn (4)]. Beer’s law describes the time-averaged profile of light distribution in the canopy reasonably well. But instantaneous light gradients are not very well described by Beer’s law because it assumes that every leaf in a given horizontal layer in the canopy receives the same amount of light. Leaves in sun flecks receive more light than Beer’s law would predict. Additionally, the interception of direct beam irradiance is strongly determined by the leaf inclination angle that may differ considerably between leaves in a canopy (e.g. Spitters, 1986). The present model therefore distinguishes two classes of leaf area: shaded and sunlit leaf area. This method has proven to give accurate estimates of canopy photosynthesis [De Pury & Farquhar, 1997 and citations therein]. The PFDs incident on the shaded \((I_{\text{sh},i})\) and sunlit \((I_{\text{sl},i})\) leaf area are thus calculated according to eqns (2)–(9) in Anten (1997). The extinction coefficient for direct irradiance is estimated as a function of the leaf angle distribution following Goudriaan (1988) by dividing leaves into three inclination classes (0–30, 30–60 and 60–90°) with all the leaves in a class having an inclination angle equal to the center angle of their class i.e. 15, 45 and 75°. For the extinction coefficient for diffuse PFD \((K_{\text{df}})\) I used measured values (see Anten, 1997).

### LEAF AND PLANT PHOTOSYNTHESIS

The advantage of using a rectangular hyperbola is that it permits a simple solution for the partial derivative of plant photosynthesis \((P_i)\) to its leaf area \((L_i)\) [eqn (10)]. However, the non-rectangular hyperbola (Marshal & Biscoe, 1980) generally better fits experimental data than the rectangular hyperbola and is therefore used in the numerical model:

\[
p_{\text{L},i} = \frac{(p_{\text{max},i} + \Phi I_{L,i}) - [(p_{\text{max},i} + \Phi I_{L,i})^2 - 4\Phi \Theta p_{\text{max},i} I_{L,i}]^{0.5}}{2\Theta} - r_d,i
\]

with \(p_{\text{L},i}\) net photosynthesis per unit leaf area, \(I_L\) incident PFD, \(p_{\text{max}}\) light-saturated photosynthesis [eqn (6a)], \(r_d\) dark respiration [eqn (6b)] and \(\Phi\) and \(\Theta\) apparent quantum yield and curvature factor, respectively. Note, however, that the rectangular hyperbola is a special case of the non-rectangular hyperbola [i.e. eqn (17) with...
\( \Theta = 0 \) and that they are therefore similar in shape. \( \Phi \) and \( \Theta \) were assumed to be constant (Schieving et al., 1992; Anten et al., 1995a, b, 1998; Hirose et al., 1997).

The assumption of an optimal nitrogen distribution allowed for the derivation of a simple analytical equation for plant photosynthesis [eqn (7)]. Patterns of N distribution in stands of vegetation are generally observed to be similar in form (i.e. decreasing N content per unit leaf area, \( n_{L,i} \) with increasing depth in the canopy) but less skewed than the optimal distribution (see Werger & Hirose, 1991). In the numerical model I therefore use actual N distributions fitted with the following exponential equation:

\[
n_{L,i} = (n_{0,i} - n_b)\exp(-K_n t_i) + n_b,
\]

where \( K_n \) is the coefficient of N distribution, \( n_{0,i} \) the \( n_{L,i} \) at the top of the canopy and \( n_b \) the x-intercept of the \( p_{max,i} - n_{L,i} \) relationship (Anten et al., 1995a).

The photosynthetic rates of sunlit and shaded leaf area \( p_{sl,i} \) and \( p_{sh,i} \) at any depth in the canopy are calculated by substituting \( I_{L,i} \) in eqn (17) by the PFD incident on these classes of leaf area following Goudriaan (1988). Subsequently, whole plant photosynthesis (\( P_i \)) can be found as

\[
P_i = \beta_i \int_{L_T} f_{sl} p_{sl,i} + (1 - f_{sl}) p_{sh,i} \, dI_T,
\]

where \( L_T \) is the total LAI of a stand, \( f_{sl} \) the fraction of sunlit leaf area [given by eqn (19) in Spitters, 1986] and \( \beta_i \) the ratio of an individual’s leaf area to the total leaf area. Daily values of plant photosynthesis (\( P_{D,T} \)) are obtained by integrating \( P_i \) over the day, from sunrise to sunset. In this calculation, daily courses of direct and diffuse radiation above the canopy (\( I_{0,dr} \) and \( I_{0,df} \)), the solar angle and the day length are calculated as a function of the latitude and date according to eqns (6.27) and (6.31) in Gates (1980) and eqn (16) in Spitters (1986) assuming clear day conditions. Whole-stand daily canopy photosynthesis (\( P_{D,T} \)) is found by dividing plant photosynthesis \( P_{D,T} \) by \( \beta_i \).

**DETERMINATION OF OPTIMAL AND EVOLUTIONARILY STABLE LAI**

The optimal LAI for maximization of whole-stand carbon gain (\( P_{D,T} \)) per unit of nitrogen in the canopy (\( N_T \)) was determined by calculating \( P_{D,T} \) as a function of the LAI of the stand (\( L_T \)) and thus finding the \( L_T \) at which \( P_{D,T} \) is maximized. Canopy nitrogen, \( N_T \), was fixed, so that increases in \( L_T \) led to proportional reductions in leaf N contents per unit area (\( n_L \)) and vice versa. However, no leaf in the canopy was allowed to have an \( n_L \) value lower than the minimal N content (\( n_b \)), with \( n_b \) equal to the x-intercept of the \( p_{max} - n_L \) relationship.

In order to determine the ES-LAI of a stand, the LAI of an individual in the stand (\( L_i \)) was increased by 5%. The LAI of neighbors was kept constant and this 5% increase in \( L_i \) therefore not only increased the total LAI (\( L_T \)) but also the ratio of \( L_i \) to \( L_T (\beta_i) \). If this led to an increase in

| Table 3 | The photosynthetic pathway, mode of growth (mono- or dicotyledonous) and whether plants were subjected to different nitrogen treatments for the species used in this study |
|---|---|---|---|
| **Name** | **Photosynthetic pathway** | **Mode of growth** | **N treatment** |
| Sorghum bicolor* | C4 | Monocot | Yes |
| Oryza sativa* | C3 | Monocot | Yes |
| Amaranthus cruentus* | C3 | Dicot | Yes |
| Glycine max* | C3 | Dicot | No |
| Leersia hexandra† | C3 | Monocot | No |
| Paspalum fasciculatum† | C4 | Monocot | No |
| Hymenachne amplexicaulis† | C3 | Monocot | No |
| Hyparrhenia rufa† | C4 | Monocot | No |

*Data taken from Anten et al. (1995a, b).
†Data taken from Anten et al. (1998).
the daily carbon gain of the individual \( (P_{Di}) \), \( \beta_i \) was set to its original values and \( LT \) was increased, accordingly. Conversely, if it led to a reduction in \( P_{Di} \), \( LT \) was reduced after resetting \( \beta_i \) to their original values. This process was repeated through iteration until a value of \( LT \) was found at which a change in \( Li \) did not change \( PD_i \). This \( LT \) value was considered to be the ES-LAI.

EXPERIMENTAL DATA

The numeric model was applied to dense mono-specific stands of a number of herbaceous species. All data were taken from previous studies (Anten et al., 1995a, b, 1998). Table 3 shows the complete list of species with a number of their characteristics. As can be seen, the list includes: plants with \( C_3 \) and \( C_4 \) photosynthetic pathway, monocotyledonous and dicotyledonous plants and for some species, plants grown at either high or low N availability. The leaf photosynthetic characteristics of each of the species are shown in Table 4 and the canopy structural characteristics and leaf nitrogen contents in Table 5.

Results and Discussion

EVOLUTIONARILY STABLE VS. OPTIMAL LAI: MAXIMIZATION AT INDIVIDUAL OR POPULATION LEVEL

Figure 2 shows the actual, optimal and evolutionarily stable (ES) LAI as well as the whole-stand daily canopy photosynthesis calculated for each LAI value. These calculations were made assuming the leaf and canopy characteristics of the *Hymenachne amplexicaulis* stand analysed by Anten et al. (1998) (Tables 4 and 5). The optimal LAI was smaller than either the actual or the ES-LAI. These results are consistent with the predictions from the analytical model. Canopy photosynthesis for the optimal LAI was higher than the photosynthesis for the actual and ES-LAIs. These results show that the canopy structure that maximizes photosynthesis of a population (optimal LAI) is not the same as the canopy structure that maximizes photosynthesis of individuals within a population (ES-LAI).

The fact that the ES-LAI is always greater than the optimal LAI can be interpreted as follows: a simultaneous increase in leaf area of all plants in a stand will increase self-shading and as the LAI becomes larger the increase in light capture becomes increasingly marginal and will not compensate for the reduction in photosynthetic capacity. Individual plants, on the other hand, share space with neighbors and their leaves and those of their neighbors shade one another. An increase in their leaf area, keeping the leaf area of neighbor plants constant, will result in a relatively smaller increase in self-shading while these plants are able to capture a larger fraction of the available light. Thus,

<table>
<thead>
<tr>
<th>Species</th>
<th>( \alpha_p )</th>
<th>( \alpha_r )</th>
<th>( \beta_p )</th>
<th>( \beta_r )</th>
<th>( \Phi )</th>
<th>( \Theta )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sorghum*</td>
<td>0.419</td>
<td>12.5</td>
<td>0.0110</td>
<td>0.284</td>
<td>0.0494</td>
<td>0.855</td>
</tr>
<tr>
<td>Oryza*</td>
<td>0.203</td>
<td>25.7</td>
<td>0.0084</td>
<td>0.383</td>
<td>0.0431</td>
<td>0.747</td>
</tr>
<tr>
<td>Amaranthus*</td>
<td>0.307</td>
<td>24.8</td>
<td>0.0096</td>
<td>0.408</td>
<td>0.0500</td>
<td>0.826</td>
</tr>
<tr>
<td>Glycine*</td>
<td>0.143</td>
<td>29.0</td>
<td>0.0099</td>
<td>0.388</td>
<td>0.0430</td>
<td>0.722</td>
</tr>
<tr>
<td>Leersia†</td>
<td>0.324</td>
<td>18.1</td>
<td>0.0124</td>
<td>0.334</td>
<td>0.0416</td>
<td>0.651</td>
</tr>
<tr>
<td>Paspalum†</td>
<td>0.497</td>
<td>32.8</td>
<td>0.0185</td>
<td>0.099</td>
<td>0.0487</td>
<td>0.761</td>
</tr>
<tr>
<td>Hymenachne†</td>
<td>0.234</td>
<td>24.1</td>
<td>0.0114</td>
<td>0.337</td>
<td>0.0395</td>
<td>0.821</td>
</tr>
<tr>
<td>Hyparrhenia†</td>
<td>0.567</td>
<td>9.6</td>
<td>0.0207</td>
<td>0.076</td>
<td>0.0441</td>
<td>0.754</td>
</tr>
</tbody>
</table>

*Data taken from Anten et al. (1995a).  
†Data taken from Anten et al. (1998).
individuals can enhance their carbon gain by producing more leaf area even if this reduces photosynthesis of the stand as a whole.

The result regarding the difference between ES- and optimal LAI is supported by a previous study (Schieving & Poorter, 1999), which analysed the evolutionarily stable distribution of specific leaf area (SLA) of plants in stands. They then calculated numerically that the ES-LAI was greater than the optimal LAI. Unfortunately, Schieving & Poorter (1999) did not give a formal derivation of the ES-LAI and its relation to plant traits and environmental factors, nor did they validate their modeled results in any way. It should further be noted that the definition of an ESS used by Schieving & Poorter (1999) differs from the one that was used here [eqn (9)]. They assumed leaf area to be evolutionarily stable if no change in leaf area of an individual would give it a photosynthetic rate that is higher than that of its neighbors. This definition allows for a reduction in photosynthesis of an individual as long as the reduction in photosynthesis of its neighbors is greater. However, in this situation photosynthesis of the individual will be lower than that of non-neighboring plants. Competition needs to be considered on an evolutionary time-scale and the majority of competitors on such a time-scale are probably non-neighbors. For example seeds are usually spread over an area that is much larger than the area shared by canopies of neighboring plants. The definition of an ESS used by Schieving & Poorter (1999) does not take this into account. Consequently, the ES-LAI determined according to the definition of Schieving & Poorter (1999) is greater than the one predicted following the definition of an ESS used here. This is because by producing extra

<table>
<thead>
<tr>
<th></th>
<th>LAI</th>
<th>$K_{df}$</th>
<th>Leaf angle distribution</th>
<th>$N_T$</th>
<th>$K_n$</th>
<th>$n_{av}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>0–30°</td>
<td>30–60°</td>
<td>60–90°</td>
<td></td>
</tr>
<tr>
<td>Sorghum*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High N</td>
<td>5.92</td>
<td>0.632</td>
<td>0.30</td>
<td>0.27</td>
<td>0.43</td>
<td>394.4</td>
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<tr>
<td>Low N</td>
<td>4.67</td>
<td>0.604</td>
<td>0.32</td>
<td>0.28</td>
<td>0.40</td>
<td>228.6</td>
</tr>
<tr>
<td>Oryza*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High N</td>
<td>5.48</td>
<td>0.469</td>
<td>0.02</td>
<td>0.20</td>
<td>0.78</td>
<td>451.4</td>
</tr>
<tr>
<td>Low N</td>
<td>4.40</td>
<td>0.458</td>
<td>0.04</td>
<td>0.16</td>
<td>0.80</td>
<td>340.6</td>
</tr>
<tr>
<td>Amaranthus*</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>High N</td>
<td>4.99</td>
<td>0.779</td>
<td>0.69</td>
<td>0.28</td>
<td>0.03</td>
<td>421.8</td>
</tr>
<tr>
<td>Low N</td>
<td>2.13</td>
<td>0.789</td>
<td>0.68</td>
<td>0.26</td>
<td>0.06</td>
<td>172.5</td>
</tr>
<tr>
<td>Glycine*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High N</td>
<td>4.76</td>
<td>0.747</td>
<td>0.55</td>
<td>0.33</td>
<td>0.12</td>
<td>540.2</td>
</tr>
<tr>
<td>Leersia†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paspalum†</td>
<td>4.94</td>
<td>0.453</td>
<td>0.11</td>
<td>0.25</td>
<td>0.64</td>
<td>322.6</td>
</tr>
<tr>
<td>Hyparrhenia†</td>
<td>4.46</td>
<td>0.698</td>
<td>0.33</td>
<td>0.41</td>
<td>0.26</td>
<td>265.9</td>
</tr>
<tr>
<td>Dense</td>
<td>0.02</td>
<td>0.491</td>
<td>0.60</td>
<td>0.25</td>
<td>0.15</td>
<td>105.0</td>
</tr>
<tr>
<td>Open</td>
<td>2.64</td>
<td>0.470</td>
<td>0.63</td>
<td>0.22</td>
<td>0.15</td>
<td>82.8</td>
</tr>
</tbody>
</table>

*Data taken from Anten et al. (1995b).
†Data taken from Anten et al. (1998) except for the data for leaf angle distribution, which have not been reported before.
leaf area beyond the value that maximizes its own photosynthesis, a plant shades and thus reduces the photosynthesis its neighbors.

LAI is not the only case in which the optimal characteristics at the stand level are not the same as those for individual plants within a stand. For example, because the fractional allocation of biomass to leaves decreases with plant height, whole-stand assimilation would be maximized if plants would be relatively short. Yet within such a stand any individual can increase its carbon gain by growing taller and placing its leaves above those of its neighbors (Givnish, 1982). In the case of leaf angle distribution, photosynthesis of dense stands increases with the vertical inclination of the leaves of plants in the stand. This is because vertical leaves facilitate a better light penetration into the canopy (Monsi & Saeki, 1953). Yet, within such a stand any individual can enhance its photosynthesis by producing more horizontally projected leaves (Hikosaka & Hirose, 1997). Like the ES-LAI, both these cases are related to the fact that plants influence each other’s light climate.

It should be noted that the analysis presented in this study is based on a number of simplifying assumptions. Most importantly, e.g. LAI and N availability are assumed to be homogeneously distributed within a stand and plants are assumed to be of the same size. In real plant communities this is often not the case. For example, leaf area distribution is usually clumped rather than homogeneous. The light extinction coefficients ($K_L$) and the average amount of light incident on leaves will be lower in canopies where leaves are clumped (Spitters, 1986). The model presented here would thus predict that in such a situation optimal leaf N contents would be lower (greater LAI for a given amount of N) than when leaves are not clumped (see below). It should also be noted that since leaves tend to clump around the stem the ratio of a plant’s own leaf area to the total leaf area ($\beta$) will decrease with increasing distance from the stem and $\beta$ would not be constant as assumed in the model.

In contrast to the assumption of uniform plant size, natural stands often consist of plants of different sizes that grow under very different light conditions; taller plants shade shorter ones (Ford, 1975). However, for such a stand Anten & Hirose (2001) showed that the main conclusion from the present paper would still apply. With a sensitivity analysis they showed that if the stand had optimal LAI for maximum whole-stand carbon gain each individual plant could increase its own carbon gain by increasing its leaf area, irrespective of its size, showing that their optimal LAI was not evolutionarily stable.

This study only considered the nitrogen and leaf respiratory costs of leaf area production and it did not consider the carbon costs of additional stem and root tissue that provide leaves with water, nutrients and mechanical support. Inclusion of these costs would probably yield lower calculated optimum leaf areas than those estimated here (Givnish, 1988).

![Figure 2](image-url)
In the model an increase in leaf area of a plant was assumed to only increase its LAI and the associated ratio of its leaf area to the total leaf area ($\beta$). However, an increase in leaf area may also result in a horizontal expansion of the canopy, which has the advantage of only minimally increasing self-shading. On the other hand, it also implies that leaves are placed further away from the vertical stem of the plant and this requires a greater investment in support structures (e.g. Niklas & Kerchner, 1984). This would have a negative effect on the carbon balance of a plant.

The optimization criterion in this study was maximization of daily carbon gain per unit nitrogen. Inclusion of real growth processes, including leaf turnover, would probably yield new insights. Many plants have canopies in which leaves are continuously produced and lost over time (e.g. tropical pioneer trees). Resorption of nitrogen from senescing leaves is incomplete, and some nitrogen is lost when leaves are dropped. As a consequence, when calculating the optimal LAI for such plants, leaf turnover and associated nitrogen losses should be taken into account. Many other plants, however, form canopies in which all leaves are produced at the beginning and dropped at the end of the growing season (e.g. deciduous trees) and their leaf areas are therefore relatively static.

Other factors, apart from light and nitrogen may affect photosynthesis of plants. For example, water stress or photoinhibition may reduce the photosynthetic nitrogen-use efficiency (Field \textit{et al}., 1983) while herbivores tend to prefer leaves with high N contents (Mooney & Gulmon, 1979). These factors may favor selection for leaves with lower N contents than those predicted by the model for optimal LAI.

From an evolutionary perspective, it is important to look at a plant’s strategy in relation to lifetime fitness. Maximum instantaneous carbon gain and growth do not always result in maximum lifetime fitness. For example, the ability to grow fast may conflict with the ability to survive, particularly under adverse growth conditions. However, in dense stands of plants competing for light, small differences in instantaneous growth rates early in the season are crucially important in determining reproductive output later on and the present analysis, which focuses on LAI and light competition, is obviously most clearly applicable to such cases.

The present analysis did not consider how differences in leaf N content per unit area ($n_L$) come about. Variation in $n_L$ may result from variation in the amount of nitrogen per unit mass ($n_{\text{mass}}$) or from differences in the amount of mass per unit area (LMA): $n_L = n_{\text{mass}}LMA$. The LMA of a leaf reflects its structural characteristics (thickness and number of cell layers) and $n_{\text{mass}}$ its chemical characteristics (the concentration of proteins). When comparing between species, low LMA is often associated with high $n_{\text{mass}}$, and also with high maximum photosynthesis per unit leaf nitrogen (leaf-PPNUE), short leaf lifespan and rapid growth (Reich \textit{et al}., 1995; Poorter & Evans, 1998). The species in the present study however are an exception to this trend; the C$_4$ species had higher LMA and considerably lower $n_{\text{mass}}$ but they had higher photosynthesis, leaf-PPNUE and growth rates (data not shown) than the C$_3$ species. However if LMA and $n_{\text{mass}}$ are negatively correlated, an increase in LMA would yield relatively little change in $n_L$ and photosynthesis per unit area and would therefore result in a lower photosynthesis per unit mass. A high LMA will also tend to increase self-shading within a leaf (thus reducing the light incident on individual chloroplasts), which further reduces photosynthesis. It should finally be noted that while photosynthesis depends on light capture and is therefore primarily related to the amount of leaf area, other processes such as respiration are more closely related to leaf biomass and these are commonly analysed on a mass basis (e.g. Reich \textit{et al}., 1998). Future studies on optimal leaf area growth and leaf N content per unit area should therefore explicitly address variation in LMA and $n_{\text{mass}}$ in their analyses.

**EVOLUTIONARILY STABLE LAI IN RELATION TO LEAF AND CANOPY CHARACTERISTICS**

The ES-LAI increased and canopy photosynthesis decreased with the degree to which neighboring plants in the stand influence each others light climate, i.e. with decreasing values of $\beta$ (Table 2; Fig. 2). $\beta$ values close to 1 mean that
plants hardly influence each other’s light climate and ES-LAI should be close to the optimal LAI (i.e. optimal LAI is equivalent to the ES-LAI for $\beta = 1$). Such $\beta$ values may be expected in stands of plants with very broad canopies such as large trees. By contrast, in stands of herbaceous plants with relatively narrow canopies, $\beta$ should be expected to be lower (Hikosaka & Hirose, 1997). Very low $\beta$ values may be realized when leaves are spatially scattered due to longer internodes or longer petioles, which reduce self-shading (Chazdon, 1986; Takenaka, 1994; Hikosaka et al., 2001). For example, in a stand of the herbaceous annual Xanthium canadense, Hikosaka et al. (2001) estimated that only about 30% of the light gradient across the leaves of individuals was caused by self-shading while the remainder was caused by leaves of neighbors; suggesting $\beta$ to be about 0.3. X. canadense plants tend to have leaves with exceptionally long petioles (the distance between leaf tips and stems was more than twice the distance between closest neighbors) and Hikosaka et al. (2001) argued that in stands of other herbaceous species with shorter petioles, $\beta$ will likely be higher.

Both the analytical and the numerical models show that the optimal and ES-LAIs increase and the respective average $n_L$ values decrease with the potential leaf photosynthetic nitrogen use efficiency (leaf-PPNUE); with higher leaf-PPNUEs resulting from either higher slopes ($a_p$) or lower x-intercepts ($n_b$) of the relationship between light-saturated photosynthesis and leaf N content (Table 2; Fig. 3). The actual data support these predictions. The C4 plants generally had higher leaf-PPNUEs (Table 4) and lower average $n_L$ values than the C3 plants (Table 5). However, the C4 dicot Amaranthus cruentus had a higher leaf-PPNUE (Table 4) and also a higher average $n_L$ values than the C3 monocot Oryza sativa (Table 5), which seems to be in contrast with the predictions from the model. Nevertheless, various other studies have found C4 plants to have higher leaf-PPNUEs and lower $n_L$ than C3 plants (Brown, 1978; Sage & Pearcy, 1987). It has further been shown that among C3 plants those with high leaf-PPNUEs have lower $n_L$ values than those with low PPNUEs (Poorter et al., 1990; Poorter & Evans, 1998). In the latter case, the lower $n_L$ values result from a lower leaf mass
per area (LMA) (see Discussion above on the importance of LMA).

The ES-LAI was predicted to increase and the average $n_L$ value ($n_{av}$) to decrease with the vertical inclination angle of leaves in the canopy (Fig. 3). Plants with more vertically inclined leaves produce stands with lower extinction coefficients for light ($K_L$) and the analytical model predicted a negative correlation between ES-LAI and $K_L$ (Table 2). Two factors may contribute to this negative correlation. First, average daily incident light intensity decreases with the leaf inclination angle (Monsi & Saeki, 1953) and horizontally projected leaves would thus require a higher optimal $n_L$ than vertically inclined leaves (i.e. optimal $n_L$ increases with incident light intensity). Second, in stands with a high $K_L$ there is a greater degree of self-shading and thus a smaller marginal increase in light capture with increasing LAI. The data support the model predictions. Dicotyledons generally had more horizontally projected leaves, produced stands with higher $K_L$ values and had higher $n_{av}$ values than the monocotyledons (Table 5). The predicted effect of the leaf angle on ES-LAI could also explain why *Amaranthus* had a higher average $n_L$ than *Oryza* in spite of its greater leaf-PPNUE, since *Amaranthus* plants had considerably lower leaf inclination angles than *Oryza* plants. Unfortunately, I know of no other studies that have compared leaf area production and $n_L$ values between plants with different leaf angle distributions.

The predicted ES-LAI decreases (and the ES average N content increases) with the apparent quantum yield ($\Phi$, Fig. 3), which was also predicted by the analytical model (Table 2). This seems to be inconsistent with the general notion that LAI should increase with $\Phi$ (Saeki, 1960; Pearcy & Björkman, 1983). A greater $\Phi$ means leaves have lower light compensation points and following the model for optimal LAI of Saeki (1960) (see Introduction) it can be argued that the optimal LAI should therefore increase. However, Saeki (1960) did not consider nitrogen limitation on leaf area production as was done here. The reduction in ES-LAI with $\Phi$ predicted in the present study can be understood as follows. At a given incident PFD, leaves with a higher $\Phi$ will not only have higher photosyn-

**COMPARISONS BETWEEN PREDICTED AND ACTUAL LEAF AREAS**

This study showed that there was a strongly significant positive correlation between the optimal and measured LAIs [Fig. 4(A); Table 6] and between the optimal ($n_{op}^{av}$) and measured average N content [$n_{av}$, Fig. 4(C); Table 6]. However, for all the stands, optimal LAIs were considerably lower and $n_{op}^{av}$ were considerably higher than the measured values. This is shown in the linear regression of optimal against measured LAIs where the slope value was significantly smaller than 1 while the constant was not significantly different from 0 (Table 6; $P<0.05$). This indicates that while differences in leaf area production per unit nitrogen between stands of different species are well predicted by the model for optimal LAI, actual leaf areas are considerably underestimated.

The optimal LAIs calculated here were lower than those calculated by Anten et al. (1995b, 1998) for the same stands. As noted above however, those studies used Beer’s law to calculate light distribution in the canopy. Beer’s law incorrectly assumes that all leaves in a horizontal layer receive the same average PFD. This leads to overestimation of canopy carbon gain because of the curvilinear relationship between leaf photosynthesis and light. This overestimation increases with depth in the canopy because the difference in incident PFD on sunlit and shaded leaf area increases. The marginal gains in photosynthesis with increasing LAI and consequently the optimal LAI are therefore overestimated when using Beer’s law.

The predicted ES-LAIs and average N contents $n_{av}^{ES}$ corresponded very well to the measured values, i.e. all data seemed to cluster around the line of 1:1 correspondence [Fig. 4(B) and (D); Table 6]. The slope values in the linear regressions of the ES-LAIs and $n_{av}^{ES}$ values on the respective measured values were not significantly different from 1, while the intercepts were not significantly different from 0 (Table 6). Thus, in
contrast to the model for optimal LAI, the theory of ES-LAI predicted leaf area production per unit nitrogen in stands of many species very well.

It should be noted that the values of ES-LAI were calculated assuming the degree to which the canopies of individuals and neighbors are mixed ($\beta$) to be 0.5. Since $\beta$ was not measured, $\beta = 0.5$ is an arbitrary value. However, all species included in this analysis were erect herbaceous plants with narrow canopies. As noted above, in stands of such plants the light climate of any

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Independent variable</th>
<th>Slope value (S.E.)</th>
<th>$p(0)$</th>
<th>$p(1)$</th>
<th>Intercept value (S.E.)</th>
<th>$p(0)$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Optimal LAI</td>
<td>Actual LAI</td>
<td>0.509 (0.096)</td>
<td>0.0004</td>
<td>0.0003</td>
<td>0.224 (0.447)</td>
<td>0.624</td>
<td>0.72</td>
</tr>
<tr>
<td>$n_{av}^{\text{opt}}$</td>
<td>$n_{av}$</td>
<td>1.876 (0.172)</td>
<td>&lt;0.0001</td>
<td>0.0002</td>
<td>-6.292 (12.4)</td>
<td>0.622</td>
<td>0.92</td>
</tr>
<tr>
<td>ES-LAI</td>
<td>Actual LAI</td>
<td>1.098 (0.178)</td>
<td>&lt;0.0001</td>
<td>0.562</td>
<td>-0.634 (0.824)</td>
<td>0.461</td>
<td>0.79</td>
</tr>
<tr>
<td>$n_{av}^{\text{ES}}$</td>
<td>$n_{av}$</td>
<td>1.031 (0.105)</td>
<td>&lt;0.0001</td>
<td>0.738</td>
<td>1.985 (7.48)</td>
<td>0.796</td>
<td>0.91</td>
</tr>
</tbody>
</table>

Note: S.E. denotes standard errors, and $p(0)$ and $p(1)$ indicate the probability that a value equals 0 or 1 based on a Student’s $t$-test. Data are the same as those presented in Fig. 4.
individual is probably strongly determined by its neighbors and $\beta$ values should be expected to be well below 1. On the other hand, extremely low $\beta$ values should not be expected since none of the plants in this study produced very long internodes or petioles that would minimize self-shading (Hikosaka et al., 2001). Thus, $\beta$ values in stands studied here might be expected to have been reasonably close to 0.5. It is also important to note that $\beta$ should be determined on an evolutionary time-scale with evolutionarily significant competitors. In other words, the “neighbors” should be defined as the set of genotypes with whom a particular genotype will compete over the course of multiple generations.

Conclusions

In this paper, I showed analytically that there exists an evolutionarily stable leaf area index (ES-LAI) at which no individual can increase its carbon gain by changing its leaf area and that this ES-LAI should always be greater than the optimal LAI that maximizes whole-stand carbon gain. The model presented here correctly predicted the differences in leaf area between plants and the resulting canopy structure of stands (i.e. the LAI). On the other hand, extremely low $\beta$ values should not be expected since none of the plants in this study produced very long internodes or petioles that would minimize self-shading (Hikosaka et al., 2001). Thus, $\beta$ values in stands studied here might be expected to have been reasonably close to 0.5. It is also important to note that $\beta$ should be determined on an evolutionary time-scale with evolutionarily significant competitors. In other words, the “neighbors” should be defined as the set of genotypes with whom a particular genotype will compete over the course of multiple generations.

REFERENCES


