Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons

FEIKE SCHIEVING AND HENDRIK POORTER*

Department of Plant Ecology and Evolutionary Biology, P.O. Box 800.84, 3508 TB Utrecht, The Netherlands

SUMMARY

Models have been formulated for monospecific stands in which canopy photosynthesis is determined by the vertical distribution of leaf area, nitrogen and light. In such stands, resident plants can maximize canopy photosynthesis by distributing their nitrogen parallel to the light gradient, with high contents per unit leaf area at the top of the vegetation and low contents at the bottom. Using principles from game theory, we expanded these models by introducing a second species into the vegetation, with the same vertical distribution of biomass and nitrogen as the resident plants but with the ability to adjust its specific leaf area (SLA, leaf area:leaf mass). The rule of the game is that invaders replace the resident plants if they have a higher plant carbon gain than those of the resident plants. We showed that such invaders induce major changes in the vegetation. By increasing their SLA, invading plants could increase their light interception as well as their photosynthetic nitrogen-use efficiency (PNUE, the rate of photosynthesis per unit organic nitrogen). By comparison with stands in which canopy photosynthesis is maximized, those invaded by species of high SLA have the following characteristics: (1) the leaf area index is higher; (2) the vertical distribution of nitrogen is skewed less; (3) as a result of the supra-optimal leaf area index and the more uniform distribution of nitrogen, total canopy photosynthesis is lower. Thus, in dense canopies we face a classical tragedy of the commons: plants that have a strategy to maximize canopy carbon gain cannot compete with those that maximize their own carbon gain. However, because of this strategy, individual as well as total canopy carbon gain are eventually lower. We showed that it is an evolutionarily stable strategy to increase SLA up to the point where the PNUE of each leaf is maximized.

Key words: analytical model, canopy, game theory, nitrogen, photosynthetic nitrogen-use efficiency, specific leaf area.

INTRODUCTION

For the past three decades the process of photosynthesis has been studied extensively. This has improved our understanding to such an extent that relatively simple biochemically based models can now adequately describe the processes that occur at leaf level (Farquhar *et al.*, 1980). Similarly, there have been considerable achievements in modelling the carbon gain of the whole canopy. One of the first steps has been to describe the decrease in irradiance with increasing depth of the vegetation by the Lambert–Beer law (Monsi & Saeki, 1953). Field (1983) showed that for maximal carbon gain by a canopy, nitrogen should be distributed so that in each layer of the vegetation the slope of the graph of

*Author for correspondence (fax +31 30 251 8366; e-mail h.poorter@bio.uu.nl).

photosynthesis against nitrogen should be equal. An implication of this condition is that nitrogen distribution within the canopy follows the distribution of light and, consequently, that photosynthetic capacity is lower in lower parts of the vegetation (Field, 1983). Especially in dense stands this has been recurrently found (Werger & Hirose, 1991).

Hirose & Werger (1987) developed a model of the distribution of leaf area, light and nitrogen in the vegetation to evaluate the consequences of different patterns of nitrogen investment for the carbon gain of the canopy. This static model, later refined by Anten *et al.* (1995b), showed that in dense canopies the actual, non-uniform distribution of nitrogen results in a carbon gain 10–30 % higher than in a stand with a similar amount of nitrogen, distributed uniformly over the vertical axis (Fig. 1a). However, these models also show that total canopy photo-
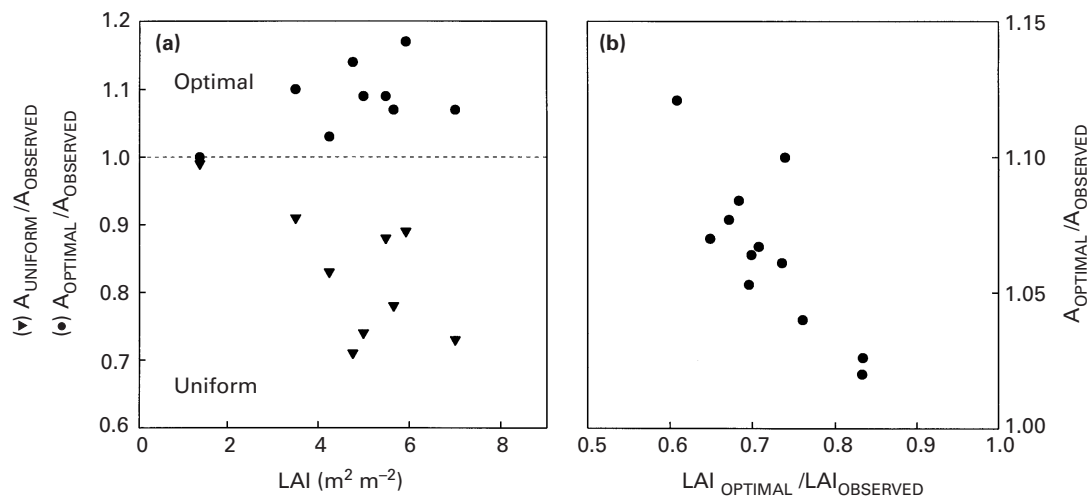
Fig. 1. (a) The rate of photosynthesis of a canopy with a uniform distribution of nitrogen over the vertical axis compared with the actual canopy photosynthesis ($A_{UNIFORM}/A_{OBSERVED}$) (closed triangles) and the values at the optimal nitrogen distribution relative to the observed values ($A_{OPTIMAL}/A_{OBSERVED}$) (closed circles). Data are from herbaceous canopies studied by Hirose & Werger (1987); Pons *et al.* (1989); Schieving *et al.* (1992b); Evans (1993); Anten *et al.* (1995a) and are plotted against the LAI of the stand. (b) Calculated canopy photosynthesis in a stand in which LAI is presumed to be optimized (with respect to canopy photosynthesis) relative to the canopy photosynthesis observed in stands growing naturally ($A_{OPTIMAL}/A_{OBSERVED}$), plotted against the ratio of LAI in an optimized stand compared with the observed LAI. Data are from Schieving *et al.* (1992b) and Anten *et al.* (1995a, 1998).

synthesis could have been even higher than the actual rate for a similar amount of leaf nitrogen per unit ground area. Extra fixation of carbon could be achieved in two ways: (1) by allocating even more nitrogen to the upper layers of the vegetation and less to the lower parts (Fig. 1a), and (2) by decreasing the total leaf area per unit ground area (leaf area index (LAI); Fig. 1b), thus decreasing the respiratory burden imposed by the lower leaves. For each of the two alternatives, the benefits to be gained in herbaceous vegetations are estimated to be 5–10 % (Hirose & Werger, 1987; Pons *et al.*, 1989; Evans, 1993; Anten *et al.*, 1995a). In stands of shrubs or trees the situation might be more complicated, and benefits might be lower (Field, 1983; Leuning *et al.*, 1991).

Why are the nitrogen distribution and LAI actually observed in herbaceous vegetation not optimized for maximal carbon gain? Most papers have studied a monospecific stand, in which all individual plants behave in exactly the same way. However, most natural vegetation consists of a mix of plant species that do not necessarily follow exactly the same strategy (Hikosaka & Hirose, 1997). In this paper we shall analyse the consequences of differing specific leaf area (SLA, leaf area per unit leaf mass) of plants competing for light. For ease of reference we shall define these different plants as being of different species. We shall examine the interaction between the species by using game theory (Maynard Smith, 1982): a model is formulated in which a monostand of a resident species (R), with an SLA that ensures maximal canopy photosynthesis, will be invaded by plants of another species (I). We analyse the

consequences of species I being able to change its SLA at a given vertical distribution of nitrogen and biomass. We shall show that the evolutionarily stable strategy is such that SLA and LAI are higher and nitrogen distribution is less skewed than in a monostand in which the total carbon gain for the stand is maximized. A consequence of these differences is that total canopy carbon gain is lower.

DESCRIPTION OF THE MODEL

The model basically extends the work of Hirose & Werger (1987) and Anten *et al.* (1995a,b). To keep this section brief, we describe the model somewhat loosely; a full and rigorous derivation is given by Schieving (1998). The derivation of some of the equations is given in detail in Appendix 1. Abbreviations and parameters are listed in Table 1.

The assumptions

(1) A canopy is a perfect, homogeneous mixture of two plant species. We shall characterize the total leaf area of the canopy by the variable F_T, the cumulative leaf area of the canopy per m² of ground and thus the LAI. As a descriptor of the distribution of total leaf area over the vertical axis, we use F^h, which is the cumulative leaf area above canopy depth h, h being the distance from the top of the canopy.

(2) Leaf angle and absorption coefficient are the same for the two species and constant with vegetation depth. The absorption coefficient is independent of the amount of nitrogen per unit leaf area. For simplicity we consider leaf angle and absorption of both

Table 1. *List of parameters used in the model, and explanation of the abbreviations and units*

Parameter	Definition	Units
a	Leaf absorbance	–
C_{Tj}	Net rate of carbon gain (gross photosynthesis − respiration) per individual of species j, with $j =$ R(esident), I(nvader) or A(verage of all plants)	mol CO_2 s^{-1} per individual
F^h	Cumulative leaf area at canopy depth h	m² leaf m^{-2} ground
f^h	Leaf area density at canopy depth h	m² leaf m^{-3} space
F_T	Total cumulative leaf area of the canopy	m² leaf m^{-2} ground
G_{Tj}	Gross photosynthetic rate per individual of species j	mol CO_2 s^{-1} per individual
g^h	Gross photosynthetic rate per unit leaf area at depth h	mol CO_2 m^{-2} leaf s^{-1}
g^h_{max}	Capacity of the gross photosynthesis-light curve at depth h	mol CO_2 m^{-2} leaf s^{-1}
h	Depth in the canopy, defined as distance from the top	m
i^0	Irradiance in the horizontal plane just above the stand	mol quanta m^{-2} ground s^{-1}
i^h_a	Irradiance absorbed per unit leaf area at canopy depth h	mol quanta m^{-2} leaf s^{-1}
K	Light extinction coefficient	–
m^h_j	Leaf mass density per individual of species j at depth h	g m^{-3}
N_T	Total cumulative leaf nitrogen in the canopy	mol N m^{-2} ground
n^h_m	Leaf nitrogen concentration at depth h	mol N kg^{-1} leaf
n^h_a	Leaf nitrogen content per unit leaf area at depth h	mol N m^{-2} leaf
$n_{a\,min}$	Threshold leaf nitrogen content per unit leaf area for positive g_{max}	mol N m^{-2} leaf
l^h	(Dark) leaf respiration rate per unit leaf mass at depth h	mol CO_2 kg^{-1} leaf s^{-1}
L_{Tj}	(Dark) respiration rate per individual of species j	mol CO_2 s^{-1} per individual
s_g	Slope of the g_{max}-n_a relation	mol CO_2 mol^{-1} N s^{-1}
s_r	Slope of the l–n_a relation	mol CO_2 mol^{-1} N s^{-1}
α	Leaf angle (from horizontal)	degrees
Φ	True quantum yield	mol CO_2 mol^{-1} quanta
Π	(Gross) photosynthetic nitrogen-use efficiency (PNUE)	mol CO_2 mol^{-1} N s^{-1}
θ	Curvature factor of the gross photosynthesis-irradiance curve	–
σ^h	SLA at canopy depth h	m² leaf kg^{-1} leaf

species to be equal, but the outcome of the model does not critically depend on this. For a given leaf area distribution and a given irradiance (i) just above the canopy (i^0), we can calculate both the irradiance (i^h) at each depth of the vegetation and, for a given leaf angle and absorbance, the amount of light intercepted by each leaf.

(3) The daily carbon gain of the stand is the difference between the gross assimilation rate (G) and the respiration rate (L) of all the leaves. We consider the area-based assimilation rate for a given leaf of a given species to be related to the amount of nitrogen per leaf area, whereas we assume the mass-based respiration of that leaf to be correlated with the amount of nitrogen per unit leaf mass. Area-based rates and contents can be converted to mass-based values through multiplication by the SLA, σ.

(4) The distribution of leaf mass and organic nitrogen (and consequently the organic nitrogen concentration) can vary throughout the depth of the vegetation, but is the same for the two species. The plants might, however, differ in their SLA distributions. Thus, invading plants play the game by distributing at each depth their leaf mass and nitrogen over a larger or smaller leaf area, thereby changing specific leaf area σ and nitrogen content per unit leaf area.

(5) Water is assumed to be nonlimiting. There are no differences in height between the species. Below-ground processes and interspecific differences in leaf longevity are not taken into account, and neither are acclimation processes at the cellular level due to changes in irradiance. Light intensity above the canopy is constant during the day.

The winner of the game

The winner of the game is the species that forms a monostand which cannot be successfully invaded by any other species that adjusts its SLA. An invasion is considered successful if individuals of invading plants have a greater carbon gain than individuals of the resident plants. The model is not dynamic and does not keep track of changes in the number of individuals of species R and I within or between growing seasons. Rather, the absolute minimum of an equation describing the difference in carbon gain between the I plants and the average plant in the vegetation is sought. In biological terms one could envisage this as the process by which I plants, if successful, completely replace R plants. New invaders then change SLA relative to the new resident plants, and the game is replayed. The end situation is reached if no SLA mutation in any direction and at any height in the vegetation can be found that is more successful within the framework of the model than the mutation analysed penultimately. Plants of this species are considered to have an evolutionarily stable strategy.

The rules

(1) Irradiance within the vegetation decreases with increasing distance from the top, following the Lambert–Beer law. Taking into account the angle of the leaf (α), the intercepted irradiance for leaves at depth h (i_a^h) becomes:

$$i_a^h = i^0 K \exp^{-KF^h}, \quad \text{with} \quad K = a\cos\alpha \qquad \text{Eqn 1}$$

(i^0 is the irradiance in the horizontal plane just above the vegetation, K the light-extinction coefficient and F^h the LAI above canopy depth h for which the irradiance has to be calculated).

(2) Gross leaf photosynthesis is a function of the nitrogen content of the leaf and of the prevailing irradiance. Gross leaf photosynthetic capacity per unit leaf area (g_{max}) is a linear function of the nitrogen content per unit leaf area (n_a), taking into account a threshold value ($n_{a\,min}$):

$$g_{max} = s_g(n_a - n_{a\,min}). \qquad \text{Eqn 2}$$

(3) Whether a leaf achieves the maximum rate of photosynthesis depends on the light climate. A standard non-rectangular hyperbola is used to calculate the actual rate of photosynthesis at each depth h in the vegetation:

$$g^h = \frac{(g_{max}^h + \Phi i_a^h - \sqrt{(g_{max}^h + \Phi i_a^h)^2 - 4\Theta\Phi g_{max}^h i_a^h}}{2\Theta}, \qquad \text{Eqn 3}$$

(θ is the curvature of the non-rectangular hyperbola and Φ the true quantum yield of photosynthesis).

(4) Leaf respiration per unit leaf mass (l) is a linear function of the nitrogen concentration (nitrogen per unit leaf mass):

$$l = s_r n_m. \qquad \text{Eqn 4}$$

No distinction is made between day and night respiration. Rates of photosynthesis and respiration on a leaf mass or area basis can be easily interconverted if the SLA, σ, is known.

(5) Net carbon gain of an individual plant, neglecting respiration of stem and roots, can be written:

$$C_T = G_T - L_T \qquad \text{Eqn 5}$$

with G_T (gross carbon gain) being a function of the leaf area of the plant and the rate of photosynthesis per unit leaf area at each depth in the vegetation. The rate of photosynthesis itself is determined by the nitrogen content (n_a) and the absorbed irradiance (i_a^h) at that depth in the vegetation. Respiration of all leaves of the plant taken together (L_T) is a function of the mass at each height and the nitrogen concentration per unit mass. Thus, total carbon gain per plant is given by the integral:

$$C_T = \int_0^{h_T} dh\,[f^h g(i_a^h, n_a^h) - m^h l(n_m^h)]$$
$$= \int_0^{h_T} dh\,m^h[\sigma^h g(i_a^h, n_a^h) - l(n_m^h)], \qquad \text{Eqn 6}$$

(h_T is the total depth of the vegetation). Because Eqn 6 integrates processes over the depth of the vegetation, the leaf area and mass at depth h are now indicated as leaf area density (f^h; leaf area per unit volume) and leaf mass density (m^h; mass per unit volume), respectively. So far these equations are similar to those given in Anten *et al.* (1995b). Anten *et al.* also give the equations to calculate the optimal distribution of nitrogen and leaf area that leads to a maximal carbon gain per unit ground area.

(6) Having arrived at the 'optimal' distribution of nitrogen and leaf area in a monostand, we then introduce a second species into the model. In the first round of the game, resident plants (R) have the distribution characteristics of the optimal plants. The second species (I) will follow another strategy, by adjusting its SLA. The total carbon gain of an individual of each of the species j, integrated over all layers of the vegetation, is given by:

$$C_{T,j} = \int_0^{h_T} dh\,m^h[\sigma_j^h g(i_a^h, n_{a,j}^h) - l(n_m^h)], \qquad \text{Eqn 7}$$

(nitrogen content per unit leaf area is given by $n_{a,j}^h = n_m^h/\sigma_j^h$).

Thus, according to Eqn 7 the difference in performance between plants of species R and I is solely the result of a difference in SLA.

(7) Given the fractions ϕ_R and ϕ_I of plants of species R and I, respectively (with $\phi_R + \phi_I = 1$), the average carbon gain in the stand per plant (C_{TA}) is given by:

$$C_{TA} = \phi_R C_{TR} + \phi_I C_{TI}. \qquad \text{Eqn 8}$$

(8) In its simplest form, a multispecies canopy consists of two species. However, in principle, more species could be involved. Therefore, following the rules of game theory, we evaluate the performance of species I, that is the carbon gain of invader I expressed per individual (C_{TI}), relative to the carbon gain of the average individual in the stand (C_{TA}). In the case that species I has increased SLA in all layers from σ to $(1+\delta).\sigma$, the difference in plant carbon gain with respect to the mean is given by:

$$C_{TI}^\delta - C_{TA}^\delta = C_{TI}^\delta - (\phi_R C_{TR}^\delta + \phi_I C_{TI}^\delta)$$
$$= (1 - \phi_I) C_{TI}^\delta - \phi_R C_{TR}^\delta$$
$$= \phi_R [C_{TI}^\delta - C_{TR}^\delta], \qquad \text{Eqn 9}$$

(C_{Tj}^δ denotes the rate of carbon gain of species j after the small increase in SLA.) Because respiration in our model is related to the nitrogen concentration n_m, which does not differ between residents and invaders, respiration disappears from Eqn 9.

This equation shows what might be expected intuitively: the greatest difference between species I and the mean of the vegetation as a whole (and thus the effect of the δ variation) occurs when the frequency of I plants is low. The difference becomes

less pronounced when relatively more I plants are present.

As a matter of convenience we keep δ constant for all layers of the canopy. However, by a calculus-of-variation argument it can be shown that the same results are obtained if δ is any smooth variation function of canopy depth.

(9) For small variations, δ, we can write:

$$C_{TI}^{\delta} - C_{TA}^{\delta} = \frac{d}{d\delta}(C_{TI}^{\delta} - C_{TA}^{\delta}).\delta \qquad \text{Eqn 10}$$

(The derivative d/dδ(…) is calculated at δ = 0.) The effect of δ on the difference between the carbon gain of the I plants and of the average plant in the vegetation depends on the explicit form of Eqn 10. In Appendix 1 we derive the following equation:

$$\frac{d(C_{TI}^{\delta} - C_{TA}^{\delta})}{d\delta} = \phi_R \int_0^{h_T} dh\, m^h\, \sigma^h \left[g(i_a^h, n_a^h) - n_a^h \cdot \frac{\partial g(i_a^h, n_a^h)}{\partial n_a} \right].$$

$$\text{Eqn 11}$$

Thus, for a given change δ, the difference in carbon gain between the I plants and the average plant in the vegetation depends on the fraction of R plants in the stand, the mass at each height, the SLA of species R, and a term in parentheses. As long as the integral is positive, a positive variation δ in the I plants leads to a higher carbon gain per plant for the I-plants than for plants of species R. In the game this could be envisaged as a replacement of R by I plants, I plants becoming the new R plants. This process recurs until any change in δ (positive or negative) causes no further increase in carbon gain. This is the case if the resident plants satisfy at every canopy depth:

$$g - n_a \frac{\partial g}{\partial n_a} = 0 \qquad \text{Eqn 12}$$

In this case, invaders will not be able to replace the resident plants and an evolutionarily stable system is reached.

Although the full model, as described by Schieving (1998), focuses on the effect of enlarging the leaf area at a given leaf biomass, SLA is not used explicitly in the model. State variables are total leaf area and total nitrogen only. To enable the visualization of the changes in SLA, it is necessary to specify the concentration of nitrogen. As a matter of convenience we assumed that the nitrogen concentration of the leaves was 2.5 mmol g^{-1} in all layers of the vegetation. The model is robust in the sense that somewhat different assumptions about the distribution of leaf area, mass and nitrogen do not affect its outcome. For example, if we assume that for each species SLA is equal for all leaves along the axis, and that invading plants can play the game by altering both SLA and leaf nitrogen distribution, we also arrive at Eqn 11.

Table 2. *List of the values of the parameters used in the graphical examples*

Parameter	Value
a	0.8
i^0	1000 μmol quanta m^{-2} s^{-1}
$n_{a\,min}$	40 mmol N m^{-2} leaf
s_g	0.33 mmol CO$_2$ mol^{-1} N s^{-1}
α	0°
Φ	0.063 mol CO$_2$ mol^{-1} quanta
θ	0.8

RESULTS

An optimal monostand

For the convenience of the reader we show the results of the analysis graphically for a given set of parameters listed in Table 2. We started our analysis with a stand consisting only of species R. Following Anten *et al.* (1995b), we calculated, for a given amount of leaf nitrogen per ground area ($N_T = 400$ mmol m^{-2}), the optimal nitrogen distribution for maximal canopy photosynthesis. Thereafter we determined the leaf area index, F_T^*, for which carbon gain of the canopy is maximized. The distribution of nitrogen, expressed as nitrogen content per unit leaf area, is shown by the broken line in Fig. 2a. Usually, such a distribution is shown as a function of cumulative leaf area. However, in the game, the total leaf area alters. Therefore, we choose to plot the relevant variables as a function of the cumulative amount of nitrogen in the vegetation, using equations given by Schieving (1998). The distribution of nitrogen follows the distribution of light in the canopy (Fig. 2b), whereas SLA follows the opposite pattern (Fig. 3a). As expected, the profile of gross photosynthesis follows that of light and nitrogen (Fig. 3b), with low values at the bottom of the canopy.

If we consider the optimal LAI for a range of leaf nitrogen content per ground area, we see that it first increases linearly with N_T, with a slight hint of saturation thereafter (Fig. 4a). Above an N_T of 500 mmol m^{-2}, larger amounts of nitrogen in the canopy do not enhance gross canopy photosynthesis but increase respiration, thereby decreasing net carbon gain (Fig. 4b).

Invasion of the monostand by species I

Let us now assume a stand in which the leaf area game is played. The game starts with the introduction of an infinitesimally small number of plants of species I in the stand of species R. These invading plants have the same distribution of biomass and nitrogen as the R plants after they have achieved the optimal carbon gain. They are well mixed in the vegetation and because they are so few they do not affect the light climate in the stand. In the game
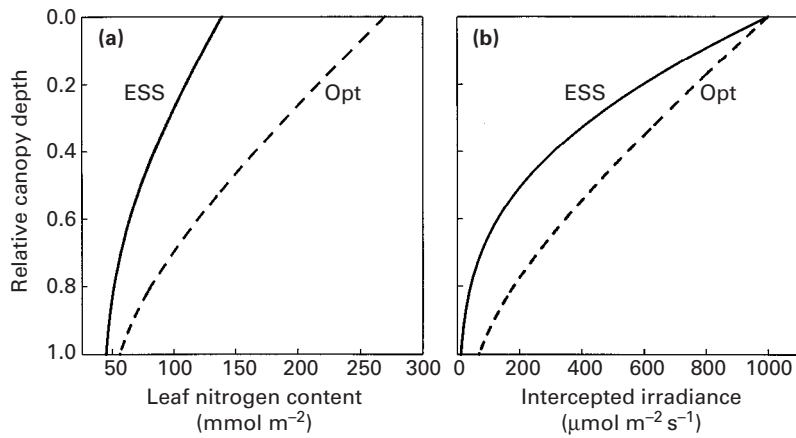
Fig. 2. (a) Leaf nitrogen content per unit area, and (b) intercepted irradiance plotted as a function of relative canopy depth. Optimal stand (Opt, broken line) with a distribution of nitrogen that maximizes canopy photosynthesis; stand in an evolutionarily stable situation (ESS, solid line) at the end of the game. Relative canopy depth is calculated as the cumulative amount of leaf nitrogen in the vegetation above a given point divided by total leaf nitrogen in the vegetation, following Schieving (1998). These graphs show a numerical example for a vegetation with a total leaf nitrogen of 400 mmol m^{-2} ground area. Parameter values used in these simulations are given in Table 2.
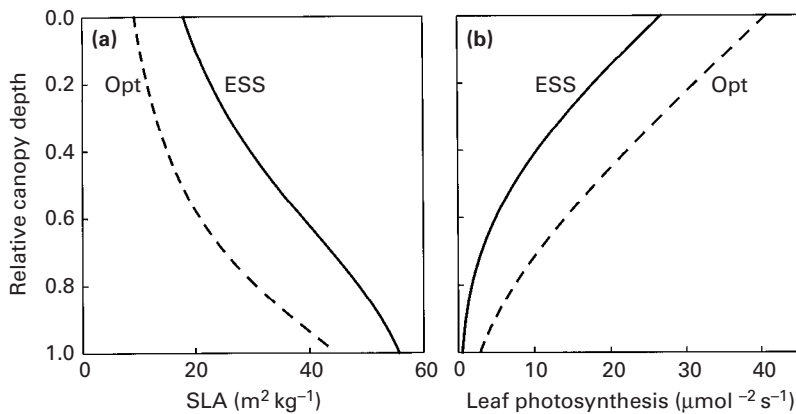

Fig. 3. (a) Specific leaf area (SLA) and (b) rate of gross photosynthesis plotted as a function of relative canopy depth in leaves of an optimal stand (Opt, broken line) and a stand in an evolutionarily stable situation at the end of the game (ESS, solid line). Relative canopy depth is calculated as the cumulative amount of leaf nitrogen in the vegetation above a given point divided by total leaf nitrogen in the vegetation, following Schieving (1998). These graphs show a numerical example for a vegetation with a total leaf nitrogen of 400 mmol m^{-2} ground area. Parameter values used in these simulations are given in Table 2.

theory model these plants have the potential to alter their SLA, and as a first option we assume that they increase SLA at every canopy depth by 10 %. As a consequence, nitrogen is diluted over a larger leaf area and the area-based rates of photosynthesis decrease. However, in I plants this is more than compensated for by a greater leaf area per plant. Consequently, in the example of a stand with an N_T of 400 mmol m^{-2}, total carbon gain of individual I plants is 5 % higher than that of resident plants. Therefore, the result of the first round is that the invaders perform better in terms of total plant carbon gain and will replace the residents.

The evolutionarily stable end situation

After the first invasion, invading plants have repeatedly outcompeted the R plants and have become the new residents, keeping their own specific SLA distri-

bution. This process continues until invaders cannot find any SLA change at any height in the vegetation to make them perform better than the residents. In this stable end situation, SLA has increased to higher values in all layers of the vegetation (Fig. 3a). By comparison with that of the initial stand, irradiance at the bottom of the canopy and the nitrogen content per unit leaf area are lower, the latter approaching the minimum value of 40 mmol N m^{-2}. Consequently, the rate of leaf photosynthesis has decreased substantially in all layers of the vegetation (Fig. 3b). Contrary to the initial phase, the increase in LAI in the end phase of the game (Fig. 4b) leads, for almost all values of N_T, to a lower rate of canopy photosynthesis than in the optimal stand. Only at very low contents of nitrogen per unit ground area in the vegetation does the leaf area game not have an effect. In such a vegetation the LAI is very low (Fig. 4a) and there is no competition for light. Thus,
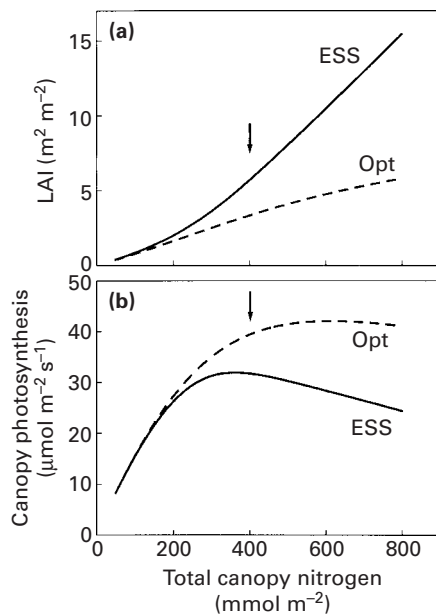
Fig. 4. (a) LAI and (b) canopy photosynthesis for an 'optimal' stand (a monostand in which canopy photosynthesis is maximized (Opt, broken line)) and a stand in an evolutionarily stable situation at the end of the game (ESS, solid line), for a range of leaf nitrogen contents per unit ground area. Arrows indicate the results for an N_T of $400 \, mmol \, m^{-2}$, used in the simulation presented in Figs 2, 3 and 6.

with the exception of very open stands, the evolutionarily stable end situation has led to an LAI higher, but to canopy photosynthesis lower than in the optimum stand. As density was not changed, this implies that carbon gain of each individual is also lower than in the situation before the game started.

DISCUSSION

Specific leaf area and leaf area index

Specific leaf area is a parameter that is, apart from environmental influences like irradiance, under strong genetic control and differentiates between functional groups of species. Thus, species from infertile habitats, especially evergreens, have an inherently low SLA, whereas species from fertile habitats have high SLAs (Monk, 1966; Poorter & De Jong, 1999). Low SLA in plants growing in nutrient-poor habitats was possibly caused by selection pressure. In such environments it might be a successful strategy to increase the time nutrients are resident in the plant (Berendse & Aerts, 1987; Aerts & Chapin, 1999). This can be achieved in part by increasing the life span of the leaves, which is correlated negatively with SLA (Reich, 1998). Mechanistically, this linkage could be explained by the accumulation of lignin and other secondary compounds in the leaves, which decrease the attractiveness to herbivores, as well as by investment in compounds and structures that facilitate survival

during dry, cold or otherwise unfavourable environmental conditions (Poorter & Garnier, 1999).

Possible evolutionary pressures leading to high SLA have received less attention in the ecological literature. Agricultural models show that before canopy closure there is an advantage in having a high SLA, both in terms of final yield in a monostand (Gutschick, 1988) and in competitive ability in a crop/weed situation (Spitters & Aerts, 1983). However, what happens after canopy closure? Obviously, in fast-developing vegetation competition for light is partly determined by the ability to position leaves high in the vegetation (Barnes *et al.*, 1990). Apart from the insertion point at which a leaf is developing, leaf angle (Hikosaka & Hirose, 1997) and amount of biomass invested in a given leaf, it is possible for the plant to modulate its SLA. Outcomes of the model presented here show that such an evolutionary pressure is possible. All else being equal, a monostand of plants that have distributed leaf nitrogen and area such that total carbon gain is maximized is susceptible to invasion by a species that can increase its SLA. The advantage of the invading species is not due directly to the fact that shade is cast on leaves lower in the vegetation, because this affects leaves of both the resident and invading species equally. Rather, it is the increased light interception resulting from enlargement of their leaves at each layer of the canopy that increases the carbon gain of the invaders (Gutschick & Wiegel, 1988). Moreover, by adjusting SLA they optimize their nitrogen economy, as will be discussed in the next section.

What is the upper limit of SLA? In the model, we constrained SLA indirectly, by setting a minimum nitrogen content per unit leaf area ($n_{a \, min}$). For a given nitrogen content per unit mass, SLA could at most increase until the nitrogen content per unit leaf area equalled $n_{a \, min}$. This seems justified from the perspective that a minimum amount of nitrogen (in the form of DNA, RNA, non-photosynthetic enzymes and other proteins) must be present before a leaf can start to fix carbon. A positive value for $n_{a \, min}$ is supported by a range of observations (Hirose & Werger, 1987; Field, 1988; Pons *et al.*, 1989, 1993) but not all (Evans, 1988). From a biomechanical perspective also, there must be an upper limit of SLA, to prevent a leaf from becoming too frail. At low irradiance SLA can occasionally exceed $80 \, m^2 \, kg^{-1}$ (Corré, 1983). However, these values seem to be extreme, found in experiments in glasshouses or growth rooms. Values for plants in nature are generally lower, at least partly because of more turbulent wind conditions, which decrease SLA (Woodward, 1983).

The effect of increased SLA in a given stand biomass is that LAI increases beyond the optimal value for canopy photosynthesis. This is shown for the numerical example (Fig. 3b), but can also be proved within the analytical framework of the model
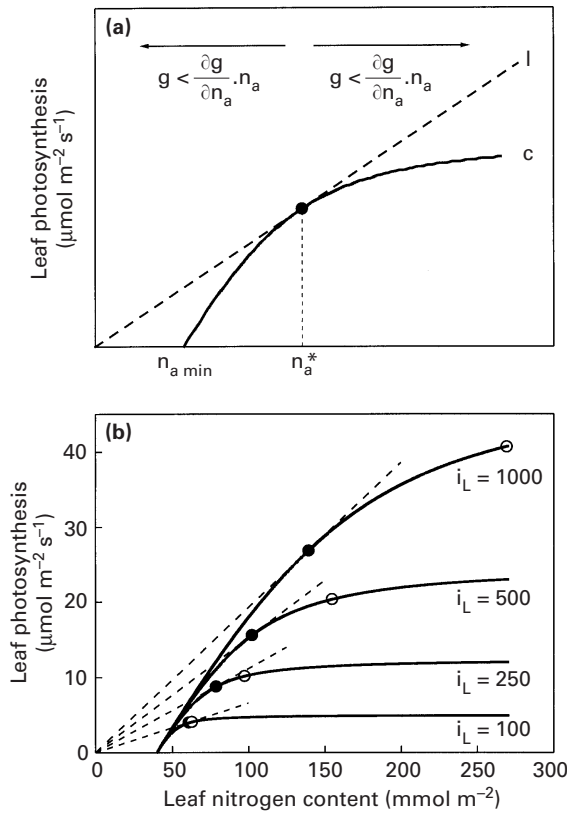
Fig. 5. (a) Continuous curve c; the rate of photosynthesis as a function of leaf nitrogen content per unit leaf area for an intermediate irradiance. Variable $n_{a\,min}$ is the threshold value for photosynthesis; n_a^* is the point at which photsynthetic nitrogen-use efficiency (PNUE) is maximal. At this point the broken line l is tangent to curve c. For more information see discussion section. (b) The rate of photosynthesis as a function of leaf nitrogen content per unit leaf area for leaves that experience different irradiances within the vegetation. Open circles, points at which leaves in the 'optimal' stand operate. Filled circles, leaves of a stand in the evolutionarily stable situation at the end of the game, where SLA is such that PNUE at leaf level is maximized.

(Schieving, 1998). It is in line with conclusions by several authors (Fig. 1b). We stress that the absolute increases in LAI shown in Fig. 3a are higher than expected. Our model is a simple one and is not aimed at realistically mimicking the development over time of a vegetation, including the carbon economy of stems and roots and the water economy of the stand. Rather, it is a framework in which we focus on qualitative trends that follow from some simple relations. Given the results of this game theory model, we suggest in plants growing in dense stands a selective pressure towards a relatively high SLA.

Distribution of nitrogen and maximization of photosynthetic nitrogen-use efficiency

Another phenomenon related to the carbon gain of vegetation is the distribution of nitrogen. In plants growing in dense stands the distribution of nitrogen is more skewed (with higher content per unit leaf area at the top than at the bottom) than in plants in open

stands. Therefore, one would expect that in the end situation of the leaf area game, when LAI has increased compared with that of the 'optimal' stand, nitrogen distribution would be more skewed. However, this is not so. As in observations in analyses of stands growing naturally, nitrogen distribution is less skewed (Hirose & Werger, 1987; Pons *et al.*, 1989; cf. De Pury & Farquhar, 1997) (Fig. 1a). How is this possible?

For plants growing naturally, several hypotheses have been put forward to explain this phenomenon. It might be that higher concentrations of nitrogen in top layers are physiologically not achievable, as there must be an upper limit to the amount of chlorophyll and protein contained in 1 g of plant material (Pons *et al.*, 1989). It could also be that there is a limitation to decreasing nitrogen in bottom layers. Retranslocation might not be possible, or the costs for retranslocation might be high and not met by the relatively small benefits (Field, 1983). Sunfleck penetration into the vegetation could increase the return on investment lower in the canopy (Terashima & Hikosaka, 1995; but see De Pury & Farquhar, 1995). Moreover, with potential herbivory at the top of the canopy an extra layer of leaves lower down would be valuable (Gutschick & Wiegel, 1988), requiring for its function a certain amount of nitrogen; consequently, distribution cannot be skewed too much.

Another explanation follows from the model and requires some insight into the relationship between photosynthesis and leaf organic nitrogen. The ratio between the two is the photosynthetic nitrogen-use efficiency (PNUE) (Field & Mooney, 1986; Evans, 1989) and is for a leaf at depth h in the vegetation given by:

$$\Pi(i_a^h, n_a^h) = g(i_a^h, n_a^h)/n_a^h \qquad \text{Eqn 13}$$

Of interest in this respect is how a dilution of the available nitrogen over a range of leaf areas affects PNUE. Fig. 5a shows an example of gross photosynthesis as a function of leaf nitrogen content per unit leaf area, at an intermediate irradiance, combining Eqns 1–3. Mathematically, the leaf nitrogen content at which PNUE is maximal can be found by differentiating PNUE with respect to n_a:

$$\frac{\partial \Pi(n_a^h)}{\partial n_a^h} = \frac{1}{(n_a^h)^2}\left[n_a^h \frac{\partial g(i_a^h, n_a^h)}{\partial n_a^h} - g(i_a^h, n_a^h)\right]. \qquad \text{Eqn 14}$$

Eqn 14 becomes zero at the nitrogen content at which $n_a \partial g/\partial n_a = g$. From Fig. 5a it can be shown that this must be where the straight line (l) through the origin is tangent to the curve (c). This is the point at which PNUE is maximal, n_a^* indicating the leaf nitrogen content at which this occurs.

How do these equations relate to the leaf-area game described earlier? In the description of the model, it was stated that variation in SLA had no effect any more when $n_a \partial g/\partial n_a = g$ at every canopy
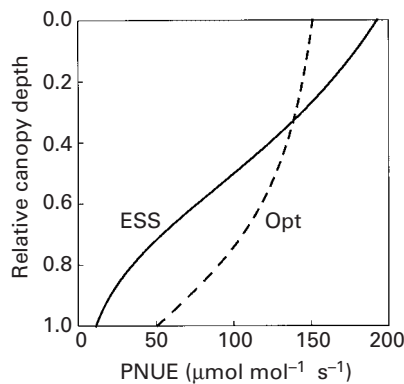
Fig. 6. *In situ* photosynthetic nitrogen-use efficiency (PNUE) as a function of the depth of the vegetation, for an optimal stand (Opt, broken line) and a stand in an evolutionarily stable situation at the end of the game (ESS, continuous line). For more detail see the Fig. 2 legend.

depth (Eqns 11, 12). This coincides exactly with the condition in which PNUE is at a maximum (Eqn 14). Therefore, within the model, a population that can resist invasion of leaf area players must have maximized PNUE for all its leaves.

A consequence of PNUE maximization is that nitrogen distribution of plants in these stands does not maximize the carbon gain of the canopy. A visual proof is given in Fig. 5b, where a family of curves, each representing a different irradiance, relates gross photosynthesis to nitrogen content per unit leaf area. Because leaves lower in the canopy experience low levels of light, photosynthesis curves saturate at low n_a levels, implying that the n_a^* for which PNUE reaches a maximum is lower for leaves at the bottom than at the top of the canopy (Fig. 5b, closed circles). However, it also implies that the slope $n_a \partial g / \partial n_a$ is different for the different layers. This is at variance with the condition formulated by Field (1983), that slopes should be equal at each depth in order to maximize canopy carbon gain. These operating points are indicated in Fig. 5b by the open circles. As shown by Hikosaka & Terashima (1995), differences between leaves that maximize PNUE and those that maximize carbon gain are very small at low irradiance but substantial at high irradiance. The consequence of the strategy of maximizing the PNUE of individual leaves is that the carbon gain of the stand is not maximal (Fig. 4b). This is the tragedy of the commons: the strategy that would maximize the carbon gain of all individual plants in the stand is not evolutionarily stable. Such a stand will be replaced by plants that play a different strategy, the end result being a stand in which total carbon gain is lower.

An implication of the lower carbon gain of the canopy at a given amount of leaf nitrogen per ground area is that the PNUE is lower in the evolutionarily stable situation at stand level. At first, this might be surprising, because we have concluded that the leaf area game is played up to the point at which PNUE

is maximized. However, it should be stressed that invaders maximize the PNUE of each leaf *for the light climate that they experience*. Stands in the end-game situation have higher LAI and consequently are characterized by lower light levels, especially low in the canopy (Fig. 2b). Consequently, at a given depth *h* the rate of photosynthesis of the lower leaves is less in the evolutionarily stable than in the optimal stand, as is PNUE (Fig. 6). This is not fully compensated for by higher PNUE in the upper part of the evolutionarily stable stand, thus PNUE of the whole stand decreases. The form of the photosynthesis–nitrogen relationship is crucial to this analysis. The family of curves shown in Fig. 5 has a threshold value for nitrogen content ($n_{a\,min}$), below which no photosynthesis would occur. If such a threshold did not exist, no SLA could be found for which PNUE is maximal and there would be a tendency to ever-increasing SLA. This is in line with simulations of Evans (1998), who showed that leaves with the lowest photosynthetic capacity per unit area and the highest SLA have the highest daily rate of photosynthesis per unit biomass.

Our model suggests a tendency for SLA and thereby PNUE of plants in dense vegetation to increase. Interestingly, in comparative experiments a strong correlation between SLA and PNUE is often found (Poorter & Evans, 1998); species with higher SLA also have higher PNUE. In plants grown in controlled conditions at intermediate light intensities the main reason is that nitrogen content per unit area in low-SLA species is high, resulting in high photosynthetic capacity. Because light is the limiting factor for photosynthesis in such an environment, part of the assimilatory machinery is not used, leading to low PNUE (Pons *et al.*, 1994; Poorter & Evans, 1998). In plants grown at high irradiance, additional factors play a role, but PNUE of low-SLA species would still increase if they were to spread their leaf biomass and nitrogen over a larger leaf area (Poorter & Evans, 1998).

Outlook

We stress that the model presented in this paper is a rather simplified representation of real vegetation. Although more complexity would not necessarily improve insight, we think that there are at least four points at which progress could be made. First, we assumed constant and uniform light conditions throughout the day. Changes in irradiance, the angle at which light penetrates the vegetation and the separation between direct and diffuse light can be of importance in determining the distribution of nitrogen within the canopy (Gutschick & Wiegel, 1988; Evans, 1998). Second, we did not consider differences in shoot height or leaf angle between the two species, factors known to have a strong effect on light competition (Barnes *et al.*, 1990; Hikosaka &

Hirose, 1997). Third, we assumed respiration to be directly dependent on nitrogen content, as found by Hirose *et al.* (1997), Anten *et al.* (1998) and Reich *et al.* (1998). However, at least part of night respiration is related to the amount of photosynthesis fixed during the preceding day (Ludwig *et al.*, 1975; Pons & Pearcy, 1994). Because leaves low in the vegetation operate close to the light-compensation point, the implication could be that their respiration rate is lower than would be expected on the basis of their nitrogen content. This in turn could imply that the net carbon gain of the canopy is underestimated at high LAIs (Ludwig *et al.*, 1965). A fourth point is that we focused on the 24-h carbon gain of a stand with a given amount of leaf nitrogen. Inclusion of the real growth process, including turnover of leaves, might yield further insights. However, the consequence of including these processes into the model would be that results could be obtained only by means of numerical simulations rather than by a relatively simple analytical solution.

CONCLUSIONS

The model formulated here shows the tragedy of the commons: plants that distribute their nitrogen at a given stand biomass in such a way that canopy photosynthesis is maximized are outcompeted by plants that follow a different strategy. Within the framework of the model, an evolutionarily stable strategy is achieved by increasing SLA to the point at which PNUE is maximized for each individual leaf. Consequences at stand level are that LAI is higher and nitrogen distribution less skewed than in a canopy in which carbon gain is maximized. Therefore, canopy carbon gain as well as carbon gain of the individual plants are lower.

ACKNOWLEDGEMENTS

REFERENCES

Aerts R, Chapin FS. 1999. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*. (In press).

Anten NPR, Schieving F, Medina E, Werger MJA, Schuffelen P. 1995a. Optimal leaf area indices in C_3 and C_4 mono- and dicotyledonous species at low and high nitrogen availability. *Physiologia Plantarum* **95**: 541–550.

Anten NPR, Schieving F, Werger MJA. 1995b. Patterns of light and nitrogen distribution in relation to whole canopy carbon gain in C_3 and C_4 mono- and dicotyledonous species. *Oecologia* **101**: 504–513.

Anten NPR, Werger MJA, Medina E. 1998. Nitrogen distribution and leaf area indices in relation to photosynthetic nitrogen use efficiency in savanna grasses. *Plant Ecology* **138**: 63–75.

Barnes PW, Beyschlag W, Ryel R, Caldwell MM, Flint SD. 1990. Plant competition for light analysed with a multispecies canopy model. III. Influence of canopy structure in mixtures and monocultures of wheat and wild oat. *Oecologia* **82**: 560–566.

Berendse F, Aerts R. 1987. Nitrogen-use efficiency: a biologically meaningful definition? *Functional Ecology* **1**: 293–296.

Corré WJ. 1983. Growth and morphogenesis of sun and shade plants. III. The combined effects of light intensity and nutrient supply. *Acta Botanica Neerlandica* **32**: 277–294.

De Pury DGG, Farquhar GD. 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant Cell and Environment* **20**: 537–557.

Evans JR. 1988. Acclimation by the thylakoid membranes to growth irradiance and the partitioning of nitrogen between soluble and thylakoid proteins. *Australian Journal of Plant Physiology* **15**: 93–106.

Evans JR. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* **78**: 9–19.

Evans JR. 1993. Photosynthetic acclimation and nitrogen partitioning within a lucerne canopy. II. Stability through time and comparison with a theoretical optimum. *Australian Journal of Plant Physiology* **20**: 69–82.

Evans JR. 1998. Photosynthetic characteristics of fast- and slow-growing species. In: Lambers H, Poorter H, Van Vuuren MMI, eds. *Inherent variation in plant growth. Physiological mechanisms and ecological consequences*. Leiden, The Netherlands: Backhuys, 101–119.

Farquhar GD, Von Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* **149**: 78–90.

Field CB. 1983. Allocating leaf nitrogen for maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* **56**: 348–355.

Field CB. 1988. On the role of photosynthetic responses in constraining the habitat distribution of rainforest plants. *Australian Journal of Plant Physiology* **15**: 343–358.

Field C, Mooney HA. 1986. The photosynthesis–nitrogen relationship in wild plants. In: Givnish TJ, ed. *On the economy of form and function*. Cambridge, UK: Cambridge University Press, 25–55.

Gutschick VP. 1988. Optimization of specific leaf mass, internal CO_2 concentration, and chlorophyll content in crop canopies. *Plant Physiology and Biochemistry* **26**: 525–537.

Gutschick VP, Wiegel FW. 1988. Optimizing the canopy photosynthetic rate by patterns of investment in specific leaf mass. *American Naturalist* **132**: 67–86.

Hikosaka K, Hirose T. 1997. Leaf angle as a strategy for light competition: optimal and evolutionary stable light-extinction coefficient within a leaf canopy. *Ecoscience* **4**: 501–507.

Hikosaka K, Terashima I. 1995. A model of the acclimation of photosynthesis in the leaves of C_3 plants to sun and shade with respect to nitrogen use. *Plant Cell and Environment* **18**: 605–616.

Hirose T, Ackerly DD, Traw MB, Ramseier D, Bazzaz FA. 1997. CO_2 elevation, canopy photosynthesis, and optimal leaf area index. *Ecology* **78**: 2339–2350.

Hirose T, Werger MJA. 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern. *Oecologia* **72**: 520–526.

Leuning R, Wang YP, Cromer RN. 1991. Model simulations of spatial distributions and daily totals of photosynthesis in *Eucalyptus grandis* canopies. *Oecologia* **88**: 494–503.

Ludwig LJ, Saeki T, Evans LT. 1965. Photosynthesis in artificial communities of cotton plants in relation to leaf area. I. Experiments with progressive defoliation of mature plants. *Australian Journal of Biological Sciences* **18**: 1103–1118.

Ludwig LJ, Charles-Edwards DA, Withers AC. 1975. Tomato leaf photosynthesis and respiration in various light and carbon dioxide environments. In: Marcelle R, ed. *Environmental and biological control of photosynthesis*. The Hague, The Netherlands: Junk, 29–36.

Maynard Smith J. 1982. *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press.

Monk CD. 1966. An ecological significance of evergreenness. *Ecology* **47**: 504–505.

Monsi M, Saeki T. 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine bedeutingen für die Stoffproduktion. *Japanese Journal of Botany* **14**: 22–52.

Pons TL, Pearcy RW. 1994. Nitrogen reallocation and photosynthetic acclimation in response to partial shading in soybean plants. *Physiologia Plantarum* **92**: 636–644.

Pons TL, Schieving F, Hirose T, Werger MJA 1989. Optimization of leaf nitrogen allocation for canopy photosynthesis in *Lysimachia vulgaris*. In: Lambers H, Cambridge ML, Konings H, Pons SPB, eds. *Causes and consequences of variation in growth rate and productivity of higher plants*. The Hague, The Netherlands: Academic Publishing, 175–186.

Pons TL, Van der Werf A, Lambers H. 1994. Photosynthetic nitrogen use efficiency of inherently slow- and fast-growing species: possible explanations for observed differences. In: Roy J, Garnier SPB, eds. *A whole plant perspective on carbon–nitrogen interactions*. The Hague, The Netherlands: Academic Publishing, 71–77.

Pons TL, Van Rijnberk H, Van der Werf A. 1993. Importance of the gradient in photosynthetically active radiation in a vegetation stand for leaf nitrogen allocation in two monocotyledons. *Oecologia* **95**: 416–424.

Poorter H, De Jong R. 1999. Specific leaf area, chemical composition and leaf construction costs of plant species from productive and unproductive habitats. *New Phytologist* **143**: 000–000.

Poorter H, Evans JR 1998. Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia* **116**: 26–37.

Poorter H, Garnier E. 1999. Ecological significance of inherent variation in relative growth rate. In: Pugnaire FI, Valladares F, eds. *Handbook of functional plant ecology*. New York, USA: Marcel Dekker 81–120.

Reich PB. 1998. Variation among plant species in leaf turnover rates and associated traits: implications for growth at all life stages. In: Lambers H, Poorter H, Van Vuuren MMI, eds. *Inherent variation in plant growth. Physiological mechanisms and ecological consequences*. Leiden, The Netherlands: Backhuys, 467–487.

Reich PB, Walters MB, Ellsworth DS, Vose JM, Volin JC, Gresham C, Bowman WD. 1998. Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and life-span: a test across biomes and functional groups. *Oecologia* **114**: 471–482.

Schieving, F. 1998. *Plato's plant: on the mathematical structure of simple plants and canopies*. Leiden, The Netherlands: Backhuys.

Schieving F, Pons TL, Werger MJA, Hirose T. 1992a. The vertical distribution of nitrogen and photosynthetic activity at different plant densities in *Carex acutiformis*. *Plant and Soil* **142**: 9–17.

Schieving F, Werger MJA, Hirose T. 1992b. Canopy structure, nitrogen distribution and whole canopy photosynthetic carbon gain in growing and flowering stands of tall herbs. *Vegetatio* **102**: 173–181.

Spitters CJT, Aerts R. 1983. Simulation of competition for light and water in crop–weed associations. *Aspects of Applied Biology* **4**: 467–483.

Terashima I, Hikosaka K. 1995. Comparative ecophysiology of leaf and canopy photosynthesis. *Plant Cell and Environment* **18**: 1111–1128.

Werger MJA, Hirose T. 1991. Leaf nitrogen distribution and whole canopy photosynthetic carbon gain in herbaceous stands. *Vegetatio* **97**: 11–20.

Woodward FI. 1983. The significance of interspecific differences in specific leaf area to the growth of selected herbaceous species from different altitudes. *New Phytologist* **95**: 313–323.

APPENDIX I. A FORMAL DERIVATION OF THE PHOTOSYNTHETIC ADVANTAGE OF THE INVADING SPECIES I

The difference in net carbon gain between the plants of invading species I and the average plant in the stand is given by:

$$C_{TI}^{\delta} - C_{TA}^{\delta} = C_{TI}^{\delta} - \phi_R C_{TR}^{\delta} - \phi_I C_{TI}^{\delta}$$
$$= (1 - \phi_I) C_{TI}^{\delta} - \phi_R C_{TR}^{\delta}$$
$$= \phi_R (C_{TI}^{\delta} - C_{TR}^{\delta}) \qquad \text{Eqn 15}$$

Expanding the above expression gives:

$$C_{TI}^{\delta} - C_{TA}^{\delta} = \phi_R \int_0^{h_T} \mathrm{d}h\, m^h \sigma^h \left[(1+\delta) g\left(i_a^h, \frac{n_a^h}{1+\delta}\right) - g(i_a^h, n_a^h) \right] \qquad \text{Eqn 16}$$

Here σ^h and n_a^h are the SLA and nitrogen content per unit leaf area of species R plants. The nitrogen content of the I plants can be written as:

$$n_{aI}^h = n_a^h(\delta) = n_a^h/(1+\delta) \qquad \text{Eqn 17}$$

It should be noted that the respiration rates disappear from the expression $C_{TI} - C_{TA}$ and that the $(1+\delta)$ variation affects the total leaf area, the nitrogen content per unit leaf area and the irradiance at the leaf level.

Because δ is small, we can write:

$$C_{TI}^{\delta} - C_{TA}^{\delta} = \frac{\mathrm{d}}{\mathrm{d}\delta}(C_{TI}^{\delta} - C_{TA}^{\delta})|_{\delta=0} \cdot \delta \qquad \text{Eqn 18}$$

Interchanging differentiation and integration gives:

$$\frac{\mathrm{d}}{\mathrm{d}\delta}(C_{TI}^{\delta} - C_{TA}^{\delta})\bigg|_{\delta=0} = \phi_R \int_0^{h_T} \mathrm{d}h\, m^h \sigma^h \times$$
$$\frac{\mathrm{d}}{\mathrm{d}\delta}\left[(1+\delta) g\left(i_a^h(\delta), \frac{n_a^h}{1+\delta}\right) - g(i_a^h(\delta), n_a^h) \right]\bigg|_{\delta=0}. \qquad \text{Eqn 19}$$

Expanding the derivative $\mathrm{d}/\mathrm{d}\delta\,[..]$ in the integrand part of Eqn 19 gives:

$$\frac{\mathrm{d}}{\mathrm{d}\delta}[..] = g\left(i_a^h(\delta), \frac{n_a^h}{1+\delta}\right) + (1+\delta)\frac{\mathrm{d}}{\mathrm{d}\delta} g\left(i_a^h(\delta), \frac{n_a^h}{1+\delta}\right)$$
$$- \frac{\mathrm{d}}{\mathrm{d}\delta} g(i_a^h(\delta), n^h). \qquad \text{Eqn 20}$$

By the chain rule:

$$\frac{\mathrm{d}}{\mathrm{d}\delta} g\left(i_a^h(\delta), \frac{n_a^h}{1+\delta}\right) = \frac{\partial g^h}{\partial i_a^h}\frac{\mathrm{d}i_a^h}{\mathrm{d}F^h}\frac{\mathrm{d}F^h}{\mathrm{d}\delta} - \frac{\partial g^h}{\partial n_a}\frac{n_a^h}{(1+\delta)^2}, \qquad \text{Eqn 21}$$

This gives for Eqn 20, evaluated at $\delta = 0$:

$$\frac{\mathrm{d}}{\mathrm{d}\delta}[..]|_{\delta=0} = g(i_a^h, n_a^h) + \frac{\partial g(i_a^h, n_a^h)}{\partial i_a^h}\frac{\mathrm{d}i_a^h}{\mathrm{d}F^h}\frac{\mathrm{d}F^h}{\mathrm{d}\delta}\bigg|_{\delta=0}$$
$$- \frac{\partial g(i_a^h, n_a^h)}{\partial n_a} n_a^h - \frac{\partial g(i_a^h, n_a^h)}{\partial i_a^h}\frac{\mathrm{d}i_a^h}{\mathrm{d}F^h}\frac{\mathrm{d}F^h}{\mathrm{d}\delta}\bigg|_{\delta=0}$$
$$= g(i_a^h, n_a^h) - \frac{\partial g(i_a^h, n_a^h)}{\partial n_a} n_a^h. \qquad \text{Eqn 22}$$

Substitution of the above expression into Eqn 19 gives:

$$\frac{\mathrm{d}}{\mathrm{d}\delta}(C_{TI}^{\delta} - C_{TA}^{\delta})|_{\delta=0} =$$
$$\phi_R \int_0^{h_T} \mathrm{d}h\, m^h \sigma^h \left[g(i_a^h, n_a^h) - \frac{\partial g(i_a^h, n_a^h)}{\partial n_a} n_a^h \right], \qquad \text{Eqn 23}$$

As pointed out in the main text, if this integral is positive, the invading plants will outcompete the resident plants.