REVIEW

# Optimal Photosynthetic Characteristics of Individual Plants in Vegetation Stands and Implications for Species Coexistence

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● *Aims* This paper reviews the way optimization theory has been used in canopy models to analyse the adaptive significance of photosynthesis-related plant characteristics and their consequences for the structure and species composition of vegetation stands.
● *Scope* In most studies simple optimization has been used with trait values optimal when they lead to maximum whole-stand photosynthesis. This approach is subject to the condition that the optimum for one individual is independent of the characteristics of its neighbours. This seems unlikely in vegetation stands where neighbour plants strongly influence each other's light climate. Not surprisingly, there are consistent deviations between predicted plant traits and real values: plants tend to be taller, distribute nitrogen more evenly among their leaves and produce more leaf area which is projected more horizontally than predicted by models.
● *Conclusions* By applying game theory to individual plant-based canopy models, other studies have shown that optimal vegetation stands with maximum whole-stand photosynthesis are not evolutionarily stable. They can be successfully invaded by mutants that are taller, project their leaves more horizontally or that produce greater than optimal leaf areas. While these individual-based models can successfully predict the canopy structure of vegetation stands, they are invariably determined at unique optimal trait values. They do not allow for the co-existence of more than one species with different characteristics. Canopy models can contribute to our understanding of species coexistence through (*a*) simultaneous analysis of the various traits that determine light capture and photosynthesis and the trade-offs between them, and (*b*) consideration of trade-offs associated with specialization to different positions in the niche space defined by temporal and spatial heterogeneity of resources.   © 2004 Annals of Botany Company

**Key words:** Agricultural productivity, canopy structure, game theory, leaf area index, light, nitrogen, optimization, photosynthesis, species co-existence.

## INTRODUCTION

One of the long-standing challenges in plant biology is the development of a quantitative theoretical framework for scaling from organ-level processes to individual plant form and growth and from there to the structure and productivity of vegetation stands. This understanding is important in agriculture and global change biology, where it is instrumental in predicting how changes at the organ-level, e.g. effects of $CO_2$ elevation on leaf photosynthesis, may translate into changes in the productivity at the stand level. But it is also important in ecology, which seeks to understand how certain physiological and structural traits enable plants to photosynthesize, grow and compete with neighbours, and how these processes at the individual level in turn determine the structure and species composition of vegetation.

Canopy models have long been used to quantitatively relate the leaf area distribution and leaf photosynthetic characteristics of plants to their net photosynthetic carbon gain. Most of these canopy models, however, estimate daily carbon gain at the level of the stand, i.e. per unit soil area and not at the level of the individual plants within the stand (stand-based models *vs.* individual-based models, hereafter). These stand-based models are now widely used to estimate whole-stand canopy carbon gain and to determine

the characteristics that would maximize canopy carbon gain (e.g. Monsi and Saeki, 1953; Saeki, 1960; Hirose and Werger, 1987; Anten *et al.*, 1995*a*, *b*). In agronomy they form the basis of crop growth models (e.g. de Wit, 1965; Goudriaan and van Laar, 1994), which are useful for determining optimal crop characteristics that maximize per unit land area yields (see van Ittersum *et al.*, 2003). Yet the use of stand-based models implicitly makes two assumptions that are not realistic (see Anten and Hirose, 2001): (1) that the performance of one individual is independent of characteristics of its neighbours—this entirely ignores competitive interactions between plants; (2) that vegetation stands are summations of close to identical individuals—this ignores the fact that most vegetation stands consist of many species that differ from each other in stature, leaf distribution and leaf photosynthesis.

More recently, crop and plant growth modellers have developed models that estimate light capture and photosynthesis of individual plants in stands (e.g. Barnes *et al.*, 1990; Kropff and Spitters, 1991; Shugart *et al.*, 1992; Hikosaka *et al.*, 1999; Anten and Hirose, 2001, 2003). This review discusses how such individual-based models have yielded new insights into the relationship between characteristics of individual plants and the structure, productivity and coexistence of multiple species in vegetation stands. It starts with a brief but critical appraisal of the use of the optimization theory in canopy studies. It then shortly

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reviews whole-stand-based canopy photosynthesis models and will focus on the conclusions that can be drawn from such models regarding the optimal stand characteristics for maximum whole-canopy carbon gain. The next part deals with models that analyse photosynthesis of individuals in mono-species stands. It will focus on the use of competitive optimization in photosynthesis models to determine evolutionarily stable strategies, making the point that stands with optimal characteristics for maximum carbon gain are not evolutionarily stable. The final section discusses the possibilities of extending optimization analyses in canopy models of multi-species stands such that they can predict co-existence between species.

## THE USE OF OPTIMIZATION THEORY IN CANOPY MODELS

A frequently used approach in canopy modelling is the application of the optimization theory. This review will deal extensively with this use of the optimization theory and the concept will therefore be briefly discussed. The definition of optimization is: 'making the best or most effective use of a situation, opportunity or resource'. Most optimization studies in canopy research define 'use of' as the use of some kind of resource, light, nitrogen or water, and consider this use to be 'most effective' when net daily carbon gain is maximal. The reason for this definition of 'most effective' is that photosynthesis provides the structural substrates for growth and reproduction and that plants with a high carbon gain should have the greatest amount of resources with which to compete for additional water, light and nutrients (Givnish, 1982). But assuming maximum photosynthesis as most effective is, of course, a simplification of reality; many other factors may determine the lifetime performance of a plant. In general, the application of optimization to natural systems has been criticized, as being too anthropomorphic; why should plants follow our design of what is best or most effective (Chen *et al.*, 1993; Kull and Jarvis, 1995)? It should therefore be emphasized that optimization is simply a mathematical assessment of marginal gains and that by applying it in canopy research one cannot make the claim that all plants are designed to maximize their carbon gain. It should be used strictly as a null hypothesis to analyse the adaptive significance of photosynthesis-related characteristics of plants.

## WHOLE-STAND CANOPY PHOTOSYNTHESIS MODELS: THE CASE OF SIMPLE OPTIMIZATION

### Optimal vegetation stands under light limitation

Monsi and Saeki (1953) were the first to apply optimization theory to leaf area distribution in vegetation. They determined that whole-stand canopy photosynthesis is maximized if the total amount of leaf area per unit soil area (leaf area index, LAI) of a stand is such that the leaves in the lowest part of the canopy receive an amount of light that is equal to their light compensation point (see also Hirose, 2005). From this they determined that, under low-light conditions, canopies should have a small LAI, consisting of horizontally oriented leaves in a manner to minimize self-shading, whereas the optimal strategy in high-light environments is to have steeply inclined leaves with a large LAI (Saeki, 1960). This idea can be expanded to consider the optimal crown structure of trees: shaded trees should have broad shallow crowns where leaves are arranged in a single planar array while, in sunny sites, crowns should be deeper and narrower (Horn, 1971; King, 1991).

As predicted, under high-light conditions plants tend to form stands with a relatively large LAI, while under low light conditions canopies of plants tend to be mono-layered and tend to have horizontally projected leaves (see Hirose, 2005). Contrary to these predictions, however, studies on tropical forests found that later successional shade-tolerant species formed deeper canopies with more leaf layers (Sterck *et al.*, 2001) and a greater LAI (Kitajima *et al.*, 2005) than early successional ones. Also, even under highly illuminated conditions, stands may have LAIs that are well below the optimum, particularly where soil resources are limiting. The prediction that, in stands with high LAI, vertical leaves would be favourable for photosynthesis was verified in experiments where leaf angles were manipulated (Monsi *et al.*, 1973). Nevertheless many plant species with horizontal leaves form dense stands with high extinction coefficients under high-light conditions (Hikosaka and Hirose, 1997; Kitajima *et al.*, 2005).

### Optimal nitrogen use for photosynthesis

The analyses described above assume that light availability is the primary limiting resource that constrains photosynthetic performance. However, many factors may limit photosynthetic productivity, one of the most important of these being nitrogen availability. A large proportion of nitrogen in leaves is incorporated into photosynthesis-related enzymes (Evans, 1989) and leaves with higher leaf N contents also have higher photosynthetic rates (Field and Mooney, 1986). In view of this, the idea has been proposed that plant canopies might be designed to maximize photosynthesis for a given amount of N allocated to leaves ($N_{canopy}$) (Mooney and Gulmon, 1979).

A large number of studies have investigated patterns of leaf nitrogen distribution within plant canopies (see also Hirose, 2005). It was theoretically determined that the optimal $N_{area}$ distribution for maximum whole-stand carbon gain per unit nitrogen, should follow the light gradient in the canopy such that $N_{area}$ is highest at the well-illuminated part of the canopy (Field, 1983; Sellers *et al.*, 1992; Anten *et al.*, 1995a; Sands, 1995). In accordance with this prediction, actual stands of vegetation were found to exhibit strongly non-uniform N distribution patterns in stands of various species (e.g. Werger and Hirose, 1991; Anten *et al.*, 2000). In all cases, model calculations estimated that N distribution resulted in a considerable (1–42 %) enhancement of canopy photosynthesis compared with the uniform distribution in which $N_{area}$ of all leaves equals the mean (Fig. 1).
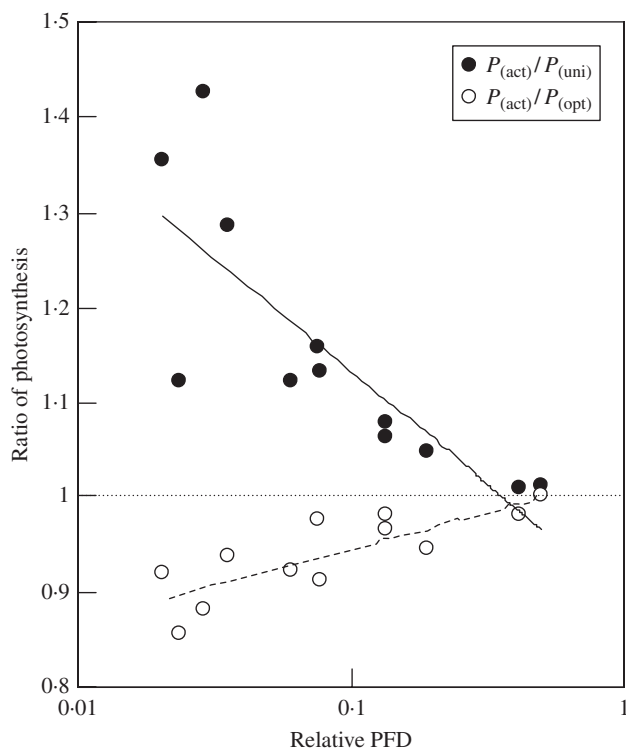
FIG. 1. The ratio between canopy photosynthesis for the actual and the uniform nitrogen distribution ($P_{(act)}/P_{(uni)}$) and the ratio between the canopy photosynthesis at the actual and optimal nitrogen distribution ($P_{(act)}/P_{(opt)}$) as a function of the relative PFD below the canopy (log scale). Data were taken from Field (1983), Hirose and Werger (1987), Schieving *et al*. (1992*a*, *b*) and Anten *et al*. (1995*a*, *b*).
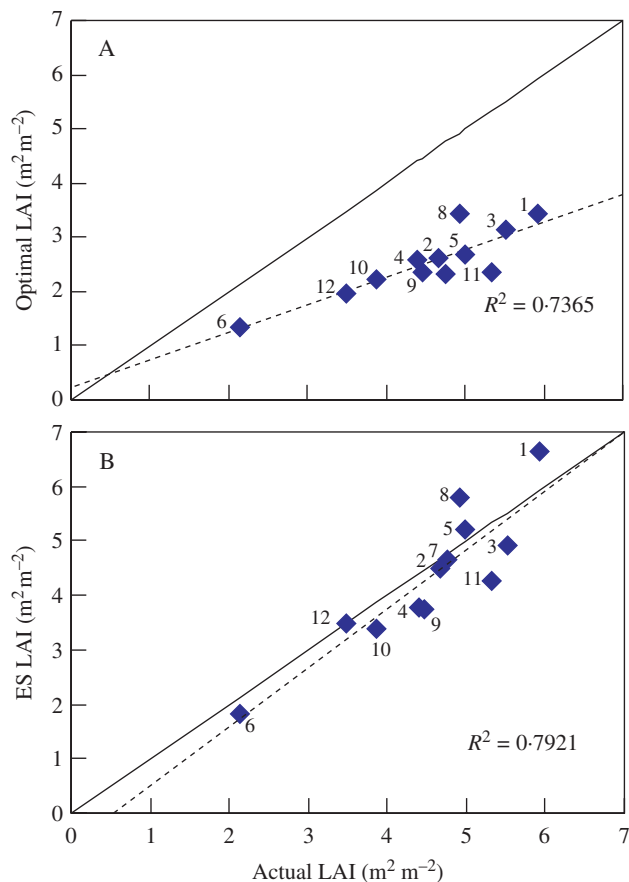


FIG. 2. (A) Optimal (optimal LAI) and (B) evolutionarily stable leaf area indices (ES LAI) plotted against the LAI actually measured. Solid lines indicate 1:1 correspondence and dashed lines linear regressions. Numbers indicate: 1 and 2, *Sorghum bicolor* high and low N availability; 3 and 4, *Oryza sativa* high and low N availability; 5 and 6 *Amaranthus cruentus* high and low N availability; 7, *Glycine max*; 8, *Leersia hexandra*; 9, *Hymenachne amplexicaulis*; 10, *Paspalum fasciculatum*; 11 and 12, *Hyparrhenia rufa* dense and open stand [raw data taken from Anten *et al*. (1995*b*) for 1–7, from Anten *et al*. (1998) for 8–12]. Figure redrawn from Anten (2002).

However, there were systematic differences between predicted and measured N distributions; all the measured N distribution patterns were considerably more uniform than the calculated optimal patterns. Leaf N contents at the top of the canopy were generally 30–60 % lower than those predicted by the model, and canopy photosynthesis calculated for the actual distributions was 5–14 % lower than estimated maximum rates (e.g. Hirose and Werger, 1987; Schieving *et al*., 1992*a*, *b*; Anten *et al*., 1995*a*; Fig. 1).

Canopy photosynthesis per unit nitrogen does not only depend on the way nitrogen is distributed among leaves but also on the total amount of leaf area (the LAI) of the stand. By increasing their leaf area, plants increase the amount of light captured and thus their photosynthesis. But if the total of leaf N in the canopy ($N_{canopy}$) is restricted, then this increase implies that the average leaf N content per unit area ($N_{area(av)}$; $N_{area(av)} = N_{canopy}/LAI$) and associated photosynthetic capacities of leaves are also reduced. Theoretically it was shown that there is consequently an optimal LAI (and $N_{area}$), beyond which a further increase in light capture no longer compensates for the lower photosynthetic capacities and canopy photosynthesis is maximized (Anten *et al*., 1995*b*). Furthermore, plants with a high potential leaf-level PNUE (photosynthetic nitrogen use efficiency, i.e. photosynthetic capacity for a given $N_{area}$) should produce higher LAIs for a given $N_{canopy}$ and thus have lower $N_{area}$ than those with low leaf PNUEs, and plants with horizontal

leaves producing stands with high extinction coefficients for light should produce less leaf area per unit $N_{canopy}$ and have higher $N_{area}$ than those with vertical leaves (Anten *et al*., 1995*b*). In accordance with these predictions, plants with the C$_4$ photosynthetic pathway were found to have higher leaf-PNUEs and to produce more leaf area for a given amount of nitrogen than C$_3$ plants, while dicotyledonous plants had more horizontal leaves and less leaf area for a given amount of N than monocots (Sage and Pearcy, 1987; Anten *et al*., 1995*b*, 1998). When the data for a number of species were combined there was a strong correlation ($r^2 = 0.73$) between the predicted optimal LAI and N$_{area}$ values and the measured ones; suggesting that the model for optimal LAI explained >70 % of the variation in leaf area production between species (Fig. 2A). The model was also well able to predict the effects of elevated CO$_2$ on LAI (Hirose *et al*., 1997; Anten *et al*., 2004). Yet, while observed trends generally match the prediction by the optimization theory, real LAI values are consistently larger and N$_{area}$ values lower than the predicted optima (Fig. 2A) and canopy photosynthesis at actual LAI

was estimated to be 2–20 % lower than the maximum values (Schieving *et al*., 1992*a*; Anten *et al*., 1995*b*, 1998, 2004; Hirose *et al*., 1997; Anten and Hirose, 2001).

In short, while the models for optimal stand characteristics for maximizing whole stand net photosynthesis make reasonably good predictions of the general trends that can be observed, there are important and consistent differences between predictions and actually measured values. A number of reasons have been proposed to explain these differences (see Anten *et al*., 2000). Mostly these reasons refer to simplifying assumptions in the models. For example, the models do not take into account the additional costs of root and stem biomass associated with leaf area production (Givnish, 1988). The models also do not consider the energy costs of N distribution included (Field, 1983), while none of them, with one exception (Stockhoff, 1994), consider leaf herbivory. Including these aspects would surely make the models more realistic and could in principle contribute to better predictions. However, the more essential reason for the consistent deviations between actual and optimal may lie in the optimization criterion to maximize photosynthesis at the stand level rather than at the individual plant level as explained in detail in the next section.

## MONO-SPECIES INDIVIDUAL-BASED CANOPY PHOTOSYNTHESIS MODELS: IS CANOPY STRUCTURE THE RESULT OF A GAME?

In the models discussed so far, optimal stand characteristics were defined as those that maximize canopy photosynthesis or canopy PNUE of the stand per unit of soil area. However, stands of vegetation consist of individual plants. Thus the above definition implicitly assumes that characteristics that maximize fitness of individuals within a stand are manifested as optimal characteristics at the stand level. This in turn is subject to the condition that the optimum for one individual is independent of the characteristics of its neighbours (i.e. the condition for simple optimization; Parker and Maynard-Smith, 1990). It is very unlikely that this holds true for dense stands of vegetation, where plants grow closely together and strongly influence the amounts of light, water and nutrients that come available to their neighbours. It is therefore more appropriate to analyse canopy characteristics in terms of density dependent optimization or evolutionarily stable strategies (ESSs; Maynard-Smith, 1974; Parker and Maynard-Smith, 1990).

### Plant height

Plant height is one of the most obviously density-dependent characteristics of plants. Height growth involves costs. As height increases, plants have to invest disproportionate amounts of biomass in support structures (stems, branches and petioles) to maintain mechanical stability (McMahon, 1973). As a consequence, the fractional allocation of biomass to leaves generally decreases with height (Givnish, 1982; Anten and Hirose, 1998, 1999). Thus, whole-stand net carbon gain for a given combination of LAI and leaf angles would be maximized when plants are short because

this entails a relatively high allocation of resources to leaves. Yet, within such a population, any mutant plant can increase its carbon gain by growing slightly taller, and by placing its leaves above those of its neighbours. The higher carbon gain of the mutant will enable it to grow and reproduce more and eventually invade the population. With a very simple canopy model, Givnish (1982) derived that this process of mutant invasion will repeat itself until the added benefits of increased height no longer compensate for the added costs. At this stage a stable equilibrium canopy height, i.e. an ESS, is achieved at which no individual plant can increase its carbon gain by changing its height.

The ESS canopy height increases when plants strongly influence each other's light climate (Givnish, 1982; Iwasa *et al*., 1984). Such a strong interaction will occur when plants grow closely together in crowded stands and when individual plants produce large leaf areas, which will happen in productive environments with high soil fertility (Lambers *et al*., 1990; Anten *et al*., 1995*b*). On the other hand, in a more open stand, with little interaction between the canopies of neighbouring plants, the increase in photosynthesis with plant height will be negligible and shorter stature should be favoured (Givnish, 1982; Iwasa *et al*., 1984; Sakai, 1991). Short stature should also be favoured in a situation where the cost of height growth, the necessary increased investment of resources in support structures, is large (Givnish, 1982). This situation arises, for example, when plants grow in windy environments where they experience strong mechanical loadings (Telewski and Pruyn, 1998).

These predictions are all consistent with real observations. Particularly the increase in plant height with increasing density has been well documented (see Schmitt *et al*., 1999); plants typically produce longer and thinner stems when they grow in the proximity of neighbours through phytochrome-mediated responses. The prediction that taller individuals should have higher fitness in crowded stands while shorter individuals should do better in sparser vegetation (Givnish, 1982; Iwasa *et al*., 1984) has also been verified experimentally (Dudley and Schmitt, 1996).

The idea of density-dependent height growth can be expanded to include the basic architecture of plants. High-density sites should favour an architectural design that allows plants to grow tall at the lowest costs of construction or support. This could be achieved though the production of a vertical stem and restricted horizontal branching (Koyama, 1987; King, 1991; Sakai, 1991). On the other hand, low-density sites would favour an architecture that involves simply a minimal investment in support. This can be achieved, for example, by producing a rosette or a creeping stem (Sakai, 1991).

### Leaf angle

As noted above, under high light conditions, whole-stand canopy photosynthesis would be maximized if plants had vertically inclined leaves that facilitate penetration of light to lower canopy layers. Yet, it was also noted that many
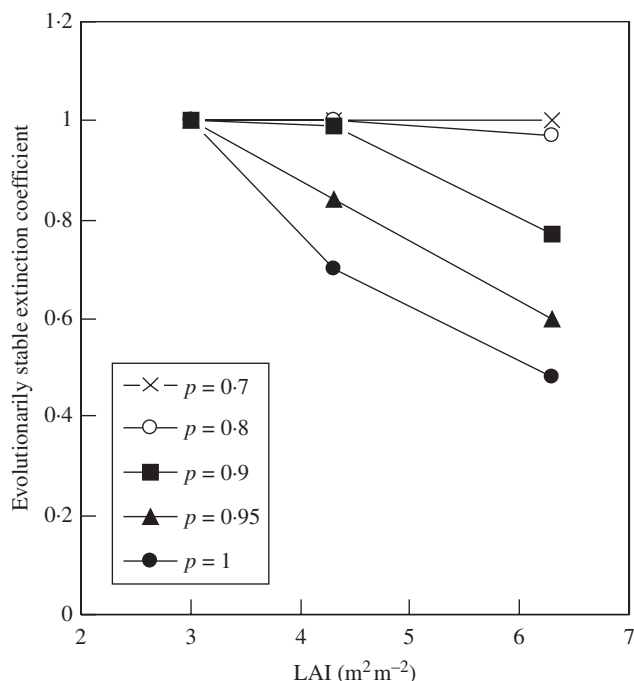
Fɪɢ. 3. Effects of *p*, the degree to which plants determine their own light climate, and LAI on the evolutionarily stable extinction coefficient for light. Redrawn from Hikosaka and Hirose (1997).

plants that form dense canopies at sunny sites, tend to have horizontal leaves. Why is this? A similar argumentation as in the case of optimal stature could apply here as well. Assume a stand in which all plants have vertical leaves such that whole-canopy carbon gain is maximized. This stand can be successfully invaded by a mutant, that displays leaves more horizontally above its competitors, because it can capture more of the available light and thus increase its carbon gain at the expense of others. The difference in photosynthesis would result in relatively higher growth and reproductive rates of the mutant, enabling it to invade the population. This process would repeat itself until there is a stable situation where no change in leaf angle gives any advantage in terms of photosynthesis; the leaf angle distribution and associated extinction coefficient of the stand would be evolutionarily stable.

Hikosaka and Hirose (1997) devised a canopy model with which they analysed the effect of leaf angle distribution on competition between plants. They explicitly considered the degree of interaction between individuals in the stand by introducing the parameter *p*, which denotes the degree to which the light environment experienced by a plant is determined, either by its own leaves or that of its neighbours. A *p* value of 1 (*p* ranges between 0 and 1) means that plants only influence their own light climate, while a very low *p* means that the light climate of plants is mostly determined by their neighbours.

They showed that, in most vegetation stands, horizontal leaves would be evolutionarily stable. The only exception would be formed by stands with minimal interaction between plant canopies (*p* ≥ 0·9) or a very high LAI (Fig. 3). High *p* values might be expected in plants with broad canopies such as large trees. On the other hand, plants

with narrow canopies such as herbaceous plants probably have relatively low *p* values. For example, Hikosaka *et al.* (2001) estimated that, in dense stands of the herbaceous annual *Xanthium canadense*, only about 30 % of the light gradient that plants experienced was caused by self-shading (*p* ≈ 0·3). Interestingly, *X. canadense* tends to have horizontally projected leaves and forms stands with high K values (Anten and Hirose, 1998, 2001). Unfortunately, there are no other data available of light interference in canopies, so an assessment of whether the predicted relationship between leaf angle distribution and *p* holds true is not possible.

Tremmel and Bazzaz (1993) conducted an experiment where they let target and neighbour plants of different species compete against each other. They found that target plants performed better than their neighbours if they had more horizontal leaves than the neighbours, which supported the prediction from Hikosaka and Hirose (1997).

### Leaf area production

As discussed above, plants consistently form canopies with LAI values greater than the predicted optima for maximal whole stand PNUE and, consequently, have leaf N contents that are lower than optimal. To address this discrepancy, Anten and Hirose (2001) conducted a sensitivity analysis in which they increased the leaf area of target plants in *Xanthium canadense* by 10 % while keeping the leaf area of neighbours constant. Total leaf nitrogen of both target and neighbour plants was also kept constant. The increase in leaf area of target plants therefore resulted in a concomitant reduction in the N content per unit area of their leaves ($N_{area}$). The greater leaf area of target individuals resulted in an increase in their photosynthesis, and this was simulated for stands growing at both high and low N availabilities (Fig. 4). This was in spite of the fact that the measured LAI of the stand was greater than the optimal for maximum whole-stand photosynthesis (see fig. 6 in Anten and Hirose, 2001). This analysis thus suggested that the optimal LAI is not evolutionarily stable.

Theoretical studies that have further analysed leaf area growth from an evolutionary perspective, demonstrated that the evolutionarily stable LAI (ES-LAI) should always be greater than the optimal one (Schieving, 1998; Anten, 2002). Most of the predictions about differences in leaf area growth between plants with different physiological or morphological characteristics or those growing under different conditions were similar to those made with the model for simple optimal LAI (Anten *et al.*, 1995*b*; see above). The ES-LAI was further predicted to increase strongly with the degree to which plants influence each other's light climate (decreasing *p* see above; Fig. 5).

But is the model for ES-LAI a better predictor of real LAI values than the model for optimal LAI? Anten (2002) found a very close correspondence between predicted ES-LAI values and measured values (Fig. 2B), suggesting that this is indeed the case. It should be noted though that Anten (2002) assumed a *p* value of 0·5; the light climate of a plant in stand is for 50 % determined by self-shading
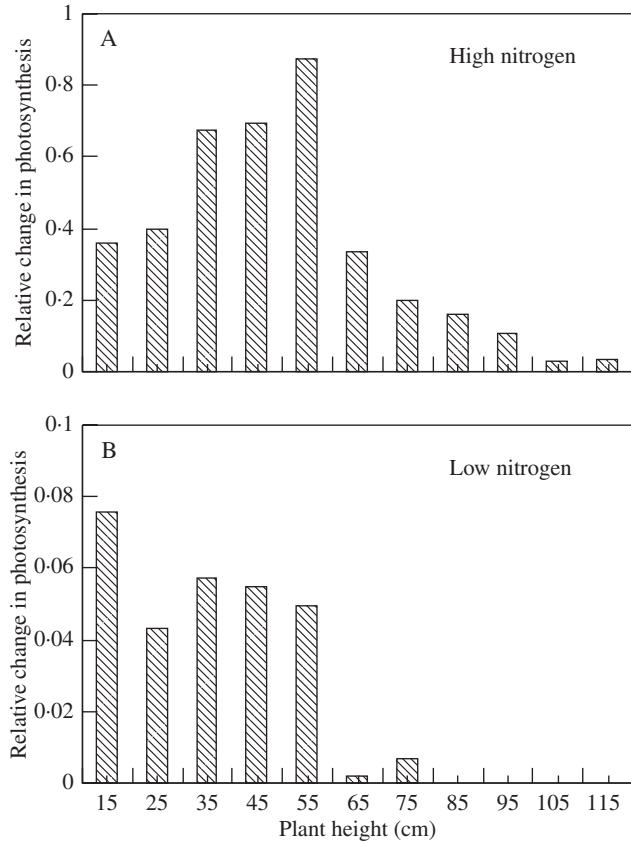
FIG. 4. Effects of a simulated increase in leaf area on daily photosynthesis of target plants of different height in *Xanthium canadense* stands growing at either high (A) or low (B) nitrogen availability. The stand consisted of plants that differed in height, and individuals were divided into 10-cm height classes. Each bar indicates the relative change in photosynthesis for plants of a given height class (e.g. 15 on the *x*-axis indicates the height class 10–20 cm; 25 indicates 20–30 cm, etc.), while keeping the leaf area of plants in the other height classes constant. Relative change in photosynthesis is calculated as $(P_D{}^* - P_D)/P_D$ where $P_D$ is daily plant photosynthesis and $P_D{}^*$ the $P_D$ value after changing the leaf area by 10 %. For further details of the calculation procedure, see Anten and Hirose (2001) from which this figure was taken.
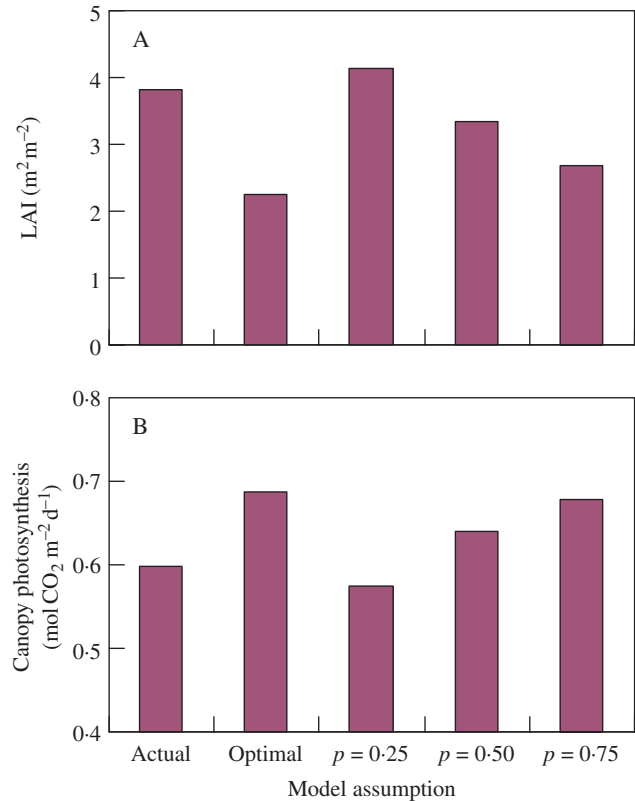


FIG. 5. (A) The actual, optimal and evolutionarily stable leaf area indices (ES LAI) for a stand of the savanna grass *Hymenachne amplexicaulis*. The ES LAI was calculated for three values of $p$ (the degree to which plants determine their own light climate): $p = 0.25$, $0.5$ and $0.75$. Implicitly, a reduction in $p$ implies that plant density increases (see Anten, 2002). (B) Daily whole-stand net photosynthesis for each LAI in (A).

and for 50 % by neighbours. The predicted ES-LAI is very sensitive to the value of $p$ (Fig. 5). Unfortunately only one study (Hikosaka *et al.*, 2001, see above) has measured $p$. Thus, to test whether the model for ES-LAI is indeed a good predictor of real LAIs, it will be important to obtain more measurements of the degree to which plants in vegetation influence each other's light climate.

### Clonal plant

One group of plants that deserves special attention in the discussion about individual- *vs.* stand-level optimization are clonal plants. In stands of clonal plants, neighbouring shoots (ramets) are likely to be part of the same genetic individual. Depending on the growth form of the plant (phalanx *vs.* guerrilla), a given ramet is more likely to interact with ramets of the same clone than with ramets of different clones. The question thus arises: do ramets of clonal plants grow differently when they interact with ramets of the same

clone than when they interact with ramets of a different one? From the arguments developed so far in this paper, one would expect that, in the latter case, they would invest relatively more biomass in resource harvesting structures than in the former case. To date unfortunately there are no studies that have analysed the canopy structure of clonal plants from a game theoretical perspective. But, a recent study (Gruntman and Novoplansky, 2004) on below-ground interactions appears to support this prediction. It had earlier been shown that plants in general tend to over-invest in root growth just as they appear to over-invest in above-ground light harvesting structures (Gersani *et al.*, 2001). Gruntman and Novoplansky (2004) found that cuttings of the grass *Buchloe dactyloides* invest relatively more mass in roots when they interact with cuttings of a different clone than when they interact with ones from the same clone.

### Canopy structure is the result of a game

It can be concluded that the structure and productivity of vegetation stands apparently exhibit the result of a tragedy of the commons (Donald, 1968) because maximization of individual fitness may be in conflict with maximization of stand productivity. Plants consistently over-invest in

height growth and leaf area production, and produce leaves at a more horizontal orientation than optimal. This over-investment goes at the expense of the net photosynthetic rate and the associated growth of the vegetation stand. As noted above, this pattern is not only observed above ground but also below ground where plants that grow in the proximity of neighbours appear to over-invest in roots to acquire soil resources that would otherwise be acquired by neighbours. In short, competitive optimization provides a useful quantitative theoretical framework for scaling from organ-level processes to individual plant form and growth and from there to the structure and productivity of vegetation stands.

This tragedy of the commons has important consequences for agriculture, as first noted by Donald (1968). Traditionally, plant breeding involves the selection of the most productive individuals from a population and using those for further breeding. It is now clear that those plants achieved their advantage over other plants by over-investing in resource harvesting structures at the expense of growth and yield potential. Thus, it is very likely that in many cases their characteristics are not those that would give the highest per unit area yields (Donald, 1968; Zhang *et al.*, 1999).

## MIXED-SPECIES CANOPIES: CAN MORE THAN ONE PLAYER STAY IN THE GAME?

The majority of the world's vegetation stands consist of various species differing from each other in many ways. Understanding this biological diversity has long been one of the central questions in plant ecology, and a whole suite of theories has been proposed in an attempt to explain species coexistence (see review by Palmer, 1994).

Canopy models may provide an invaluable tool when addressing the issue of species diversity. Because of their mechanistic nature, they can be used to quantify the consequences of different combinations of trait values for the competitive interactions between species (Pronk, 2004). Unfortunately, within the canopy modelling community, very little effort has been made to use models to analyse species diversity in vegetation stands. The optimization studies discussed above all predict unique optimal trait values; all alternative strategies are selected against and will eventually disappear from the vegetation. So these models in fact predict mono-species stands containing close to identical individuals.

In this section, ideas are presented that have or can be implemented into canopy models to make these models better suited to address the issue of species diversity. It is therefore not a review of all theories about species co-existence but focuses on three avenues through which advances have or can be made: (1) considering several plant characteristics rather than only one; (2) taking time and space into account; and (3) considering competition for different resources.

*Trade-offs between different characteristics*

A large number of plant characteristics contribute to whole-plant net photosynthesis, e.g. plant height, leaf area, leaf geometry, photosynthetic capacity, dark respiration. Yet all studies discussed so far have considered optimization of one characteristic with all other characteristics held equal. For example, ES plant height is calculated while keeping LAI, leaf angle and leaf photosynthetic characteristics constant (Givnish, 1982; Iwasa *et al.*, 1984). If there are trade-offs between different characteristics, an investment in one would go at the expense of the others, and plants would not be able to maintain optimal values for all characteristics.

Such a trade-off exists between two characteristics that determine light capture in dense vegetation: leaf area growth and stature. To grow tall, plants have to invest a disproportionate amount of mass in support structures in order to maintain mechanically stable (McMahon, 1973) and consequently taller plants have a lower leaf mass ratio (LMR) and leaf area ratio (LAR) (Givnish, 1982; Anten and Hirose, 1999; see Figs 6A and B and 7A and B). A number of studies (Hirose and Werger, 1995; Anten and Hirose, 1999, 2003; Werger *et al.*, 2002) have quantified above-ground growth patterns and light capture for different species in mixed herbaceous stands. In all these studies, taller more dominant species captured more light both in total amount and per unit leaf area ($\phi_{area}$; Fig. 6C). However, shorter subordinate species were able to capture equal or even greater amounts of light per unit mass ($\phi_{mass}$; Fig. 6D) than dominants in spite of the fact that they were heavily shaded. Subordinates achieved this relatively high $\phi_{mass}$ because they had substantially higher LAR values ($\phi_{mass} = LAR \times \phi_{area}$; Hirose and Werger, 1995) and, to a lesser extent, because they oriented their leaves horizontally with little overlap between leaves (Anten and Hirose, 1999). If above-ground mass is considered to be an investment to capture light, then $\phi_{mass}$ (light capture per unit mass) can be taken to be the efficiency of this investment. Thus, species of different stature seemed to be equally efficient in capturing light and this could help explain their coexistence (Hirose and Werger, 1995; Anten and Hirose, 1999).

Interestingly, comparisons between plants of different stature but of the same species in a mono-species stand found that shorter plants had considerably lower $\phi_{mass}$ values than taller plants (Anten and Hirose, 1998; Fig. 7), even though the subordinate plants in this mono-specific stand were not more heavily shaded than the subordinate plants in the mixed stands. The result came about because differences in LAR between plants of different stature were much less in the mono than in the mixed stand (Figs 6 and 7). This difference can be explained as follows. Plants tend to respond plastically to neighbours through an increase in stem elongation (Schmitt *et al.*, 1999). This elongation results in a reduced allocation to leaves. This can be seen by comparing isolated *X. canadense* plants to those in dense stands (Fig. 7A; Anten and Hirose, 1998). The isolated plants had considerably higher LMR values than the plants from the stand, even when compared at the same plant height. There are large genotypical differences in this plasticity: some species, particularly shade-intolerant ones, respond very strongly, while others hardly respond at all (Kitajima, 1994; Gilbert *et al.*, 2001). In a mixed stand the subordinate species are probably much less plastic than the
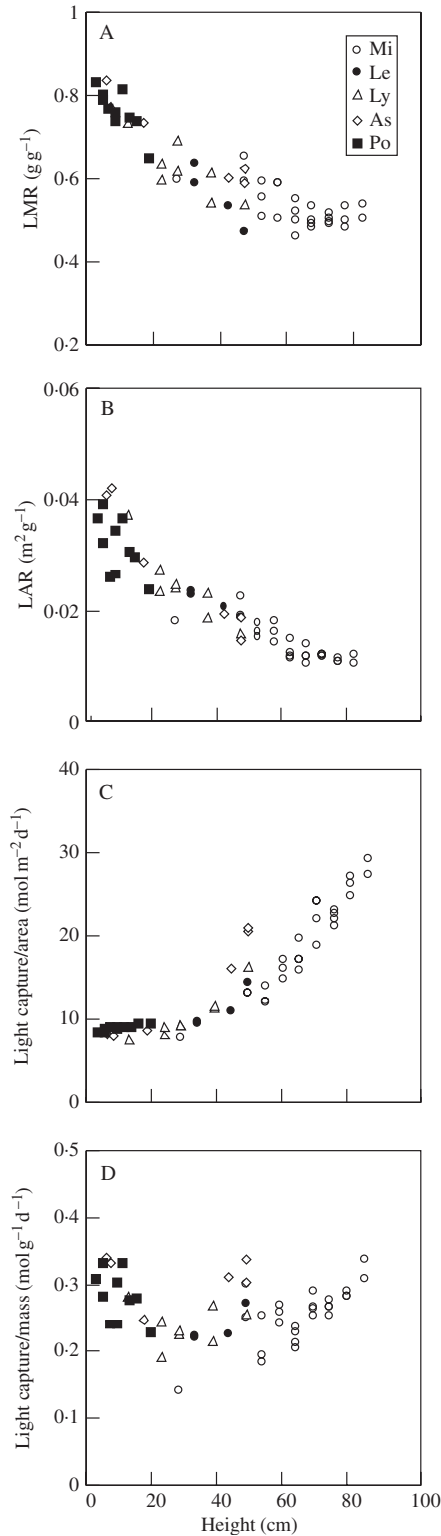
FIG. 6. (A) The leaf mass ratio (LMR; leaf mass per unit plant mass), (B) leaf area ratio (LAR; leaf are per unit above-ground plant mass), (C) average daily light absorption per unit leaf area ($\phi_{area}$) and (D) per unit mass ($\phi_{mass}$) as a function of shoot height for individual shoots of five species in a tall-grass meadow. Mi is *Miscanthus sinensis*, the dominant grass; Le, Ly, As and Po are *Lespedeza bicolour*, *Lysimachia clethroides*, *Astilbe thunbergii* and *Potentilla freyniana*, respectively (all dicot forbs). Redrawn from Anten and Hirose (1999).
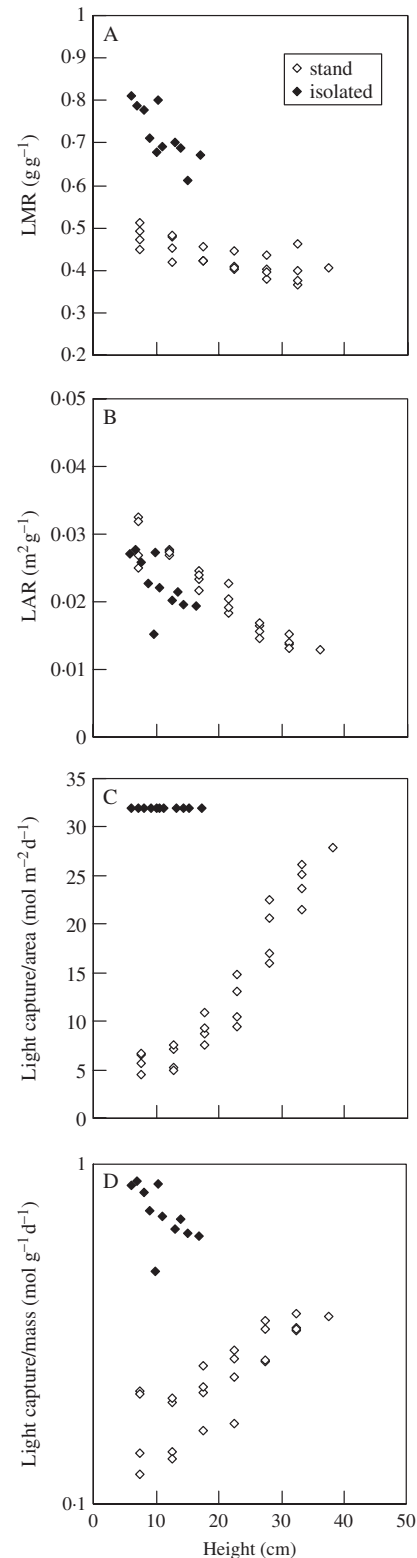
FIG. 7. (A) The leaf mass ratio (LMR; leaf mass per unit plant mass), (B) leaf area ratio (LAR; leaf area per unit above-ground plant mass), (C) average daily light absorption per unit leaf area ($\phi_{area}$) and (D) per unit mass ($\phi_{mass}$; *y*-axis logarithmically transformed) as a function of plant height for individuals of different height of the annual *Xanthium canadense* either growing in a dense mono-species stand or in isolation. Redrawn from Anten and Hirose (1998).

dominants, they do not exhibit this enhanced stem elongation and maintain a relative high allocation to leaf area growth. As can be seen, the subordinate species in the mixed stand had high LMR values comparable to the isolated *X. canadense* plants. Thus, interspecific differences in plasticity in height growth in combination with the trade-off between height and leaf area growth could partially explain the coexistence of species with different stature.

The trade-off between height and leaf area also has interesting implications when used in the analysis of optimal LAI. As discussed above, in the absence of N limitation the LAI of a plant is optimal if the light intensity on the lowest leaf is equal to the light compensation point of the leaf, where the difference between photosynthesis and respiratory costs of the leaf is zero. In this calculation the costs should not only include leaf respiration but also costs of producing and maintaining additional stems and roots that are to support the leaf and supply it with water and nutrients (Givnish, 1988; Anten and Hirose, 2001). The latter costs increase disproportionately with plant height. Consequently, one would expect that the LAI would go down with increasing plant stature (Givnish, 1988) because of the respiratory costs of maintaining an increase in leaves. Consequently, as the light compensation point of the lowest leaf increases more light reaches below the canopy of the taller plants, which could be utilized by shorter individuals whose leaves have lower respiratory costs (Huisman *et al.*, 1999). In other words, in dense stands tall stature might be a mono-morphic ESS when only height is considered. But the trade-off with LAI means that these taller plants cannot exploit all of the available light, thus creating a niche for shorter plants to co-exist.

*Time*

The studies discussed in the previous section considered whole-plant carbon gain at one point in time. As such they ignored two important aspects: the dynamics of growth and the fact that growth conditions can change dramatically in time. Considering the first aspect, there is probably a trade-off between trait values that confer an early competitive advantage and those that facilitate long-term survival of the plant structure. A good example might be the characteristics that determine height growth. Rapid height growth can be achieved either by growing fast overall or by achieving a relatively large height increment per unit of mass invested in the stem. The latter in turn results from a small stem diameter or a low stem mass density both of which would make the plant structure more susceptible to mechanical failure (Niklas, 1992; Telewski and Pruyn, 1998). Thus, rapid height growth trades off with longevity of the plant structure and with the maximal achievable height. This distinction in stem characteristics exists between herbaceous and woody plants and between early successional and late successional tree species. A similar trade-off exists between the photosynthesis rate per unit leaf area and leaf longevity. Leaves with high photosynthetic rates tend to be more palatable and have higher protein contents, and are therefore more susceptible

to herbivory and other forms of leaf damage than leaves with low photosynthetic rates (Coley, 1988).

As regards the second aspect, growth conditions can change dramatically during the course of a growing season. For example, in temperate environments there is an increase in temperature from spring to summer, while in many (sub)tropical areas there is often a substantial difference in water availability between the dry and rainy seasons. Thus, the optimal characteristics that maximize whole plant carbon gain at one point in time will be different from those that maximize it at another point in time. Yet because plants are plastic, this point in itself does not exclude the possibility of one species optimally adjusting its characteristics to a changing environment. But this possibility will not exist if plant characteristics are structurally or physiologically constrained to the extent that an optimal adjustment to one set of environmental conditions excludes an optimal adjustment to another set of conditions. A good example of this might be prairie vegetation in parts of North America as well as other grasslands, where $C_3$ plants dominate during cooler spring months, while $C_4$ plants are dominant during the hotter summer (Kemp and Williams, 1980; Turner and Knapp, 1996; Anten and Hirose, 1999). This shift in dominance is likely to be directly associated with different temperature optima for maximum activity of the photosynthetic enzymes associated with the two pathways (Pearcy *et al.*, 1981). Thus if the characteristic in question is photosynthetic pathway, the optimal strategy for the summer would be $C_4$ but that for the spring would be $C_3$. Both types can use the same area but at different times.

Apart from predictable changes such as general seasonal trends, growth conditions can also vary unpredictably both in time and space. The occurrence of gaps in the forest, rainfall, severe events such as droughts or infections by diseases or pests and seed dispersal and related plant density are all, to some degree, random. Thus it is by no means certain that plants, which are optimally adjusted to a certain set of conditions will also grow under these conditions. An interesting example of how this may lead to diversity in trait values is the case of density-dependent height growth as studied by Pronk (2004). As noted above, the ESS height strongly depends on plant density; greater density favours taller plants. But plant density can vary unpredictably in time and space and Pronk (2004) showed that consequently plants with different height growth strategies can co-exist because each will have a chance of ending up in a site where density is such that its height growth is optimal, in the sense that it will win the competition from its immediate neighbours.

*Competition for different resources*

So far only models that consider plant performance to be limited by light only or by light and nitrogen availability have been covered. There are, of course, many other resources, $CO_2$, water, phosphorus and other mineral nutrients, which can limit photosynthesis and growth. In many cases, being a good competitor for one resource implies being a poor competitor for one or more of the others.

The most obvious example would be the trade-off between the abilities to acquire above- and below-ground resources. There are also trade-offs in the efficiency with which plants use different resources for photosynthesis and growth. For example, at the leaf-level a high photosynthetic nitrogen-use efficiency (PNUE) probably goes at the expense of a high water-use efficiency (photosynthesis/transpiration) (Field *et al.*, 1983). PNUE probably also trades-off with light use efficiency (photosynthesis per unit of absorbed light). An increase in leaf nitrogen content tends to increase LUE but can decrease PNUE (Hikosaka and Terashima, 1995; Hirose and Bazazz, 1998; Anten *et al.*, 2000).

A number of studies (Tilman, 1980; Grover, 1997) have used resource competition models to predict the outcome of competitive interactions and species diversity. These models are based on Liebig's Law of the Minimum, which assumes that each species is limited by only one resource at a time. Consequently, the theory predicts that the species that has the minimum requirement for the most limiting resource would win the competition at equilibrium. However, if *n* different resources limit growth through temporal and spatial heterogeneity of these resources, a maximum of *n* different species could co-exist, provided that growth of each species is limited by a different resource (Tilman, 1980).

The problem with the competition theory is that, while there are maybe six to ten different resources that limit growth there can easily be more than 50 species of plants that coexist with each other. A recent study (Huisman and Weissing, 1999), however, demonstrated that competition models could produce oscillations when plants compete for three or more resources and that these oscillations allow for the coexistence of larger species on fewer resources. Yet it should be noted that all resource competition models are based on highly simplified relationships between growth and resource availability and provide no mechanistic details with regards to the physiology of plant growth or the nature of interaction between neighbouring plants.

## CONCLUDING REMARKS

Species coexistence can be further understood by (*a*) simultaneously analysing the various traits that determine light capture and photosynthesis and the trade-offs between them, and (*b*) by analysing the trade-offs associated with specialization to different positions in the niche space defined by temporal and spatial heterogeneity of resources. The challenge is to design canopy models in such a way that they are suited to analyse these aspects in a mechanistic way. Firstly, canopy models should be able to describe the structure of vegetation stands with enough accuracy such that the consequences of interspecific differences in shoot structure (e.g. height, and leaf area and leaf angle distribution) for photosynthesis can be estimated. Relatively few models (e.g. Barnes *et al.*, 1990; Anten and Hirose, 1999, 2003) can adequately account for this variation. Secondly, models for daily canopy photosynthesis should be expanded to incorporate the dynamics of growth (for example, see Pronk, 2004). In this respect, much can be learned from crop

growth models (van Ittersum *et al.*, 2003). Next, trade-offs between the different traits associated with light capture and photosynthesis need to be further understood and implemented mechanistically into models. The same applies for trade-offs in the ability to acquire and use different resources and time-dependent trade-offs. Current models often use empirical relationships [e.g. the relationship between leaf allocation and plant height (Givnish, 1982; Iwasa *et al.*, 1984; Anten and Hirose, 1998, 1999) or stem diameter and height (Yokozawa and Hara, 1992)] and as such provide little added understanding of the trade-off. Inclusion of these aspects will make canopy models better able to describe and analyse species diversity in vegetation stands.

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