

How light competition between plants affects their response to climate change

Marloes P. van Loon^{1,2}, Feike Schieving¹, Max Rietkerk³, Stefan C. Dekker³, Frank Sterck⁴ and Niels P. R. Anten²

¹Ecology and Biodiversity Group, Utrecht University, Postbox 80084, 3508 TB, Utrecht, the Netherlands; ²Centre for Crop Systems Analysis, Wageningen University, Postbox 430, 6700 AK, Wageningen, the Netherlands; ³Department of Environmental Sciences, Copernicus Institute for Sustainable Development, Utrecht University, Postbox 80115, 3508 TC, Utrecht, the Netherlands; ⁴Forest Ecology and Forest Management Group, Wageningen University, Postbox 47, 6700 AA, Wageningen, the Netherlands

Author for correspondence:

Marloes P. van Loon

Tel: +31 030 2536848

Email: m.p.vanloon@uu.nl

Received: 19 February 2014

Accepted: 26 April 2014

New Phytologist (2014)

doi: 10.1111/nph.12865

Key words: canopy, FACE data, gas exchange, leaf area index (LAI), modeling, optimality principle, photosynthesis, soybean (*Glycine max*).

Summary

- How plants respond to climate change is of major concern, as plants will strongly impact future ecosystem functioning, food production and climate. Here, we investigated how vegetation structure and functioning may be influenced by predicted increases in annual temperatures and atmospheric CO₂ concentration, and modeled the extent to which local plant–plant interactions may modify these effects.
- A canopy model was developed, which calculates photosynthesis as a function of light, nitrogen, temperature, CO₂ and water availability, and considers different degrees of light competition between neighboring plants through canopy mixing; soybean (*Glycine max*) was used as a reference system.
- The model predicts increased net photosynthesis and reduced stomatal conductance and transpiration under atmospheric CO₂ increase. When CO₂ elevation is combined with warming, photosynthesis is increased more, but transpiration is reduced less. Intriguingly, when competition is considered, the optimal response shifts to producing larger leaf areas, but with lower stomatal conductance and associated vegetation transpiration than when competition is not considered. Furthermore, only when competition is considered are the predicted effects of elevated CO₂ on leaf area index (LAI) well within the range of observed effects obtained by Free air CO₂ enrichment (FACE) experiments.
- Together, our results illustrate how competition between plants may modify vegetation responses to climate change.

Introduction

Atmospheric CO₂ concentration is predicted to rise in the future, and, partly as a result of this, global temperature will increase (IPCC, 2007). How plants respond to changing climate is of major concern, as this strongly affects basic vegetation functions such as crop production in the future. Vegetation in turn may modify climate change through climate–vegetation feedbacks (Claussen, 1997; Brovkin *et al.*, 1998; Bonan, 2008; Dekker *et al.*, 2010), because vegetation affects the radiative flow, water balance and carbon in the atmosphere itself (Scheffer *et al.*, 2005). These vegetation–climate feedbacks necessitate the inclusion of vegetation in climate models.

Currently, in many climate models, vegetation functioning is directly linked to the leaf area index (LAI, i.e. the leaf area per unit soil area). This is because LAI, being the amount of light-intercepting tissue, is a key trait driving the exchange of CO₂, water vapor and energy between vegetation and atmosphere (Running & Coughlan, 1988; Sellers *et al.*, 1997; Van den Hurk *et al.*, 2003). However, LAI is highly variable and can differ as a

function of vegetation type and climatic and soil conditions (Asner *et al.*, 2003; Iio *et al.*, 2014).

Climate models are often used for climate change predictions and studying climate–vegetation feedbacks. However, these models generally ignore local interactions between plants. In fact, there are frequent calls for the inclusion of the role of the interactions between plants in modifying the effects of climate change on plant structure and functioning, and on species composition (e.g. Dewar *et al.*, 2009; Lloyd *et al.*, 2010), but so far this has rarely been done. Incorporating local interactions between plants in climate–vegetation models can result in different predictions of transpiration rates and net primary production, which are likely to have major but largely unknown consequences for the future climate (Nicotra *et al.*, 2010).

Optimization theory can be a good addition to climate–vegetation models, as it is a simple but elegant way to scale from individual physiological processes to vegetation functioning, and has been applied to different natural forest stands (Schymanski *et al.*, 2007; Dewar *et al.*, 2009; Sterck *et al.*, 2011; Dekker *et al.*, 2012). Optimization models assume that plants optimize their

traits to maximize performance (usually canopy photosynthesis or net primary production) at the whole-stand level. Thus, they implicitly quantify the maximum contribution of trait acclimation to whole-stand performance (Anten & During, 2011). Several optimization models have been developed that predict the response of plants to elevated CO₂ (e.g. Franklin, 2007; McMurtrie *et al.*, 2008). However, while these optimization models make qualitatively good predictions, because there is usually a strong positive correlation between predicted and observed LAIs, quantitatively they often underestimate measured LAIs, and overestimate canopy photosynthesis (Anten *et al.*, 1998; Anten, 2005).

By defining performance maximization at the level of vegetation stands rather than at the individual level, optimization models implicitly assume that the optimal trait values of one plant are independent of the trait values of its neighbors. This in turn ignores the fact that plants strongly compete for resources (Anten, 2002). Competitive optimization (also known as density-dependent optimization; Maynard Smith, 1974) may overcome this problem as this assesses the payoff of a given set of trait values in relation to the characteristics of neighbor plants (Reichert & Hammerstein, 1983; Anten, 2002). Through this approach, stable strategies can be defined (also known as evolutionarily stable strategies), whereby a population adopting such a strategy cannot be invaded by individuals adopting any other strategy, because this will not increase the payoff of the individual (Parker & Maynard-Smith, 1990). This approach can for example be used to predict the allocation of biomass to leaves, wood and roots (Dybziński *et al.*, 2011; Farrior *et al.*, 2013). In the current study, we applied this approach to analyze the effects of climate change on LAI and associated vegetation functioning, because, as noted already, the LAI is a key trait in driving the exchange of CO₂, water vapor and energy between vegetation and atmosphere. Application of the evolutionarily stable strategy approach to analyze vegetation structure and functioning under current climate conditions resulted in a closer fit of predicted stable LAI to real values compared with predictions from simple optimization, in which only the total stand is optimized (Anten, 2002; Lloyd *et al.*, 2010). However, although adding competitive optimization at the individual level provides a relatively simple means of assessing how competition may modify plant responses to climate change, very few studies (e.g. Friend *et al.*, 1993, 1997; Medvigy *et al.*, 2010) have used it to investigate vegetation functioning under future climate scenarios.

The aim of this study was therefore to analyze how vegetation structure and functioning may be influenced by climate change and to what extent competition for light through canopy overlap may modify these effects. We have developed a canopy model in which we used soybean (*Glycine max*) as a reference system. Soybean was chosen because this species is widely grown all over the world and is one of the most studied species for response to elevated CO₂ (Ainsworth *et al.*, 2002) and therefore ample experimental data are available. Here, the effect of CO₂ on vegetation structure and functioning predicted by the model was validated against a large data set from several Free air CO₂ enrichment (FACE) experiments on soybean. In addition, the model

predictions of seasonal dynamics in LAI at current and elevated CO₂ concentrations were validated against data from a detailed study on this (Dermody *et al.*, 2006). The canopy model we developed calculates the canopy photosynthesis of soybean as a function of light, nitrogen, temperature, CO₂ and water. A water balance was included in the model to enable calculation of water transport through the plant and transpiration of the plant.

There are three different versions of the canopy model. The first model version is the baseline version (hereafter called No-Opt), assuming that LAI will remain constant under climate change. The second model version uses simple optimization (hereafter called SimOpt), where plants optimize their LAI to maximize the performance at the whole-stand level (so competition is not included). The last version uses competitive optimization (hereafter called ComOpt), where plants optimize their LAI in a competitive setting. SimOpt is included because comparison of its results with those of the ComOpt version allows us to determine the effect of competition separately from that of acclimation itself (included in the SimOpt version). With these model versions, we studied the effects of the predicted gradual increases in temperature and elevated CO₂ on soybean, and how these effects differ if competition is included.

Materials and Methods

Introduction of the canopy model

To answer our main research question, a canopy model is developed. This canopy model is based on steady-state assumptions of water transport and of CO₂ inflow and consumption, and these are solved with the given parameters (Supporting Information Table S1) and for the given constraints (for a given amount of nitrogen (N) that plants allocate to leaves, water availability as reflected by soil water potential, incident light, temperature, and atmospheric CO₂ concentration). The model uses parameter values obtained from experimental studies on soybean (*Glycine max* (L.) Merr) from Anten *et al.* (1995a) and Dermody *et al.* (2006) (Table 1). Parameter values given in Table S1 were used for all simulation unless otherwise specified. All variables names with units are supplied in Table S2. Here we present a short description of the canopy model; a full description can be found in Methods S1. After the canopy model has been presented, a description is given of the three different model versions, the climate change scenarios and how we compared the model outcomes with experimental data.

Plant structure

From a whole stand (Fig. 1a), a target plant is defined (Fig. 1b), whose leaves are confined within area A . The total leaf area of the target plant (f_i) per unit of ground area (A) is the LAI (F_i), as we standardized A to 1 m². Neighboring plants can also have leaves within A , thereby influencing the light climate of the target plant (Fig. 1f). Our competitive optimization criterion is defined as maximization of an individual plant's photosynthesis in the presence of neighbors, but does not consider the photosynthesis of

Table 1 Parameters used in the model which were obtained from experimental studies on soybean, with their units, a description of the parameter and the input value

Symbol	Units	Explanation	Input value
c_{rl}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Intercept of the $R_l N_l$ relation ¹	0.388 ²
F_T	–	Leaf area index	6.58 ^{3,4}
h_t	m	Top height of the canopy	0.66 ²
K_{df}	–	Extinction coefficient for diffuse PFD	0.747 ²
K_n	–	Extinction coefficient for nitrogen	0.298 ²
N_b	mmol m^{-2}	Leaf N concentration not associated with photosynthesis	29.0 ²
N_T	mmol m^{-2}	Total canopy leaf N	526.6 ³
x_c	$\mu\text{mol CO}_2 \text{mmol N}^{-1} \text{s}^{-1}$	Slope of the V_{cmax} N_l-N_b relation ¹	0.17 ²
x_j	$\mu\text{mol CO}_2 \text{mmol N}^{-1} \text{s}^{-1}$	Slope of the J_{max} N_l-N_b relation ¹	1.03 ²
x_r	$\mu\text{mol CO}_2 \text{mmol N}^{-1} \text{s}^{-1}$	Slope of the $R_l N_l$ relation ¹	0.0099 ²
θ	–	Curvature factor	0.9 ³

¹ J_{max} , V_{cmax} and R_l are assumed to be linearly related to leaf nitrogen content per unit leaf area.

²Source: Anten *et al.* (1995a).

³Source: Dermody *et al.* (2006).

⁴This value was only used for the NoOpt version of the model. For SimOpt and CompOpt, leaf area index is an emerging property.

those neighbors. The number of neighbor plants having part of their leaves in A therefore does not affect the calculation; only their combined total leaf area in A matters. The interaction between the target and the neighboring plants through canopy mixing was modeled following Anten (2002). A summary of this approach is given here.

The total LAI (F_T) is a summation of the LAI of the target plant (F_i) and of the neighboring plants (F_n) in the same area A (Fig. 1f). All plants are assumed to be identical (same height, LAI etc.). The leaf areas of the target plant and neighbors are assumed to be uniformly distributed, horizontally and vertically.

The ratio of the target plant's leaf area to the total leaf area (β) in the area A describes the degree to which canopies of plants are mixed, which in turn determines the degree to which plants influence each other's light climate.

$$\beta = \frac{F_i}{F_T} \quad \text{Eqn 1}$$

A value of $\beta = 1$ means that the leaves of the target plant in area A are not mixed with leaves of neighboring plants, and the target plant only influences its own light climate through self-shading (Fig. 1b). Conversely, decreasing values of β indicate an increased degree of mixing and thus mutual shading between the plants (Fig. 1f). It should be noted that β values approaching zero are unrealistic as $\beta = 0$ entails that a target plant has no leaf area, which is evidently impossible.

Light distribution

The light interception of the leaves was calculated with the model of Spitters *et al.* (1986), which distinguishes between direct light (i.e. direct beam irradiance) and diffuse light (i.e. radiation from the sky dome as well as radiation that is scattered by leaves in the canopy). Furthermore, two leaf classes were distinguished: shaded leaf area and sunlit leaf area. This model has been shown to be sufficiently accurate for estimates of canopy photosynthesis (De Pury & Farquhar, 1997).

Nitrogen distribution

The N content of the leaves (N_l) in the canopy is calculated as a negative exponentially declining function of depth in the canopy (i.e. similar in shape but less steep than the light distribution) following Anten *et al.* (1995b). Plants are assumed to have a fixed total amount of leaf N (N_T); thus, increasing the leaf area results in a reduced leaf N content.

Photosynthesis

The net photosynthesis of a leaf per unit area (P_{nl}) was calculated with the Farquhar photosynthesis model (Farquhar *et al.*, 1980), where the net photosynthesis is calculated as the gross photosynthetic rate of a leaf per unit ground area (P_{gl}) minus the leaf respiration rate (R_l); and P_{gl} is the minimum of the carboxylation or Rubisco-limited photosynthetic rate P_{cl} and the electron transport-limited photosynthetic rate P_{j1} (Farquhar *et al.*, 1980).

Gross and net daily photosynthesis rates of a plant (P_{gT} and P_{nT} , respectively) are obtained by integration of the leaf gross and net photosynthetic rates over the cumulated LAI of the canopy (thus taking account of variation in light and N between leaves) and over the time of the day (yielding a whole-vegetation value with area A) and subsequently multiplying the integrands by β .

$$P_{nT} = \beta \int_{t=0}^{t=24} \int_{f_i=0}^{f_i=F_T} P_{nl} df dt \quad \text{Eqn 2}$$

$$P_{gT} = \beta \int_{t=0}^{t=24} \int_{f_i=0}^{f_i=F_T} P_{gl} df dt \quad \text{Eqn 3}$$

(t , time (in h).)

The photosynthetic parameters are dependent on temperature. The temperature dependency of the maximum carboxylation rate (V_{cmax}) and of the maximum electron transport rate (J_{max}) were calculated according to a peak model (Johnson *et al.*, 1942); for all other photosynthetic parameters we used an Arrhenius model (Farquhar *et al.*, 1980).

J_{max} , V_{cmax} and R_l are assumed to be linearly related to leaf N content per unit leaf area N_l (Harley *et al.*, 1992). Thus, because of the fixed total amount of leaf N (N_T), increasing the leaf area results in a reduced leaf N content and an associated lower photosynthetic capacity per leaf.

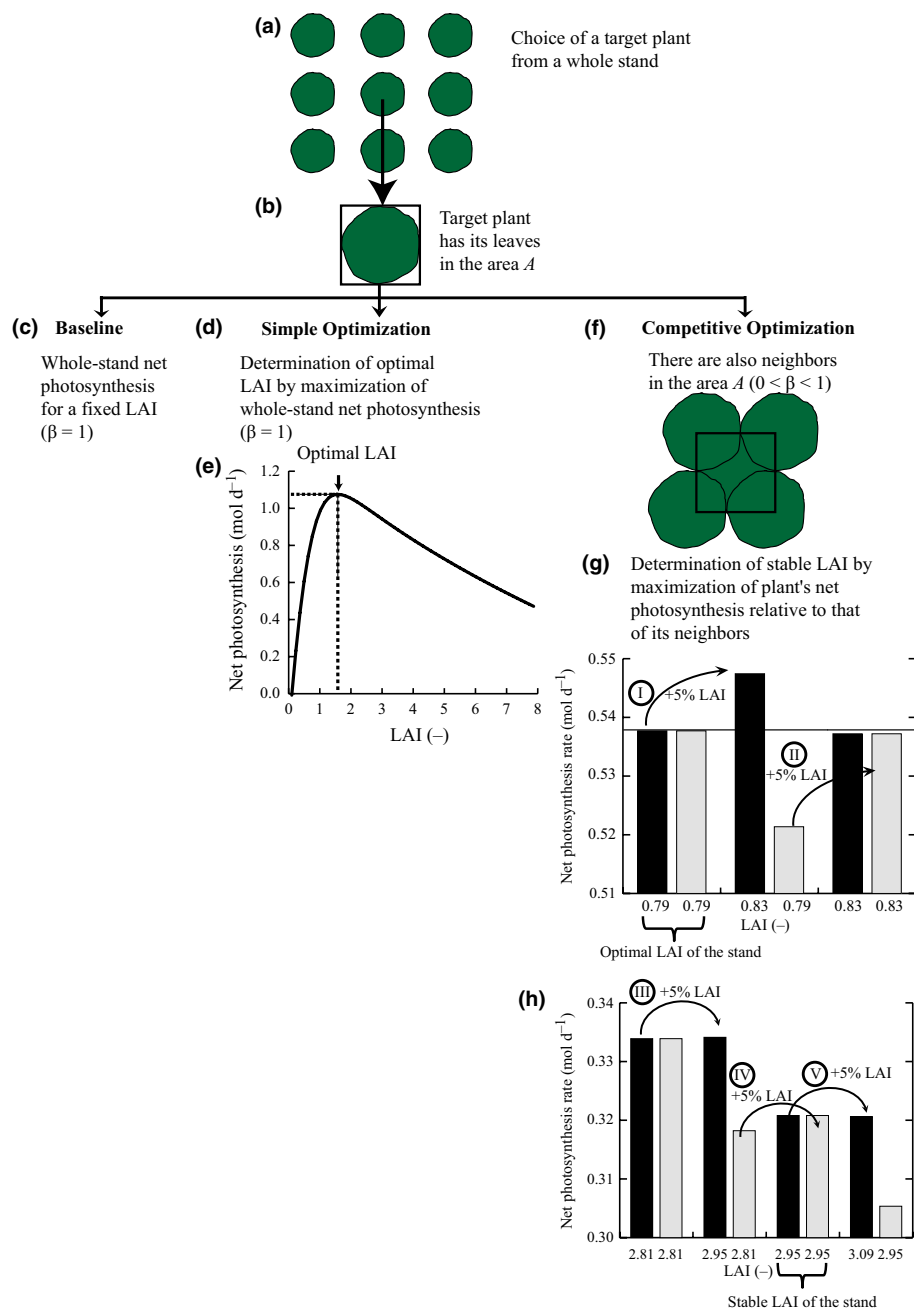


Fig. 1 Overview of the determination of optimal leaf area index (LAI) and stable LAI. (a) From a whole stand, a target plant is defined (top-down view). (b) The target plant has its leaves in a specified area (area A ; A is 1 m^2). (c) If there are no neighbors in the area A , then the simple optimization is performed ($\beta = 1$; β is the ratio of the target's leaf area to the total leaf area in the area A), (d) by maximization of whole-stand net photosynthesis to determine the optimal LAI. (e) If there are neighbors next to the target plant in the area A ($0 < \beta < 1$), then competitive optimization is performed (f). The stable LAI is defined by maximization of the plant's net photosynthetic rate relative to that of its neighbors. To determine this, several steps are necessary. (Step I) Increase the LAI of the target plant to 5% above the optimal LAI (which maximizes net photosynthesis for the whole stand, indicated by a black line). By unilaterally increasing its leaf area, the target plant captures a larger fraction of the available light, resulting in an increase in the net photosynthetic rate of the target plant. (Step II) The neighbor also increases its LAI by 5%, and so the LAI of the whole stand is also increased by 5%. Increasing the LAI of the stand above its optimal LAI will reduce the net photosynthesis of the whole stand (g). This process is repeated (Steps III and IV), until a value of the LAI of the stand is found at which a further change in the LAI of the target plant does not increase the net photosynthetic rate of the target plant (Step V), which is then the stable LAI (h).

Steady-state flow of CO_2 and water transport

We assume that there is a steady state of inflow of CO_2 for photosynthesis and consumption of CO_2 . Solving the steady-state condition for the internal CO_2 results in the net photosynthetic rate. The inflow of CO_2 is determined by the stomatal conductance (G_{sT}) and the difference between the atmospheric and internal CO_2 concentrations (C_a and C_i , respectively), in which both G_{sT} and C_i are calculated according to Tuzet *et al.* (2003). This means that both G_{sT} and C_i are a function of the leaf water potential (Ψ_l). Furthermore, we assume a steady state of plant transpiration E_{entry} and plant water transport through the stem W_{entry} , that is, $E_{\text{entry}} = W_{\text{entry}}$ (Sterck & Schieving, 2011). Water transport is calculated for the

whole plant. This assumes that all leaves have the same leaf water potential. Transpiration depends on the canopy stomatal conductance of the plant (G_{sT}) and on the vapor pressure difference between leaf and air (VPD). The VPD depends on the relative humidity (RH) and on the temperature (Tetens, 1930). We assume that RH remains constant with a change in temperature, resulting in an increased VPD with increased temperature. The plant water transport through the stem depends on a constant stem conductance and on the difference in base water potential, gravity potential and leaf water potential.

So the steady state of both water transport and CO_2 inflow and consumption should hold. Then we can solve these steady states for Ψ_l with the given parameters (Sterck & Schieving, 2011; Table S1) and for the given constraints (constant total

canopy N, base water potential, temperature, atmospheric CO₂ concentration, and RH; we assume for all simulations a fixed and relatively high base water potential; see Fig. S1 for results of a wide range water availabilities and total canopy N contents). With this Ψ_1 , we can calculate the C_i of the plant and thus the net photosynthesis.

Model versions: baseline model, simple optimization model, and competitive optimization model

Three model versions are developed to show the effects of competition on vegetation functioning. All model versions use the same canopy model; the only difference is the way in which LAI is calculated (Fig. 1). The first model version is the baseline version (NoOpt) where we show responses of plants with a fixed LAI (Fig. 1c). For the LAI, a measured value for soybean was used of 6.58 (Table 1); this value was obtained for atmospheric CO₂ of 37 Pa and a temperature of 24°C (Dermody *et al.*, 2006), that is, the ‘current climate’ treatment (representing the year 2000). The LAI was kept constant if simulations were performed for different climate conditions.

The second model version is the simple optimization model (SimOpt). Here the optimization procedure determines the optimal LAI that maximizes the whole-stand net photosynthesis (P_{nT}), and it assumes that plants do not compete for light ($\beta = 1$; leaves of the target plant are not mixed with those of neighbors; Fig. 1d). An optimal LAI at which net photosynthesis is maximized exists, as light interception increases with LAI but with decreasing marginal returns (i.e. for LAI = 1, c. 50% of available light is captured; for LAI = 2, 75% is captured, etc.), while increasing LAI also entails a reduction in leaf N content and thus in leaf photosynthetic capacity (Anten *et al.*, 1995b) (Fig. 1e). Thus, the underlying assumption of the simple optimization is that trait acclimation to climate change will be such that whole-stand performance is maximized (Fig. 1d).

The third model version is the competitive optimization model (ComOpt) where plants are able to change their LAI and individual plants are assumed to interact with neighboring plants ($\beta < 1$; leaves of the target plant are mixed with those of neighbors; Fig. 1f). With this model, the stable LAI of the stand, that is, the LAI at which no individual can increase its performance with a change of its leaf area (often denoted as the evolutionarily stable state; Maynard Smith, 1974), is determined (Fig. 1g). Thus, plant–plant interactions are taken into account to determine the optimal trait values of individual plants (Fig. 1g).

In order to find the stable LAI of a stand, we followed the same approach as Anten (2002), which is briefly described here. We defined a certain degree of mixture between a target plant and other plants in the same area (β ; Eqn 1; $\beta = 1$ is no mixture, and the closer β is to zero, the higher the degree of mixture; Fig. 1f). Then the LAI of the target plant (F_i) was increased by 5%, while the LAI of the neighbors (F_n) was kept constant (Fig. 1g, step I). This 5% increase in F_i increased not only the total LAI of the stand (F_{entry}), but also β . That is, by increasing its leaf area, the target plant captures a larger fraction of the available light. When this resulted in an increase in the net photosynthetic

rate of the target plant (Fig. 1g), the LAI of neighbors was also increased by 5% (all plants have the same leaf area and β was thus restored to its original value), and as such the LAI of the whole stand (F_{entry}) was also increased by 5% (Fig. 1g, step II). This process was repeated (Fig. 1h, steps III and IV) until a value of F_{entry} was found at which a further change in F_i did not increase the net photosynthetic rate of the target plant (Fig. 1h, step V), which is then the stable LAI for a certain value of β (Fig. 1h). In all simulations with the ComOpt model, we used a value of β of 0.5. This value was based on the results from an independent study (Anten, 2002) which found that this $\beta = 0.5$ gave good predictions of real LAIs for a variety of herbaceous species grown under ambient conditions (Anten, 2002); that is, for a wide range of LAI values there was a strong correlation between predicted and observed LAI values ($r^2 = 0.8$) and the slope of the regression line (1.09 ± 0.178) was not significantly different from 1.

Note that neither SimOpt and ComOpt specify whether changes in trait values occur through plasticity, genotypic adaptation or the replacement of less optimal genotypes by more optimal ones that come from elsewhere. This issue will be discussed further in the Discussion section. By comparing ComOpt and SimOpt, we can show the extent to which competition modifies vegetation structure and functioning.

Climate change scenarios

For the climate change scenarios, we assume an increase in atmospheric CO₂ concentration from 37 Pa to 97 Pa (IPCC, 2007) between the years 2000 and 2100. In the first climate change scenario, we assume that the temperature stays constant (24°C; average over the experiments) over this period, while for the second scenario we assume a temperature increase of 4°C over this period (A1FI scenario of the Special Report on Emissions Scenarios (SRES); IPCC, 2007). We assume that the RH remains constant with increasing temperature, which means that there is an increase in VPD. Consequently, the stomatal conductance has to decrease to maintain the same rate of transpiration. Thus, an increase in temperature causes a certain degree of water stress.

Model validation against experimental data

First, we tested the extent to which SimOpt and ComOpt could predict the seasonal dynamics in LAI using data from Dermody *et al.* (2006). Dermody *et al.* (2006) measured the total canopy leaf N content and the LAI under ambient and elevated CO₂ concentrations at different times during the season. For our model, we used the total canopy leaf N content as an input value and compared the resulting LAI obtained under ambient and elevated CO₂ concentrations with those of Dermody *et al.* (2006).

Secondly, we tested the extent to which the three model versions (NoOpt, SimOpt and ComOpt) could correctly predict measured effects of elevated CO₂ on LAI, leaf photosynthesis and stomatal conductance in soybean obtained in a wide range of FACE experiments. The data were taken from Rogers *et al.* (2004), Bernacchi *et al.* (2005, 2006), Dermody *et al.* (2006),

Leakey *et al.* (2006), Ainsworth *et al.* (2007), A. D. B. Leakey (unpublished), and J. M. McGrath (unpublished). These experiments compare plants grown under an atmospheric CO₂ concentration of *c.* 37.5 Pa with plants grown under an atmospheric CO₂ concentration of *c.* 55.0 Pa. We specifically compared the relative changes of simulated and measured LAIs (107 measurements), as well as the net photosynthetic rate (186 measurements on the topmost leaves in the canopy) and stomatal conductance (258 measurements on the topmost leaves in the canopy) under saturating light conditions with our simulations over the same increase in CO₂. Here we compared relative changes, as the total canopy N content is not known for all studies. To assess the impact of variation in the assumed total canopy N, we ran the model for the range in canopy N (45–1023 mmol N m⁻²).

Results

The effect of β on the competitive optimization model version

First we analyzed the degree to which the predicted plant traits depended on the assumed plant–plant interaction (indicated by

the parameter β ; $\beta=1$, simple optimization model SimOpt, Fig. 1d; reduction in β from 1 towards zero, competitive optimization model ComOpt, Fig. 1f) under current climate conditions (year 2000: temperature of 24°C, atmospheric CO₂ concentration of 37 Pa). The stable LAIs were found to be clearly larger than the optimal LAI ($\beta=1$) and the predicted stable LAIs increased as β values decreased (Fig. 2a). Predicted canopy photosynthesis in turn showed the opposite trend, becoming lower with decreasing values of β (Fig. 2b). Both canopy-level stomatal conductance (Fig. 2c) and transpiration rate (Fig. 2d) decreased with increasing β . As with a fixed canopy N, LAI is increased beyond the optimum for maximizing whole-stand net photosynthesis, so leaf photosynthesis and associated conductance decrease. The nonlinear responses to β (Fig. 2) are the result of the nonlinearity of the empirical logistic function (Eqn S27; this function determines the stomatal conductance which influences the rate of transpiration and therefore the leaf water potential and the internal CO₂ concentration). Thus, our model results reveal that including competition results in higher predicted values of LAI, but with a lower total transpiration rate. However, even though transpiration is reduced with a higher degree of mixture (Fig. 2d), the reduction in photosynthesis is even stronger such

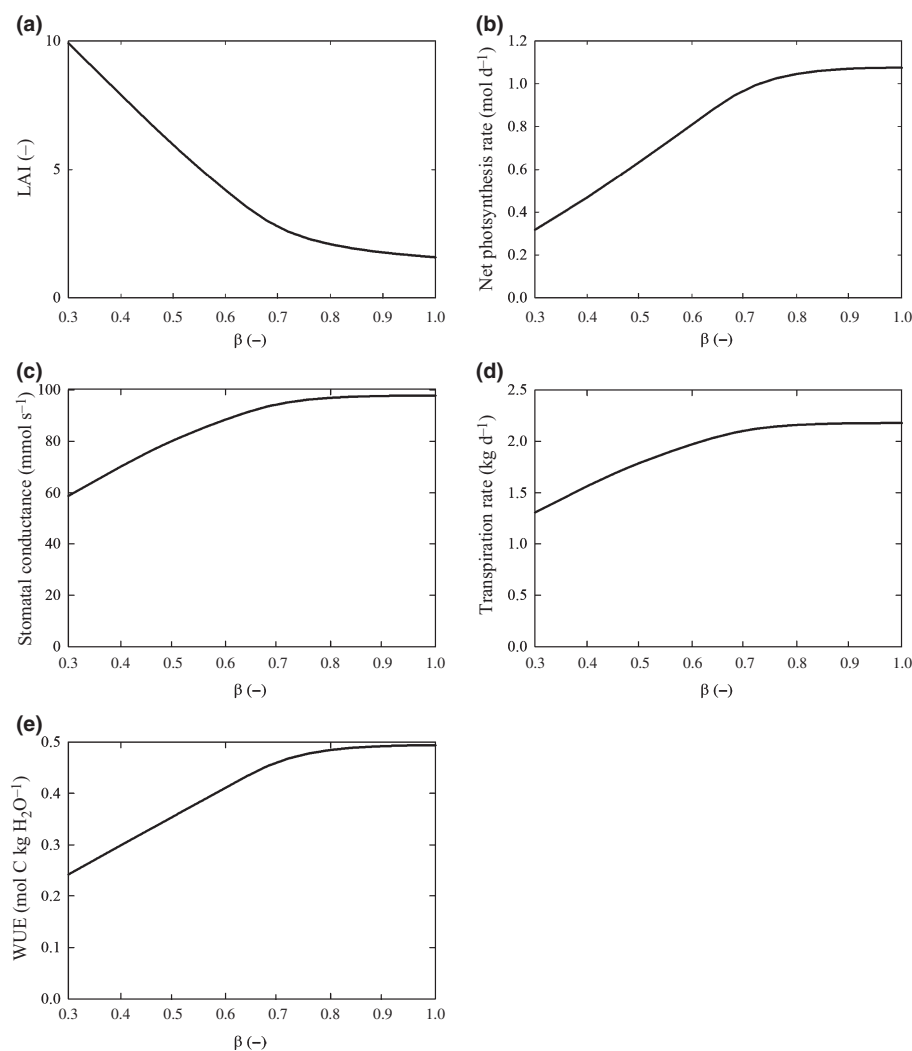


Fig. 2 (a) Total leaf area index (LAI), (b) net photosynthetic rate, (c) stomatal conductance, (d) transpiration rate and (e) water use efficiency (WUE) for different degrees to which canopies are mixed (β ; $\beta=1$ is no mixture; the closer β is to zero, the higher the degree of mixture).

that water use efficiency (WUE) is reduced (Fig. 2e). As the amount of N in the canopy is the same for the two model versions, predicted whole-plant photosynthetic N use efficiency also decreases with increasing mixture (data not shown). However, model results are highly sensitive to β (Eqn 1), indicating that this is a key parameter in the model (Fig. 2).

Climate change

By the year 2100, SimOpt ($\beta=1$) and ComOpt (constant $\beta=0.5$) predicted that with constant temperature and increased CO₂ concentration LAI would increase by 0.3% and 14%, respectively, and with increases in both temperature and CO₂ concentration LAI would increase by 14% and 4%, respectively, while for NoOpt a constant LAI was assumed (Fig. 3a). For ComOpt the LAI increases because, as a consequence of the increase in CO₂ concentration, leaf photosynthesis becomes more electron-transport limited, and thus indirectly light limited. When light is limiting, the benefits of investing in leaf area and the associated ability to compete for light increase. There is a smaller increase in LAI when the temperature is also increased, because an increase in temperature results in an increase in the vapor pressure difference between leaf and air (VPD; Eqn S30; we assumed constant relative humidity) which causes a certain degree of water stress, causing lower LAI. However, for SimOpt, an increase in temperature resulted in more leaf area as the negative effects of water stress are much smaller as a result of the lower initial leaf area, and therefore increasing LAI will result in higher photosynthesis. Given the fact that total canopy N was assumed to be constant, the model predicts a small reduction in leaf N content per unit leaf area (see Fig. S1 for results for a wide range of total canopy N contents and water availabilities).

All three models predict an increase in the net photosynthetic rate from 2000 to 2100 (Fig. 3b). With a constant temperature, NoOpt, SimOpt and ComOpt predict an increase of 58%, 61% and 40%, respectively. All models predict a stronger increase if the temperature increases over time, as a result of the increase in the efficiency of photosynthesis (64%, 68% and 58% for NoOpt, SimOpt and ComOpt, respectively; Fig. 3b).

All three models predict a reduction in stomatal conductance with increasing CO₂ concentration over the simulation period (2000–2100), but this reduction is smaller for both ComOpt and NoOpt when temperature is also assumed to increase over this period. The latter is because temperature increases the rate of photosynthesis and thus the demand for CO₂. For SimOpt this decrease is larger, as a consequence of the stronger increase in LAI with an increase in temperature. The ComOpt version predicts a larger reduction (41% and 48% with and without warming, respectively) than the NoOpt version (41% and 45%, respectively) and SimOpt (33% and 31%, respectively; Fig. 3c).

The transpiration rate decreases with increasing CO₂ according to all model versions, with the largest reduction in ComOpt (Fig. 3d). With a constant temperature, NoOpt predicts a reduction of 45%, SimOpt a reduction of 31% and ComOpt a reduction of 48%. These reductions mirror the reductions in stomatal conductance because there is no change in VPD. If the

temperature also increases, the reduction in the transpiration rate is smaller than the reduction in stomatal conductance; NoOpt predicts a reduction of 25%, SimOpt a reduction of 15% and ComOpt a reduction of 25% (Fig. 3d). The smaller reduction in transpiration rate with an increase in temperature is because VPD increases (we assumed constant relative humidity), and because of the mentioned positive effect of temperature on stomatal conductance.

The WUE (i.e. the net photosynthetic rate divided by the transpiration rate of the whole canopy) will increase under elevated CO₂ conditions as a result of the increase in net photosynthesis and the decrease in transpiration rate (Fig. 3e). The temperature rise increases the VPD, which increases the transpiration rate. This increase in transpiration rate with an increase in temperature is greater than the increase in net photosynthesis, so WUE increases less if temperature also increases.

Model validation against experimental studies

The seasonal pattern in LAI development of the crop under both ambient and elevated CO₂ concentrations (Dermody *et al.*, 2006) corresponded well with the predictions of the ComOpt model version (Fig. S2). This was illustrated by the fact that predicted and measured values clustered around the 1 : 1 correspondence line, when plotted against all points. Conversely, the simple optimization model (SimOpt: no competition, $\beta=1$; optimal LAI) greatly underestimated the LAI values throughout the season under both ambient and elevated CO₂ concentrations (Figs 4a,b, S2).

Secondly, ComOpt predicted the relative change in LAI attributable to an increase in CO₂ concentration from 37.5 to 55.0 Pa well within the wide range of data (107 observed values) obtained from a set of FACE experiments (Fig. 5). The average increase in LAI across all these observations was 11% (95% confidence interval ranging from 2 to 19%). For the same increase in atmospheric CO₂, ComOpt predicted an 8% increase (0.5% lower bound and 17% higher bound, as a result of variation in observed canopy leaf N values obtained by Dermody *et al.*, 2006). Conversely, SimOpt predicted a very small change (0.2%), well below the observed range, and this was also the case if the sensitivity of the model was included (lower bound 0.15%; higher bound 0.30%); and for NoOpt there was no change in LAI by definition (Fig. 5). The FACE experiments showed a mean increase in the net photosynthetic rate of the top leaves in the canopy of 24% (20% lower bound; 28% higher bound). All model versions predicted changes that fell within this range (NoOpt, 21%; SimOpt, 26%; and ComOpt, 23%; Fig. 5). The experiments showed a mean reduction in stomatal conductance of 11% (lower bound -16%; higher bound -5%); NoOpt, SimOpt and ComOpt predicted a decrease of 17%, 9% and 14%, respectively (Fig. 5). Across all simulations, higher values of total canopy N content resulted in more positive relative responses to elevated CO₂; that is, larger relative increases in LAI and photosynthesis and lower relative reductions in stomatal conductance (Fig. 5; higher bounds; Fig. S1). Thus, all three model versions gave good predictions of the relative effects of CO₂ elevation on leaf fluxes. However, the

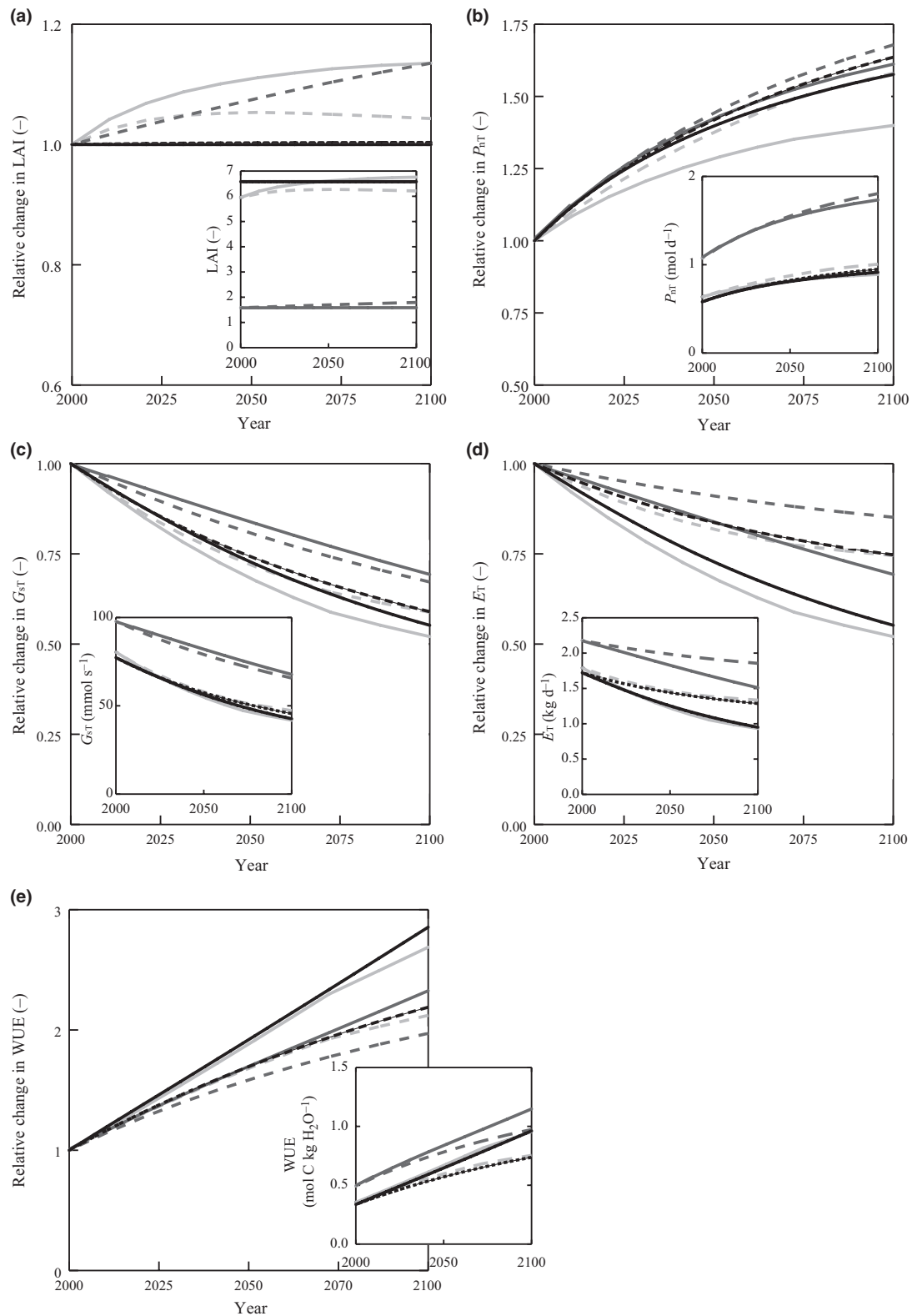


Fig. 3 Fractional changes in (a) total leaf area index (LAI), (b) net photosynthetic rate (P_{nT}), (c) stomatal conductance (G_{sr}), (d) transpiration rate (E_{tr}), and (e) water use efficiency (WUE) as predicted by the baseline model (black lines), the simple optimization model (dark gray lines) and the competitive optimization model (light gray lines; $\beta = 0.5$); the inserts show the absolute values. In 2000, the atmospheric CO_2 concentration is 37 Pa and it is assumed to increase linearly to 97 Pa in 2100. The temperature is 24°C in 2000; the striped lines indicate the results for a linear increase in temperature to 28°C; the continuous lines indicate a constant temperature of 24°C over the years.

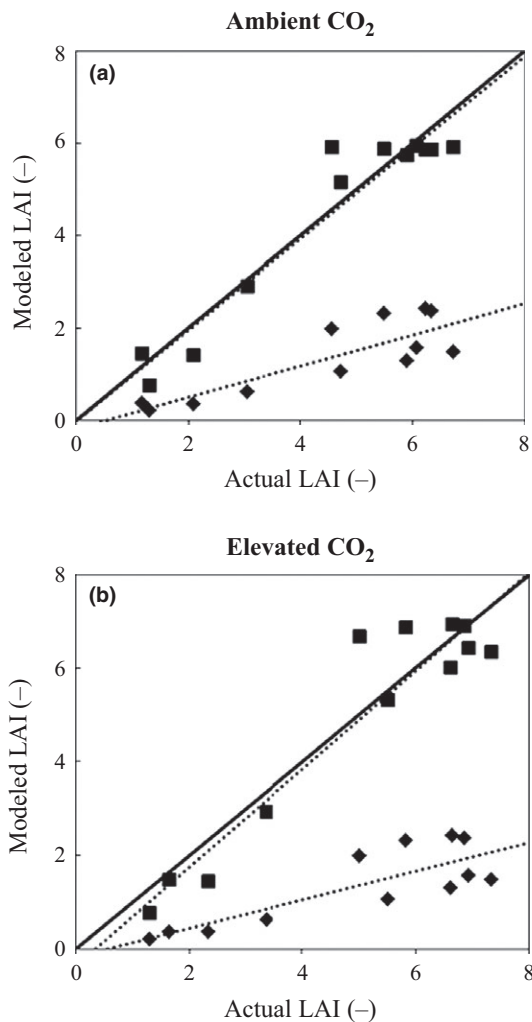


Fig. 4 Predicted leaf area index (LAI) by the simple optimization model (diamonds) and the competitive optimization model (squares) as a function of actual LAI (Dermody *et al.*, 2006), for an atmospheric CO₂ concentration of 37 Pa (a) and 55 Pa (b). Solid lines indicate the 1 : 1 correspondence line and dashed lines the linear regressions.

absolute values of the fluxes for both ambient and elevated CO₂ concentrations were greatly overestimated by SimOpt (not shown). Similarly, SimOpt greatly underestimated the absolute LAI values (Figs 4, 5). Thus, ComOpt was the only model version of the three that gave good predictions of the effects of CO₂ on both LAI and leaf fluxes.

Discussion

This study shows that it is important to consider local plant–plant interactions in models that predict vegetation structure and functioning under climate change. Our simulations reveal that including competition in the model (ComOpt; degree of interaction, $\beta < 1$) results in predicted vegetation stands with higher LAIs, but with lower transpiration rates and lower photosynthetic rates compared with simple optimization (SimOpt; $\beta = 1$). As the reduction in photosynthesis is proportionally larger than the

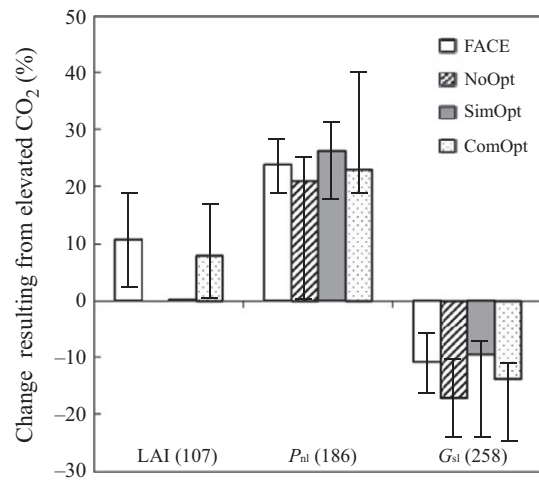


Fig. 5 Percentage changes in leaf area index (LAI), leaf net photosynthetic rate (P_{ni}) and stomatal conductance (G_{si}) of the topmost leaf resulting from an increase in CO₂ from 37.5 to 55 Pa. White bars represent the mean percentage change according to Free air CO₂ enrichment (FACE) experiments with the 95% confidence interval as an error bar; sample size appears in parentheses next to the symbol. Striped, gray and dotted bars represent the percentage change according to the baseline model (NoOpt), the simple optimization model (SimOpt) and the competitive optimization model (ComOpt), respectively; error bars are the result of changes in canopy leaf nitrogen (N) content (45–1023 mmol N m⁻²).

reduction in transpiration, inclusion of competition also results in lower predicted WUE. This finding is contrary to the simple positive relationship between LAI and transpiration often assumed by climate and ecology modelers (e.g. Van den Hurk *et al.*, 2003). Thus, our results illustrate how competition between plants may modify vegetation responses to climate.

With the CO₂ elevation predicted for the 21st Century, our model simulated an increase in both LAI and net canopy photosynthesis, while transpiration rates decreased. This CO₂ fertilization mechanism is known from many studies (e.g. Cao & Woodward, 1998) and, in turn, entails a considerable increase in photosynthetic WUE. However, with the predicted increase in temperature, transpiration is reduced less but photosynthesis is increased more, while LAI is increased less. The result is that plants are predicted to become more efficient with elevated CO₂, but because of the temperature rise WUE increases less.

The competitive optimization model has been shown to be a good predictor of LAIs under current conditions (Anten, 2002), and here we show that it also accurately predicts the effects of elevated CO₂ on this trait observed in a large number of FACE experiments (Fig. 5) as well as the seasonal dynamic in LAI over the season (Fig. 4), at least in soybean. LAI is a key trait in driving vegetation climate feedbacks through its effects on CO₂ and water vapor exchange between vegetation and the atmosphere and its effect on surface albedo.

Degree of interaction between plants

The ecological implications of light competition among plants has been the subject of extensive research (e.g. Weiner, 1990; Schmitt *et al.*, 1999; Falster & Westoby, 2003; Niinemets, 2010)

but, to our knowledge, the degree to which competition may mediate plant responses to climate change has not been quantitatively studied. Here we show that the degree to which canopies of neighboring plants are mixed and thus influence each other's light climate has a large influence on model outcomes. This was shown by the strong increase in LAI with the degree to which plants influence each other's light climate. This result suggests that the degree of plant–plant interaction may strongly affect vegetation responses to climate change and that more work is therefore needed to quantify this interaction. In this respect it is important to note that this degree of self to nonself interaction (β) in plant canopies probably differs between plant types. For example, trees have relatively broad canopies and probably a higher degree of self-interaction (larger β) than herbaceous plants with much narrower canopies (Anten & During, 2011). Clonal plants may also differ markedly in the degree of self/nonself interaction, depending on the spatial pattern in which they produce their vegetative offspring. If placed close together, such plants may produce large monoclonal patches and competition between genetically different individuals is very limited, which would be reflected in β values close to 1. Thus, we emphasize that, if our approach were to be extended to more plant types, careful consideration should be given to the assumptions of self/nonself interactions.

Our model predicts that, with increasing interaction among plants in vegetation (decreasing β), the leaf area of plants increases while their stomatal conductance declines, resulting in both a larger LAI and lower transpiration at the vegetation level. The pattern observed in our simulations can be explained as follows. If a plant is competing, increasing its LAI to more than the optimal LAI (determined for a given canopy N and water availability) will result in a smaller increase in self-shading, while the plant is able to capture a larger fraction of the available light. Thus, the individual plant can increase its carbon gain by increasing the LAI even if this reduces the photosynthesis of the stand as a whole. It will thus have a higher relative fitness and can invade, resulting in a new population with a larger leaf area. As canopy N remains unchanged, this implies that plants reduce N use efficiency in order to shade competitors. So, with an increase in the degree of mixture between plants, the LAI of the stand as a whole will increase while the net photosynthesis of the stand decreases. As a consequence of the decreased consumption of CO₂ of the stand, this will decrease the stomatal conductance of the stand which results in a lower transpiration rate compared with plants that are not mixed.

Model compared with experimental studies

The correspondence between model predictions and observed values was dependent on the type of competition, the trait and whether absolute or relative effects were considered. However, ComOpt was the only model version that correctly predicted both the seasonal course in LAI under ambient and elevated CO₂ concentrations from Dermody *et al.* (2006) and the average relative effect of CO₂ elevation on LAI as determined by 107 FACE experiments. By contrast, SimOpt greatly underestimated

absolute LAIs and the relative effects of elevated CO₂ on LAI. This indicates that inclusion of competition in vegetation models may greatly improve predictions of LAI and effects of climate change thereupon. For stomatal conductance and net photosynthetic rate, all three model versions simulated the relative changes with increasing CO₂ well within the range of observed effects obtained by FACE experiments. However, in absolute terms SimOpt considerably overestimated net photosynthesis and stomatal conductance.

All three models showed amplified responses to elevated CO₂ with higher N contents, which is consistent with the general finding that growth stimulation by CO₂ is larger at high than at low N availability (Rogers *et al.*, 1996; Poorter, 1998). In the model, the mechanism that drives the stronger response to CO₂ at high N is that LAI and thus shading in the canopy increase with N availability and thus plants benefit more from the CO₂ stimulation of quantum yield (Anten *et al.*, 2004). In addition, inhibition of photosynthesis by carbohydrate accumulation at high CO₂ tends to be weaker at high than at low N (Rogers *et al.*, 1996).

Vegetation responses to climate change

Plants were predicted to respond to climate change (i.e. warming and CO₂ elevation) by increasing LAI, and decreasing leaf N, stomatal conductance and transpiration rate. Plants decrease their stomatal conductance when the atmospheric CO₂ concentration increases, in order to maintain the ratio of internal CO₂ to atmospheric CO₂ (Goudriaan & Unsworth, 1990), resulting in a decrease in the transpiration rate. An increase in temperature resulted in a lower LAI for ComOpt compared with the situation where only CO₂ was increased. This can be explained by the optimality hypothesis of gas exchange. According to the optimality theory, plants maximize carbon gain while having minimum water loss (e.g. Cowan, 1978; Katul *et al.*, 2010). The increased temperature results in higher transpiration rates. To keep transpiration constant, LAI is reduced but photosynthesis is increased as a result of increased efficiency of the photosynthetic apparatus. However, in the case of SimOpt, this issue plays a much smaller role as this model version predicts much lower LAIs (as it does not consider competition).

The magnitude of the change in transpiration rate projected by the models strongly depends on the extent of future warming. We used the climate predictions of the A1FI climate scenario of the IPCC, which predicts that the temperature will increase by 4°C from the year 2000 to 2100, and we had a scenario where the temperature stayed constant. This variation in temperature resulted in a broad range of predicted transpiration rates.

Limitations of the model and considerations for future work

Our main objective was to show that inclusion of competition in vegetation models may strongly affect predictions of vegetation structure and functioning in response to climate, and not to provide a tailor-made predictive tool. We therefore used a canopy model that was based on a number of simplifications that more

predictive studies should consider in the future. For example, while we did include leaf respiration costs, added costs of leaf construction and investments in stems and roots needed to support leaves were not taken into account. We also did not set an upper limit to the specific leaf area. These factors were likely to impose limitations on LAI, particularly where LAI was predicted to be very high, for example at very low values of β .

All three model versions predicted a decreased transpiration rate; this may affect climate predictions through effects of climate-vegetation feedbacks (e.g. Bonan, 2008; Dekker *et al.*, 2010). A decreased transpiration rate can cause a drying of the near surface atmosphere as well as a warming of the canopy itself (as a consequence of less evaporative cooling), which subsequently increases the vapor pressure difference between leaf and air. Depending on soil water availability, this can lead to further stomatal closure or, if stomatal opening remains unchanged, higher transpiration (Friend & Cox, 1995; Bernacchi *et al.*, 2007). The latter feedback probably occurred in the SoyFACE experiments as plants were well watered, but this was not considered in our model. Thus, while our predicted effects of CO₂ elevation on stomatal conductance were consistent with results from FACE experiments (Fig. 5), it is possible that we overestimated the reduction in transpiration. Indeed, other studies predicted smaller reductions in transpiration (e.g. Bernacchi *et al.*, 2007; Drewry *et al.*, 2010).

Our analysis was constrained at the canopy level, as we addressed the question of how plants compete for light given the amount of resources allocated to their leaves. As our model was developed for well-watered systems, biomass allocation to the root was not simulated. Therefore, we did not extend the model with inclusion of acquisition and competition for belowground resources. Interestingly, while game theoretical models exist analyzing either aboveground traits (e.g. Hikosaka & Hirose, 1997; Anten, 2002; Falster & Westoby, 2003) or belowground traits (Gersani *et al.*, 2001) separately, combined analyses of both components have not been performed. Such analyses would constitute an important step forward.

We did not consider growth-related processes that underlie leaf area production. LAI increment arises from the balance between leaf production with associated construction costs and senescence with associated losses of resources (e.g. Hikosaka, 2005). In spite of this simplification, ComOpt is able to accurately simulate the seasonal dynamics in LAI. This indicates that, if one knows the seasonal pattern in N uptake by the crop, which can be modeled fairly realistically (e.g. Franklin, 2007), ComOpt can provide fairly accurate estimates of LAI.

In our approach of defining a stable LAI, we assumed that there is a stand of identical plants and assessed whether this stand can be invaded by a plant with a slightly different LAI. If this invader plant has a higher assimilation rate, it will invade, resulting in a new situation in which all individuals have this different LAI. However, it has not been shown whether these changes in LAI occur through plasticity, genotypic adaptation or replacement of less competitive resident genotypes by more competitive ones. Moreover, it is unlikely that such changes in canopy traits would occur completely through genotypic adaptation, given the short time-span of the predicted effects (100 yr). Thus, the

patterns as predicted by us could be the result of phenotypic plasticity or of invasions of existing populations by individuals from outside. Regarding the former, plant acclimation to elevated CO₂ (e.g. Sage, 1994; Ainsworth & Long, 2005) and temperature has been reported (e.g. Hikosaka *et al.*, 2006; Yamori *et al.*, 2009). Regarding the potential contribution of invasions from outside, this process is likely to take place with respect to increased temperature, as populations from warmer areas (i.e. lower latitudes or altitudes) could competitively replace those from cooler habitats (e.g. Dukes & Mooney, 1999; Parmesan & Yohe, 2003). For CO₂ this seems to be an unlikely scenario, as the CO₂ concentration is rather constant across the globe. Thus, within this time-span it is most likely that plants show acclimation to elevated CO₂. So, although our model is relatively simple, as it was not our objective to produce a detailed model of vegetation functioning, our study does strongly imply that inclusion of trait acclimation in a competitive setting in vegetation models is ecologically more realistic and may improve predictions of climate change effects on vegetation structure and functioning.

Acknowledgements

We thank Elisabeth Ainsworth for the provision of the FACE data set. This work was financially supported by a Focus & Mass grant from Utrecht University awarded to N.P.R.A., M.R. and S.C.D.

References

- Ainsworth EA, Davey PA, Bernacchi CJ, Dermody OC, Heaton EA, Moore DJ, Morgan PB, Naidu SL, Yoo Ra H, Zhu X *et al.* 2002. A meta-analysis of elevated [CO₂] effects on soybean (glycine max) physiology, growth and yield. *Global Change Biology* 8: 695–709.
- Ainsworth EA, Long SP. 2005. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytologist* 165: 351–372.
- Ainsworth EA, Rogers A, Leakey AD, Heady LE, Gibon Y, Stitt M, Schurr U. 2007. Does elevated atmospheric [CO₂] alter diurnal C uptake and the balance of C and N metabolites in growing and fully expanded soybean leaves? *Journal of Experimental Botany* 58: 579–591.
- Anten NPR, Schieving F, Werger MJ. 1995a. Patterns of light and nitrogen distribution in relation to whole canopy carbon gain in C₃ and C₄ mono- and dicotyledonous species. *Oecologia* 101: 504–513.
- Anten NPR. 2002. Evolutionarily stable leaf area production in plant populations. *Journal of Theoretical Biology* 217: 15–32.
- Anten NPR. 2005. Optimal photosynthetic characteristics of individual plants in vegetation stands and implications for species coexistence. *Annals of Botany* 95: 495–506.
- Anten NPR, During HJ. 2011. Is analysing the nitrogen use at the plant canopy level a matter of choosing the right optimization criterion. *Oecologia* 167: 293–303.
- Anten NPR, Hirose T, Onoda Y, Kinugasa T, Kim HY, Okada M, Kobayashi K. 2004. Elevated CO₂ and nitrogen availability have interactive effects on canopy carbon gain in rice. *New Phytologist* 161: 459–471.
- Anten NPR, Schieving F, Medina E, Werger MJA, Schuffelen P. 1995b. Optimal leaf area indices in C₃ and C₄ mono- and dicotyledonous species at low and high nitrogen availability. *Physiologia Plantarum* 95: 541–550.
- 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.

- Asner GP, Scurlock JMO, Hicke JA. 2003. Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Global Ecology and Biogeography* 12: 191–205.
- Bernacchi CJ, Kimball BA, Quarles DR, Long SP, Ort DR. 2007. Decreases in stomatal conductance of soybean under open-air elevation of [CO₂] are closely coupled with decreases in ecosystem evapotranspiration. *Plant Physiology* 143: 134–144.
- Bernacchi CJ, Leakey ADB, Heady LE, Morgan PB, Dohleman FG, Mcgrath JM, Gillespie KM, Wittig VE, Rogers A, Long SP *et al.* 2006. Hourly and seasonal variation in photosynthesis and stomatal conductance of soybean grown at future CO₂ and ozone concentrations for 3 years under fully open-air field conditions. *Plant, Cell & Environment* 29: 2077–2090.
- Bernacchi CJ, Morgan PB, Ort DR, Long SP. 2005. The growth of soybean under free air [CO₂] enrichment (FACE) stimulates photosynthesis while decreasing *in vivo* Rubisco capacity. *Planta* 220: 434–446.
- Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320: 1444–1449.
- Brovkin V, Claussen M, Petoukhov V, Ganopolske A. 1998. On the stability of the atmosphere-vegetation system in the Sahara/Sahel region. *Journal of Geophysical Research* 103: 31613–31624.
- Cao M, Woodward FI. 1998. Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. *Global Change Biology* 4: 185–198.
- Claussen M. 1997. Modeling bio-geophysical feedback in the African and Indian monsoon region. *Climate Dynamics* 13: 247–257.
- Cowan I. 1978. Stomatal behaviour and environment. *Advances in Botanical Research* 4: 117–228.
- De Pury DGG, Farquhar G. 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell & Environment* 20: 537–557.
- Dekker SC, De Boer H, Brovkin V, Fraedrich K, Wassen M, Rietkerk M. 2010. Biogeophysical feedbacks trigger shifts in the modelled vegetation-atmosphere system at multiple scales. *Biogeosciences* 7: 1237–1245.
- Dekker SC, Vrugt JA, Elkington RJ. 2012. Significant variation in vegetation characteristics and dynamics from ecohydrological optimality of net carbon profit. *Ecohydrology* 5: 1–18.
- Dermody O, Long SP, DeLucia EH. 2006. How does elevated CO₂ or ozone affect the leaf-area index of soybean when applied independently? *New Phytologist* 169: 145–155.
- Dewar RC, Franklin O, Makela A, McMurtrie RE, Valentine HT. 2009. Optimal function explains forest responses to global change. *BioScience* 59: 127–139.
- Drewry D, Kumar P, Long S, Bernacchi C, Liang X, Sivapalan M. 2010. Ecohydrological responses of dense canopies to environmental variability: 2. Role of acclimation under elevated CO₂. *Journal of Geophysical Research: Biogeosciences (2005–2012)* 115: G04023.
- Dukes JS, Mooney HA. 1999. Does global change increase the success of biological invaders? *Trends in Ecology & Evolution* 14: 135–139.
- Dybzinski R, Farrior C, Wolf A, Reich PB, Pacala SW. 2011. Evolutionarily stable strategy carbon allocation to foliage, wood, and fine roots in trees competing for light and nitrogen: an analytically tractable, individual-based model and quantitative comparisons to data. *The American Naturalist* 177: 153–166.
- Falster DS, Westoby M. 2003. Plant height and evolutionary games. *Trends in Ecology & Evolution* 18: 337–343.
- Farquhar GD, von Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* 149: 78–90.
- Farrior CE, Dybzinski R, Levin SA, Pacala SW. 2013. Competition for water and light in closed-canopy forests: a tractable model of carbon allocation with implications for carbon sinks. *The American Naturalist* 181: 314–330.
- Franklin O. 2007. Optimal nitrogen allocation controls tree responses to elevated CO₂. *New Phytologist* 174: 811–822.
- Friend A, Schugart H, Running S. 1993. A physiology-based gap model of forest dynamics. *Ecology* 74: 792–797.
- Friend A, Stevens A, Knox R, Cannell M. 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3. 0). *Ecological Modelling* 95: 249–287.
- Friend AD, Cox PM. 1995. Modelling the effects of atmospheric CO₂ on vegetation-atmosphere interactions. *Agricultural and Forest Meteorology* 73: 285–295.
- Gersani M, O'Brien EE, Maina GM, Abramsky Z. 2001. Tragedy of the commons as a result of root competition. *Journal of Ecology* 89: 660–669.
- Goudriaan J, Unsworth MH. 1990. Implications of increasing carbon dioxide and climate change for agricultural productivity and water resources. *ASA Special Publication* 53: 111–130.
- Harley PC, Thomas RB, Reynolds JF, Strain BR. 1992. Modelling photosynthesis of cotton grown in elevated CO₂. *Plant, Cell & Environment* 15: 271–282.
- Hikosaka K. 2005. Leaf canopy as a dynamic system: ecophysiology and optimality in leaf turnover. *Annals of Botany* 95: 521–533.
- Hikosaka K, Hirose T. 1997. Leaf angle as a strategy for light competition: optimal and evolutionarily stable light-extinction coefficient within a leaf canopy. *Ecoscience* 4: 501–507.
- Hikosaka K, Ishikawa K, Borjigidai A, Muller O, Onoda Y. 2006. Temperature acclimation of photosynthesis: mechanisms involved in the changes in temperature dependence of photosynthetic rate. *Journal of Experimental Botany* 57: 291–302.
- Iio A, Hikosaka K, Anten NPR, Nakagawa Y, Ito A. 2014. Global dependence of field-observed leaf area index in woody species on climate: a systematic review. *Global Ecology and Biogeography* 23: 274–285.
- IPCC. 2007. In Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, eds. *Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK & New York, NY, USA: Cambridge University Press.
- Johnson FH, Eyring H, Williams RW. 1942. The nature of enzyme inhibitions in bacterial luminescence: sulfanilamide, urethane, temperature and pressure. *Journal of Cellular and Comparative Physiology* 20: 247–268.
- Katul G, Manzoni S, Palmroth S, Oren R. 2010. A stomatal optimization theory to describe the effects of atmospheric CO₂ on leaf photosynthesis and transpiration. *Annals of Botany* 105: 431–442.
- Leakey AD, Bernacchi CJ, Ort DR, Long SP. 2006. Long-term growth of soybean at elevated [CO₂] does not cause acclimation of stomatal conductance under fully open-air conditions. *Plant, Cell & Environment* 29: 1794–1800.
- Lloyd J, Patiño S, Paiva RQ, Nardoto GB, Quesada CA, Santos AJB, Baker TR, Brand WA, Hilke I, Gielmann H *et al.* 2010. Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees. *Biogeosciences* 7: 1833–1859.
- Maynard Smith J. 1974. The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology* 47: 209–221.
- McMurtrie R, Norby RJ, Medlyn BE, Dewar RC, Pepper DA, Reich PB, Barton GVM. 2008. Why is plant-growth response to elevated CO₂ amplified when water is limiting, but reduced when nitrogen is limiting? A growth-optimisation hypothesis. *Functional Plant Biology* 35: 521–534.
- Medvigy D, Wofsy SC, Munger JW, Moorcroft PR. 2010. Responses of terrestrial ecosystems and carbon budgets to current and future environmental variability. *Proceedings of the National Academy of Sciences, USA* 107: 8275–8280.
- Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F *et al.* 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* 15: 684–692.
- Niinemetts Ü. 2010. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecological Research* 25: 693–714.
- Parker GA, Maynard-Smith JM. 1990. Optimality theory in evolutionary biology. *Nature* 348: 27–33.
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- Poorter H. 1998. Do slow growing species and nutrient stressed plants respond relatively strongly to elevated CO₂? *Global Change Biology* 4: 693–697.

- Reichert SE, Hammerstein P. 1983. Game theory in the ecological context. *Annual Review of Ecology and Systematics* 14: 377–409.
- Rogers A, Allen DJ, Davey PA, Morgan PB, Ainsworth EA, Bernacchi CJ, Cornic G, Dermody O, Dohleman FG, Heaton E *et al.* 2004. Leaf photosynthesis and carbohydrate dynamics of soybeans grown throughout their life-cycle under free-air carbon dioxide enrichment. *Plant, Cell & Environment* 27: 449–458.
- Rogers G, Milham P, Gillings M, Conroy J. 1996. Sink strength may be the key to growth and nitrogen responses in N-deficient wheat at elevated CO₂. *Functional Plant Biology* 23: 253–264.
- Running SW, Coughlan JC. 1988. A general model of forest ecosystem processes for regional applications I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecological Modelling* 42: 125–154.
- Sage RF. 1994. Acclimation of photosynthesis to increasing atmospheric CO₂: the gas exchange perspective. *Photosynthesis Research* 39: 351–368.
- Scheffer M, Holmgren M, Brovkin V, Claussen M. 2005. Synergy between small- and large-scale feedbacks of vegetation on the water cycle. *Global Change Biology* 11: 1003–1012.
- Schmitt J, Dudley SA, Pigliucci M. 1999. Manipulative approaches to testing adaptive plasticity: phytochrome-mediated shade-avoidance responses in plants. *The American Naturalist* 154: S43–S54.
- Schymanski SJ, Roderick ML, Sivapalan M, Hutley LB, Beringer J. 2007. A test of the optimality approach to modelling canopy properties and CO₂ uptake by natural vegetation. *Plant, Cell & Environment* 30: 1586–1598.
- Sellers PJ, Dickinson RE, Randall DA, Betts AK, Hall FG, Berry JA, Collatz GJ, Denning AS, Mooney HA, Nobre CA *et al.* 1997. Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science* 275: 502–509.
- Spitters CJT, Toussaint HAJM, Goudriaan J. 1986. Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. Part I. Components of incoming radiation. *Agricultural and Forest Meteorology* 38: 217–229.
- Sterck F, Markesteijn L, Schieving F, Poorter L. 2011. Functional traits determine trade-offs and niches in a tropical forest community. *Proceedings of the National Academy of Sciences, USA* 108: 20627–20632.
- Sterck F, Schieving F. 2011. Modelling functional trait acclimation for trees of different height in a forest light gradient: emergent patterns driven by carbon gain maximization. *Tree Physiology* 31: 1024–1037.
- Tetens O. 1930. Über einige meteorologische Begriffe z. *Geophysik* 6: 297–309.
- Tuzet A, Perrier A, Leuning R. 2003. A coupled model of stomatal conductance, photosynthesis and transpiration. *Plant, Cell & Environment* 26: 1097–1116.
- Van den Hurk BJJM, Viterbo P, Los SO. 2003. Impact of Leaf Area Index seasonality on the annual land surface evaporation in a global circulation model. *Journal of Geophysical Research* 108: 4191–4199.
- Weiner J. 1990. Asymmetric competition in plant populations. *Trends in Ecology & Evolution* 5: 360–364.
- Yamori W, Noguchi K, Hikosaka K, Terashima I. 2009. Cold-tolerant crop species have greater temperature homeostasis of leaf respiration and photosynthesis than cold-sensitive species. *Plant and Cell Physiology* 50: 203–215.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Comparison of the LAI and net photosynthetic rate of the baseline model, the simple optimization model and the competitive optimization model for different total canopy N contents and different water availabilities.

Fig. S2 Comparison of seasonal dynamics of LAI of model predictions with measurements.

Table S1 List of symbols for the model parameters mentioned in the main text, with their units, description of the variable, input value and the source of the input value

Table S2 List of symbols for the model variables mentioned in the main text, with their units, description of the variable and their equation number as mentioned in the main text

Methods S1 A full description of the canopy model; this canopy model calculates the net photosynthetic rate as a function of light, nitrogen, temperature, water availability and atmospheric CO₂ concentration.

Please note: Wiley Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.