

Optimal Function Explains Forest Responses to Global Change

RODERICK C. DEWAR, OSKAR FRANKLIN, ANNIKKI MÄKELÄ, ROSS E. McMURTRIE, AND HARRY T. VALENTINE

Plant responses to global changes in carbon dioxide (CO₂), nitrogen, and water availability are critical to future atmospheric CO₂ concentrations, hydrology, and hence climate. Our understanding of those responses is incomplete, however. Multiple-resource manipulation experiments and empirical observations have revealed a diversity of responses, as well as some consistent patterns. But vegetation models—currently dominated by complex numerical simulation models—have yet to achieve a consensus among their predicted responses, let alone offer a coherent explanation of the observed ones. Here we propose an alternative approach based on relatively simple optimization models (OMs). We highlight the results of three recent forest OMs, which together explain a remarkable range of observed forest responses to altered resource availability. We conclude that OMs now offer a simple yet powerful approach to predicting the responses of forests—and, potentially, other plant types—to global change. We recommend ways in which OMs could be developed further in this direction.

Keywords: adaptation, global change, modeling, optimization, resource availability

Terrestrial ecosystems continue to be subjected to major human-induced perturbations in their supply of three essential resources: (1) global mean atmospheric carbon dioxide concentration ([CO₂]; the square brackets denote concentration) increased during 1995–2005 by 1.9 parts per million per year (IPCC 2007); (2) over Western Europe and the United States, rates of total (wet and dry) nitrogen (N) deposition of up to 1.5 grams N per square meter (m²) per year have been estimated for the period 1990–1993 (Holland et al. 2005, Magnani et al. 2007); and (3) according to the Intergovernmental Panel on Climate Change (IPCC 2007), human influences have “more likely than not” altered regional patterns of precipitation, with increases of both the area affected by drought since the 1970s and the frequency of heavy precipitation events.

In turn, future [CO₂], hydrology, and hence climate change will depend on how net CO₂ uptake and water use by terrestrial ecosystems respond to these perturbations. However, some outstanding questions limit our ability to predict those responses. To what extent is the stimulation of plant growth by rising [CO₂] limited by soil nutrient and water availability, and on what timescales? Will atmospheric N deposition alleviate soil N constraints on the CO₂ stimulation of plant growth? Do plants use water more efficiently at elevated [CO₂]? If so, will this lead to less water use by ecosystems, or

will greater water-use efficiency be offset by enhanced leaf-area development? Ultimately, these questions challenge our fundamental understanding of how plants and ecosystems operate under multiple resource constraints, and how they respond when those constraints are perturbed.

The physiology of photosynthesis, nutrient acquisition, water uptake, and transpiration are each reasonably well understood. It is the balance among these processes, and how that balance shifts when resource availability changes, that is the real unknown. Data from CO₂ enrichment experiments and other empirical studies have provided important clues here.

First, the data reveal strong CO₂-N and CO₂-H₂O (water) interactions. In Free-Air CO₂ Enrichment (FACE) and open-top chamber experiments, N limitation and N fertilization have been shown to reduce and enhance, respectively, the CO₂ stimulation of growth across a wide range of plant types (e.g., Wand et al. 1999, Oren et al. 2001, Nowak et al. 2004, Reich et al. 2006a). Regulation of plant growth by N is also apparent at ecosystem scales; net CO₂ uptake by European forests may be correlated with regional N deposition (Magnani et al. 2007). In contrast to these CO₂-N interactions, water limitation has been shown to increase the percentage response of plant growth to elevated [CO₂] (e.g., Morgan et al. 2004).

Second, these whole-system responses to changing resource availability can be understood from experiments focusing on the responses of some key underlying processes and plant functional traits. Those responses act on a variety of timescales and include the direct positive response of photosynthesis to elevated $[\text{CO}_2]$ (“instantaneous”), subsequent physiological acclimation such as changes in leaf stomatal conductance and leaf N concentration ($[\text{N}]$) (“short-term”—i.e., less than 1 year), adaptive shifts in the allocation of plant productivity between different plant organs (“intermediate term”—1 to 10 years), and, potentially, changes in soil N availability (“long-term”—10 to 1000 years).

On short timescales, both stomatal conductance and leaf $[\text{N}]$ are consistently reduced under elevated $[\text{CO}_2]$ (e.g., Ainsworth and Long 2005, Ainsworth and Rogers 2007). At intermediate timescales, increased fine-root production and plant N uptake at elevated $[\text{CO}_2]$ have been reported (e.g., Norby et al. 2006, Finzi et al. 2007). A meta-analysis of allocation patterns in forest ecosystems revealed that increased nutrient availability leads to little change in the fraction of photosynthesis partitioned to foliage production, whereas the fraction partitioned to wood production increases and that to belowground pools decreases (Litton et al. 2007). On longer timescales, it has been proposed that soil N availability will decrease under elevated $[\text{CO}_2]$ as a result of increased N immobilization in plant litter, biomass, and soil organic matter (Luo et al. 2004). However, the evidence for responses in microbial activity or N mineralization under elevated $[\text{CO}_2]$ remains mixed (e.g., Zak et al. 2003, Barnard et al. 2004, Reich et al. 2006a, 2006b).

Models of plant and ecosystem function can play a key role both conceptually, in making sense of the diverse responses observed in multiple-resource manipulation experiments, and practically, as components of global-scale models predicting future $[\text{CO}_2]$, hydrology, and climate. However, we would argue that modeling in this area—currently dominated by complex numerical simulation models—has reached something of a crossroads. In this article we propose an alternative approach based on relatively simple optimization models (OMs). Although OMs have been studied for a number of years (e.g., Givnish 1986, Mäkelä et al. 2002), it is only recently that their ability to predict and synthesize a wide range of plant responses to global change has begun to emerge, from comparisons with a growing body of data from FACE experiments and other empirical studies.

Plant and ecosystem modeling at a crossroads

Modeling in terrestrial ecology is dominated by complex numerical simulation models that represent explicitly the many physical, successional, and biogeochemical processes governing plant and ecosystem function. To an extent, this approach has been driven by a demand from the global change research community for land-surface models that operate over a wide range of vegetation types, environments, and timescales. Concurrently, advances in computer speed and

memory have relaxed the computational constraints on model complexity.

Complex models introduce plausible assumptions about each process for each plant type, requiring typically hundreds of parameters to be specified, few of which are identifiable from available data (e.g., Wang et al. 2001). These processes are then coupled together in various ways, often without considering simplifying principles that govern the balance between individual processes (but see, e.g., Sitch et al. 2003). And crucially, when used to simulate the plant functional responses to elevated $[\text{CO}_2]$ mentioned above, complex models—despite their focus on process detail—often fail to represent those responses mechanistically, if at all. For example, the biogeochemical-cycling model G'DAY (Comins and McMurtrie 1993) predicts reduced leaf $[\text{N}]$ at elevated $[\text{CO}_2]$ as a consequence of reduced soil N availability (“progressive N limitation”; Luo et al. 2004), which, in the short term, is the correct response but the wrong mechanism. Reduced stomatal conductance is incorporated in some complex models by assuming a fixed percentage decline or an increase in water-use efficiency (i.e., growth per unit transpiration) (e.g., Pepper et al. 2007). Shifts in growth allocation are either overlooked or imposed by assuming fixed percentage changes. Longer-term changes in soil N availability are omitted completely from several models in the IPCC *Fourth Assessment Report* (IPCC 2007; see, e.g., Cramer et al. 2001, Friedlingstein et al. 2006).

Unsurprisingly, therefore, uncertainties in model parameter values, differences among model structures, and the nonmechanistic treatment or omission of key acclimation processes have led to a great divergence in the predicted responses of complex vegetation models to elevated $[\text{CO}_2]$ (e.g., Cramer et al. 2001), to N enrichment (e.g., Levy et al. 2004), and to combined changes in $[\text{CO}_2]$, precipitation, and temperature (e.g., Luo et al. 2008). This situation makes it difficult to establish a theoretical consensus on plant responses to global change. An alternative approach is called for.

Optimization modeling: An alternative approach

Theories of optimal plant function offer an alternative approach to modeling in plant ecology (e.g., Givnish 1986, Kull 2002, Mäkelä et al. 2002). OMs identify an apparent goal or objective function F that is maximized with respect to one or more plant functional traits f . The maximization of F is usually subjected to one or more physiological or environmental constraints C . The advantage of this approach is that it avoids the need for an explicit submodel for f with its attendant parameters; instead, f is simply determined by the optimality condition that F is stationary with respect to variations in f permitted by the constraints C .

The optimization approach has been used to predict a variety of functional traits, including stomatal conductance (e.g., Cowan and Farquhar 1977), leaf and canopy N content (e.g., Dewar 1996, Haxeltine and Prentice 1996), shoot to root biomass ratio (e.g., Reynolds and Thornley 1982), N allocation within canopies (e.g., Field 1983), allocation

between height and diameter growth in trees (Mäkelä and Sievänen 1992), and leaf area index (e.g., McMurtrie 1985, Franklin and Ågren 2002). OMs incorporating multiple resource constraints have also been developed (e.g., Farquhar et al. 2002, Wright et al. 2003).

However, the optimization approach comes with its own set of contentious issues. Three key issues of principle are (1) What do plants maximize? Often F is proposed as a proxy for individual fitness—such as shoot or canopy photosynthesis, canopy photosynthesis minus plant respiration, or canopy photosynthesis minus plant respiration and foliage production (e.g., Dewar 1996, Dewar et al. 1998, Ackerly 1999, Hikosaka 2003, Anten 2005)—although the link with individual fitness is seldom quantified, and usually only a verbal justification of F is offered. (2) On what timescale τ does trait f adjust to a new optimum when the environment changes? (3) Why should one even expect that a trait f that has optimally adapted to a given environment will behave optimally in a new atypical environment? These theoretical issues remain largely unresolved today.

Perhaps partly as a result of this situation, OMs—although recognized and applied in terrestrial ecology for more than 30 years—remain relatively underexploited by the global change research community as components of land-surface models. Nevertheless, “maximization of objective function F with respect to traits f subject to constraints C ” constitutes a well-defined scientific hypothesis $H(F, f, C)$, and its predictions can be experimentally tested. So, rather than stalling on those unresolved theoretical issues, perhaps we should simply go ahead and see whether the optimization approach actually works as a predictive tool in global change research.

In the following two sections we highlight three recent forest OMs (McMurtrie et al. 2008, Franklin 2007, Mäkelä et al. 2008—hereafter models 1, 2, and 3, respectively) and their ability to predict and synthesize observed forest responses to changing resource availability. The main point we wish to demonstrate is that OMs have matured sufficiently to make quantitatively reasonable stand-level predictions of those responses, and could thus make a greater contribution to global change research than they have done until now. Then, in the final section, we identify future challenges for OMs and recommend ways in which they might be developed and applied as tools for global change research more generally, without excluding other modeling approaches.

Three forest optimization models

The three OMs (table 1, figure 1) predict the behavior of monospecific forests at the canopy scale. The models treat the canopy as a homogeneous “big leaf”; in predicting canopy photosynthesis, the big leaf approach has been shown to work as well as more detailed models that resolve individual tree crowns (e.g., Duursma and Mäkelä 2007). Respiration and growth processes are also represented. The models take soil nutrient availability as a given quantity and describe its effect on forest function; they do not include the feedback effect of forest function on soil nutrient availability through tree litter production and soil decomposition processes. Their extension to multispecies forests (e.g., Kull 2002), to tree-soil feedbacks (e.g., Comins and McMurtrie 1993), and to other plant types are areas for future research, which we include in our recommendations at the end of this article.

A full description of each model is given in the original articles (McMurtrie et al. 2008, Franklin 2007, Mäkelä et al.

Table 1. Key features of the three optimization models.

Feature	Model 1 (McMurtrie et al. 2008)	Model 2 (Franklin 2007)	Model 3 (Mäkelä et al. 2008)
Applicability	Deciduous forest	Expanding and closed-canopy forest	Closed-canopy, steady-state forest
Objective function F	Gross primary productivity (GPP, equation 1)	Net growth rate (G , equation 2)	Net primary productivity (NPP, equation 3)
Optimized traits f	Stomatal conductance (g_s) Leaf area index (L) Foliage N concentration ($[N]_f$)	Leaf area index (L) Canopy nitrogen (N) content (N_c)	Foliage biomass (W_f) Fine-root biomass (W_r) Foliage N concentration ($[N]_f$)
Constraints C	Steady-state water and above-ground N balance Fixed rainfall and N flux to above-ground pools	Fixed leaf to sapwood to fine-root N content ratios Fixed N_c (for optimal L)	Steady-state carbon (C) and N balance Fixed maximum C uptake and N uptake
Timescale	Annual	Annual for L , decadal for N_c	Decadal
Physiology	LUE saturates with g_s and $[N]_f$ APAR saturates with L Respiration proportional to GPP	GPP saturates with L and $N_c - n_o L$ Maintenance respiration proportional to N_c Foliage and fine-root turnover proportional to N_c	GPP saturates with $[N]$ and W_f Maintenance respiration proportional to $[N]_f$ N uptake saturates with W_r ; pipe model
Benefits versus costs	High LUE versus low APAR	APAR versus nonphotosynthetic canopy N GPP versus maintenance respiration and turnover	GPP versus maintenance respiration Foliage versus wood and fine-root allocation

APAR, canopy-absorbed photosynthetically active radiation; LUE, light-use efficiency = GPP/APAR; n_o , nonphotosynthetic leaf N.

2008). Only the key features are described here (figure 1, table 1). Each model represents a different optimization hypothesis $H(F, f, C)$. Each model also makes some simplifying physiological assumptions in order to quantify how the objective function F depends on the functional traits f (table 1); these can be viewed as a physiological component

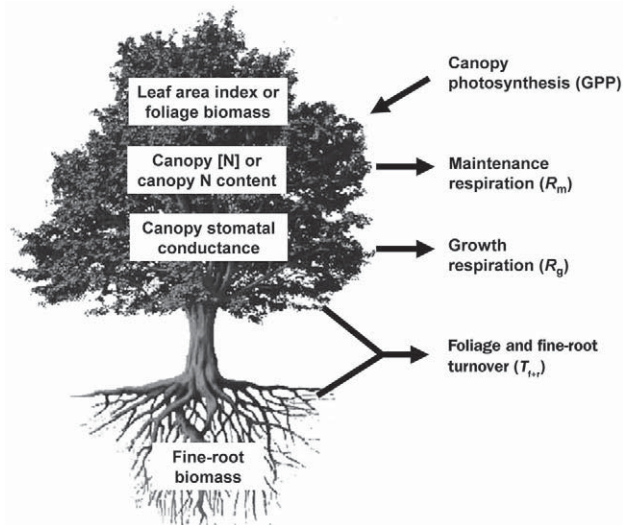


Figure 1. Boxes (left) indicate the functional traits (f) optimized by models 1, 2, and 3 (see table 1). Arrows indicate carbon gains and losses defining the objective function (F) in each model. Model 1 maximizes canopy photosynthesis (gross primary productivity, GPP) with respect to leaf area index, canopy-average leaf nitrogen concentration ($[N]$), and canopy-average stomatal conductance. Model 2 maximizes net growth rate $G = GPP - R_g - R_m - T_{f+r}$ with respect to leaf area index and canopy N content. Model 3 maximizes net primary productivity $NPP = GPP - R_g - R_m$ with respect to canopy-average $[N]$, foliage biomass, and fine-root biomass. The constraints (C) under which the objective functions are maximized are summarized in table 1. Each model represents an optimization hypothesis $H(F, f, C)$.

of C . Although the models do not predict the timescale τ over which trait f is optimized, their use of steady-state resource balance constraints (see below) implies that τ is related to the equilibration time for key processes in each model. Broadly speaking, the progression from model 1 to model 2 to model 3 represents a shift in focus from short-term trait responses (leaf $[N]$, stomatal conductance) to intermediate responses (leaf area or biomass, fine-root biomass, growth allocation), although overlap between the models is considerable. As already mentioned, none of the models predicts long-term changes in soil N availability.

Figures 2, 3, and 4 illustrate a maximum in the objective function F as a function of various traits f , for models 1, 2, and 3, respectively. Each panel shows plots of F against f at two different resource availabilities ($[CO_2]$ in models 1 and 2, soil N availability in model 3), thus illustrating how the optimal value of f for maximum F shifts in response to a change in resource availability.

Model 1. This model (McMurtrie et al. 2008) applies to a stand of deciduous trees. The model maximizes canopy photosynthesis (also known as gross primary productivity, or GPP) with respect to three functional traits (figure 1, table 1): stomatal conductance averaged over the canopy and growing season (g_s), canopy-average foliage N concentration ($[N]_p$), and canopy leaf area index (i.e., m^2 leaf per m^2 ground, L). Maximizing GPP is reasonable from an evolutionary perspective, because GPP constitutes the input of chemical free energy (photosynthate), which, through respiration, drives all

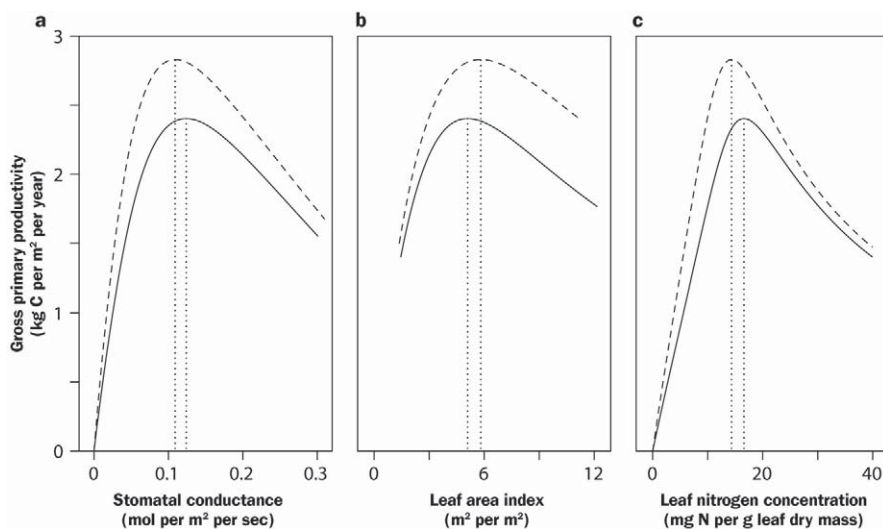


Figure 2. Model 1 (McMurtrie et al. 2008). Gross primary productivity (GPP, kilograms of carbon per square meter $[m^2]$ per year; equation 1) at carbon dioxide concentrations ($[CO_2]$) of 375 (solid curves) and 550 parts per million (dashed curves) as a function of (a) stomatal conductance (g_s , moles per m^2 per second), (b) leaf area index (L , m^2 leaf per m^2 ground), and (c) canopy-average leaf nitrogen concentration ($[N]_p$, milligrams of N per gram (g) of leaf dry mass), for a stand of sweetgum with annual N uptake to aboveground pools = $6 \text{ g N per } m^2 \text{ per year}$ and annual rainfall = $1200 \text{ millimeters per year}$. Given any one of the three traits g_s , L , and $[N]_p$, the other two are determined by annual steady-state N and water balance. As indicated by the dotted vertical lines, increased $[CO_2]$ shifts the optimal operating point (g_s , L , $[N]_p$) for maximum GPP from (0.124, 5.1, 16.6) to (0.109, 5.8, 14.3); GPP, light-use efficiency ($LUE = GPP/APAR$), and canopy light absorption ($APAR$) increase by 18%, 13%, and 4%, respectively.

the metabolic processes that contribute to sustainable plant function and survival.

Two resource supply constraints are imposed: (1) steady-state, annual aboveground N balance (N allocation to annual sapwood and foliage production = fixed annual N input to aboveground tree pools), and (2) steady-state annual water balance (annual water use by trees = fixed fraction of annual rainfall). The application of the N balance constraint to deciduous trees permits the simplifying assumption that annual foliage production is proportional to the peak L during the growing season, and implies an optimization timescale $\tau = 1$ year.

GPP is calculated using a canopy photosynthesis model that was derived by integrating a leaf photosynthesis model vertically through the canopy. The resulting expression for GPP is a product of two factors:

$$\text{GPP} = \text{LUE} \times \text{APAR}. \quad (1)$$

Here, APAR denotes the total amount of photosynthetically active radiation (PAR) absorbed by the canopy, and is a saturating function of L because of mutual shading by leaves. LUE (light-use efficiency), a saturating function of g_s and $[\text{N}]_f$ encapsulates the interactive $\text{CO}_2 \times \text{N}$ dependence of leaf photosynthesis; g_s regulates both CO_2 diffusion into leaves and canopy transpiration, leading also to a $\text{CO}_2 \times \text{H}_2\text{O}$ interaction.

With annual water use by the canopy fixed, there is a trade-off between total leaf area (L) and annual transpiration per unit leaf area (regulated by g_s). This translates directly into a trade-off between APAR and LUE, leading to a maximum in their product, GPP, at optimal stomatal conductance (figure 2a) and leaf area index (figure 2b). A simultaneous trade-off between L and $[\text{N}]_f$ arises from the constraint that annual N input to aboveground tree pools is fixed, leading to a maximum in GPP at an optimal leaf $[\text{N}]$ (figure 2c). The optimal g_s , optimal L , and optimal $[\text{N}]_f$ in figure panels 2a, 2b, and 2c all correspond to the same operating point because, under the two resource constraints, only one of the three functional traits g_s , L , and $[\text{N}]_f$ can be varied independently.

Model 2. This model (Franklin 2007) applies to a forest stand both during the canopy expansion phase and at steady-state canopy closure (when leaf production matches leaf turnover). The model maximizes net stand growth rate (G) with respect to leaf area index (L) during canopy expansion, and with respect to canopy N content (N_c) at steady-state canopy closure. This implies two distinct optimization timescales, respectively, of $\tau \approx 1$ year for L and $\tau \approx 10$ years for N_c .

Net growth rate (G) is defined as net primary productivity (NPP) minus foliage and fine-root turnover (T_{f+r}), where NPP is defined as GPP minus respiration for tree growth (R_g) and maintenance (R_m) (figure 1, table 1). Of the total photosynthate flux available for growing new tissue ($\text{GPP} - R_m$), a fraction Y (the growth efficiency) ends up in plant structure (represented by NPP) and a fraction $1 - Y$ is respired during the growth process (represented by R_g). Thus, G can be expressed as a balance equation of the form

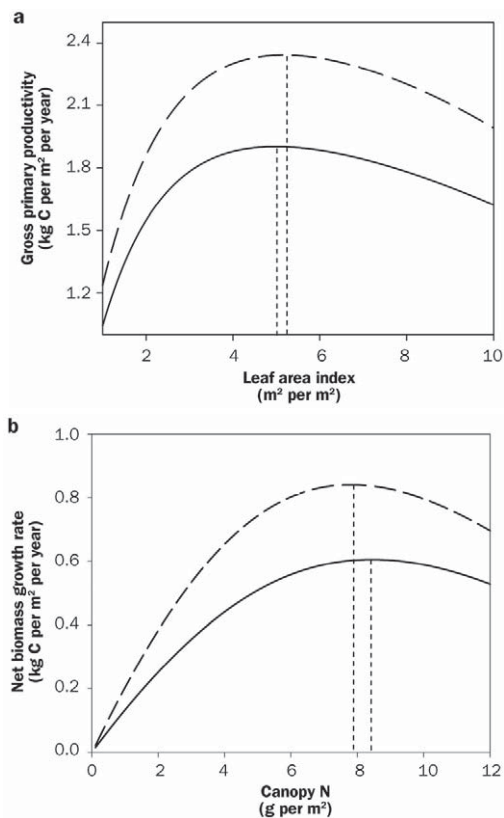


Figure 3. Model 2 (Franklin 2007). (a) Gross primary productivity (GPP, kilograms carbon per square meter $[\text{m}^2]$ per year) as a function of leaf area index (L , m^2 leaf per m^2 ground) at ambient (solid curve) and elevated (dashed curve) carbon dioxide concentrations ($[\text{CO}_2]$), for a fixed canopy nitrogen (N) content ($N_c = 7.8$ grams of N per m^2) and measured root N : foliage N ratios (f_r). Increased $[\text{CO}_2]$ was effected in the model by increased leaf photosynthetic responses to N and light, and increased f_r (Franklin 2007). As indicated by the dotted vertical lines, the optimal L for maximum GPP increases from 5.0 to 5.3 under elevated $[\text{CO}_2]$; GPP, light-use efficiency ($\text{LUE} = \text{GPP}/\text{APAR}$), and canopy light absorption (APAR) increase by 23%, 22%, and 1%, respectively. (b) Net growth rate (G , kilograms of carbon per m^2 per year; equation 2) as a function of canopy N content (N_c grams N per m^2) at ambient $[\text{CO}_2]$ with $f_r = 0.18$ (solid curve) and elevated $[\text{CO}_2]$ with $f_r = 0.36$ (dashed curve); leaf area index is optimal at each N_c as in (a). As indicated by the dotted vertical lines, the optimal N_c for maximum G decreases from 8.5 to 7.8 grams of N per m^2 under elevated $[\text{CO}_2]$.

$$G = Y(\text{GPP} - R_m) - T_{f+r}. \quad (2)$$

Once foliage and fine roots have reached steady state, G equates to wood production. The proposed evolutionary rationale for maximizing G is that tree survival is largely determined by the ability to avoid being overtopped by neighbors (Franklin 2007). Since tree size (height) is an integrated

measure of wood growth, survival should be closely related to G .

GPP is derived as a function of N_c and APAR by integrating a leaf photosynthesis model over the canopy (similarly to model 1). A key assumption here is that a given canopy N content is distributed within the canopy such that GPP is maximized (Franklin and Ågren 2002), so already an aspect of optimal function is introduced. Another key assumption is that only a part ($n_{\text{tot}} - n_0$) of the total N content of a leaf (n_{tot}) is assumed to be photosynthetically active. Although this last assumption with a fixed n_0 is not strictly correct at the leaf biochemical level (Kull 2002), it describes reasonably well the relationship between leaf photosynthetic capacity and leaf N for many species. Finally, APAR is a saturating function of L due to leaf mutual shading (as in model 1). As a result, GPP is a saturating function of $N_c - n_0L$ and L (table 1), n_0L being the amount of nonphotosynthetic canopy N per unit ground area. On the cost side of equation 2, R_m is proportional to N_c , based on the assumptions that R_m reflects the energy cost of resynthesising degraded N-rich proteins (e.g., Reich et al. 2006c), and that the N contents of foliage, live sapwood, and fine roots are in fixed ratios (constraint C). Also proportional to N_c is T_{f+r} , from the additional assumption that annual biomass turnover is proportional to live biomass.

Consequently, for a fixed N_c (corresponding to $\tau \approx 1$ year), GPP (and hence net growth rate, G) has a maximum with respect to leaf area index L (figure 3a) because the benefit of increased APAR (a saturating function of L) is eventually offset by the cost of increased nonphotosynthetic N (proportional to L). Then, as N_c increases through the canopy-expansion phase, G eventually attains a maximum (figure 3b) because the benefit of increased GPP (a saturating function of N_c) is eventually offset by the increased costs of R_m and T_{f+r} (proportional to N_c), at which point it is assumed no further expansion occurs (steady-state canopy, corresponding to $\tau \approx 10$ years).

In summary, model 2 applies three nested optimizations: (1) maximize G with respect to the distribution of N within the canopy (L and N_c fixed, $\tau \leq 1$ year); (2) maximize G with respect to L (N_c fixed, $\tau \approx 1$ year); and (3) maximize G with respect to N_c ($\tau \approx 10$ years). The first two procedures are equivalent to maximizing GPP because N_c is fixed on these shorter timescales.

Model 3. This model (Mäkelä et al. 2008) applies to a steady-state, closed-canopy forest, implying a timescale of $\tau \approx 10$ years. It was developed for sites at which water is not a limiting resource. The

model maximizes NPP with respect to three functional traits: canopy-average foliage N concentration ($[N]_f$), foliage biomass (W_f), and fine-root biomass (W_r) (figure 1, table 1). Live-wood biomass is determined by assuming that the live-wood cross-sectional area is proportional to W_f (the pipe model; Shinzaki et al. 1964) and that stem height is proportional to $[N]_f$. The predicted stem height corresponds to a stand age between canopy closure and stand senescence. NPP is expressed as

$$\text{NPP} = Y(\text{GPP} - R_m), \quad (3)$$

as in model 2. A possible evolutionary rationale for maximizing NPP derives from the observation that, in closed forest stands, the greater the productivity of larger trees, the faster the self-thinning of the shorter, less productive trees.

Instead of deriving GPP from a leaf-scale model (cf. models 1 and 2), GPP is formulated at the canopy scale as a saturating function of W_f (mimicking the effect of leaf mutual shading), where the plateau value of this function is itself a saturating function of $[N]_f$. Maintenance respiration (R_m) is proportional to $[N]_f$ (similarly to model 2). In contrast to model 1, where annual N uptake to aboveground pools is fixed, model 3 assumes that N uptake is a saturating function of fine-root biomass, with a plateau value that depends on soil N availability. The steady-state assumption leads to two resource constraints: steady-state C balance ($\text{NPP} = \text{litter production}$, which includes deactivation of live wood) and steady-state N balance (N uptake by roots = N losses in litter and sequestration in dead wood).

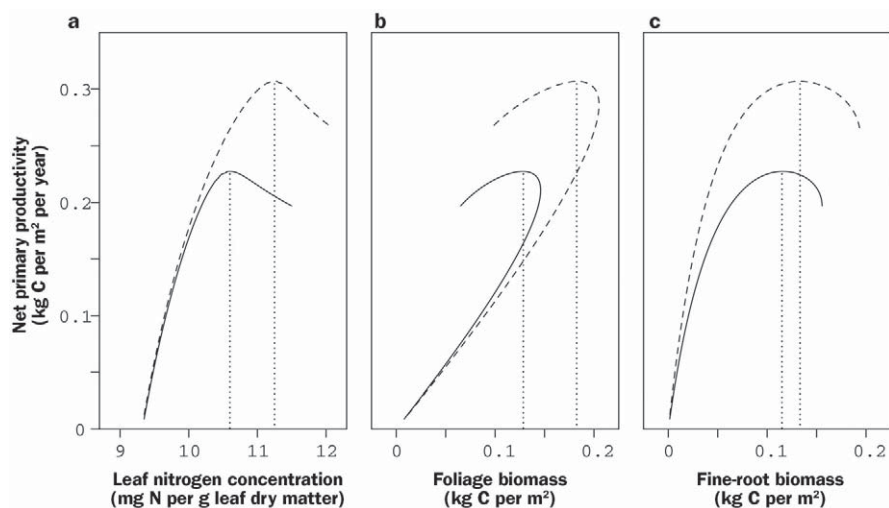


Figure 4. Model 3 (Mäkelä et al. 2008). Net primary productivity (NPP; equation 3) as a function of (a) canopy-average leaf nitrogen concentration ($[N]_f$, milligrams of N per gram of leaf dry matter), (b) leaf biomass (W_f , kilograms of carbon [C] per square meter), and (c) fine-root biomass (W_r , kilograms of C per square meter), at soil N availabilities of 20 (solid curves) and 25 (dashed curves) milligrams of N per gram of fine-root dry matter per year. Given any one of the three traits $[N]_f$, W_f , and W_r , the other two are determined by annual steady-state C and N balance. As indicated by the dotted vertical lines, increased soil N availability shifts the optimal operating point ($[N]_f$, W_f , W_r) for maximum NPP from (10.6, 0.129, 0.115) to (11.25, 0.182, 0.133).

Under the two resource constraints, only one of the three functional traits $[N]_p$, W_p and W_r can be varied independently (figure 4). The maximum NPP with respect to $[N]_f$ reflects the balance between increased GPP (a saturating function of $[N]_p$) and increased R_m (proportional to $[N]_p$), as in model 2. However, through the N balance constraint, there is an additional C cost of increasing $[N]_f$ incurred by greater investment in fine-root biomass. Moreover, the link between stem height and $[N]_p$ together with the pipe model, implies that increased $[N]_f$ (longer pipe) is associated with greater allocation of NPP to live-wood production. Model 3 optimizes leaf biomass (W_f), whereas models 1 and 2 optimize leaf area index (L). Optimization of L and W_f are equivalent if the ratio $W_f:L$ is fixed, as assumed here.

Predicted responses to changing resource availability

We now highlight some key forest responses to changing resource availability predicted by models 1, 2, and 3. These range from shorter-term trait responses (leaf [N], stomatal conductance) to longer-term trait responses (leaf area index, foliage biomass, fine-root biomass, growth allocation). The two dotted vertical lines in each of figures 2, 3, and 4 indicate how the optimal operating point shifts in response to a change in resource availability, in models 1, 2, and 3 respectively. Figures 5, 6, and 7 compare the model predictions with observations from FACE experiments and other empirical studies. Our aim here is to demonstrate how OMs can explain and predict a wide variety of forest responses over a range of timescales, and this is reflected in the diversity of model outputs plotted in figures 5, 6, and 7.

Responses of leaf N concentration (models 1, 2, and 3). In response to elevated $[CO_2]$, all three models predict a decrease in the canopy-average leaf N concentration ($[N]_f$ in models 1 and 3, N_c/L in model 2), as illustrated in figures 2c, 3a, 3b, and 6a. This response is consistent with the general trend observed in FACE experiments (e.g., Ainsworth and Long 2005). Reduced leaf [N] is not detrimental to the GPP of high- CO_2 plants because their photosynthesis per unit leaf N is higher. High- CO_2 plants can then afford to reduce their leaf [N] and associated costs, thereby maintaining a higher leaf area. This fundamental photosynthetic $CO_2 \times N$ interaction is encapsulated into the GPP component of all three models, and explains why they all predict reduced leaf [N] under elevated $[CO_2]$. This explanation based on whole-plant optimization contrasts with previous leaf-level mechanistic explanations of this response (e.g., Ellsworth et al. 2004).

However, the costs and constraints associated with maintaining a high leaf [N] are different in each model (table 1, “Benefits versus costs”): low leaf area index and light interception in model 1, high maintenance respiration and turnover in model 2, and high maintenance respiration and allocation to fine roots and live wood in model 3. As a result, the implied timescales for the leaf [N] response to elevated $[CO_2]$ are

also different ($\tau \approx 1$ year in model 1, $\tau \approx 10$ years in models 2 and 3).

Model 1 not only captures the qualitative response of leaf [N] to elevated $[CO_2]$ (figure 2c) but also makes very reasonable quantitative predictions in comparison with experimental data from the Oak Ridge FACE site (figure 5). Figure 6a shows leaf [N] responses to elevated $[CO_2]$ across a gradient of soil N availability, as predicted by model 3. In addition to the decrease in $[N]_f$ at elevated $[CO_2]$, $[N]_f$ displays a ramp response to soil N availability consistent with observations, particularly of deciduous species (e.g., Le Maire et al. 2005). At low N availability, productivity is limited by N uptake and $[N]_f$ attains a lower bound. At high N availability, the marginal benefit of increasing $[N]_f$ is small so that $[N]_f$ approaches its upper bound, productivity being limited here by canopy light absorption. Between these two extremes, $[N]_f$ increases with N availability.

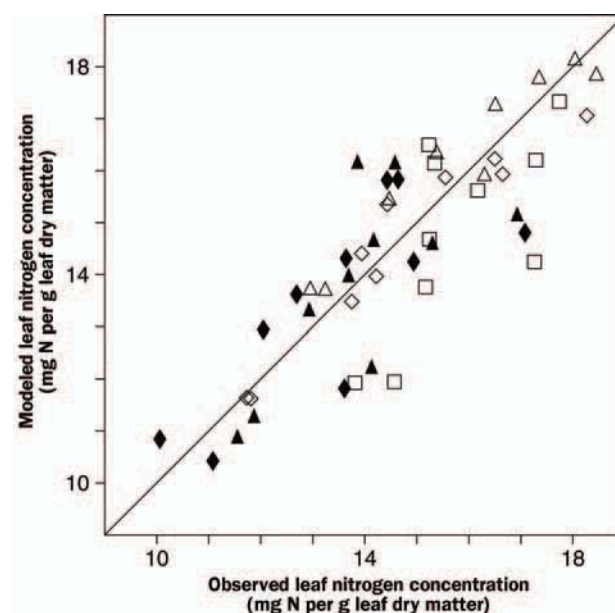


Figure 5. Model 1 (McMurtrie et al. 2008). Modeled versus observed leaf nitrogen concentration [N] (milligrams N per gram of leaf dry matter) for the Oak Ridge FACE experiment ($r^2 = 0.84$). The five symbols correspond to the five FACE experimental rings, three at ambient carbon dioxide concentrations ($[CO_2]$) (375 parts per million, open symbols) and two at elevated $[CO_2]$ (550 parts per million, solid symbols). Values are shown over several years, from 1998 to 2007 (Norby et al. 2007). Leaf [N] tends to be lower at elevated $[CO_2]$ than at ambient $[CO_2]$, but the interannual variation in leaf [N] is large for each ring. According to model 1, the interannual variation in leaf [N] is a consequence of variation in annual N input to aboveground pools (U). The model was fitted to net primary productivity, leaf area index, and leaf [N] data simultaneously, using least-squares estimation with different values of U estimated for each year.

Likewise, model 1 predicts a positive response of $[N]_f$ to increased N supply to the aboveground pools (McMurtrie et al. 2008). By contrast, in response to increased precipitation, model 1 predicts a reduction in $[N]_f$ (McMurtrie et al. 2008), consistent with field observations (Reich et al. 1999, Wright et al. 2003). Optimization thus explains the acclimation responses of leaf [N] to changes in $[CO_2]$, N availability, and precipitation.

Responses of stomatal conductance (model 1). Model 1 generally predicts a decrease in stomatal conductance (g_s) under elevated $[CO_2]$ (figure 2a). The explanation is similar to that for the decrease of leaf [N] in high- CO_2 plants. For a given stomatal opening, the CO_2 diffusion rate into the leaf is higher at elevated $[CO_2]$, so, with a fixed annual water use, high- CO_2 plants can maximize their GPP by partially closing their stomata and increasing their leaf area. The behavior of conifer species, which tend not to close their stomata very much under elevated $[CO_2]$ (e.g., Medlyn et al. 2001), does not disprove the optimization hypothesis of model 1. For example, if canopy photosynthesis is relatively insensitive to stomatal conductance (corresponding to a very flat peak in figure 2a), then there would be little advantage for high- CO_2 plants to close their stomata (McMurtrie et al. 2008).

The predicted reductions in $[N]_f$ and g_s under elevated $[CO_2]$ are both consistent with the trends observed in FACE experiments (Ainsworth and Long 2005). Model 1 puts reduced leaf [N], reduced g_s , and increased leaf area index on an equal footing, as emergent whole-plant responses to elevated $[CO_2]$ when annual GPP is maximized (figure 2). This integrative C-N-H₂O response is consistent with evidence that stomatal closure at elevated $[CO_2]$ can actually contribute to down-regulation of the dark reactions of photosynthesis, usually attributed to declining leaf [N] alone (Lee et al. 2001).

Responses of productivity, leaf area, and light-use efficiency (models 1, 2, and 3). All three models predict increased productivity under elevated $[CO_2]$. Moreover, all three models explain this response as being due primarily to increased LUE (i.e., GPP per unit of canopy light absorption), rather than to increased APAR, in

agreement with the conclusions from FACE experiments (Norby et al. 2005, McCarthy et al. 2006). Because of the effect of mutual shading, a given relative increase in leaf area translates into a much smaller relative increase in APAR. For example, in the scenario depicted in figure 2, model 1 predicts increases in GPP, LUE (= GPP/APAR), L (or W_f), and APAR of 18%, 13%, 14%, and 4%, respectively; the corresponding predictions of model 2 at fixed canopy N content (figure 3a) are 23%, 22%, 6%, and 1%; and those of model 3 at high N availability (figure 6) are 21%, 16%, 19%, and 5%.

Model 1 provides further insights into CO_2 -N and CO_2 -H₂O interactions. The predicted percentage of CO_2 stimulation of productivity is reduced under N limitation but enhanced under water limitation, as observed (e.g., Morgan et al. 2004, Nowak et al. 2004). Model 1 explains this behavior from the fact that leaf photosynthesis is less sensitive to CO_2 at lower leaf [N] (the $CO_2 \times N$ interaction already mentioned) but is more sensitive to CO_2 at lower stomatal conductance (because photosynthesis is then strongly limited by CO_2 diffusion into leaves).

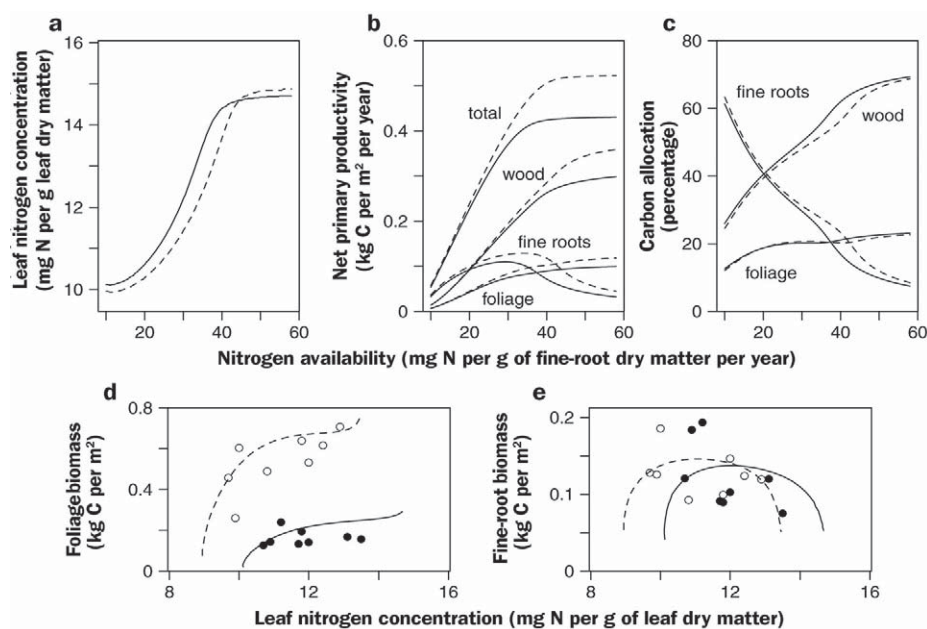


Figure 6. Model 3 (Mäkelä et al. 2008). (a–c) Model responses to soil nitrogen (N) availability (milligrams N per gram of fine-root dry matter per year) at ambient (solid curves) and elevated (dashed curves) carbon dioxide concentrations ($[CO_2]$), for Scots pine (*Pinus sylvestris* L.) in Finland. Elevated $[CO_2]$ was effected in the model by a 15% increase in the maximum rate of photosynthesis per unit of foliage biomass. (a) Foliage [N] (milligrams of N per gram of leaf dry matter); (b) total net primary productivity (NPP) (kilograms of carbon per m² per year) and its components; and (c) percentage NPP allocated to the production of foliage, live sapwood, and fine roots. At high N availability, gross primary productivity (GPP), light-use efficiency (LUE = GPP/APAR), and canopy light absorption (APAR) increase by 21%, 16%, and 5%, respectively, under elevated $[CO_2]$. (d–e) Modeled (lines) and observed (circles) relations between leaf biomass (W_f , kilograms of carbon per square meter), fine-root biomass (W_r , kilograms of carbon per square meter), and foliage [N] for stands of Scots pine (*Pinus sylvestris* L., solid circles and lines) and Norway spruce (*Picea abies* L., open circles, dashed lines) across Finland.

Figure 7 shows the responses of GPP, NPP, and L to elevated $[\text{CO}_2]$, as predicted by model 2. The predictions are in reasonable quantitative agreement with the responses observed in four forest FACE experiments—remarkably so, given the simplicity of the model.

Figure 6b shows productivity responses to elevated $[\text{CO}_2]$ and soil N availability, as predicted by model 3. In the intermediate regime where $[\text{N}]_f$ increases with N availability (figure 6a), the co-allocation of C and N to foliage and fine roots is finely tuned to maximize NPP, which is then tightly correlated with soil N availability (cf. Magnani et al. 2007). However, NPP is roughly constant once $[\text{N}]_f$ approaches its upper bound (figure 6a, 6b). A strong $\text{CO}_2 \times \text{N}$ interaction is evident here (as in model 1), in which CO_2 stimulation of foliage, fine-root, and live-wood production is magnified at higher N availability (figure 6b).

Figure panels 6d and 6e show that both the foliage biomass versus $[\text{N}]_f$ and fine-root biomass versus $[\text{N}]_f$ trait relationships predicted by model 3 are in reasonable quantitative agreement with sample-based estimates from stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.) in Finland. The predictions here were based on standard parameter sets for these two species (Mäkelä et al. 2008); no attempt was made to fit the model to these estimates in view of the bivariate sampling errors involved. Moreover, as figure panels 4b and 4c illustrate, the value of NPP is close to maximal over a rather wide range of values of foliage and fine-root biomass, and so we should not expect field data to fall on, or be necessarily close to, the optimal response curves in figure panels 6d and 6e. Nevertheless, as with models 1 and 2 (figures 5 and 7), the degree of agreement here with data is very reasonable.

Growth allocation responses (model 3). Figure 6c shows how elevated $[\text{CO}_2]$ and increased soil N availability shift the allocation of NPP between the production of foliage, live sapwood, and fine roots, according to model 3. In response to increased N availability, the predominant trade-off is between fine-root and wood production, with fine roots favored on N-poor sites. Significantly, the fraction of NPP allocated to foliage production is remarkably insensitive to soil N availability (18% to 22% over the normal range of soil N availability, excluding very low values). This insensitivity arises because modeled increases in $[\text{N}]_f$ and foliage biomass across the gradient of N availability maintain an approximately constant GPP and NPP per unit of foliage biomass. Because annual foliage turnover is a fixed fraction of foliage biomass, and is matched in the steady state by the production of new foliage, it follows that foliage production is a fairly constant fraction of GPP and NPP. These modeled allocation responses to N availability are remarkably consistent with reported trends (Litton et al. 2007).

In response to elevated $[\text{CO}_2]$ (figure 6b, 6c), model 3 predicts increased investment in fine roots, consistent with the intermediate-term responses of the Oak Ridge FACE experiment (Norby et al. 2006). The predicted increase in

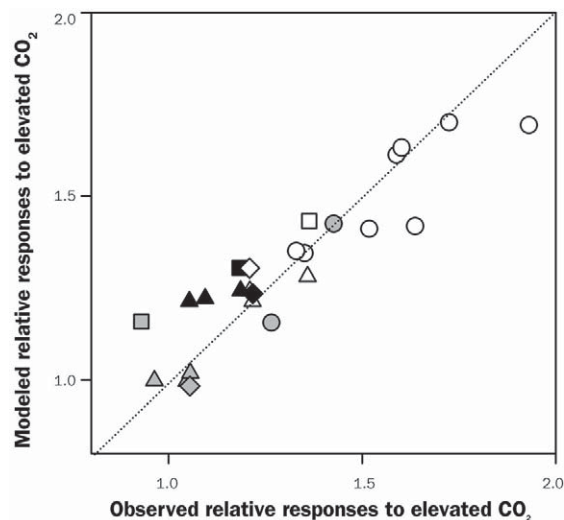


Figure 7. Model 2 (Franklin 2007). Modeled versus observed relative responses to elevated carbon dioxide concentration ($[\text{CO}_2]$) of net primary productivity (open symbols), gross primary productivity (black symbols), and leaf area index (L , gray symbols) for four FACE sites (POPFACE, circles; Aspen FACE, triangles; Oak Ridge, diamonds; Duke forest, squares). For all modeled versus observed data, $r^2 = 0.83$. Differences between some of these data values (Franklin 2007) and those obtained in other analyses of the same experiments (Schäfer et al. 2003, McCarthy et al. 2007) may be attributed to differences in sampling methods and in the sampling period. Reproduced from Franklin (2007).

fine-root biomass at elevated $[\text{CO}_2]$ leads to an increase in plant N uptake, qualitatively consistent with the trend observed in other FACE experiments (e.g., Finzi et al. 2007).

Further analysis (data not shown) shows that model 3 is also broadly consistent with empirical relationships between leaf area, NPP, and total belowground C allocation (TBCA) obtained from four FACE experiments (Palmroth et al. 2006). In particular, the model predicts a peaked relationship between TBCA and leaf area (cf. figure 3 of Palmroth et al. 2006), and predicted impacts of elevated $[\text{CO}_2]$ on productivity and growth allocation are in line with observations. However, model 3 underestimates the leaf area and net primary productivity observed in these experiments, as expected for this model, which was parameterized for Finnish forests.

What has been achieved? The key challenge for plant modeling, we recall, is to explain the balance between the various processes of resource capture and use. Many complex models currently fail that challenge through their inability to explain plant adaptations to different environments. In contrast, OMs offer a simple yet powerful approach to describing the balance between different processes, and how that balance shifts when resource availability changes (e.g., Givnish 1986, Mäkelä et al. 2002).

Models 1, 2, and 3 reproduce many of the forest responses observed in multiple-resource manipulation experiments, including multiple-resource interactions ($\text{CO}_2 \times \text{N}$, $\text{CO}_2 \times \text{H}_2\text{O}$). Unlike complex models, they explain trait responses as emergent properties of optimal plant function. Moreover, the quantitative agreement with data is very reasonable, given the simplicity of the models. This agreement suggests that optimization itself goes a long way toward explaining integrative forest function, so that relatively little parameter fitting is required. The three OMs highlighted here are restricted to monospecific, homogeneous forest stands and ignore tree-soil feedbacks. Nevertheless, the results demonstrate that OMs have matured sufficiently to make quantitatively reasonable stand-level predictions, and could, with further development, make a much greater contribution to global change research than they have done until now.

Future challenges for optimization modeling in global change research

Where do we now stand in our efforts to understand and predict plant responses to global change? Following May (2004), we recall here the three historical stages that led to the discovery of the universal inverse-square law of gravitation—observed facts, patterns that give coherence to the observations, fundamental laws that explain the patterns—associated, respectively, with Tycho Brahe, Johannes Kepler, and Isaac Newton. In the context of global change research, FACE experiments and other empirical studies represent the observational Brahe stage, and meta-analyses of their results represent the pattern-seeking Keplerian stage. We are now embarking on the Newtonian stage of searching for the deeper general principles that govern those patterns. OMs, we suggest, now have much to offer in this Newtonian stage, in terms of both understanding and predicting plant responses to global change.

We return now to the three outstanding theoretical issues raised earlier, which provide the backdrop to some specific recommendations for the future development and application of OMs in global change research.

What do plants maximize? We have approached this question from a practical perspective (which objective function F appears to work in practice?) rather than from a theoretical perspective (what “should” plants maximize?). In its contribution to the objective functions in models 1, 2, and 3, GPP constitutes a universal benefit in all three models. The consistency between predicted and observed forest responses to altered resource availability suggests that maximizing GPP captures an essential aspect of plant function.

The models differ in the costs incorporated into the objective function (figure 1, table 1). How can we decide between these alternatives? Further analysis might tease out key differences in the models’ predictions (e.g., does some plant trait f increase with rising $[\text{CO}_2]$ in one model but decrease with rising $[\text{CO}_2]$ in another model?), which can then be tested experimentally. Nevertheless, one would like to derive the objective function F from a more fundamental theoretic

cal basis. From the perspective of evolutionary theory, it is not clear that plants should maximize stand-scale properties (e.g., GPP, NPP, net growth rate). Stand-scale optimization might be viewed as an approximate description of natural selection at the level of individuals, for which game theory provides useful insights (e.g., Schieving and Poorter 1999, Anten 2005).

Recently, however, an alternative thermodynamic perspective on biological adaptation and evolution has emerged (Dewar 2004, Whitfield 2005, 2007, Martyushev and Seleznev 2006), which identifies a fundamental objective function based on entropy concepts. Within this perspective, living systems are viewed as examples of a wider class of nonequilibrium structures—including nonliving systems such as growing crystals and weather cyclones—that import energy in one form and export it in a higher-entropy form. The hypothesis of maximum entropy production (MEP) conjectures that these systems self-organize (acclimate, evolve) under given constraints so as to maximize this rate of entropic export. The proposed theoretical explanation for MEP is statistical (Dewar 2004): in systems forced out of thermodynamic equilibrium by external constraints, MEP structures emerge simply because they are by far the most probable ones: “survival of the likeliest” (Whitfield 2007).

According to MEP, such statistical selection can extend beyond individual plants to ecosystems. For the ensemble of living cells in a plant or ecosystem, MEP is approximately equivalent to maximizing whole-system respiration (i.e., the total dissipation rate of chemical free energy by metabolic reactions), which, in turn, is equivalent to maximizing GPP on timescales when these two fluxes are in approximate balance. MEP offers a novel statistical perspective on plant and ecosystem function, the implications of which we are currently exploring.

On what timescale? The resource constraints built into models 1, 2, and 3 all relate to steady-state C, N, or water balance. However, the models are concerned with different timescales, ranging from annual (model 1) to decadal (models 2 and 3), that reflect the time constants for equilibration of key processes in each model. For example, model 3 implicitly assumes a timescale ($\tau \approx 10$ years) that is appropriate to a steady-state canopy. Moreover, a fixed constraint on one timescale may be a variable trait on longer timescales, as in model 2, where a nested sequence of optimizations is applied (optimize the distribution of N within the canopy at fixed L and $N_c \rightarrow$ optimize L at fixed $N_c \rightarrow$ optimize N_c). This points to a key future challenge: how to incorporate longer-term plant-soil feedbacks (not considered by models 1, 2, and 3) when soil N availability is no longer a fixed constraint. These feedbacks are important for long-term CO_2 uptake by ecosystems (Comins and McMurtrie 1993, Luo et al. 2004).

Is plant function always optimal? There is no a priori guarantee that a functional trait that is optimal in a given environment will attain the new theoretical optimum when a

new atypical environment is imposed. But again, the hypothesis that it does so remains open to experimental testing. Indeed, experimental failure to reach a theoretical optimum need not call into question the optimization approach itself; rather, it could serve to indicate the existence of a previously unidentified constraint (or an overconstrained system).

Whatever its success in describing actual plant function, optimization remains useful because it defines the theoretical limits of plant function (e.g., maximum productivity, maximum CO₂ uptake) on the basis of identified environmental and physiological constraints, and thus defines the biological bounds on future [CO₂], hydrology, and climate predictions.

Specific recommendations. In order to enhance the contribution of OMs to global change research, we encourage scientists to do the following:

- Compare the predictions of different candidate objective functions (e.g., GPP, NPP, net growth rate, entropy production) with patterns emerging from meta-analyses of multiple-resource manipulation experiments, functional trait databases, and satellite-derived regional NPP estimates, to better identify the general optimization principle(s) governing plant function.
- Apply OMs in a hierarchical fashion to different functional traits on different timescales (short → intermediate → long); this could be achieved by applying quasi-steady state resource constraints to different subsystems on different timescales.
- Develop more comprehensive OMs of forest function (see table 1) under multiple resource limitations (energy, carbon, water, nutrients), and extend them to other plant types.
- Incorporate soil decomposition processes within OMs, to predict adaptive changes in soil nutrient availability; one approach would be to replace the N balance constraints in models 1, 2, and 3 (fixed soil N availability) with the longer-term nutrient-cycling constraints (e.g., fixed N deposition rate) applied in previous models of plant-soil feedbacks that adopt the quasi-steady state approach (e.g., Comins and McMurtrie 1993).
- Develop OMs for multispecies ecosystems; game theory of individual-level selection is one approach (e.g., Anten 2005). Alternatively, entropy-based concepts have recently been used to predict the most likely species abundance distribution of an ecological community as a function of resource availability (Dewar and Porté 2008). This statistical approach, hitherto applied to a very crude model of resource use by individuals, could be developed to incorporate more realistic physiology.
- Develop operational methods to incorporate OMs into land-surface models; for example, feed optimal traits (e.g., stomatal conductance, leaf [N], leaf area index, allocation fractions) or optimal composite parameters (e.g., LUE, APAR) as input to dynamic global vegetation models (DGVMs), or integrate optimization directly into DGVM code (e.g., Sitch et al. 2003).

Acknowledgments

We are grateful for financial support from TERACC (NSF grant 0090238), the Academy of Finland (MereGrowth Project, grant 206307), and INRA for modeling workshops in Sydney, 13–17 November 2006, and Biarritz, 27–29 November 2007. R. E. M. and O. F. acknowledge support received from the Australian Research Council, the Australian Department of Climate Change, and the US Department of Energy's Office of Science, Biological and Environmental Research Program (grant DE-FG02-96ER62291). We thank three anonymous reviewers for helpful comments on the manuscript.

References cited

- Ackerly DD. 1999. Self-shading, carbon gain and leaf dynamics: A test of alternative optimality models. *Oecologia* 119: 300–310.
- 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. 2007. The response of photosynthesis and stomatal conductance to rising [CO₂], mechanisms and environmental interactions. *Plant Cell and Environment* 30: 258–270.
- Anten NPR. 2005. Optimal photosynthetic characteristics of individual plants in vegetation stands and implications for species coexistence. *Annals of Botany* 95: 495–506.
- Barnard R, Barthes L, Le Roux X, Harmens H, Raschi A, Soussana J, Winkler B, Leadley PW. 2004. Atmospheric CO₂ elevation has little effect in nitrifying and denitrifying enzyme activity in four European grasslands. *Global Change Biology* 10: 488–497.
- Comins HN, McMurtrie RE. 1993. Long-term response of nutrient-limited forests to CO₂-enrichment; equilibrium behaviour of plant-soil models. *Ecological Applications* 3: 666–681.
- Cowan IR, Farquhar GD. 1977. Stomatal function in relation to leaf metabolism and environment. *Society of Experimental Biology Symposium* 31: 471–505.
- Cramer WA, et al. 2001. Global responses of terrestrial ecosystem structure and function to CO₂ and climate change: Results from six dynamic global vegetation models. *Global Change Biology* 7: 357–373.
- Dewar RC. 1996. The correlation between plant growth and intercepted radiation: An interpretation in terms of optimal plant nitrogen content. *Annals of Botany* 78: 125–136.
- . 2004. Maximum entropy production and non-equilibrium statistical mechanics. Pages 41–55 in Kleidon A, Lorenz R, eds. *Non-equilibrium Thermodynamics and Entropy Production: Life, Earth and Beyond*. Heidelberg (Germany): Springer.
- Dewar RC, Porté A. 2008. Statistical mechanics unifies different ecological patterns. *Journal of Theoretical Biology* 251: 389–403.
- Dewar RC, Medlyn BE, McMurtrie RE. 1998. A mechanistic analysis of light and carbon use efficiencies. *Plant, Cell and Environment* 21: 573–588.
- Duursma RA, Mäkelä A. 2007. Summary models for light interception and light-use efficiency of non-homogeneous canopies. *Tree Physiology* 27: 859–870.
- Ellsworth DS, Reich PB, Naumburg ES, Koch GW, Kubiske ME, Smith SD. 2004. Photosynthesis, carboxylation and leaf nitrogen responses of 16

- species to elevated pCO₂ across four free-air CO₂ enrichment experiments in forest, grassland and desert. *Global Change Biology* 10: 2121–2138.
- Farquhar GD, Buckley TN, Miller JM. 2002. Optimal stomatal control in relation to leaf area and nitrogen content. *Silva Fennica* 36: 625–637.
- Field CB. 1983. Allocating leaf nitrogen for the maximization of carbon gain—leaf age as a control on the allocation program. *Oecologia* 56: 341–347.
- Finzi AC, et al. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *Proceedings of the National Academy of Sciences* 104: 14014–14019.
- Franklin O. 2007. Optimal nitrogen allocation controls tree responses to elevated CO₂. *New Phytologist* 174: 811–822.
- Franklin O, Ågren GI. 2002. Leaf senescence and resorption as mechanisms of maximizing photosynthetic production during canopy development at N limitation. *Functional Ecology* 16: 727–733.
- Friedlingstein P, et al. 2006. Climate-carbon cycle feedback analysis, results from the C⁴MIP model intercomparison. *Journal of Climate* 19: 3337–3353.
- Givnish TJ, ed. 1986. *On the Economy of Plant Form and Function*. Cambridge (United Kingdom): Cambridge University Press.
- Haxeltine A, Prentice IC. 1996. A general model for the light use efficiency of primary production. *Functional Ecology* 10: 551–561.
- Hikosaka K. 2003. Leaf canopy as a dynamic system: Ecophysiology and optimality in leaf turnover. *Annals of Botany* 95: 521–533.
- Holland EA, Braswell BH, Sulzman J, Lamarque JF. 2005. Nitrogen deposition onto United States and Western Europe: Synthesis of observations and models. *Ecological Applications* 15: 38–57.
- [IPCC] Intergovernmental Panel on Climate Change. 2007. *Fourth Assessment Report: Climate Change 2007*. Cambridge (United Kingdom): Cambridge University Press. (2 December 2008; www.ipcc.ch/ipccreports/ar4-syr.htm)
- Kull O. 2002. Acclimation of photosynthesis in canopies: Models and limitations. *Oecologia* 133: 267–279.
- Lee TD, Tjoelker MG, Ellsworth DS, Reich PB. 2001. Leaf gas exchange responses of 13 prairie grassland species to elevated CO₂ and increased nitrogen supply. *New Phytologist* 150: 405–418.
- Le Maire G, Davi H, Soudani K, Francois C, Le Dantec V, Dufréne E. 2005. Modeling annual production and carbon fluxes of a large managed temperate forest using forest inventories, satellite data and field measurements. *Tree Physiology* 25: 859–872.
- Levy PE, Wendler R, van Oijen M, Cannell MGR, Millard P. 2004. The effect of nitrogen enrichment on the carbon sink in coniferous forests: Uncertainty and sensitivity analyses of three ecosystem models. *Water, Air and Soil Pollution: Focus* 4: 67–74.
- Litton CM, Raich JW, Ryan MG. 2007. Carbon allocation in forest ecosystems. *Global Change Biology* 13: 2089–2109.
- Luo Y, et al. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* 54: 731–739.
- Luo Y, et al. 2008. Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology* 14: 1986–1999.
- Magnani F, et al. 2007. The human footprint in the carbon cycle of temperate and boreal forests. *Nature* 447: 849–851.
- Mäkelä A, Sievänen R. 1992. Height growth strategies in open-grown trees. *Journal of Theoretical Biology* 159: 443–467.
- Mäkelä A, Givnish TJ, Berninger F, Buckley TN, Farquhar GD, Hari P. 2002. Challenges and opportunities of the optimality approach in plant ecology. *Silva Fennica* 36: 605–614.
- Mäkelä A, Valentine HT, Helmisääri H-S. 2008. Optimal co-allocation of carbon and nitrogen in a forest stand at steady state. *New Phytologist* 180: 114–123.
- Martyushev LM, Seleznev VD. 2006. Maximum entropy production principle in physics, chemistry and biology. *Physics Reports* 426: 1–45.
- May RM. 2004. Uses and abuses of mathematics in biology. *Science* 303: 790–793.
- McCarthy HR, Oren R, Finzi AC, Johnsen KH. 2006. Canopy leaf area constrains [CO₂]-induced enhancement of productivity and partitioning among aboveground carbon pools. *Proceedings of the National Academy of Sciences* 103: 19356–19361.
- McCarthy HR, Oren R, Finzi AC, Ellsworth DS, Kim H-S, Johnsen KH, Millar B. 2007. Temporal dynamics and spatial variability in the enhancement of canopy leaf area under elevated atmospheric CO₂. *Global Change Biology* 13: 1–19.
- McMurtrie RE. 1985. Forest productivity in relation to carbon partitioning and nutrient cycling: A mathematical model. Pages 194–207 in Cannell MGR, Jackson JE, eds. *Attributes of Trees as Crop Plants*. Huntingdon (United Kingdom): Institute of Terrestrial Ecology.
- McMurtrie RE, Norby RJ, Medlyn BE, Dewar RC, Pepper DA, Reich PB, Barton CVM. 2008. Why is plant-growth response to elevated CO₂ amplified when water is limiting, but reduced when nitrogen is limiting? A growth-optimization hypothesis. *Functional Plant Biology* 35: 521–534.
- Medlyn BE, et al. 2001. Stomatal conductance of forest species after long-term exposure to elevated CO₂ concentration: A synthesis. *New Phytologist* 149: 247–264.
- Morgan JA, et al. 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia* 140: 11–25.
- Norby RJ, et al. 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences* 102: 18052–18056.
- Norby RJ, Wullschlegel SD, Hanson PJ, Gunderson CA, Tschaplinski TJ, Jastrow JD. 2006. CO₂ enrichment of a deciduous forest: The Oak Ridge FACE experiment. *Ecological Studies* 187: 231–251.
- Norby RJ, Iversen CM, Tharp ML. 2007. ORNL FACE Nitrogen Concentrations: Leaves, Litter, Fine Roots, Wood. Carbon Dioxide Information Analysis Center, US Department of Energy, Oak Ridge National Laboratory, Oak Ridge, Tennessee. (2 December 2008; <http://cdiac.ornl.gov>)
- Nowak RS, Ellsworth DS, Smith SD. 2004. Functional responses of plants to elevated atmospheric CO₂—do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist* 162: 253–280.
- Oren R, et al. 2001. Soil fertility limits carbon sequestration by a forest ecosystem in a CO₂-enriched atmosphere. *Nature* 411: 469–472.
- Palmroth S, Oren R, McCarthy HR, Johnsen KH, Finzi AC, Butnor JR, Ryan MG, Schlesinger WH. 2006. Aboveground sink strength in forests controls the allocation of carbon below ground and its [CO₂]-induced enhancement. *Proceedings of the National Academy of Sciences* 103: 19362–19367.
- Pepper DA, Eliasson PE, McMurtrie RE, Corbeels M, Ågren GI, Strömgren M, Linder S. 2007. Simulated mechanisms of soil N feedback on the forest CO₂ response. *Global Change Biology* 13: 1265–1281.
- Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD. 1999. Generality of leaf trait relationships: A test across six biomes. *Ecology* 80: 1955–1969.
- Reich PB, Hobbie SE, Lee T, Ellsworth DS, West JB, Tilman D, Knops JMH, Naem S, Trost J. 2006a. Nitrogen limitation constrains sustainability of ecosystem response to CO₂. *Nature* 440: 922–925.
- Reich PB, Hungate BA, Luo Y. 2006b. Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology, Evolution, and Systematics* 37: 611–636.
- Reich PB, Tjoelker MG, Machado JL, Oleksyn J. 2006c. Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature* 439: 457–461.
- Reynolds JE, Thornley JHM. 1982. A shoot:root partitioning model. *Annals of Botany* 49: 585–597.
- Schäfer KVR, Oren R, Ellsworth DS, Lai C-T, Herrick JD, Finzi AC, Richter DD, Katul GG. 2003. Exposure to an enriched CO₂ atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. *Global Change Biology* 9: 1378–1400.
- Schieving F, Poorter H. 1999. Carbon gain in a multispecies canopy: The role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. *New Phytologist* 143: 201–211.
- Shinozaki K, Yoda K, Hozumi K, Kira K. 1964. A quantitative analysis of plant form—the pipe model theory, I: Basic analysis. *Japanese Journal of Ecology* 14: 97–105.

- Sitch S, et al. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* 9: 161–185.
- Ward S, Midgeley G, Jones M, Curtis PS. 1999. Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentration: A meta-analytic test of current theories and perceptions. *Global Change Biology* 5: 723–741.
- Wang Y-P, Leuning R, Cleugh HA, Coppin PA. 2001. Parameter estimation in surface exchange models using nonlinear inversion: How many parameters can we estimate and which measurements are most useful? *Global Change Biology* 7: 495–510.
- Whitfield J. 2005. Order out of chaos. *Nature* 436: 905–907.
- . 2007. Survival of the likeliest? *PLoS Biology* 5: e142. (3 December 2008; www.duke.edu/philosophy/bio/Papers/Whitfield_Survival.pdf)
- Wright IJ, Reich PB, Westoby M. 2003. Least-cost input mixtures of water and nitrogen for photosynthesis. *American Naturalist* 161: 98–111.
- Zak DR, Holmes WE, Finzi AC, Norby RJ, Schlesinger WH. 2003. Soil nitrogen cycling under elevated CO₂: A synthesis of forest FACE experiments. *Ecological Applications* 13: 1508–1514.

Roderick C. Dewar (e-mail: roderick.dewar@anu.edu.au) is with the Research School of Biological Sciences at the Australian National University in Canberra. Oskar Franklin is with the International Institute for Applied Systems Analysis in Laxenburg, Austria. Annikki Mäkelä is with the Department of Forest Ecology at the University of Helsinki in Finland. Ross E. McMurtrie is with the School of Biological Earth and Environmental Sciences at the University of New South Wales in Sydney, Australia. Harry T. Valentine is with the US Forest Service in Durham, New Hampshire.