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Invited review: Part of an invited issue on carbon allocation

# Modeling carbon allocation in trees: a search for principles

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We review approaches to predicting carbon and nitrogen allocation in forest models in terms of their underlying assumptions and their resulting strengths and limitations. Empirical and allometric methods are easily developed and computationally efficient, but lack the power of evolution-based approaches to explain and predict multifaceted effects of environmental variability and climate change. In evolution-based methods, allocation is usually determined by maximization of a fitness proxy, either in a fixed environment, which we call optimal response (OR) models, or including the feedback of an individual's strategy on its environment (game-theoretical optimization, GTO). Optimal response models can predict allocation in single trees and stands when there is significant competition only for one resource. Game-theoretical optimization can be used to account for additional dimensions of competition, e.g., when strong root competition boosts root allocation at the expense of wood production. However, we demonstrate that an OR model predicts similar allocation to a GTO model under the root-competitive conditions reported in free-air carbon dioxide enrichment (FACE) experiments. The most evolutionarily realistic approach is adaptive dynamics (AD) where the allocation strategy arises from eco-evolutionary dynamics of populations instead of a fitness proxy. We also discuss emerging entropy-based approaches that offer an alternative thermodynamic perspective on allocation, in which fitness proxies are replaced by entropy or entropy production. To help develop allocation models further, the value of wide-ranging datasets, such as FLUXNET, could be greatly enhanced by ancillary measurements of driving variables, such as water and soil nitrogen availability.

***Keywords***: acclimation, evolutionarily stable strategy, functional balance, game theory, partitioning, plasticity, soil depth, theory, tree growth.

## Introduction

The question of how plants allocate carbon among different organs has long been a topic of ecological interest. In times of rising atmospheric carbon dioxide, forest carbon (C) allocation has drawn particular interest due to its responsiveness and potential effect on carbon sequestration and the global carbon balance. The differences in lifespan and decomposition rates among tree organs, such as stems and leaves, imply that C allocation in trees strongly influences forest carbon cycling rates. Whereas the importance of C allocation is undisputed, there is little consensus on how it should be modeled. As a result, a plethora of contrasting approaches exist. Although many promising approaches have been developed for the purpose of scientific insight, it is remarkable how rudimentary the representation of C allocation is in comparison to C assimilation (photosynthesis) in many applied forest models. For example, most dynamic global vegetation models (DGVMs) that are used for future carbon budget projections have fixed or only water-dependent C allocation (Ostle et al. 2009). The lack of consensus on how to model C allocation may be part of the reason for the diverging predictions of the future global forest carbon balance among large-scale models (Purves and Pacala 2008, Ise et al. 2010).

The deficiency of large-scale models in their allocation components seems not to be due to a lack of empirical evidence, but rather to the difficulty in interpreting the available information in the form of well-defined principles that are valid under a wide range of conditions. Because allocation is the outcome of many processes rather than a process in itself (Cannell and Dewar 1994), it is natural to derive allocation mechanistically by combining the individual underlying processes in a bottom-up fashion (Lacointe 2000). However, while the individual processes of different organs are relatively well understood, it is not straightforward to predict their concerted responses under variable environmental conditions. Consequently, allocation is the Achilles' heel of most forest models (Le Roux et al. 2001, Landsberg 2003).

In contrast to the limited allocation schemes in large-scale applied models, a number of promising approaches have been tested at smaller scales for the purpose of scientific insight. These approaches range from simple empirical scaling functions to complex mechanistic representations of the ecological and evolutionary dynamics of the whole forest. In order to elucidate the state of the art in forest allocation modeling and as an initial step towards improving allocation in applied forest models, we discuss a range of C allocation approaches in terms of their underlying assumptions, strengths and limitations. Because C allocation does not differ from nutrient allocation in terms of controlling principles, most of the discussion applies to both types of allocation, together referred to simply as 'allocation'. We discuss the principles that control allocation in trees in response to internal or environmental factors (e.g., allometric scaling, optimization) rather than the processes themselves (growth, respiration and exudation). In order to promote fruitful use of eco-evolutionary theory in forest modeling, we put emphasis on approaches rooted in ecological or evolutionary concepts. We identify conditions where simpler individual optimization-based approaches are consistent with evolutionary theory and when more complex approaches including feedbacks between individual behavior and the environment are called for. Emerging entropy-based approaches are discussed in terms of their probabilistic interpretation and their potential to address allocation strategies in a computationally efficient way. Finally, because model testing and empirical data are essential for model development, we suggest statistical methods and types of data that would be most helpful for further development of models and theories on C allocation in forests.

## Overview of approaches to allocation modeling in forest models

In this paper, we review a range of approaches used to predict allocation in forest models in terms of underlying principles. Although most of the concepts and terms used are well established in forest modeling or tree physiology, terms that may be less commonly used in these fields, or may have variable meanings depending on the context, are explained in a glossary (Table 1). Examples of models are used to illustrate the approaches, which are introduced in order of increasing complexity, ranging from empirically based factors to mechanistic representations of evolutionary dynamics. Before the different approaches are discussed in detail in the following sections, here the main categories of methods are summarized (Table 2) and put into a common framework to facilitate comparison (Figure 1).

Five main categories of approaches to allocation modeling are identified, based on the key principles used to predict

Table 1. Glossary—terms and their meanings as used in this paper.

| Term | Meaning[1] |
|---|---|
| Density dependence | The number and size of individuals in a given area influences the environment of each individual. |
| Entropy | Statistically interpreted, a measure of the probability of a certain state of a complex, non-equilibrium system, compared with other states. |
| Environmental feedback | An individual's *strategy* affects the environment in a way that feeds back on the *fitness* of the individual. |
| Feedback environment | Properties of the environment that are part of the environmental feedback. |
| Evolutionarily stable strategy (ESS) | A *strategy* that cannot be invaded by another strategy in the environment it creates. |
| Fitness | Per capita population growth rate. |
| Fitness proxy | A substitute approximation for *fitness* used for convenience (e.g., growth rate). |
| Game theory | A theory where the success of an individual's *strategy* depends on the *strategy* of others. |
| Optimization | A modeling technique for finding the strategy that maximizes a goal function (e.g., fitness proxy) in a model. |
| Plasticity | Non-genetic change or acclimation of a *strategy* of an individual during its lifetime, usually in response to the environment. |
| Reaction norm | A *plastic strategy*, i.e., a strategy that changes in response to the environment. |
| Strategy | A combination of *traits* that defines an individual or its behavior (phenotype). |
| Trait | An attribute of an individual, usually with influence on *fitness*, e.g., the reaction norm for allocation, wood density or photosynthetic capacity. |

[1] Italicized words are explained in the glossary.

Table 2. Summary of carbon allocation principles.

| Name | Description[1] | Examples |
|---|---|---|
| Empirical approaches | | |
| Fixed ratios | Fixed fractions of the assimilated carbon (C) is allocated to each organ. | Fixed leaf : fine-root allocation ratio in most dynamic global vegetation models (DGVMs; Ostle et al. 2009). |
| Allometric approaches | | |
| Allometric scaling | Scaling relationships between organs that vary with individual size but not with the environment. | Metabolic scaling with body size leads to universal scaling relationships between organs (metabolic theory of ecology; West et al. 2009). |
| Functional-balance approaches | | |
| Coordination theory | Equalization of the limiting effects of different resources via preferential allocation of C to the organ responsible for acquisition of the most limiting resource. | Root versus shoot growth in response to C and nitrogen (N) supply (Reynolds and Chen 1996) and C and water supply (Chen and Reynolds 1997) in small plants. |
| Eco-evolutionarily-based approaches | | |
| Optimal response (OR) | Optimization of a strategy (e.g., allocation) in order to maximize a fitness proxy in a fixed environment. | Allocation of C and N controlled by maximization of photosynthesis at the canopy scale (McMurtrie et al. 2008) and net growth at the whole plant level (Franklin et al. 2009). |
| Game-theoretic optimization (GTO) | Models where the success of an individual's *strategy* depends on the *strategy* of other individuals. In forest modeling it accounts for the feedback of allocation on the abiotic and biotic environment. | Prediction of root, foliage and wood allocation in a growing even-aged stand (King 1993; Figures 3 and 4). |
| Adaptive dynamics (AD) | Modeling of the emergence of strategies through evolution, via explicitly modeled population dynamics. It may result in an *ESS*. | Derivation of ESS for root, foliage and wood allocation in a steady-state forest (Dybzinski et al. 2011). |
| Thermodynamic approach | | |
| Maximum entropy production (MEP) | Optimization of *traits* (including allocation) to maximize the rate of entropy production (free energy dissipation) under a fixed environment. | Plant C allocation control at different timescales and levels of organization (Dewar 2010; Figure 7, and Appendix B). |

[1] Italicized words are explained in Table 1.

allocation: empirical, allometric scaling, functional balance, evolution based and entropy based. The distinction is not clear-cut as all models have empirical components and—because this classification is not a purpose per se but a vehicle for readability—we accept some overlap between categories. For example, allometric scaling may be based on metabolic theory or solely on empirical data, i.e., it can be a mechanistic or an empirical method. However, we distinguish between allometric scaling and empirical methods in general due to an important and distinct feature of allometric scaling: it accounts for ontogenetic effects on allocation in individuals but not environmental effects (plasticity) (Figure 1a). We categorize an approach as empirical if it is based on observed relationships rather than a theoretically justified principle, e.g., if it accounts for environmental effects based on empirical relationships (Figure 1b). In functional-balance approaches, allocation is controlled in order to maintain internal homeostasis of physiological processes or element concentrations, without reference to an ultimate goal or purpose of the behavior. In contrast, the evolution-based methods are teleonomic, meaning that, from a modeler's perspective, allocation is predicted based on its ultimate effect on future success, i.e., fitness or a fitness proxy. The evolution-based approaches include optimal response (OR) models, which maximize a fitness proxy in a fixed environment (Figure 1c), game theoretically based approaches (GTO, Figure 1d), which maximize a fitness proxy including the feedback of an individual's strategy on its environment, and adaptive dynamics (AD, Figure 1e), which models the evolution of strategies (e.g., allocation) in the context of population dynamics. Whereas OR and GTO models usually address acclimation (or plasticity) of allocation, AD can be used to predict the evolution of allocation strategies. Entropy-based approaches resemble OR or GTO, but the controlling principle is based on thermodynamics rather than evolutionary theory and involves maximization of entropy or entropy production (Figure 1e).

## What is the simplest way to model allocation?

### *Empirical and allometric approaches*

In forest modeling or any other scientific modeling, it is advisable to follow 'Einstein's razor', i.e., make the model as simple

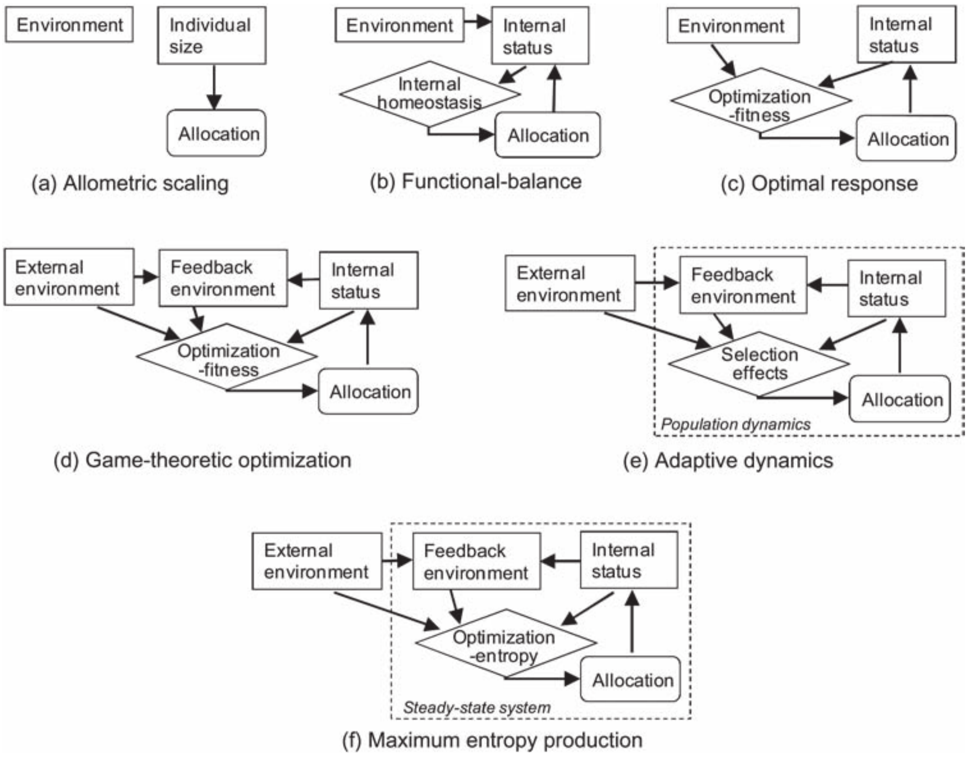

Figure 1. Examples of interactions between environment (abiotic and biotic), internal status (e.g., size and growth rate) and allocation of carbon (C) addressed to determine C allocation in different modeling approaches. In allometric scaling (a) allocation only depends on individual size. Functional balance (b) can be used to link the size of each organ (internal status) to the acquisition of a particular resource and allocate C among organs in order to maintain internal homeostasis, e.g., fixed biomass C : N ratio. In an OR approach (c) effects of environmental and internal factors are integrated to get the optimal allocation that maximizes fitness or a fitness proxy (optimization fitness). In addition to the interactions of the OR approach, a GTO approach (d) accounts for the effect of individuals (internal status) on their environment, e.g., competition effects. The AD approach (e) includes the interactions applied in GTO but instead of prescribing a fitness proxy, allocation at the individual level evolves through the effect of selection via explicit modeling of population dynamics. The MEP approach (f) is based on similar interactions to the evolution-based approaches but has a different organizing principle, i.e., maximum entropy production (optimization entropy). The exact formulation of the MEP principle depends on which part of the system is assumed to be in steady state (dashed box), which is determined by the level of organization (e.g., forest, tree or canopy) and corresponding temporal scale addressed.

as possible, but no simpler. There exist some very simple approaches to C allocation, but the question is when are they too simple and under which circumstances are they acceptable?

The simplest way to model C allocation is to assume that a fixed fraction of the C assimilated in photosynthesis is allocated to each organ (e.g., fixed leaf : fine-root allocation ratio in most DGVMs; Ostle et al. 2009). Although in reality the allocation of C varies with both individual status (such as size and age) and environmental conditions, the fixed allocation approach may be justified under certain conditions for models operating at the scale of stands or larger. If the forest tree size-distribution and productivity are assumed to be in a steady state, large-scale allocation is also likely to be in a steady state even though the allocation of each tree changes with time. Similarly, a large-scale perspective can average out spatial variability in environmental factors and their effects on allocation. However, a potentially critical limitation of the fixed allocation approach, commonly used in long-term simulations of terrestrial C budgets, is the lack of allocation response to environmental changes, such as climate change, N deposition and elevated atmospheric $CO_2$. This lack of response contradicts experimental results and physiologically more sophisticated models, showing that rising $CO_2$ levels lead to large shifts in C allocation between fine roots and wood that strongly interact with soil N availability and stand age (Iversen et al. 2008).

Whereas fixed allocation may be justified at large scales for steady-state forests in constant environments, at the individual level allocation clearly varies with size (and age) of a tree. This intrinsic (ontogenetic) allocation pattern can be described by allometric scaling relationships based on empirical data or allometric theory (e.g., West et al. 2009) (Figure 1a). Allometric scaling provides a simple way of deriving a typical or mean behavior of a species and even to derive structural and functional properties at the population level (West et al. 2009). An often used allometric relationship in forest models is the pipe model (Shinozaki et al. 1964) that links the sapwood cross-sectional area of the stem to leaf area, based on the relationship between leaf water use and stem transport capacity. Because the pipe model relationship is mainly governed by the internal relationship between plant organs for a single resource (water), it is likely to be more invariant across environments than most other allometric relationships, such as among root, stem and leaf biomasses that are each linked to acquisition of different resources from the environment. Because allometric scaling among organs does not address the plastic response of allocation to environmental factors, it cannot be used to model effects of resource availability and climate change on C allocation in trees.

If we are interested in the effects of a changing or variable environment (abiotic and biotic) on forests, the variation in allocation in response to these variables must also be considered, i.e., the reaction norm (explanation in Table 1) for allocation. A conceptually simple way to address environmental effects on allocation is through heuristic rules that mimic observed responses (Figure 1b). For example, observations that reduced nutrient availability increases root allocation (Landsberg and Waring 1997), or that low light increases relative C allocation to the stem, can be used to construct empirically based allocation functions, which are fitted to observations. Because empirically based allocation relationships are usually based on functions of simple shape, e.g., monotonic, they should be most easily derived and accurate for simple allocation patterns, such as the rather universal trend of increasing allocation to wood with site productivity (Litton et al. 2007). In contrast, deriving empirical allocation relationships may be more problematic for more complex, e.g., non-monotonic, relationships, such as the allocation to fine roots in response to soil N availability (Mäkelä et al. 2008, Franklin et al. 2009), which likely contributes to the low predictive power of empirical root-allocation models (Gower et al. 1996).

### *Functional-balance approaches*

Compared with empirical and allometric approaches, the functional-balance concept, first suggested by Davidson (1969), leads to more mechanistic representations of the allocation process. In this approach, allocation is driven by bottom-up responses to maintain an optimal (usually fixed) internal resource status or element ratio (e.g., biomass C : N). Similar approaches have been referred to as optimal partitioning theory (McCarthy and Enquist 2007), which—as they do not specify an overarching eco-evolutionarily rooted optimality criterion—should not be confused with the OR approach described below. Coordination theory is another approach rooted in the functional-balance concept, which states that the plant strives to equalize the limiting effects of different resources via preferential allocation of C to the organ responsible for acquisition of the most limiting resource in each time step (Reynolds and Chen 1996, Chen and Reynolds 1997). Because the limiting effects are calculated in terms of growth rate, this approach may lead to allocation that approximates a growth rate maximization behavior without foresight. This method offers a practical bottom-up way of simulating adaptive responses to temporal variability in resource availability without the need to account for conceptually and computationally more challenging long-term goals, such as fitness maximization.

The bottom-up perspective also means that an evolutionary underpinning of the choice of the particular goal or 'balance' variable used (whole-plant instantaneous growth rate) is lacking. It is not self-evident why whole-plant growth should be maximized rather than, e.g., shoot growth, which may be critical for survival under the asymmetric competition for light experienced by most plants in nature. In addition, for trees these methods may be hampered by the assumed direct linking of each organ to the acquisition of a particular resource or need, e.g., between stem height and light capture in trees, as done in Scheiter and Higgins (2009). For trees in forests such simple links may not always hold as organs interact, e.g., leaf area and stem height both influence light absorption, and the optimal C allocation to leaf versus stem growth will depend on the local light environment. Such interactive and variable relationships among organs can be addressed in a general manner by applying an overarching control principle, such as a goal function of the integrated effects of all organs based on evolutionary, fitness-maximizing arguments. Nevertheless, even in such an evolution-based allocation model (discussed below), many elements from functional-balance models (e.g., C and N mass balances) and allometric scaling (e.g., the pipe model) remain essential for the representation of physiological constraints in the model.

## Eco-evolutionarily-based models: theory for insight and prediction

Few physicists would choose to ignore the guiding principles of their field, such as the conservation of mass and energy, when modeling a physical phenomenon. In contrast, in applied ecological modeling it has been common practice to ignore the guiding principles of ecological and evolutionary theory. However, an increasing number of forest modelers have recognized that ecological and evolutionary theory are not only fundamental for understanding biology and ecology but also provide powerful tools for improving predictive models (Dewar et al. 2009, Anten and During 2011). An organizing eco-evolutionary principle can limit the uncertainty in models by imposing a top-down control that selects one (most likely or fittest) behavior out of the otherwise infinite number of possibilities. In addition, this way of deriving allocation eliminates the need for empirical estimation of allocation factors and the associated practical difficulties and uncertainties, e.g., measuring fine-root production. However, although the practical and theoretical advantages of an accurate organizing principle are clear, finding the most appropriate principles and assumptions is not straightforward.

Allocation, like all biological processes, is a product of evolution, which suggests that to fully understand allocation, it may be necessary to model the underlying evolutionary process in considerable detail. This is easier said than done, particularly for trees and forests, where long generation times and a large number of environmental and internal variables interacting on different temporal and spatial scales create a system that is exceptionally challenging to model. In addition, whereas in empirical approaches C allocation can be modeled separately from C acquisition (photosynthesis), in an evolutionary approach, allocation is linked to all other physiological processes, and the integrated whole-plant behavior is subjected to selection or optimization (Figure 1). Due to the complexity of the evolutionary process, its effects must be simplified to bring out the consequences for allocation in a form that can be applied for predictive purposes, e.g., to predict allocation plasticity in response to environmental variables. A common feature of simplification in most tree allocation models is the use of a proxy for fitness, such as instantaneous growth rate, that can be readily measured and modeled. This simplification is natural for short timescale models, addressing acclimation responses (plasticity) of existing trees rather than the long-term community composition or evolution. However, although the observed behavior of the existing forest can guide the selection of a fitness proxy, it is not always possible to discern the most appropriate fitness measure based on the resulting correspondence with empirical data (Anten and During 2011). This uncertainty is minimized by using a fitness measure that accounts for the whole life cycle, such as mean number of offspring produced per individual during its lifetime ($R_0$). Perrin (1992) derived a theoretical framework based on maximization of $R_0$ that leads to allocation that maximizes net productivity increase in each time step followed by a complete switch to reproductive allocation. However, an important limitation of the approach by Perrin (1992) is that the environment must be specified externally (exogenously), which is not a straightforward task for the life cycle of a tree in a forest. In addition, the fixed external environment implies that interactions between individuals, in particular effects of competition, are not explicitly addressed. However, competition is ubiquitous in forests, as evident from the existence of tall tree stems as a result of competition for light (Mäkelä 1985, King 1990, Falster and Westoby 2003). It turns out that competition plays an important role when selecting the most appropriate type of evolution-based allocation approach.

### A single tree optimality perspective: OR models

The most widely used evolution-based models for trees and forests, the OR models, are based on maximization of a goal function that reflects fitness on the timescale addressed by the model. The underlying assumption is that evolution has led to a behavior that optimizes this goal function due to its importance for fitness. Consequently, the reaction norm for allocation in an OR model is implicitly defined by the goal function, e.g., maximization of net growth. In contrast to a game-theoretic approach, an OR model does not explicitly address a feedback loop between the plant's strategy (behavior) and its abiotic or biotic environment (Figure 1c). Practically speaking, the most important consequence of the absence of explicit environmental feedback is that allocation can be optimized in a fixed environment, which reduces mathematical complexity compared with a GTO model. Due to its power and relative simplicity, the OR approach is useful for scaling up processes across organizational levels, i.e., by assuming optimal functioning at each level from chloroplasts to forest canopies, the number of parameters and the accumulation of uncertainty at each new organizational level added to a model can be minimized (Schymanski 2008). Although OR is not a new approach to model plant behavior (e.g., Vincent and Pulliam 1980), it is only recently that its 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 free-air carbon dioxide enrichment (FACE) experiments and other empirical studies (Dewar et al. 2009).

Theoretically, OR is a valid approach when plant behavior on the timescale addressed by the model is not significantly influenced by environmental feedback, such as competition. For example, within-canopy distribution of leaf area and N usually do not significantly affect the environment of neighboring trees. Consistent with this observation, an OR model was successfully used to determine covariations in leaf traits in agreement with the observed leaf economic spectrum (McMurtrie and Dewar 2011): leaf acclimation of specific leaf area, N concentration and stomatal conductance to elevated $CO_2$ (McMurtrie et al. 2008); leaf-N per leaf-area in trees at ambient and elevated $CO_2$ (Franklin 2007); and leaf-N per leaf-area in crops (Franklin and Ågren 2002). Although these models address slightly different leaf and canopy properties, they all derive optimal C and N allocation through maximization of net C gain, i.e., photosynthesis minus C costs of respiration and leaf turnover, for a given amount of canopy N.

For OR modeling of whole trees, the benefits and costs of all organs (canopy, stem and roots) must be included in the goal function of the model. In addition, the effect of competition can rarely be neglected. However, the effects of competition can sometimes be subsumed in the optimization target of an OR model. For example, C and N allocation to stem wood, fine roots and leaf area index (LAI) in response to soil N availability and $CO_2$ was determined by maximization of net stem growth (plus reproduction, which was negligible; Franklin et al. 2009). This goal function (fitness proxy) is based on the idea that stem growth rate determines the success of an individual due to strong and asymmetric competition (disproportional advantage for larger versus smaller individuals) for light. Thus, by letting the goal function represent the most competitive strategy, OR can be used to address an effect of environmental feedback, such as competition, despite the absence of explicit modeling of the feedbacks.

The OR model by Franklin (2007) applies nested optimizations to determine C and N allocation at three hierarchical levels: optimal total canopy N at the whole-plant level, LAI (for a steady-state canopy N) at the canopy level and leaf N per area (for steady-state canopy N and LAI) at the leaf level. Steady state is assumed in each optimization and for the levels above, which means that canopy N and LAI are in steady state only when the canopy is in steady state, i.e., fully expanded (Figure 2a). For expanding (young) canopies, LAI and leaf N per area are optimized for each value of canopy N, which is not in steady state (canopy N increases with canopy expansion). This leads to different relationships between productivity and canopy N for expanding and fully grown canopies (Figure 2b). For example, this result explains why growth per canopy N (canopy nitrogen use efficiency) decreases with canopy N and age in expanding canopies (Franklin 2007, van Kuijk and Anten 2009) but does not decrease with canopy N (e.g., in response to N additions) in fully closed canopies. Thus, OR applied at different levels and corresponding equilibrium timescales can be combined in the same model to address allocation responses on different timescales and for different life stages.

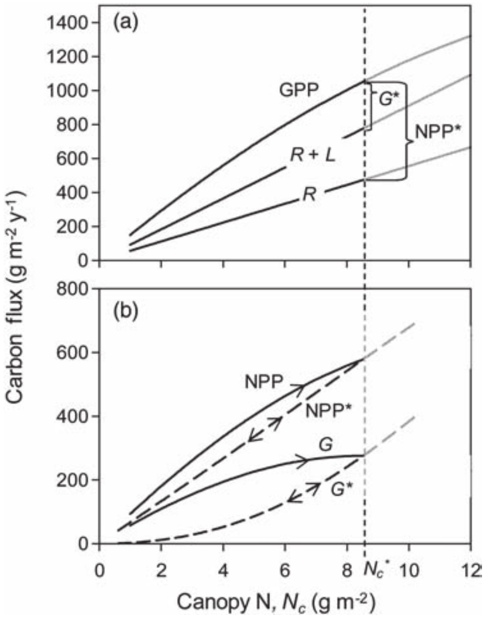

Figure 2. Model of canopy expansion and optimal steady-state canopy in an OR model. (a) The steady-state optimal canopy nitrogen ($N_c$*) that maximizes net growth ($G$), where $G$ equals the difference between carbon gain (GPP) and C costs (respiration, $R$ + litter production, $L$). (b) The paths of net production as a function of canopy N of expanding (young) canopies (NPP and $G$, solid lines) and steady-state canopies (NPP* and $G$*, dashed lines). For expanding canopies, NPP and $G$ are functions of increasing $N_c$ for fixed slopes of $R$ and $L$ as shown in (a). For steady-state canopies, the curves of NPP* and $G$* do not correspond to the fixed slopes of $R$ and $L$ as shown in (a) but are drawn by varying the slope of $R + L$ versus $N_c$ (the C cost per $N_c$) and deriving a new $N_c$* for each $R + L$ slope. In nature, the $R + L$ slope changes with age or soil fertility as a result of shifts in stem-wood N : canopy-N ratio or root-N : canopy-N ratio. For example, increasing stem wood respiration with stem height causes a decrease of NPP* and $G$* along the dashed lines. The model is described in Franklin (2007).

Optimal response models have also been developed based on fitness proxies defined at organizational levels above the individual, e.g., at the stand level. Because selection mainly operates at the individual level, it is not straightforward to evaluate the applicability of an OR model based on a fitness proxy defined at the stand level. Nevertheless, allocation to stem wood, fine roots and foliage in response to N uptake and $CO_2$ was successfully determined by maximization of net primary productivity (NPP) at the stand level for steady-state (old) pine and spruce forests (Mäkelä et al. 2008). Thus, although not obviously defendable from a theoretical perspective, it appears that maximization of NPP provides a sufficiently good approximation for predicting the behavior of the forests on the timescale addressed in this model. In general, various productivity-related fitness proxies appear to provide good approximations of allocation plasticity in OR models of existing trees and forests. However, with increasing time horizon, the impact of any mismatch between a fitness proxy and actual fitness will increase. On timescales including different life stages (reproductive, vegetative growth), a single productivity-based fitness proxy is clearly not sufficient to explain a tree's allocation strategy.

The validity of the OR approach in forest modeling is mainly limited by two interrelated factors: potential inadequacy of the fitness proxy, and environmental feedback through competition. In an OR model, it is necessary to use an integrated measure of an individual's performance, including any environmental feedbacks (Table 1; Heino et al. 1998; e.g., competition) in the form of a single variable (fitness proxy, e.g., height growth), which is maximized. In practice, this implies that the potential to address competitive effects in an OR model should be limited to one dimension of competition, i.e., a one-dimensional feedback environment. For example, it appears that vegetative growth in even-aged stands dominated by competition for light is one example where the feedback environment can be sufficiently one-dimensional to use OR. This means that fitness increases monotonically with height growth rate because there is no other way to gain an advantage over your competitors. However, if there is competition for another limiting resource (another dimension of competition), such as soil N, it is also possible for a tree to influence its height growth rate relative to the other trees by increasing its share of nutrient uptake at the expense of the others, by diverting C allocation from stem to roots (see below). Because the competitors respond in the same way, there is an interactive relationship between individuals that influence the optimal allocation strategy. Thus, it is no longer possible to derive the optimal allocation strategy without reference to the interaction with neighbors (the feedback environment in Figure 1d).

### Addressing competition: GTO models

Continuous-trait game theory in ecology and evolution is centered around the concept of the evolutionarily stable strategy (ESS), which is a strategy (e.g., a reaction norm for C allocation) that cannot be invaded by a different strategy when it is in equilibrium with its environment (it is the resident strategy) (McGill and Brown 2007). Whereas the optimal strategy in an OR model is determined in a fixed environment, a GTO approach includes the interaction of the strategy and the environment (Figure 1c and d), e.g., competition with neighbors (biotic environment). Critically, the result of a GTO model, the ESS, is optimal in the sense that it cannot be invaded and thus successfully holds a site, but it may or may not maximize a particular aspect of productivity, such as carbon sequestration, reproduction, height growth, etc. (Dybzinski et al. 2011). Game-theoretic optimization has mainly been applied to explain height growth in trees (Mäkelä 1985, King 1990) but also to root : stem : foliage allocation ratios in trees, suggesting that competition for soil N can significantly influence allocation (King 1993).

One of the most interesting findings from the use of GTO in forest modeling is that ESS allocation, particularly to roots, will not maximize 'stand fitness' (e.g., stand growth rate; King 1993). This result, also shown for grasses (Craine 2006) and herbs (Gersani et al. 2001), is caused by competition and the fact that it is beneficial for an individual to increase its marginal N uptake at the expense of others. Thus, each individual will increase N uptake beyond the 'collective optimum' until a competitive optimum (or equilibrium) is reached at a higher root allocation than would maximize stand productivity, i.e., a tragedy of the commons occurs.

The explicit modeling of environmental feedback in GTO models means that, in comparison to an OR approach, an additional level of interaction must be included in the solution, i.e., in the derivation of an ESS. Thus, for most modeling purposes, GTO models are more complex and computationally costly than OR models. However, competition effects based on GTO can be modeled at similar computational cost as for OR models under simplifying assumptions, such as identical trees maximizing wood growth (King 1993). In this case, whole-forest (stand) properties can be derived directly without the need to simulate interactions among individuals or size classes explicitly. However, if interactions between different size classes and non-equilibrium conditions are addressed, explicit simulation of individuals in one way or another will likely be necessary, which increases computational cost considerably and makes the results less tractable.

In conclusion, the scarcity of GTO in forest models despite its power to address important aspects of competition suggests that GTO has a large potential to further improve and extend forest allocation models, particularly in combination with simplifying assumptions to limit the computational costs. For example, GTO may be helpful in addressing the often overlooked allocation of C to mycorrhizal fungi that supply N in a C–N trading relationship with the plants that may span from mutualism to parasitism (Kummel and Salant 2006).

### How do the optimal response and game-theoretic approaches compare in practice?

As discussed above, the advantage of using an OR approach compared with GTO is the lower complexity and computational cost obtained by omitting explicit environmental feedback, i.e., not explicitly addressing the effect of a strategy on the plant's (abiotic and biotic) environment. On the other hand, environmental feedback such as competition may be an important driver of plant behavior, in which case an OR may fail unless it implicitly accounts for the environmental feedback. Because of the relatively widespread use of the simpler OR approach in comparison to GTO in forest modeling, a potentially interesting question is how different are their predictions in practice?

In theory, an OR approach is insufficient and GTO is required to model allocation when the feedback environment has more than one dimension, e.g., when there is competition for both light and soil nutrients. King (1993) compared a GTO model with an OR model, where both models maximize stem wood production but only the GTO model accounted for root competition for N. In particular, root allocation differed greatly between the two approaches, a result also predicted by a more comprehensive model based on AD (Dybzinski et al. 2011). Both these models assume an N uptake–root relationship that leads to almost complete uptake of the potentially available soil N. Thus, an individual can increase its N uptake almost exclusively at the expense of its neighbors, which promotes very strong root competition. However, in reality the competition intensity may vary among forests and it has not been evaluated how the intensity of competition in forests influences the difference between an OR and a GTO model in practice.

In order to evaluate the effect of competition intensity for predicted root allocation, we constructed a simple tree growth and allocation model based on elements from the models by King (1993) and Franklin et al. (2009) described in Appendix A. The degree of root competition was evaluated as the relative difference in marginal N uptake per root between a non-competitive (OR) version of the model and a GTO version, which includes root competition (but otherwise is identical to the OR version). This measure of competition is similar to a relative competition index (RCI, Grace 1995). The effect of root-competition intensity was then evaluated by comparing model results based on parameters representative of an observed N uptake–root growth relationship from the Oak Ridge National Laboratory (ORNL) FACE experiment (Franklin et al. 2009) to a more competitive relationship, representing shallower soil depth (Figure 3). For each model and the two soil depths, allocation to fine roots, wood and foliage was modeled in response to soil N availability and in response to C availability for photosynthesis, not specifying the underlying cause (e.g., atmospheric [$CO_2$], light intensity or stomatal conductance).

The difference in predicted allocation between the GTO and OR approaches increases with the intensity of root competition (which is not accounted for in the OR model), which is strongly influenced by soil depth (Figure 4e and f). This root-competition effect has a maximum at rather low soil N availability and vanishes at high soil N availability, whereas it increases monotonically with C availability for photosynthesis. Allocation and root-competition intensity is affected by C availability and N availability to a similar extent but following different functional shapes. However, the observed competitive intensity in ORNL FACE was relatively low, resulting in an overall small modeled root-competition effect on allocation (Figure 4a–c). Only a substantially smaller soil depth significantly increased the competitive effect on allocation (Figure 4d–f). Increased C availability increases wood allocation most strongly for large soil depths and high soil N availability, suggesting that rising $CO_2$ will enhance stem wood C sequestration particularly in forests with deep and N-rich soils. Although a proper evaluation of this result is beyond the scope of this paper, it illustrates a potentially important use of GTO in accounting for effects of soil depth on C allocation.

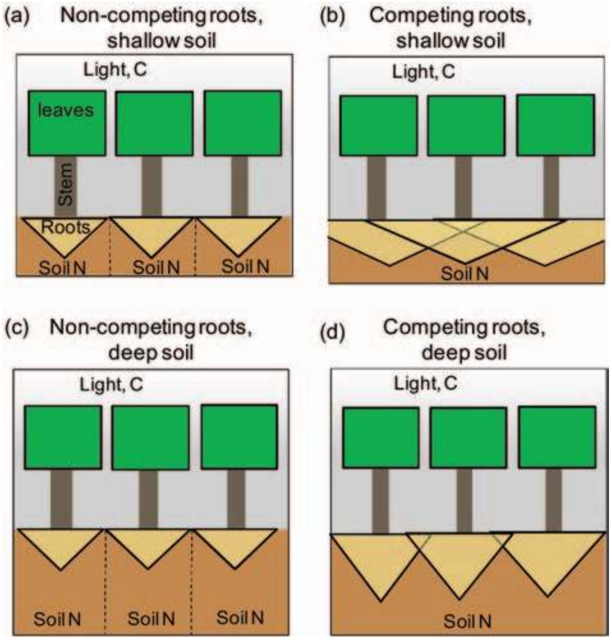

Figure 3. Comparison of GTO and OR models for different soil depths used for evaluation of the effect of root competition on carbon (C) allocation, shown in Figure 4. In both models (defined in Appendix A), growth is limited by light, carbon availability for photosynthesis and soil nitrogen (N) availability. Both models are based on maximization of stem growth but employ different assumptions for root-competition : no root-competition (OR model, (a) and (c)) and root competition (GTO model, (b) and (d)). Each model is evaluated for shallow soil (c) and (d) and deep soil (a) and (b). Shallow soil leads to a more complete exploration of the soil volume and more overlap among roots than in the deep soil, which leads to a stronger competition for N in the presence of root competition. Thus shallow soil amplifies the difference between the model predictions with root competition and without root competition, as shown in Figure 4.

Our analysis shows that the intensity of competition can strongly affect modeled allocation and thus the difference in the results between a GTO model that includes this effect and an OR model that does not. A comprehensive evaluation of the importance of root competition in forests is beyond the scope of this paper. However, in the intensively studied Oak Ridge and Duke FACE sites, stand N uptake increased almost linearly with increased fine-root production in response to elevated $CO_2$ (Franklin et al. 2009), which suggests a relatively minor root-competition effect. A small root-competition effect explains why the OR model by Franklin et al. (2009) was able to predict the observed responses in these FACE experiments, despite not accounting for root competition. In contrast, there are forests where root competition is more pronounced, e.g., in nutrient-poor dry conditions (Montgomery et al. 2010), which may accentuate the differences between OR and GTO models. In general however, the OR model by Franklin et al. (2009) produces qualitatively similar allocation relationships to the GTO model by King (1993) and the AD model by Dybzinski et al. (2011; see below), such as a trade-off between root and wood allocation and increasing root allocation at decreasing N availability. These general patterns are supported by a meta-analysis of a large range of experimental data (Litton et al. 2007).

If indeed the competition intensity is the key limitation of using an OR model for C allocation in forests, this can be used to identify in which types of forests an OR model is sufficient and when GTO models should be preferred. Based on the results presented here, we suggest that factors influencing below-ground density dependence should be important, such as soil volume, as has been shown for annual plants (O'Brien and Brown 2008). In addition, the distribution and mobility of resources should be important for the intensity of competition and thus for the selection of the modeling approach. Because competition should be stronger for more mobile soil resources than for less mobile resources (Casper and Jackson 1997), the predictions of GTO and OR approaches may differ more in water-limited forests and less in phosphorus-limited forests compared with N-limited forests.

In conclusion, despite the theoretical differences, OR and GTO approaches predict similar allocation patterns in forests

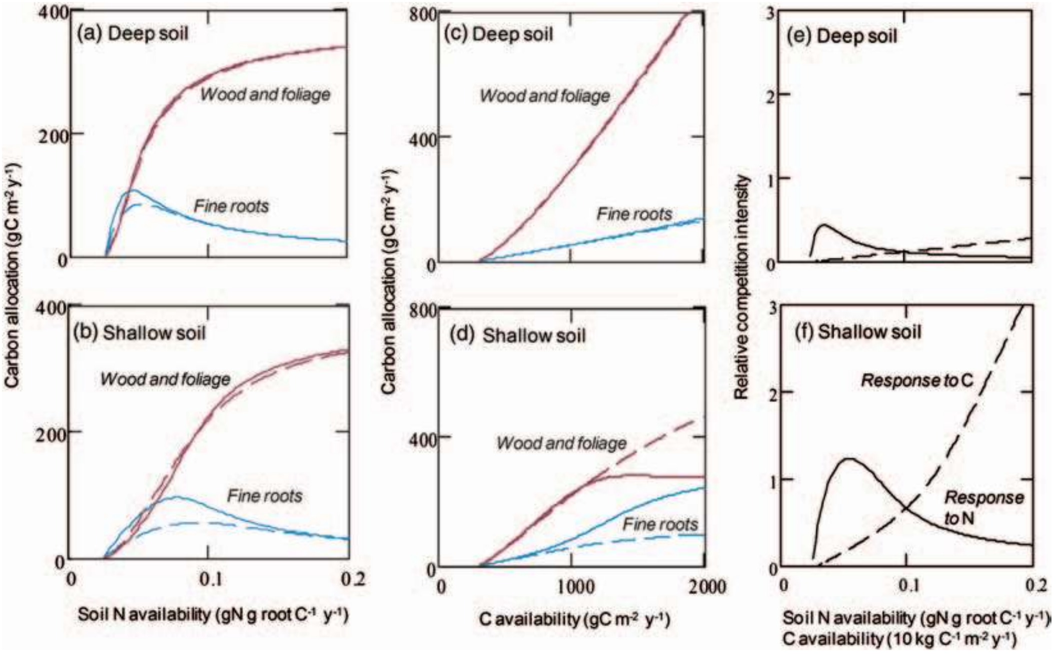

Figure 4. Effect of root competition and competition intensity on modeled forest carbon (C) allocation. Model predictions of allocation (a–d) and competition intensity (e and f) are based on two optimization models that both maximize individual wood production but differ in their assumptions of root competition for soil nitrogen (N). As explained in Figure 3 and Appendix A, the GTO model (solid lines) accounts for root-competition effects while the OR model (dashed lines) does not. Optimal allocation of carbon to foliage and wood and fine roots is shown in response to soil N availability (a, b) and C availability for photosynthesis (c, d). (e and f) show root-competition intensity, i.e., relative difference in marginal gain in N uptake per C allocated to roots for a competitive individual (GTO model) compared with a non-competitive individual (OR model), in response to soil N availability (solid line) and C availability (dashed line). Top figures (a, c, e) are based on parameters representative of observations in ORNL FACE, while bottom figures (b, d, f) are based on the same parameters except that soil depth has been reduced by a factor of 4.5 to increase root competition. In modeling variable soil N availability, C availability was fixed at 1000 g C $m^{-2}$ $year^{-1}$. In modeling variable C availability, soil N availability was fixed at 0.1 g N g root $C^{-1}$ $year^{-1}$. Other parameters and the models are described in Appendix A.

where root competition for soil resources is weak, as observed in the ORNL and Duke FACE experiments. However, stronger root competition is likely to be common, which would amplify the difference between the modeling approaches.

### *Evolving allocation: AD*

In forest modeling, OR and GTO models are mainly used to predict allocation plasticity in response to environmental variables such as resource availability, while assuming that the fitness proxy that governs allocation plasticity remains fixed. In contrast, adaptive dynamics theory (AD; e.g., Dieckmann and Law 1996, Metz et al. 1996, Geritz et al. 1998, Meszéna et al. 2001, McGill and Brown 2007) takes a step further by, instead of assuming a fitness proxy, letting fitness and the allocation strategy emerge dynamically, through modeling the evolution process driven by the underlying ecology. In such models, evolution gradually modifies an allocation strategy so as to increase its success relative to the currently existing strategy (or strategies). In an AD model, the success of strategies is modeled explicitly in terms of their population dynamics, based on considering the whole life cycle of the modeled organism. Although in theory several different types of outcomes of this process are possible (Geritz et al. 1997, McGill and Brown 2007), for C allocation in trees under natural conditions, a likely result is an allocation ESS (potentially involving a mixture of several coexisting strategies). As in GTO models, the ESS is optimal in the sense that it cannot be invaded by an alternative strategy.

The main advantage of AD compared with GTO and OR models is that the fittest strategy arises as an emergent property of the model, avoiding the problem of having to select an appropriate fitness proxy a priori. Like in GTO models, but unlike in OR models, the feedback environment in an AD model is also emergent, so competition and other interactions are readily accounted for. In addition, whereas the OR approach leads to a single optimal strategy (at least in a spatially homogeneous environment), the use of AD allows ESS mixtures of continuous strategies that each originate as an emergent property of the model.

The limitations of using AD in forest modeling lie mainly in the complexity and computational demand incurred by an explicit modeling of population dynamics, in particular when the latter is structured with regard to size or other physiological states. In allocation modeling, the degree of complexity will further depend on how the allocation strategy is represented: two salient options include values (scalars) for each considered

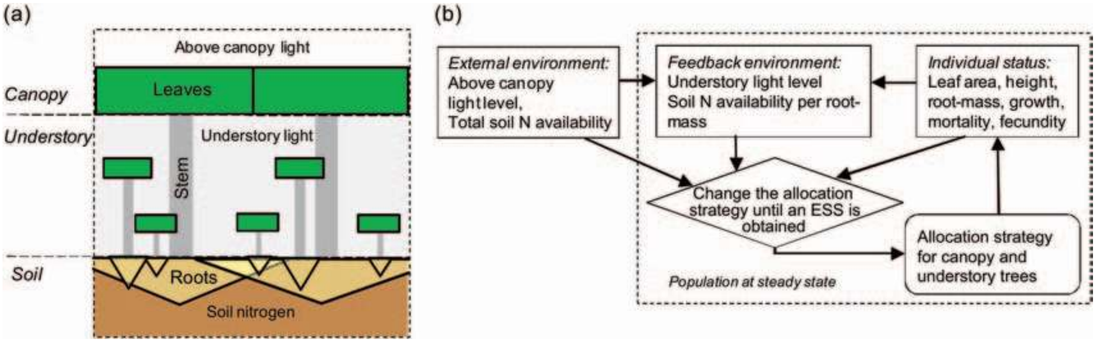

Figure 5. The AD forest model by Dybzinski et al. (2011). (a) Trees are classified as canopy trees, which experience full sunlight, and understory trees, which are shaded by the canopy trees and experience a constant understory light level. Understory trees become canopy trees when they reach the canopy height, which emerges dynamically from the model as the height at which the crowns of the tallest trees completely cover the horizontal space (the perfect plasticity approximation for light competition). Nitrogen (N) uptake of each tree is a function of its root mass relative to the total root mass of all trees and the soil N availability, i.e., all trees compete for the same N. (b) The allocation strategy (determining carbon allocation to roots, foliage, stems) affects individual size, growth and fecundity as well as the competition for light and N among trees via the feedback environment. The ESS allocation strategy is the strategy that maximizes fitness, in the sense that it cannot be invaded by a different strategy in the feedback environment that it gives rise to. By assuming a steady-state population size structure, the ESS allocation strategy can be found by maximizing the lifetime reproductive success without explicit simulation of population dynamics.

organ or a full reaction norm specifying phenotypically plastic allocation responses to a continuum of environmental situations.

Due to the importance of plasticity for C allocation of trees, it may be desirable to model the potentially complex interplay between evolutionary and plastic changes in allocation. Such a separation is feasible in AD models, by evolving a multivariate reaction norm for allocation that accounts for the key environmental factors influencing allocation plasticity (e.g., by following the approach of Ernande and Dieckmann 2004). However, perhaps due to the daunting complexity of such an allocation model, to our knowledge this possibility has not yet been pursued.

The only AD model of forest allocation that to our knowledge has been published (Dybzinski et al. 2011; Figure 5) does not differentiate between effects of evolution, community composition and plasticity on allocation. Instead, this model demonstrates how an AD model can be simplified based on an equilibrium assumption for the population size and age structure and simplification of height-structured competition based on the perfect-plasticity approximation for the spatial arrangement of tree crowns (Strigul et al. 2008). These simplifications allow results to be derived without a need for explicitly modeling the interactions among individuals or size classes. Consequently, the model yields tractable solutions, despite its basis in AD. The results of this model point to the importance of competition for root allocation and its trade-off with wood allocation (Figure 6), in line with the results by King (1993) and the GTO model presented above. More generally, the derived patterns of allocation to leaves, roots and stem are consistent with a meta-analysis of forest allocation (Litton et al. 2007) and with predictions resulting from an OR model (Franklin et al. 2009). Interestingly, the AD basis of Dybzinski et al.'s (2011) model, and its representation of height-structured competition, allowed a novel interpretation of the transition from closed-canopy to open-canopy forests as a result of increasing soil N limitation reducing the ESS for canopy height and leaf area index.

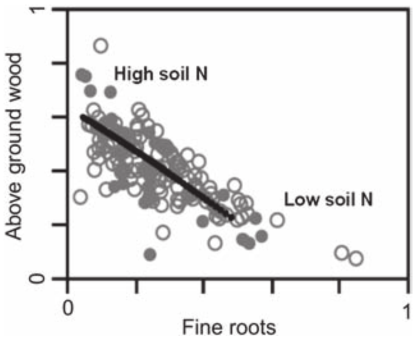

Figure 6. Fraction of NPP allocated to wood versus fine roots predicted by the Dybzinski et al. (2011) model compared with measured data. The model predictions are ESSs across a gradient from low to high soil N availability (black line). Circles represent data from the publicly available FLUXNET database (Luyssaert et al. 2007). Stands represented by open circles are dominated by gymnosperms, whereas those represented by filled circles are dominated by angiosperms.

## A statistical view of plant behavior: entropy-based approaches

The hypothesis of maximum entropy production (MEP) offers a novel thermodynamic perspective on plant behavior. Viewed from this perspective, living systems are examples of a wider class of far-from-equilibrium dissipative structures—which include non-living systems such as the Earth's climate—that import free energy from their environment and export it in a higher entropy (lower free energy) form. According to MEP, when subjected to given constraints (both external and internal), these systems will organize themselves into steady states that maximize the rate of increase in the entropy of their environment.

While MEP has made successful predictions of, for example, planetary climates, fluid turbulence, crystal growth morphology and biological design (Dewar et al. 2006, Martyushev and Seleznev 2006, Kleidon et al. 2010), its theoretical basis remains unclear. However, one proposed statistical interpretation of MEP is that it describes the most probable steady state of complex, non-equilibrium systems under a given set of constraints (e.g., Dewar 2009), in the same sense that the bulk properties of matter in equilibrium are those which can be realized microscopically in the greatest number of ways (corresponding to a state of maximum entropy). In its application to biological systems, MEP then replaces 'survival of the fittest' with 'survival of the likeliest'.

Dewar (2010) showed how various goal functions traditionally used as proxies for fitness in OR models applied at different levels (leaf, canopy, whole plant) can be replaced by chemical entropy production on different timescales and levels of organization. Thus MEP resembles an OR approach in which the goal function (fitness proxy) is replaced by entropy production in the part of the system that is assumed to be in steady state at the timescale of interest. Maximum entropy production can also replace the goal function in a GTO model (e.g., in the model used in our OR–GTO comparison example above; see Figure 1f).

In a forest stand, chemical entropy production (i.e., free energy dissipation) occurs as high free energy chemical species (e.g., photosynthates) are converted to lower free energy forms (e.g., $CO_2$). The entropy production depends on the boundaries of the system that is assumed to be in steady state, the fluxes of matter across the system boundaries, and the chemical potentials associated with those fluxes. In its application to King's (1993) model of a forest stand, foliage and fine-root dry matter are assumed to be in a steady state (Figure B1). Appendix B shows how the rate of entropy production is calculated for this system. The resulting entropy production (Eq. (B3)) depends on the relative differences among the chemical potentials of the chemical species (photosynthates, dry matter and $CO_2$) crossing the system boundary. A qualitative analysis of realistic ranges for these chemical potentials (Appendix B) suggests that MEP would predict optimal root allocation values intermediate between those from maximization of wood growth and NPP maximization (Figure 7). The results in Figure 7, and the more general agreement between allocation predictions by MEP and OR models (Dewar 2010), suggest that entropy production represents a biologically realistic goal function for OR models (under the relevant steady-state condition), and one that may be derived on more objective grounds than some of the fitness proxies currently in use.

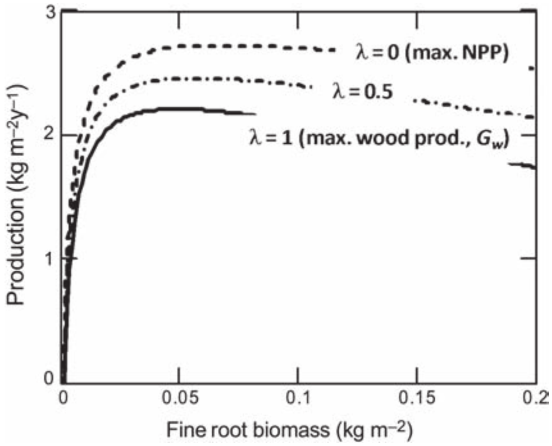

Figure 7. Rescaled entropy production (σ, Appendix B) versus fine-root biomass for three values of λ, a dimensionless number (given by Eq. (B4)) that depends on the chemical potentials of photosynthate, dry matter and $CO_2$. σ has been scaled to the same units as dry matter production (kg m$^{-2}$ year$^{-1}$; see Eq. (B5)). For $0 < \lambda < 1$, maximum entropy production predicts optimal fine-root biomass and production values that are intermediate between those predicted by the maximization of total production (NPP, case $\lambda = 0$) and maximization of wood production ($G_w$, case $\lambda = 1$). The plots were generated using the forest stand model and parameter values of King (1993).

The statistical interpretation of MEP as the most probable behavior under given constraints has its basis in another, more fundamental entropy-based concept—maximum entropy, or MaxEnt (Jaynes 1957, Dewar 2009)—which provides a common theoretical framework for both equilibrium and non-equilibrium behavior. MaxEnt has been used to unify other ecological patterns, such as species abundance patterns and self-thinning (Pueyo et al. 2007, Dewar and Porte 2008, Harte 2011). MaxEnt predicts not only the most probable plant behavior (e.g., MEP) under given environmental and internal constraints, but also the frequency distribution of different ecological or physiological strategies (e.g., allocation patterns) about the most probable strategy. In fact, MaxEnt predicts the most spread-out frequency distribution, thus accounting for the observed coexistence of many different strategies within a given environment, among which the most probable one is dominant.

The practical importance of entropy-based approaches (MEP and MaxEnt)—like OR approaches—lies in their potential to make realistic predictions of plant behavior and ecological patterns directly from a tractably reduced number of environmental and internal constraints, without the need to simulate the underlying population dynamics in great detail. Potentially therefore, MEP and MaxEnt models are much less computationally demanding than more detailed approaches based on modeling population dynamics, such as AD. But if

MEP and MaxEnt do not explicitly represent the underlying processes and feedbacks driving evolution (such as competition) in all their detail, then why (and when) can we expect it to give reasonable predictions for strategies (such as allocation) that are the result of evolution?

The answer requires a fuller appreciation of what MaxEnt is (and is not). In view of its basis in information theory, MaxEnt is not really a dynamical principle (e.g., like Newton's law of gravity) but rather an inference method for making predictions based only on the information represented by the given set of constraints (environmental and internal), and nothing else (Dewar 2009). The fact that MaxEnt and MEP do indeed appear to make reasonable predictions using only a few constraints—e.g., without simulating the dynamics of individual birth, growth, competition and reproduction in all its detail—suggests that those dynamic details that were not included in the constraint set are largely governed by stochastic rather than deterministic dynamics, and their effects average out, i.e., they represent irrelevant information. Therefore, the predictive success of MaxEnt depends entirely on whether we have put in the relevant environmental and (deterministic) internal constraints (e.g., what part of the tree or forest is in steady state). Disagreement with observations signals a missing constraint, such as significant underlying adaptive (deterministic) dynamics.

The underlying stochasticity which underpins the success of MaxEnt and MEP contrasts with evolution-based models, where the interactions and dynamics are often assumed to be sufficiently deterministic, and the environment sufficiently predictable, for one or a few distinct ESSs to crystallize. However, MaxEnt and MEP do not deny the existence and relevance of adaptive evolution. It appears that some dynamic deterministic details (e.g., competition for light, as discussed above) at the individual scale are indeed necessary to explain observed allocation patterns at the stand scale. Comparing an entropy-based approach with observations constitutes an efficient method of exposing those features of the individual population dynamics that are relevant at the community scale. In addition, further insights into the interplay and relative importance of adaptive and stochastic evolutionary processes can be obtained by combining these two aspects of evolution in the same model (Iwasa 1988, Barton and Coe 2009).

In summary, the potential of MEP and MaxEnt for improving computational efficiency in predictive models, for averaging out stochasticity and for explaining the coexistence of many strategies (i.e., biodiversity) implies that the use of entropy-based approaches in forest modeling is worth exploring further. In particular, further elaboration of the strengths and limitations of MEP and MaxEnt in relation to evolution-based approaches would be valuable for guiding future forest model development.

## What is the best way to model allocation?

Of the approaches discussed in this study, in an evolutionary perspective, AD constitutes the most theoretically comprehensive basis for predicting allocation. However, the overall accuracy of a forest model depends not only on the representation of the fundamental underlying principle—e.g., if allocation is predicted via AD or by maximization of a fitness proxy—but also on how well the physiological mechanisms and population dynamics are described. There is always a practical limitation to the complexity of a model, due to computational costs, or in order to keep the model behavior transparent, or due to accumulation of uncertainty with increasing number of parameters. Thus, when selecting the controlling principle of a model, not only its theoretical accuracy matters but also the complexity it induces and whether it allows for sufficient matching complexity in other parts of the model. Balancing the complexities of different parts in forest models may result in a tendency to a trade-off between the complexity of the controlling principle and the complexity of the reaction norm. For example, the trait-evolution model by Falster et al. (2011) addresses evolution rather explicitly based on AD, whereas allocation is determined by allometric scaling (only size dependent). In contrast, the steady-state forest OR model by Mäkelä et al. (2008) employs maximization of stand productivity (NPP as fitness proxy) as a simple controlling principle while allocation to stem, foliage and roots are all responsive to soil N availability (multivariate reaction norm). The contrasting priorities in the partitioning of complexity between these two models reflects the divergent research questions they address, i.e., the short-term plastic allocation responses of existing individuals versus the very much longer-term process of trait evolution. Thus, ultimately the research question and timescale addressed determine which allocation modeling approach is preferable.

## Model testing and improvement

### *From model tuning to scientific progress*

Although we have suggested some guidelines for identifying approaches that are appropriate to predict allocation for different purposes, it is evident that more research is warranted to further increase an understanding of allocation and how it can best be modeled. For a given research question, evaluation of alternative approaches or variants of the same basic methods leads to more scientific progress than testing of a single model (Hobbs and Hilborn 2006). For example, in the majority of plant and forest OR-based modeling studies, the consequences of a single fitness proxy were tested against empirical data and success was declared because the correspondence ($r^2$) between modeled and measured data was reasonable. While these studies represent substantial progress in terms of conceptual development, physiological parameters and numerical predictions of plant behavior, they rarely quantify the scientific progress in terms of the value of the particular controlling principle (e.g., OR or GTO) applied. The problem is that different principles (e.g., fitness proxies) often give very similar results (Anten and During 2011) and a different principle might be better than the one tested. Thus, to yield quantifiable and conclusive progress in terms of improving the controlling principles in allocation models, alternative hypotheses (e.g., fitness proxies or evolving traits) should be compared for a given research question and dataset.

However, comparison of alternative models may be complicated by differences in model complexity and the number and interdependencies of the parameters estimated. For example, increasing the number of free parameters increases wiggle room and improves the model fit to data ($r^2$), but it does not necessarily mean that the model's predictive power has increased. Instead, alternative models can be compared using methods that are independent of model differences in the number of parameters and the model structure, such as cross validation (e.g., Hastie et al. 2001). However, even the parameter estimation of a single forest allocation model can be a challenge due to model complexity. Often it is difficult to find a unique set of best-fit parameters using common parameter-optimization algorithms because the prediction error function (e.g., least squares error) has multiple local minima. Bayesian calibration is a method that suffers less from this problem, while also providing a range of useful measures regarding the model parameters, including probability distributions and correlation coefficients between parameters (Van Oijen et al. 2005). In addition to alternative hypotheses and statistical evaluation methods, comprehensive empirical data are obviously essential for model improvement, as discussed in the next section.

### *What empirical data do allocation modelers need?*

Empirical data and experiments are critical to the development of allocation models in at least three interrelated ways. First, empirical information provides a window into the relationships, mechanisms and trade-offs that are to be described mathematically in an allocation model. Second, empirical information provides the data to numerically parameterize an allocation model, which is necessary both to make quantitative predictions and to understand the implications of models not amenable to analytical solution. Third, empirical information provides the data with which to test those quantitative predictions. In a make-believe world of unlimited resources for research, allocation models would benefit from empirical information that is simultaneously comprehensive (covering all of the parameters and relationships relevant to allocation), accurate (replication sufficient to ensure that sample distributions match the true population distributions) and general (measuring all the species and habitats where an allocation model is expected to be relevant). But in the real world, empiricists must necessarily balance and compromise the degree to which the data they collect are comprehensive, accurate and general. Below, we discuss the advantages and disadvantages of these compromises for the purpose of improving allocation models.

At one extreme, empiricists may study a single site comprehensively and accurately, as has happened in the relatively small number of FACE sites (Ainsworth and Long 2005). From the empiricists' perspective, the high cost and obvious relevance of FACE experiments merit their close scrutiny, and many researchers are drawn to the sites and thus contribute a large volume of site-specific data to the literature. Mechanistic allocation models, which often include parameters that are seldom measured at other sites (e.g., effects of elevated $CO_2$ on allocation and photosynthesis), can benefit from this abundance of data. Not only are the rarely measured parameters and processes accounted for, but they are linked to the more commonly measured parameters and processes, which gives the modeler confidence in the coherence in the complete set of parameters. For example, Franklin et al. (2009) used comprehensive data from two closed-canopy forest FACE sites to inform, parameterize and test an optimization (OR) model that predicted the differing allocation responses to $CO_2$ and fertilization observed in the experiments. The potential drawback to using comprehensive data from a small number of sites with an allocation model is no different than the potential drawback of using such data in a strictly empirical study: it is possible that the site or sites are a poor representation of the population (e.g., the world's forests) and thus that the lessons learned may not generalize. Of course, in the case of costly FACE experiments, this potential drawback is unavoidable, but should be kept in mind nevertheless.

At the other extreme, empiricists may spread their research efforts out across many sites, potentially sacrificing comprehensiveness and site-specific accuracy at the altar of generality. For example, a large subset of the global FLUXNET network of eddy covariance towers measures forest carbon allocation to foliage, wood and fine roots (Jung et al. 2007), the three most basic pools of carbon in allocation models. With an AD allocation model parameterized from other sources, Dybzinski et al. (2011) tested model predictions against this general dataset. While illuminating, such large and general datasets suffer from a lack of certain key parameters. Most obviously, measuring resource availabilities (e.g., light, nitrogen, phosphorus and water), which are often the most important drivers in allocation models, would make such datasets much more valuable for allocation modelers. The potential drawback to using large-scale data with an allocation model is no different than the potential drawback of using such data in a strictly empirical study: the presence of unaccounted-for confounding variables may obscure or, worse, reverse mechanistic trends at smaller scales (e.g., Simpson's paradox; Simpson 1951).

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## References

Ainsworth, E.A. and S.P. Long. 2005. What have we learned from 15 years of Free-Air $CO_2$ Enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising $CO_2$. New Phytol. 165:351–371.

Anten, N.P.R. and H.J. During. 2011. Is analysing the nitrogen use at the plant canopy level a matter of choosing the right optimization criterion? Oecologia 167:293–303.

Barton, N.H. and J.B. Coe. 2009. On the application of statistical physics to evolutionary biology. J. Theor. Biol. 259:317–324.

Cannell, M.G.R. and R.C. Dewar. 1994. Carbon allocation in trees: a review of concepts for modelling. Adv. Ecol. Res. 25:59–104.

Casper, B.B. and R.B. Jackson. 1997. Plant competition underground. Annu. Rev. Ecol. Syst. 28:545–570.

Chen, J.L. and J.F. Reynolds. 1997. A coordination model of whole-plant carbon allocation in relation to water stress. Ann. Bot. 80:45–55.

Craine, J.M. 2006. Competition for nutrients and optimal root allocation. Plant Soil 285:171–185.

Davidson, R.L. 1969. Effects of soil nutrients and moisture on root/shoot ratios in *Lolium perenne* L. and *Trifolium repens* L. Ann. Bot. 33:571–577.

Dewar, R.C. 2009. Maximum entropy production as an inference algorithm that translates physical assumptions into macroscopic predictions: don't shoot the messenger. Entropy 11:931–944.

Dewar, R.C. 2010. Maximum entropy production and plant optimization theories. Philos. Trans. R. Soc. Lond. B Biol. Sci. 365:1429–1435.

Dewar, R.C. and A. Porte. 2008. Statistical mechanics unifies different ecological patterns. J. Theor. Biol. 251:389–403.

Dewar, R.C., D. Juretić and P. Županović. 2006. The functional design of the rotary enzyme ATP synthase is consistent with maximum entropy production. Chem. Phys. Lett. 430:177–182.

Dewar, R.C., O. Franklin, A. Mäkelä, R.E. McMurtrie and H.T. Valentine. 2009. Optimal function explains forest responses to global change. Bioscience 59:127–139.

Dieckmann, U. and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. J. Math. Biol. 34:579–612.

Dybzinski, R., C. Farrior, A. Wolf, P.B. Reich and S.W. Pacala. 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. Am. Nat. 177:153–166.

Ernande, B. and U. Dieckmann. 2004. The evolution of phenotypic plasticity in spatially structured environments: implications of intraspecific competition, plasticity costs and environmental characteristics. J. Evol. Biol. 17:613–628.

Falster, D.S. and M. Westoby. 2003. Plant height and evolutionary games. Trends Ecol. Evol. 18:337–343.

Falster, D.S., Å. Brännström, U. Dieckmann and M. Westoby. 2011. Influence of four major plant traits on average height, leaf-area cover, net primary productivity, and biomass density in single-species forests: a theoretical investigation. J. Ecol. 99:148–164.

Franklin, O. 2007. Optimal nitrogen allocation controls tree responses to elevated $CO_2$. New Phytol. 174:811–822.

Franklin, O. and G.I. Ågren. 2002. Leaf senescence and resorption as mechanisms of maximizing photosynthetic production during canopy development at N limitation. Funct. Ecol. 16:727–733.

Franklin, O., R.E. McMurtrie, C.M. Iversen, K.Y. Crous, A.C. Finzi, D.T. Tissue, D.S. Ellsworth, R. Oren and R.J. Norby. 2009. Forest fine-root production and nitrogen use under elevated $CO_2$: contrasting responses in evergreen and deciduous trees explained by a common principle. Glob. Change Biol. 15:132–144.

Geritz, S.A.H., J.A.J. Metz, É. Kisdi and G. Meszéna. 1997. Dynamics of adaptation and evolutionary branching. Phys. Rev. Lett. 78:2024–2027.

Geritz, S.A.H., É. Kisdi, G. Meszéna and J.A.J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evol. Ecol. 12:35–57.

Gersani, M., J.S. Brown, E.E. O'Brien, G.M. Maina and Z. Abramsky. 2001. Tragedy of the commons as a result of root competition. J. Ecol. 89:660–669.

Gower, S.T., S. Pongracic and J.J. Landsberg. 1996. A global trend in belowground carbon allocation: can we use the relationship at smaller scales? Ecology 77:1750–1755.

Grace, J.B. 1995. On the measurement of plant competition intensity. Ecology 76:305–308.

Harte, J. 2011. Maximum entropy and ecology: a theory of abundance, distribution, and energetics. Oxford University Press, Oxford.

Hastie, T., R. Tibshirani and J. Friedman. 2001. The elements of statistical learning. Data mining, inference, and prediction. Springer, New York.

Heino, M., J.A.J. Metz and V. Kaitala. 1998. The enigma of frequency-dependent selection. Trends Ecol. Evol. 13:367–370.

Hobbs, N.T. and R. Hilborn. 2006. Alternatives to statistical hypothesis testing in ecology: a guide to self teaching. Ecol. Appl. 16:5–19.

Ise, T., C.M. Litton, C.P. Giardina and A. Ito. 2010. Comparison of modeling approaches for carbon partitioning: impact on estimates of global net primary production and equilibrium biomass of woody vegetation from MODIS GPP. J. Geophys. Res. G Biogeosci. 115. G04025, doi:10.1029/2010JG001326.

Iversen, C.M., J. Ledford and R.J. Norby. 2008. $CO_2$ enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. New Phytol. 179:837–847.

Iwasa, Y. 1988. Free fitness that always increases in evolution. J. Theor. Biol. 135:265–281.

Jaynes, E.T. 1957. Information theory and statistical mechanics. Phys. Rev. 106:620–630.

Jung, M., G. Le Maire, S. Zaehle, S. Luyssaert, M. Vetter, G. Churkina, P. Ciais, N. Viovy and M. Reichstein. 2007. Assessing the ability of three land ecosystem models to simulate gross carbon uptake of forests from boreal to Mediterranean climate in Europe. Biogeosci. Discuss. 4:1353–1375.

King, D.A. 1990. The adaptive significance of tree height. Am. Nat. 135:809–828.

King, D.A. 1993. A model analysis of the influence of root and foliage allocation on forest production and competition between trees. Tree Physiol. 12:119–135.

Kleidon, A., Y. Malhi and P.M.E. Cox. 2010. Maximum entropy production in ecological and environmental systems: applications and implications. Philos. Trans. R. Soc. Lond. B Biol. Sci. (Theme Issue) 365:1295–1455.

Kummel, M. and S.W. Salant. 2006. The economics of mutualisms: optimal utilization of mycorrhizal mutualistic partners by plants. Ecology 87:892–902.

Lacointe, A. 2000. Carbon allocation among tree organs: a review of basic processes and representation in functional-structural tree models. Ann. For. Sci. 57:521–533.

Landsberg, J.J. 2003. Modelling forest ecosystems: state of the art, challenges, and future directions. Can. J. For. Res. 33:385–397.

Landsberg, J.J. and R.H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manag. 95:209–228.

Le Roux, X., A. Lacointe, A. Escobar-Gutiérrez and S. Le Dizès. 2001. Carbon-based models of individual tree growth: a critical appraisal. Ann. For. Sci. 58:469–506.

Litton, C.M., J.W. Raich and M.G. Ryan. 2007. Carbon allocation in forest ecosystems. Glob. Change Biol. 13:2089–2109.

Luyssaert, S., I. Inglima, M. Jung, et al. 2007. $CO_2$ balance of boreal, temperate, and tropical forests derived from a global database. Glob. Change Biol. 13:2509–2537.

Mäkelä, A. 1985. Differential games in evolutionary theory: height growth strategies of trees. Theor. Popul. Biol. 27:239–267.

Mäkelä, A., H.T. Valentine and H.-S. Helmisaari. 2008. Optimal co-allocation of carbon and nitrogen in a forest stand at steady state. New Phytol. 180:114–123.

Martyushev, L.M. and V.D. Seleznev. 2006. Maximum entropy production principle in physics, chemistry and biology. Phys. Rep. 426:1–45.

McCarthy, M.C. and B.J. Enquist. 2007. Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. Funct. Ecol. 21:713–720.

McGill, B.J. and J.S. Brown. 2007. Evolutionary game theory and adaptive dynamics of continuous traits. Annu. Rev. Ecol. Evol. Syst. 38:403–435.

McMurtrie, R.E. and R.C. Dewar. 2011. Leaf-trait variation explained by the hypothesis that plants maximize their canopy carbon export over the lifespan of leaves. Tree Physiol. 31:1007–1023.

McMurtrie, R.E., R.J. Norby, B.E. Medlyn, R.C. Dewar, D.A. Pepper, P.B. Reich and C.V.M. Barton. 2008. Why is plant-growth response to elevated $CO_2$ amplified when water is limiting, but reduced when nitrogen is limiting? A growth-optimisation hypothesis. Funct. Plant Biol. 35:521–534.

Meszéna, G., É. Kisdi, U. Dieckmann, S.A.H. Geritz and J.A.J. Metz. 2001. Evolutionary optimisation models and matrix games in the unified perspective of adaptive dynamics. Selection 2:193–210.

Metz, J.A.J., S.A.H. Geritz, G. Meszéna, F.J.A. Jacobs and J.S. Van Heerwaarden. 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. *In* Stochastic and Spatial Structures of Dynamical Systems. Eds. S.J. Van Strien and S.M. Verduyn Lunel. North-Holland, Amsterdam, pp 183–231.

Montgomery, R.A., P.B. Reich and B.J. Palik. 2010. Untangling positive and negative biotic interactions: views from above and below ground in a forest ecosystem. Ecology 91:3641–3655.

O'Brien, E.E. and J.S. Brown. 2008. Games roots play: effects of soil volume and nutrients. J. Ecol. 96:438–446.

Ostle, N.J., P. Smith, R. Fisher, *et al.* 2009. Integrating plant-soil interactions into global carbon cycle models. J. Ecol. 97:851–863.

Perrin, N. 1992. Optimal resource allocation and the marginal value of organs. Am. Nat. 139:1344–1369.

Pueyo, S., F. He and T. Zillio. 2007. The maximum entropy formalism and the idiosyncratic theory of biodiversity. Ecol. Lett. 10:1017–1028.

Purves, D. and S. Pacala. 2008. Predictive models of forest dynamics. Science 320:1452–1453.

Reynolds, J.F. and J. Chen. 1996. Modelling whole-plant allocation in relation to carbon and nitrogen supply: coordination versus optimization: opinion. Plant Soil 185:65–74.

Scheiter, S. and S.I. Higgins. 2009. Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach. Glob. Change Biol. 15:2224–2246.

Schymanski, S.J. 2008. Optimality as a concept to understand and model vegetation at different scales. Geogr. Compass 2:1580–1598.

Shinozaki, K.Y., K. Hozumi and T. Kira. 1964. A quantitative analysis of plant form—the pipe model theory. I. Basic analyses. Jpn. J. Ecol. 14:97–104.

Simpson, E.H. 1951. The interpretation of interaction in contingency tables. J. R. Stat. Soc. B (Methodol.). 13:238–241.

Strigul, N., D. Pristinski, D. Purves, J. Dushoff and S. Pacala. 2008. Scaling from trees to forests: tractable macroscopic equations for forest dynamics. Ecol. Monogr. 78:523–545.

van Kuijk, M. and N.P.R. Anten. 2009. Whole-canopy nitrogen-use efficiency of pioneer species in early secondary forest succession in Vietnam. Ecol. Res. 24:811–820.

Van Oijen, M., J. Rougier and R. Smith. 2005. Bayesian calibration of process-based forest models: bridging the gap between models and data. Tree Physiol. 25:915–927.

Vincent, T.L. and H.R. Pulliam. 1980. Evolution of life history strategies for an asexual annual plant model. Theor. Popul. Biol. 17:215–231.

West, G.B., B.J. Enquist and J.H. Brown. 2009. A general quantitative theory of forest structure and dynamics. Proc. Natl Acad. Sci. USA 106:7040–7045.

## Appendix A: Allocation model addressing the effect of root competition

This model is used to evaluate the effect of root competition for soil nitrogen (N) on the allocation to roots (fine roots), foliage and wood. No novel concepts or assumptions are used in the model; it is based on elements from the models by King (1993) and Franklin et al. (2009). We adopt the common assumption in these models that the trees adjust allocation to maximize wood production (for trees with yet insignificant reproductive production). The representation of root competition is based on the model by King (1993) while the soil N uptake function and parameters are taken from Franklin et al. (2009). In order to focus on the effects of root competition and improve tractability, we use a simpler equation for carbon (C) assimilation than in the models by King (1993) and Franklin et al. (2009).

### *Nitrogen uptake by roots*

Net N uptake (*U*, Eq. (A1)) is assumed to be a function of fine-root production (*R*), half-saturation *R* (*d*, assumed proportional to soil depth, i.e., effective soil depth usable for root N uptake), N : C ratio of roots ($c_R$) and soil N availability ($N_{av}$ = N uptake per *R* at a small *R*; Franklin et al. 2009):

$$U = \frac{N_{av}R}{(R / d) + 1} - c_R R \tag{A1}$$

*R* includes all C use by the roots (growth, respiration and exudation). Competitive interaction as modeled in King (1993) implies that $R$ of one focal individual ($R_i$) can change independently of its competitors' $R$ ($R_o$). The mean $R$ for a total of $n$ competing individuals then becomes

$$R = \frac{(n-1)R_o + R_i}{n} \tag{A2}$$

The N uptake of a focal individual under competition ($U_i$, Eq. (A3)) is given by inserting Eq. (A2) in Eq. (A1) and multiplying by the fraction root production of the focal individual relative to total root production:

$$U_i = \frac{N_{av} R_i}{((R_o(n-1) + R_i) / n d) + 1} - c_R R \tag{A3}$$

We derived a measure of the intensity of root competition (RCI, Eq. (A4)) as the relative difference in marginal uptake per $R$ between the competitive model (Eq. (A3)) and the non-competitive model (Eq. (A1)) for $U$:

$$\mathrm{RCI} = \frac{(\partial U_i / \partial R_i) - (\mathrm{d}U / \mathrm{d}R)}{(\mathrm{d}U / \mathrm{d}R)} \tag{A4}$$

### *Carbon assimilation by the canopy*

Net canopy C uptake (NCP = canopy photosynthesis − canopy respiration, Eq. (A5)) is a function of effective C availability ($C_{av}$) and canopy $N$ ($N_c$), which is proportional to both photosynthetic capacity and maintenance respiration ($r N_c$, Franklin et al. 2009):

$$\mathrm{NCP} = \frac{C_{av} N_c}{N_c + k_c} - r N_c \tag{A5}$$

In Eq. (A5), $k_c$ is the half-saturation $N_c$ of NCP. $C_{av}$ does not correspond to any particular $CO_2$ concentration but represents the total effect of the different factors controlling C assimilation efficiency of the photosynthetic machinery ($N_c$), i.e., atmospheric [$CO_2$], photosynthetically active radiation and stomatal conductance.

### *Carbon and nitrogen balance of growth*

The carbon balance of the trees (Eq. (A5)) implies that the total C used for net wood growth ($G$), foliage turnover ($N_c/(t_c c_c)$) and root production equals NCP:

$$G + \frac{N_c}{t_c c_c} + R = \mathrm{NCP} = \frac{C_{av} N_c}{N_c + k_c} - r N_c \tag{A6}$$

In Eq. (A6), $t_c$ is leaf lifespan.

The nitrogen balance of the trees is

$$G c_G + \frac{N_c}{t_c} + R c_R = U \tag{A7}$$

In Eq. (A7), $c_G$ is the N : C ratio of wood.

Net wood growth ($G$) as a function of $R$, $N_{av}$ and $C_{av}$ is derived numerically by using Eqs (A6) and (A7) to eliminate $N_c$ and solving for $G$. In this derivation, $U$ is replaced by Eq. (A1) or Eq. (A3) to model $G$ of non-competing roots $G(R, C_{av}, N_{av})$ or competing roots $G(R_i, R_o, C_{av}, N_{av})$, respectively.

### *Optimal allocation*

Following King (1993) and Franklin et al. (2009), allocation is optimized to maximize $G$. In this model $G$ is maximized by optimization of root allocation ($R$), while allocation to wood ($G$) and foliage are functions of $R$. The optimal $R$ with and without root competition is derived by numerically solving the below equations (Eqs. (A8) and (A9)) for $R$:

$$\frac{\partial G(R_i, R_o, C_{av}, N_{av})}{\partial R_i} = 0, \quad R_o = R_i \tag{A8}$$

$$\frac{\partial G(R, C_{av}, N_{av})}{\partial R} = 0 \tag{A9}$$

Equation (A8) means that the optimization (differentiation) of $R$ for each tree is made individually, i.e., with respect to root production of a focal tree ($R_i$) and not the competing trees ($R_o$). At the same time, all trees behave in the same way, i.e., Eq. (A8) is then solved for $R = R_i = R_o$.

### *Parameters*

Parameter values (Table A1) are representative of the results in Franklin et al. (2009), i.e., a young even-aged sweetgum forest.

## Appendix B: Entropy production of a forest stand described by the King (1993) model

Entropy production (i.e., free energy dissipation) occurs within the steady-state subsystem enclosed by the dashed box in Figure B1, as high free energy chemical species (e.g., photosynthates) are converted to lower free energy forms (e.g., $CO_2$). In the steady state, the rate of entropy production within the dashed box is equal to the rate of entropy export ($\sigma$, J $K^{-1}$ $m^{-2}$ $year^{-1}$) across the boundary, given by, e.g., Dewar (2010):

$$\sigma = \frac{P\mu_P - R\mu_R - G_W\mu_W - (L_f + L_r)\mu_L}{T} \tag{B1}$$

where $T$ (K) is the temperature, assumed uniform on the boundary (other symbols are defined in the legend of Figure B1). In Eq. (B1) each boundary flux $F$ contributes an entropy export equal to $F$ multiplied by $-\mu/T$, where $F$ is defined as positive in the outward direction and $\mu$ is the chemical potential of the corresponding chemical species. Since foliage and fine roots are assumed to be in a steady state, we have

Table A1. Symbols and parameters.

| Symbol | Value | Unit | Description |
|---|---|---|---|
| *Variables* | | | |
| $C_{av}$ | | g C m$^{-2}$ year$^{-1}$ | Effective C availability, equal to NCP at saturating $N_c$ |
| $G$ | | g C m$^{-2}$ year$^{-1}$ | Net wood production |
| $N_{av}$ | | g N gC$^{-1}$ year$^{-1}$ | Soil N availability, defined as N uptake per $R$ for small $R$ |
| $N_c$ | | g N m$^{-2}$ | Canopy N |
| NCP | | g C m$^{-2}$ year$^{-1}$ | Net canopy C uptake |
| $R$, $R_i$, $R_o$ | | g C m$^{-2}$ year$^{-1}$ | Fine-root production of a mean tree, a focal tree among competitors and competitors, respectively |
| RCI | | – | Relative competition intensity |
| $U$, $Ui$ | | g N m$^{-2}$ year$^{-1}$ | N uptake of a mean tree and a focal tree among competitors, respectively |
| *Parameters* | | | |
| $c_c$, $c_G$, $c_R$ | 0.03, 0.003, 0.02 | g N g C$^{-1}$ | N : C ratio of foliage, wood and fine roots, respectively |
| $D$ | 450, 100 | g C m$^{-2}$ year$^{-1}$ | Half saturation $R$ as observed in Franklin et al. (2009) and for a smaller soil depth, respectively |
| $k_c$ | 4 | g N m$^{-2}$ | Half saturation canopy N |
| $N$ | 5 | – | Number of trees competing for soil N |
| $R$ | 30 | g C g N$^{-1}$ year$^{-1}$ | Respiration rate per N |
| $t_c$, $t_r$ | 1, 1 | $Y$ | Lifespan of foliage and fine roots, respectively |

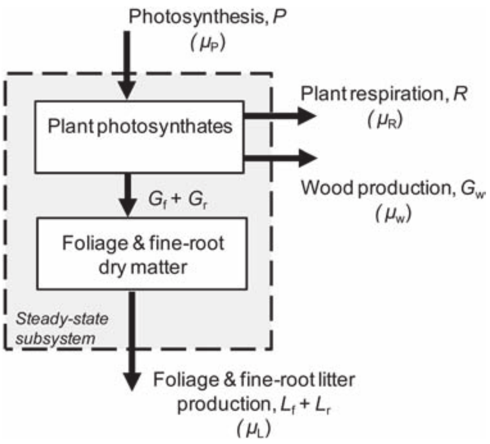

Figure B1. Entropy balance of a forest stand in which photosynthates, foliage and fine root dry matter are in a steady state, as assumed in King (1993). The dashed box indicates the steady-state subsystem. $P$, gross canopy photosynthesis; $R$, respiration for plant maintenance and dry matter growth (including wood); $G_i$, dry matter production of compartment $i$; $L_i$, litter production of compartment $i$. Following King (1993), all fluxes are in kg DM m$^{-2}$ year$^{-1}$ (DM = dry matter equivalent). For boundary fluxes, the associated chemical potentials ($\mu_i$, J kg$^{-1}$) are indicated in parentheses: $\mu_P$ (leaf photosynthate), $\mu_W$ (photosynthate at sites of wood growth), $\mu_R$ (respired CO$_2$), $\mu_L$ (foliage and fine root dry matter). Entropy production (i.e. free energy dissipation) occurs as high free energy chemical species (e.g. photosynthates) are converted to lower free energy forms (e.g. CO$_2$). The rate of entropy production within the dashed box (equal to the rate of entropy export across the boundary) is given by Eq. B1; each *outward-directed* boundary flux $F$ contributes a term $F \cdot (-\mu/T)$ where $T$ is temperature.

$G_f + G_r = L_f + L_r$ so that wood productivity is $G_W = \text{NPP} - G_f - G_r = \text{NPP} - L_f - L_r$, where NPP is total dry matter productivity. Also if we assume a fixed carbon-use efficiency $\beta$, then $P = \text{NPP} / \beta$ and $R = \text{NPP}\,(1-\beta)/\beta$. Substituting these expressions into Eq. (B1) then gives

$$T\sigma = \text{NPP}\left\{\frac{\mu_P - (1-\beta)\mu_R}{\beta} - \mu_W\right\} - (L_f + L_r)(\mu_L - \mu_W) \quad \text{(B2)}$$

If we now make the simplifying assumption that all chemical potentials and the temperature $T$ are constant in time, then Eq. (B2) implies

$$\sigma \propto \text{NPP} - \lambda(L_f + L_r) \quad \text{(B3)}$$

where

$$\lambda = \frac{\beta(\mu_L - \mu_W)}{\mu_P - (1-\beta)\mu_R - \beta\mu_W} \quad \text{(B4)}$$

is a dimensionless constant. Note that shifting each $\mu_i$ by a constant amount in Eq. (B1) does not affect $\sigma$ in the steady state, since $P - R - G_W - L_f - L_r = 0$. Therefore, we can rewrite Eq. (B4) more simply as

$$\lambda = \frac{\beta(\mu_L - \mu_W)}{\mu_P - \beta\mu_W} \quad \text{(B5)}$$

where the chemical potentials are now measured relative to $\mu_R$.

The value of $\lambda$ is a dimensionless constant that depends on the chemical potentials (Gibbs free energy, J kg$^{-1}$) of foliage and fine-root litter ($\mu_L$), of leaf (source) photosynthate ($\mu_P$) and of photosynthate near the (sink) sites of wood growth ($\mu_W$). $\mu_W$ here is the chemical potential of sink photosynthate rather than of newly synthesized wood biomass, because in Figure B1 it corresponds to matter that is physically transported across the system boundary (i.e., photosynthate) rather than to wood biomass at the sites of wood production. The latter sites lie just outside the system boundary because wood biomass is not assumed to be in a steady state.

For $\lambda = 0$ and $\lambda = 1$, $\sigma$ is proportional to NPP and $\text{NPP} - L_f - L_r = G_W$, respectively; for these two cases, therefore, MEP is equivalent to maximizing total productivity (NPP) and wood productivity ($G_W$), since foliage and fine-root dry matter are assumed to be in a steady state so that $L_f + L_r$ balances foliage and fine-root productivity. Thus, over the range $0 < \lambda < 1$, MEP predicts optimal behavior that is intermediate between max-NPP and max-$G_W$, as illustrated in Figure 7 for the King (1993) model.

Which values of $\lambda$ are realistic? In general, we expect that $\mu_P > \mu_W$ since the concentration (and hence free energy content) of photosynthate is greater in source tissues (foliage) than in sink tissues (wood). We also expect that $\mu_L > \mu_P$ (i.e., foliage and fine-root dry matter has higher free energy than photosynthate) because dry matter production is an active process driven by the free energy generated by plant respiration. Therefore, $\mu_L > \mu_W$ and also $\mu_P > \beta\mu_W$ (since $\beta < 1$), and so from Eq. (B5), $\lambda > 0$. The case $\lambda = 0$ (maximization of NPP) is thereby excluded because this would correspond to $\mu_L = \mu_W$. From Eq. (B5), the case $\lambda = 1$ (maximization of $G_W$) corresponds to the condition $\mu_L = \mu_P/\beta$, which certainly satisfies the inequality $\mu_L > \mu_P$; therefore, max-$G_W$ is consistent with MEP.