

# 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

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**ABSTRACT:** We present a model that scales from the physiological and structural traits of individual trees competing for light and nitrogen across a gradient of soil nitrogen to their community-level consequences. The model predicts the most competitive (i.e., the evolutionarily stable strategy [ESS]) allocations to foliage, wood, and fine roots for canopy and understory stages of trees growing in old-growth forests. The ESS allocations, revealed as analytical functions of commonly measured physiological parameters, depend not on simple root-shoot relations but rather on diminishing returns of carbon investment that ensure any alternate strategy will underperform an ESS in monoculture because of the competitive environment that the ESS creates. As such, ESS allocations do not maximize nitrogen-limited growth rates in monoculture, highlighting the underappreciated idea that the most competitive strategy is not necessarily the “best,” but rather that which creates conditions in which all others are “worse.” Data from 152 stands support the model’s surprising prediction that the dominant structural trade-off is between fine roots and wood, not foliage, suggesting the “root-shoot” trade-off is more precisely a “root-stem” trade-off for long-lived trees. Assuming other resources are abundant, the model predicts that forests are limited by both nitrogen and light, or nearly so.

**Keywords:** perfect plasticity approximation (PPA), FLUXNET, optimal, optimization, forest dynamics, height-structured competition.

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## Introduction

Just as the physical properties of a moving fluid depend on the characteristics and interactions of individual atoms, the dynamics of the world’s forests depend on the characteristics and interactions of individual trees. In the phys-

ical sciences, the Navier-Stokes equations successfully scale up processes at the level of atoms to those of fluids. In principle, ecologists should be able to scale up the traits, interactions, and biotic and abiotic environments of individual trees to the population, community, and ecosystem properties of forests (Purves and Pacala 2008). However, a tractable path from the idiosyncrasies of individual trees to the repeatable properties of forests is not obvious.

Building on a body of theoretical and empirical literature (von Foerster 1959; Mitchell 1975; Metz and Diekmann 1986; DeAngelis et al. 1993; Umeki 1995; Pacala et al. 1996; De Roos and Persson 2001), recent advances have produced the “perfect plasticity approximation” (PPA; Strigul et al. 2008). The PPA uses the fact that light competition regulates forest canopies in a way that is effectively independent of the spatial arrangement of individuals to scale from the “mean field” vital rates of individual trees to emergent properties at the level of forests using a physiologically structured population model (Strigul et al. 2008). It generates analyzable “macroscopic equations” that can be used to understand and predict forest structure and dynamics in much the same way that Lotka-Volterra equations can be used to understand generalized species interactions. But unlike the entirely phenomenological Lotka-Volterra equations, the PPA is based on a mechanistic treatment of height-structured competition using quantifiable, individual plant vital rates and, as such, is capable of quantitative predictions that can be tested with available data. Strigul et al. (2008) showed that the PPA captures essential dynamics of forest simulators, which themselves have been shown to capture essential properties of real forests (Di Lucca 1998). Purves et al. (2008) showed that a version of the PPA parameterized with empirically derived vital rates of the dominant tree species in the Great

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Lakes states of the United States successfully predicted aspects of forest composition and dynamics over a century of succession.

Here, we characterize the interactions of individual trees using stoichiometrically and physiologically based (i.e., as mechanistic in concept as possible and based on measurable parameters wherever possible) formulations for nitrogen and light competition that, together with quantitative allometric equations, lead to individual growth rates. With these individual growth rates, we use the macroscopic equations of the PPA to scale up to the community level. With community-level equations, we use adaptive dynamics (Geritz et al. 1998; Falster and Westoby 2003; McGill and Brown 2007) to determine the most competitive allocational strategies (i.e., evolutionarily stable strategies [ESSs]), which are not necessarily the growth-maximizing strategies in monoculture. While there are many models of plant competition for nitrogen and light (e.g., Tilman 1988; Reynolds and Pacala 1993; Rees and Bergelson 1997; Friedlingstein et al. 1999), we believe this is the first that is both analytically tractable and capable of accurate quantitative predictions of forestry data. Moreover, its ability to be modified for other types of vegetation and other types of interactions is promising.

Following Tilman (1988), we focus our ESS analysis on predictions of foliage, wood, and fine root allocation in stable-size-distribution (i.e., old-growth) stands across a nitrogen availability gradient. Although we believe that trees also shift both physiology and morphology of foliage, wood, and fine roots to remain competitive across gradients, we restrict the present analysis to shifts in allocation only, holding physiological and morphological parameters constant among strategies. This allows us to evaluate how far we can go in predicting forest processes based solely on understanding ESSs for allocation. We use parameter values for temperate deciduous broadleaf forests and remain uncommitted as to whether shifts in strategy across the gradient represent species replacement or the plastic responses of a single species. The truth is likely somewhere in between and is a worthy subject of future research. In contrast to most untested ESS models of plant dynamics (Falster and Westoby 2003), we tested the model's predictions against empirical allocational patterns from 152 primarily temperate deciduous and evergreen stands from the FLUXNET database (Luyssaert et al. 2007) and Santantonio (1989).

The organization of what follows presents the reader with options depending on his or her interest in the technical details of the model and results. The first section, "Nontechnical Model and Results Summary," provides a heuristic overview that, together with "Model Predictions Compared to Empirical NPP Data," will allow the reader to move on to the "Discussion." The second and third

sections, "Quantitative Description of the Model" and "Analytical and Quantitative Results," minimally define the model and report its results in mathematical terms. Appendix G in the online edition of the *American Naturalist* is carefully prepared to stand alone and includes a full model derivation and description, the technical derivation of the results, and additional nontechnical explanations and biological justifications. Table 1 lists all model symbols and parameters, allowing the reader to move between sections without complication. Figure 1 provides a conceptual depiction of the model.

### Nontechnical Model and Results Summary

Our model is individual based. Individuals possess strategies for allocating carbon (photosynthate) to foliage, wood, and fine roots. Individuals acquire nitrogen via belowground competition. Nitrogen uptake is proportional to fine root mass, and so individuals with relatively greater fine root mass acquire a greater relative share of the available nitrogen. A close approximation to a full nitrogen cycling model shows that the net mineralization rate is approximately constant and outside of plant control under the conditions considered here. Belowground competition is modeled as mean field, a reasonable approximation of root systems that are extensively commingled. Individuals acquire carbon via photosynthesis, which depends on light availability. Self-shading potentially diminishes the carbon fixed by leaves situated lower in a crown, and canopy individuals shade understory individuals. Carbon allocation to foliage is stoichiometrically constrained by nitrogen uptake, such that individuals cannot build more foliage than they have the nitrogen to support.

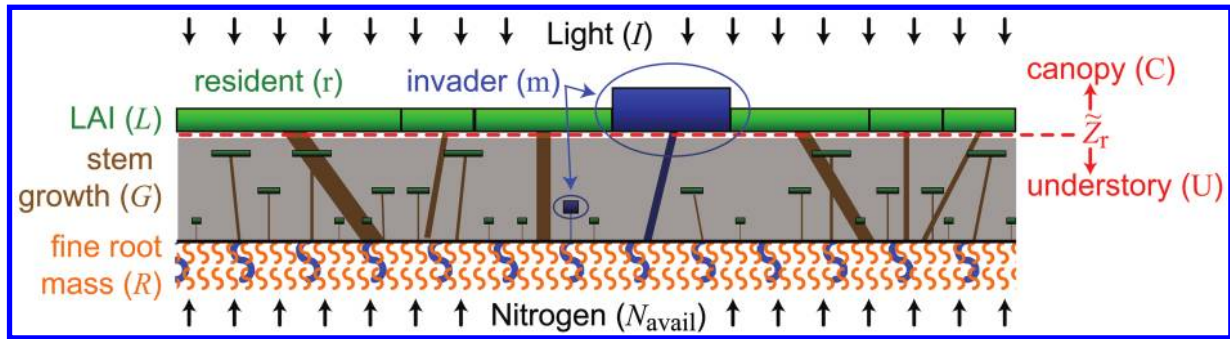
We place individuals within a forest stand that is of effectively infinite extent. We restrict our analysis to conditions in which the canopy is closed. The PPA allows us to separate an individual's life into two stages: an understory stage during which its topmost leaves are shaded by the canopy individuals above it and, assuming it survives, a canopy stage during which its topmost leaves receive full sun. Individuals transition from the understory to the canopy stage when they grow to height  $\tilde{Z}_i$ , whereupon their light environment changes instantaneously and discontinuously (derived as an approximation to a more realistic gradual transition; see app. B in the online edition of the *American Naturalist*). Individuals are subject to a constant mortality rate in the understory and a (lesser) constant mortality rate in the canopy. We assume that only individuals in the canopy stage reproduce.

To find the most competitive allocation strategy, we effectively analyze a series of invasions. We compose the stand of a resident type. Individuals of the resident type all employ the same allocational strategy in the understory

**Table 1:** Traits subject to evolutionarily stable strategy analysis, parameters, and subscripts

Symbol	Value	Units	Description
$L_{X,x}$	Any (but see eq. [2])	$m^2 m^{-2}$	Leaf area index; one-sided area of leaves per ground surface area of an individual, proportional to carbon allocation to foliage; constrained by nitrogen stoichiometry (eq. [2])
$G_{X,x}$	Any	$cm year^{-1}$	Stem diameter growth rate, proportional to carbon allocation to wood
$R_{X,x}$	Any	$g_{carbon} m^{-2}$	Live fine root mass per crown area; proportional to carbon allocation to fine roots
Nitrogen:			
$N_{avail}$	Any	$g_N m^{-2} year^{-1}$	Available nitrogen per area
$N_{X,x}$	Any	$g_N m^{-2}$	Nitrogen uptake of an individual per crown area
$\rho$	.5	None	Fraction of total plant nitrogen uptake allocated to leaves
$\delta_L$	1.595	$g_N m^{-2}$	Nitrogen per unit leaf area
$f$	.5	None	Fraction of nitrogen lost from senesced foliage
$\gamma_L$	1	$year^{-1}$	Foliage turnover
Light and photosynthesis:			
$I_X^0$	0–1	$PAR PAR_0^{-1}$	Light level of the highest leaf layer
$I_{X,x}^{bottom}$	0–1	$PAR PAR_0^{-1}$	Light level of the lowest leaf layer
$\tilde{I}$	.33	$PAR PAR_0^{-1}$	Light level at which photosynthesis is balanced between light limited and light saturated; equal to $(A_{max} + q)/\phi$
$A_{max}$	$9.9 \times 10^{-5}$	$g_{carbon} LAI^{-1} m^{-2} s^{-1}$	Maximum net carbon assimilation rate (see fig. 2)
$q$	$9.9 \times 10^{-6}$	$g_{carbon} LAI^{-1} m^{-2} s^{-1}$	Dark respiration rate (see fig. 2)
$\Phi$	$3.27 \times 10^{-4}$	$g_{carbon} LAI^{-1} m^{-2} s^{-1} PAR^{-1} PAR_0$	Quantum yield of light-limited net photosynthesis (see fig. 2)
$s$	$2.26 \times 10^6$	$s year^{-1}$	Scale conversion between measured ( $s^{-1}$ ) and yearly net photosynthesis
$k$	.5	$LAI^{-1}$	Light extinction coefficient per crown depth
$\zeta$	.75	None	Scales $k$ and $I_{C,r}$ in Beer's law light extinction to calculate $I_U^0$
Carbon:			
$E_{X,x}$	Any	$g_{carbon} m^{-2} year^{-1}$	Carbon fixed per projected crown area, net after leaf maintenance respiration
$M$	28	$g_{carbon} LAI^{-1} m^{-2}$	Leaf carbon per area
$\kappa_L$	.25	None	Foliage construction respiration, expressed as a fraction of leaf carbon
$\gamma_R$	.3	$year^{-1}$	Fine root turnover
$\kappa_R$	.25	None	Fine root construction respiration, expressed as a fraction of fine root carbon
$\Omega$	.35	$g_{carbon} g_{carbon}^{-1} year^{-1}$	Fine root respiration rate
$\omega_C$	34.6, 0	$g_{carbon} m^{-2} year^{-1}$	Carbon cost of producing seeds; 0 for understory individuals
$\Lambda$	.78	None	Fraction aboveground of the carbon allocated to wood
Perfect plasticity approximation:			
$\alpha$	.1	$m^{2\theta} cm^{-1}$	Power law coefficient relating $D$ to $A$
$\theta$	1.4	None	Power law exponent relating $D$ to $A$
$a$	81.5	$g_{carbon} cm^{-(\theta+1)}$	Power law coefficient relating $D$ to $B$
$W_x$	Any	individuals	Fitness or lifetime reproductive success of strategy $x$
$\bar{D}_r$	Any	cm	Stem diameter of shortest cohort in the canopy of a monoculture
$Z_r$	Any	m	Height of shortest cohort in the canopy of a monoculture
$\mu_x$	.013, .038	$year^{-1}$	Mortality rate, canopy and understory, respectively
$F$	.01	individuals $m^{-2} year^{-1}$	Germinants produced per unit canopy area per time

Note: Sources and derivations for values are in appendix E in the online edition of the *American Naturalist*. Subscripts and superscripts: r = variables for resident strategies; m = variables for invading strategies; x = a “placeholder” for variables that can take either an r or an m; C = variables for canopy individuals; U = variables for understory individuals; X = a “placeholder” for variables that can take either C or U; asterisk = variables for evolutionarily stable strategies; sat = variables calculated assuming saturating nitrogen uptake. PAR = photosynthetically active radiation; LAI = leaf area per ground area of an individual.



**Figure 1:** Conceptual figure. Horizontal rectangles are tree crowns with height proportional to leaf area per ground area of an individual (LAI). Vertical or slanted rectangles are stems. Orange “squiggles” are fine root mass, shown without connection to any individuals to reflect the assumption that nitrogen competition is mean field. Here, an invader type is shown that has a higher investment in fine roots per unit crown area (*larger blue squiggles*). Light is reduced due to self-shading (gradient within crowns) and transmittance through the canopy (*gray “shade” in understory*). Parenthetical symbols reflect their use in the model.

stage and the same allocational strategy in the canopy stage, that is, the allocational strategies between the two stages may differ but are uniform within a stage. We solve the system for dynamic equilibrium, such that the transition height from understory to canopy,  $\tilde{Z}_r$ , and the size distribution of the stand do not change with time.

We then add invader types to the resident stand, where the invader types differ from the resident in their allocational strategies in the understory, the canopy, or both. Importantly, if the invader’s fine root allocation is greater than that of the resident, it will be able to acquire relatively more nitrogen, allowing it to build greater stoichiometrically constrained foliage. If the invader’s fine root allocation is less than that of the resident, the opposite is true. Whether an invader will grow faster than the resident (i.e., allocate more carbon to wood) depends on the relative carbon costs and benefits of its fine root and foliage allocations in the environment set by the resident.

The population density of the invader type is assumed to be negligible, such that the resident’s allocation strategy affects the nitrogen and light availability of the invader but not the other way around. An invader will be successful if its population is expected to increase from low density. In a given habitat (here defined by nitrogen availability), we test all possible resident types against all possible invader types and deem the resident type that resists invasion by all invader types the evolutionarily stable strategy, that is, the most competitive strategy for that habitat.

Our model analysis reveals five important results. (1) In nitrogen-limited habitats, ESS allocation to foliage increases with increasing soil nitrogen availability. In nitrogen-saturated habitats, ESS allocation to foliage is independent of soil nitrogen availability and is determined solely by light availability, such that the lowest, most-shaded leaves in a crown fix just enough carbon to balance

the costs of their respiration and construction. (2) Up to the point of nitrogen saturation, ESS allocation to fine roots decreases with increasing soil nitrogen availability. For a particular soil nitrogen availability, ESS allocation to fine roots ensures that invaders with greater fine root allocation will fail to cover their cost with the additional foliage they are able to build. (3) Up to the point of nitrogen saturation, ESS allocation to wood generates increasing stem diameter growth rates with increasing soil nitrogen availability. (4) Closed-canopy forests are necessarily dual limited by nitrogen and light, or nearly so. Habitats with low soil nitrogen availability (i.e., that might be solely nitrogen limited) are always subject to successful invasion by strategies that will generate open-canopy conditions when they become residents. (5) Up to the point of nitrogen saturation, ESS allocation to foliage maximizes stem diameter growth rate in monoculture (i.e., is “optimal”), whereas ESS allocation to either fine roots or wood does not.

### Quantitative Description of the Model

Individuals compete for soil nitrogen, with net mineralization rate  $N_{\text{avail}}$  (derived from a full nitrogen cycling model; see app. G), as a function of their fine root mass  $R$ :

$$N_{x,x} \approx \frac{R_{x,x}}{R_{c,r}} N_{\text{avail}}, \quad (1)$$

where  $N_{x,x}$  is the nitrogen acquired by an individual per unit projected crown area. Following a system of subscripts that will be used again below, equation (1) can be used to calculate the per crown area nitrogen uptake of either understory or canopy individuals of either the resident or

invader strategies by substituting X with either U (understory) or C (canopy) and x with either r (resident) or m (invader). The equation states that an individual's nitrogen acquisition is proportional to the nitrogen mineralization rate and its fine root mass, relative to the resident's canopy fine root mass.

Because of stoichiometric constraints on the construction of foliage, individuals that acquire more nitrogen ( $N_{x,x}$ ; eq. [1]) can build more leaf layers (fig. 1; cf. depth of circled invader foliage to resident foliage):

$$L_{x,x} \leq \frac{N_{x,x}\rho}{\delta_L\gamma_L f}, \quad (2)$$

where  $L_{x,x}$  is the one-sided leaf area per ground area of an individual (LAI),  $N_{x,x}$  is determined by  $R_{x,x}$  via equation (1),  $\rho$  is the fraction of nitrogen taken up that is allocated to foliage,  $\delta_L$  is the nitrogen concentration of leaves per unit area (although this value is clearly different for sun leaves and shade leaves even within the same individual, we assume for simplicity no change in  $\delta_L$ ),  $f$  is the fraction of nitrogen lost from senesced foliage, and  $\gamma_L$  is leaf turnover. Note that in contrast to empirical measures of LAI, which are made at the ecosystem level, we define LAI at the individual level. However, our definition of LAI for canopy individuals will closely accord with empirical measurements in closed-canopy forests where total projected crown area and/or LAI of understory individuals is small. The inequality in equation (2) states that an individual can build less foliage than it has nitrogen for, but we show in the results that this is never adaptive for a nitrogen-limited plant and so equation (2) is more usefully understood with a strict equality under nitrogen-limited conditions.

Because light is directional, individuals shade their own leaves and the leaves of trees below them. If  $I_x^0$  is the light intensity at the top of an individual,  $L_{x,x}$  is its uniform LAI, and  $k$  is the light extinction coefficient, then the light intensity incident on its lowest leaves diminishes exponentially as a function of the leaves above:

$$I_{x,x}^{\text{bottom}} = I_x^0 e^{-kL_{x,x}}. \quad (3)$$

The light intensity at the top of the canopy is taken as full sun,  $I_C^0$ , whereas the light intensity at the top of the understory diminishes exponentially as a function of the canopy's LAI:

$$I_U^0 = I_C^0 e^{-kL_{C,r}\zeta}. \quad (4)$$

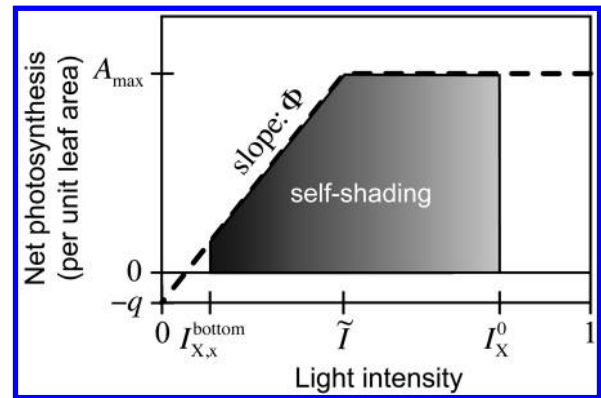
The parameter  $\zeta$  is between 0 and 1 and phenomenologically accounts for both small-scale disturbance mechanisms (e.g., single tree-fall gaps, branch breakage) and wind-driven canopy crown movements (synchronous within individuals but asynchronous among individuals)

that can cause understory light intensities to exceed those of the lowest canopy leaves.

The rate of carbon gain by a tree's crown is the sum of the photosynthetic rates of its leaf layers. Net photosynthetic rates (photosynthesis minus leaf maintenance respiration) are governed by the function in figure 2. In full sun, leaves photosynthesize at the maximum rate, but that rate diminishes in lower leaves due to self-shading (fig. 1, depicted as a gradient within each crown; fig. 2). In addition to self-shading, the photosynthesis of understory individuals is reduced by the shade of the canopy individuals above them (fig. 1; eq. [4]). There are three distinct cases, depending on whether portions of  $L_{x,x}$  are light saturated, partly light saturated and partly light limited, or solely light limited. The light intensity at which a leaf transitions from light saturated to light limited is  $\tilde{I} = (A_{\text{max}} + q)/\Phi$  (fig. 2), where  $A_{\text{max}}$  is the maximum photosynthetic rate,  $q$  is the dark respiration rate, and  $\Phi$  is the quantum yield of light-limited photosynthesis. In the first case, the entire  $L_{x,x}$  (determined by eq. [2]) is light saturated, such that  $I_x^0 > \tilde{I}$  and  $I_{x,x}^{\text{bottom}} \geq \tilde{I}$  and per-projected crown area net photosynthesis is

$$E_{x,x} = sA_{\text{max}}L_{x,x}, \quad (5)$$

where  $s$  scales per-second rates to yearly rates. In the second case, part of the  $L_{x,x}$  is light saturated and part is light limited, such that  $I_x^0 > \tilde{I}$  and  $I_{x,x}^{\text{bottom}} < \tilde{I}$ :



**Figure 2:** Simplified model of net photosynthesis, with the X-axis running from completely dark (left) to completely bright (right). Net photosynthesis is calculated by integrating across  $L_{x,x}$  from  $I_x^0$  to  $I_{x,x}^{\text{bottom}}$ , where  $I_{x,x}^{\text{bottom}}$  is determined by self-shading.  $I_x^0$  and  $I_{x,x}^{\text{bottom}}$  are free to vary along the X-axis, provided  $I_x^0 > I_{x,x}^{\text{bottom}}$ .  $\tilde{I}$  defines the transition light level between light limited and light saturated and is equal to  $(A_{\text{max}} + q)/\phi$ .

$$E_{x,x} = s \left[ \frac{A_{\max} + q}{k} \left[ 1 + \ln \left( \frac{\Phi I_x^0}{A_{\max} + q} \right) \right] - \frac{\Phi I_x^0}{k} e^{-kL_{x,x}} - qL_{x,x} \right]. \quad (6)$$

In the third and final case, all of the  $L_{x,x}$  is light limited, such that  $I_x^0 < \tilde{I}$

$$E_{x,x} = s \left[ \frac{\Phi I_x^0}{k} (1 - e^{-kL_{x,x}}) - qL_{x,x} \right]. \quad (7)$$

We note that in our treatment we always assume that  $I_C^0 > \tilde{I}$ , and thus, canopy trees are never solely light limited. In contrast, because light at the top of understory individuals is reduced by the canopy's shade, understory individuals are often partially light saturated and partially light limited or solely light limited. We use the terms "nitrogen limited" (eq. [5]), "light limited" (eq. [7]), and "dual limited" (eq. [6] or eq. [7]) to reflect their empirical interpretations, where adding only nitrogen, only light, or either nitrogen or light, respectively, would increase growth rates. To be clear, a dual-limited individual would benefit from the addition of nitrogen by itself, light by itself, or both together. All other resources, including water and phosphorus, are assumed to be nonlimiting regardless of allocation.

We assume that individuals allocate fixed carbon to support foliage, fine roots, reproductive structures (if they are in the canopy), and structural wood (branches, stem, and coarse roots). This implies diameter growth rate (see app. G):

$$G_{x,x} \approx \frac{\pi \alpha^\theta}{(\theta + 1)a} \{ E_{x,x} - (1 + \kappa_L) \gamma_L M L_{x,x} - [(1 + \kappa_R) \gamma_R + \Omega] R_{x,x} - \omega_C \}, \quad (8)$$

where  $\alpha$ ,  $a$ , and  $\theta$  are all allometric constants that relate stem diameter to projected crown area and total tree mass (see app. G);  $E_{x,x}$  is determined by equation [5], [6], or [7], depending on the environment;  $\gamma_L$  is leaf turnover;  $M$  is leaf carbon per one-sided leaf area;  $\kappa_L$  is the respiratory cost of building leaves;  $\gamma_R$  is fine root turnover;  $\kappa_R$  is the respiratory cost of building fine roots;  $\Omega$  is the maintenance respiration rate of fine roots; and  $\omega_C$  is the annual build and maintenance cost of fecundity per projected crown area. Equation (8) states that stem diameter growth rate is proportional to net photosynthesis (first term) minus the build cost of foliage (second term) minus the build and respiratory cost of fine roots (third term) minus allocation to fecundity (last term), scaled by allometric constants. The equation does not include foliage maintenance respiration, as this is already subsumed in the calculation

of net photosynthetic rate,  $E_{x,x}$ . We assume negligible wood turnover and respiration. As developed in appendix G, allocation to wood is directly proportional to the stem diameter growth rate  $G_{x,x}$  (and, via allometry, to the height growth rate). As a consequence of the allometric equations that we use and justify in online appendixes A and G, stem diameter growth rates,  $G_{x,x}$ , are constant and independent of stem diameter.

The methods of the perfect plasticity approximation, which classify individual trees as being in the canopy (as tall as or taller than the minimum canopy crown height;  $\tilde{Z}_r$ ; fig. 1) or in the understory (shorter than  $\tilde{Z}_r$ ; fig. 1) without reference to their spatial locations, allow us to rigorously scale up the individual-level ecology presented above to the community level (Adams et al. 2007; Strigul et al. 2008). Assuming the same height allometries among species, as we do here, the stem diameter  $\tilde{D}_r$  that corresponds to  $\tilde{Z}_r$  for an equilibrial monoculture is approximately

$$\tilde{D}_r \approx \frac{G_{U,x}}{\mu_U} \ln \left[ F \pi \alpha^\theta \Gamma(\theta + 1) \frac{G_{C,r}^\theta}{\mu_C^{\theta+1}} \right], \quad (9)$$

where  $\mu_C$  and  $\mu_U$  are canopy and understory mortality rates,  $F$  is per-ground area fecundity,  $\Gamma(\dots)$  is the gamma function,  $\alpha$  and  $\theta$  relate projected crown area to stem diameter, and  $G_{U,r}$  and  $G_{C,r}$  are determined by equation (8). As revealed in equation (9),  $\tilde{D}_r$  increases with growth rates and fecundity and decreases with mortality rates in a way that properly weights the understory and canopy components (Strigul et al. 2008). The lifetime reproductive success, or fitness  $W_x$ , of a strategy is approximately

$$W_x \approx e^{-\tilde{D}_r(\mu_U/G_{U,x})} F \pi \alpha^\theta \frac{G_{C,x}^\theta}{\mu_C^{\theta+1}} \Gamma(\theta + 1), \quad (10)$$

where  $G_{U,x}$  and  $G_{C,x}$  are determined by equation (8). We restrict our analysis to cases that result in closed-canopy forests, for which  $G_{U,x}$  and  $G_{C,x}$  are necessarily greater than 0. As described in appendix G, we use slightly more accurate but more cumbersome expressions for determining numerical results in figures. Qualitative results are not at all affected by this difference.

We use adaptive dynamics (Geritz et al. 1998; McGill and Brown 2007) to determine the most competitive allocations to foliage, wood, and fine roots for a given nitrogen availability, which we usefully characterize as individual leaf area index  $L_x^*$ , individual stem diameter growth rate (which is directly proportional to wood allocation)  $G_x^*$ , and fine root mass  $R_x^*$ . We use the term "strategy" to refer to a particular suite of such allocations. For a particular trait  $v$  we implicitly find the ESS  $v^*$  by finding the maxima of the fitness function  $W_m$  for  $v$ :

$$\left. \frac{dW_m(v_m, v_r)}{dv_m} \right|_{v_m=v_r, v_r=v^*} = 0,$$

$$\left. \frac{d^2W_m(v_m, v_r)}{d^2v_m} \right|_{v_m=v_r, v_r=v^*} < 0, \quad (11)$$

where  $W_m$  is a function of both the invader's strategy  $v_m$  and the resident's strategy  $v_r$  and is both continuous and smooth within the domain of analysis (Geritz et al. 1998; McGill and Brown 2007). Because of their functional connection to  $G_{x,x}$  (eq. [8]),  $L_x^*$  and  $R_x^*$  uniquely determine  $G_x^*$ ; although it is vastly more cumbersome, we could obtain the same numerical results by solving first for  $L_x^*$  and  $G_x^*$  and then substituting them for  $R_x^*$ . Equation (11) identifies local ESS candidate strategies that, as residents, are uninvadable by nearby strategies. We determine that these ESS candidate strategies are both global and convergent stable in appendix F in the online edition of the *American Naturalist*.

By subtracting carbon consumed by respiration, our growth equation (eq. [8]) lends itself to comparison with empirical net primary productivity (NPP) measurements:

$$\begin{aligned} \text{NPP}_{\text{foliage}} &\equiv \gamma_L M L_{x,x}, \\ \text{NPP}_{\text{wood}} &= \left[ \frac{\pi \alpha^\theta}{(\theta + 1)a} \right]^{-1} G_{x,x}, \\ \text{NPP}_{\text{aboveground wood}} &= \left[ \frac{\pi \alpha^\theta}{(\theta + 1)a} \right]^{-1} \Lambda G_{x,x}, \\ \text{NPP}_{\text{fine root}} &\equiv \gamma_R R_{x,x}, \end{aligned} \quad (12)$$

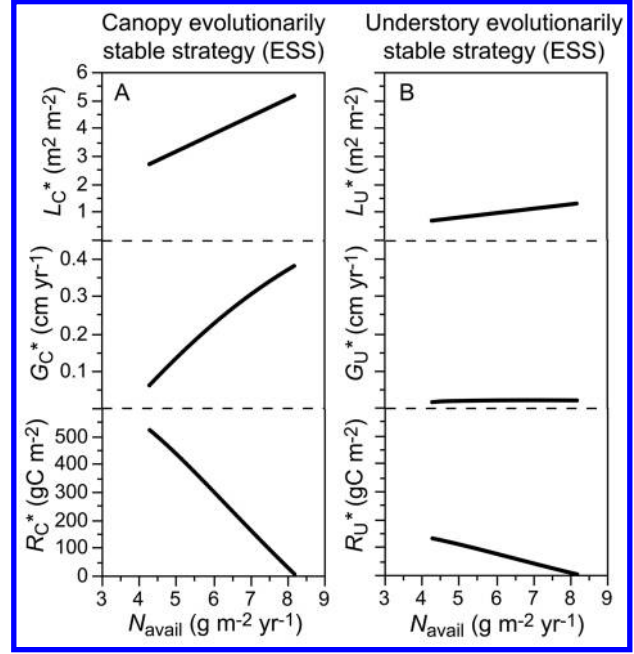
where  $\Lambda$  is the fraction of wood allocated aboveground. All four values are expressed in common units ( $\text{g}_{\text{carbon}} \text{m}^{-2} \text{year}^{-1}$  for our parameterization; table 1). Relative NPP of any component is found by dividing it by the sum of  $\text{NPP}_{\text{foliage}}$ ,  $\text{NPP}_{\text{wood}}$ , and  $\text{NPP}_{\text{fine root}}$ .

### Analytical and Quantitative Results

Appendix G contains the derivations and additional explanations for the following results.

#### Result 1

*Increasing ESS foliage with increasing nitrogen availability.* Across a fertility gradient, as  $N_{\text{avail}}$  increases, the most competitive LAIs in both the canopy,  $L_C^*$ , and in the understory,  $L_U^*$ , increase up to the point of nitrogen saturation (fig.



**Figure 3:** The evolutionarily stable strategy leaf area index ( $L_x^*$ ), stem growth rate ( $G_x^*$ ), and fine root mass ( $R_x^*$ ) across a nitrogen availability gradient for canopy (A) and understory (B) individuals. Lines begin at low  $N_{\text{avail}}$  as growth rates become sufficient to allow for closed-canopy forest. Lines end at high  $N_{\text{avail}}$  as foliage becomes nitrogen saturated, where additional nitrogen uptake would be neither competitive nor optimal and where we thus expect nitrogen to leach from the system.

3). First, we find the ESS, assuming that nitrogen is unlimited:

$$L_C^{\text{sat}} = \frac{1}{k} \ln \left[ \frac{s \Phi I_C^0}{(1 + \kappa_L) \gamma_L M + sq} \right], \quad (13)$$

where “sat” indicates that this is the nitrogen-saturated result. Interpretation of this equation is straightforward. The most competitive nitrogen-saturated LAI,  $L_C^{\text{sat}}$ , depends strongly on  $k$ , the light extinction coefficient; smaller  $k$  leads to greater  $L_C^{\text{sat}}$  because it decreases self-shading. Of those variables that may vary appreciably among species or habitats, increased  $L_C^{\text{sat}}$  occurs with increasing extrapolated net photosynthetic rate  $s$  or decreasing leaf turnover rate  $\gamma_L$ , leaf carbon per area  $M$ , or leaf dark respiration rate  $q$ . Because  $A_{\text{max}}$  and  $q$  are often positively correlated, decreasing  $A_{\text{max}}$  will likely increase  $L_C^{\text{sat}}$ . At  $L_C^{\text{sat}}$ , the lowest leaves of canopy trees are just able to pay for their own construction and respiratory costs. This is an upper limit, as it does not take into account the possibility that additional whole-plant respiratory costs are required to support those lowest leaves (Reich et al. 2009). It is easy to show that in habitats with less-than-saturating nitrogen

availability, a strategy that builds as much foliage as it can (according to eq. [2]) will invade a strategy that builds  $L_{C,r}$  less than that (see derivation of result 5 in app. G). Thus,

$$L_C^* = \min\left(\frac{N_{\text{avail}}\rho}{\delta_L\gamma_L f}, L_C^{*\text{sat}}\right), \quad (14)$$

where  $L_C^{*\text{sat}}$  is defined by equation (13). Parallel results hold for the understory and are detailed in appendix G. Together, these results show that the most competitive  $L_X^*$  strategy is that which builds as much foliage as it has nitrogen for, up to the point at which additional leaves would fail to pay for themselves due to self-shading.

### Result 2

*Decreasing ESS fine root mass with increasing nitrogen availability.* Across a soil fertility gradient as  $N_{\text{avail}}$  increases, the most competitive fine root mass,  $R_X^*$ , decreases monotonically. No closed-canopy  $R_X^*$  exists at low  $N_{\text{avail}}$  because successful invaders with greater  $R_{C,m}$  drive the system into open-canopy, nonforest conditions (see app. C in the online edition of the *American Naturalist*). For all  $N_{\text{avail}}$  sufficiently large, a stable  $R_X^*$  exists up to the point at which the canopy becomes nitrogen saturated (fig. 3). Here we show the canopy ESS  $R_C^*$ ; the understory ESS is similar and is detailed in appendix G:

$$R_C^* = \frac{s\Phi I_C^0 e^{-kL_C^*} - sq - (1 + \kappa_L)\gamma_L M}{(1 + \kappa_R)\gamma_R + \Omega} I_C^*. \quad (15)$$

Equation (15) is a ratio. The quantum yield,  $\Phi$ , is the slope of light-limited photosynthesis with light availability (fig. 2) and  $I_C^0 \exp(-kL_C^*)$  is light availability at the lowest leaf layer. Thus, the first term in the numerator describes the rate of light-limited photosynthesis at the lowest leaf layer. The second and third terms in the numerator are the respiratory and build costs of that leaf layer. Together, the numerator is the net marginal carbon benefit given to an invader with greater fine root mass than the resident. Whenever an individual is at least partially light limited, this marginal benefit will decrease with  $N_{\text{avail}}$  because  $L_C^*$  increases and thus the light at the bottom of the canopy due to self-shading will decrease. The denominator for  $R_C^*$  is the fixed carbon cost of that infinitesimally greater root investment. In contrast to the numerator, this fixed root cost never varies with  $N_{\text{avail}}$ . Simply put,  $R_C^*$  decreases with  $N_{\text{avail}}$  because the marginal benefit to greater root investment decreases due to self-shading while the cost remains fixed. It is easy to show that  $R_C^*$  goes to 0 as  $L_C^*$  goes to  $L_C^{*\text{sat}}$  (eq. [13]), demonstrating that the premium paid on fine root biomass for the purpose of nitrogen

uptake goes to 0 as nitrogen becomes nonlimiting (assuming, as we do, no leaching of nitrogen).

### Result 3

*Increasing ESS growth rates with increasing nitrogen availability.* The most competitive growth rate in the canopy,  $G_C^*$ , increases monotonically and saturates with increasing  $N_{\text{avail}}$ :

$$G_C^* = \frac{\pi\alpha^\theta}{(\theta + 1)a} \left\{ \frac{(A_{\text{max}} + q)s}{k} \left[ 1 + \ln\left(\frac{\Phi I_C^0}{A_{\text{max}} + q}\right) \right] - (kL_C^* + 1) \frac{s\Phi I_C^0}{k} e^{-kL_C^*} - \omega_C \right\}. \quad (16)$$

Over the range of  $N_{\text{avail}}$  for which the model predicts closed-canopy forest, the term involving the exponent becomes less negative with increasing  $N_{\text{avail}}$ , causing the whole function to increase but in a saturating way. Apart from the conversion constants in front and the cost of fecundity, equation (16) differs from the equation for net photosynthesis (eq. [6]) by the addition of  $kL_C^*$  to the term involving the exponent, which effectively incorporates the increasing cost of  $L_C^*$  and the decreasing cost of  $R_C^*$  with  $N_{\text{avail}}$ . It is also possible to solve analytically for  $G_U^*$ , but the resulting expression is neither simple nor illuminating.

### Result 4

*Forests composed of individuals with ESSs are dual limited up to the point of nitrogen saturation.* Up to the point of nitrogen saturation, where no tree in a stand is limited by nitrogen, our model predicts that all ESS forests are dual limited; that is, the canopy, and sometimes the understory, is limited by both nitrogen and light. At low  $N_{\text{avail}}$ , where both the canopy and understory would be solely nitrogen limited, no ESS closed-canopy forest can exist, because strategies that lead to open-canopy conditions always successfully invade closed-canopy strategies (app. C). Only after the canopy becomes dual limited with increasing  $N_{\text{avail}}$  does the possibility exist for an ESS closed-canopy forest. As  $N_{\text{avail}}$  increases, the understory transitions from dual limited to solely light limited. At the point of nitrogen saturation, no individual is limited by nitrogen, and both the understory and canopy are at  $L_X^{*\text{sat}}$  (eq. [13]; app. G).

### Result 5

*Under nitrogen-limited conditions, ESS foliage maximizes competitive ability and stem growth rate in monoculture (i.e., is "optimal"), whereas ESS fine root mass and wood allocation maximize only competitive ability (i.e., are not "op-*



timal”). By design, our method for determining ESSs (eq. [11]) finds those strategies that are uninvadable and thus the most competitive among all neighboring strategies. In much of the literature on plant ecology, plants are assumed to maximize carbon gain or individual growth rate in monoculture or in the absence of competition; that is, they are said to be “optimal.” In addition to being the most competitive strategy, ESS foliage  $L_C^*$  is optimal in this sense, but ESS fine root mass and growth rate,  $R_C^*$  and  $G_C^*$ , are not.

### Model Predictions Compared to Empirical NPP Data

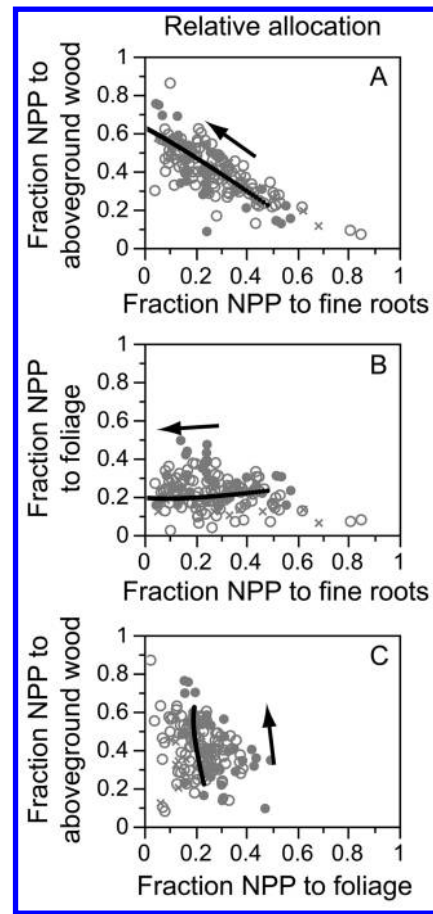
We compared our model predictions of NPP, both relative and absolute, to data from the FLUXNET database (Luyssaert et al. 2007) and Santantonio (1989); details can be found in appendix D in the online edition of the *American Naturalist*. We used common units ( $\text{g C m}^{-2} \text{ year}^{-1}$ ) for foliage, aboveground wood, and fine roots NPP as described in equation [12]. No part of the model, either its formulation or its parameterization, was based on these data, and the lines are generated as ESS solutions to the model, not as statistical fits to the data (i.e., the lines are generated without any reference to the data at all).

Both the data and our model’s predictions reveal a strong negative relationship between fractional NPP of wood and fine roots but very little relationship between fractional NPP of either wood and foliage or fine roots and foliage (fig. 4). The model’s predictions are close to the empirical relationship (i.e., regression line, not shown) and most of the range of the fractional data (fig. 4). Not surprisingly, the data reveal increasing absolute NPP of foliage, wood, and fine roots with increasing total NPP (fig. 5). The model’s predictions largely fall within the range of the absolute data but fail to find the empirical relationships (i.e., regression lines, not shown) or generate values for large ranges of the observed data (fig. 5). Moreover, whereas the data show a generally positive relationship between absolute NPP of fine roots and total NPP, the model predicts a negative relationship (fig. 5).

## Discussion

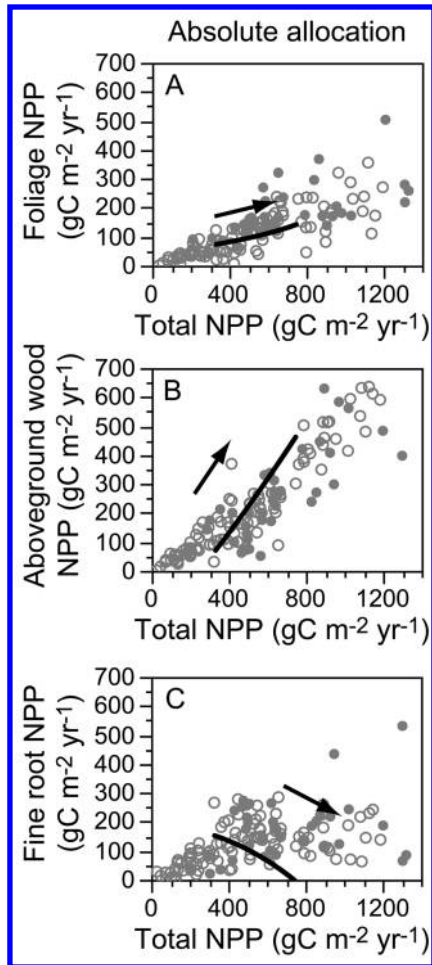
### *Allocational Strategies Are Not Necessarily “Optimal”*

Many investigators have suggested and observed that proportional allocations to foliage and stem increase and allocation to fine roots decreases with increasing nitrogen availability in both forests and other types of vegetation (Miller and Miller 1976; Aber et al. 1985; Vogt et al. 1987; Tilman 1988; Santantonio 1989; Gholz et al. 1991; Gower et al. 1992; Reynolds and Pacala 1993; Rees and Bergelson 1997; Coomes and Grubb 2000; Jimenez et al. 2009). The



**Figure 4:** Empirical relations between relative net primary productivity (NPP) allocated to foliage, fine roots, and aboveground wood (gray) compared to independent model predictions of evolutionarily stable strategies across a nitrogen gradient. Arrows show gradient of increasing  $N_{\text{avail}}$  for model predictions. Circles represent data from the publicly available FLUXNET database (Luyssaert et al. 2007), and Xs represent data from Santantonio (1989). Stands represented by open circles or Xs are dominated by gymnosperms, whereas those represented by filled circles are dominated by angiosperms. Methodological details can be found in appendix D in the online edition of the *American Naturalist*. These empirical data neither informed model parameters nor constrained the predictions and thus represent an independent test of the model.

suggested and observed distributions of standing biomass often follow the same patterns. These trends have been explained using optimization theory: optimal plants are said to allocate so that they balance their belowground and aboveground limitations and thus maximize growth rates (Poorter and Nagel 2000). In such a framework, the trade-off is between belowground and aboveground resource acquisition, where capturing more of one resource necessarily means capturing less of the other (e.g., Tilman 1988; Reynolds and Pacala 1993; Aikio and Markkola 2002; Smith and Sibly 2008).



**Figure 5:** Empirical relations between absolute net primary productivity (NPP) allocated to foliage, aboveground wood, and fine roots (gray) compared to independent model predictions of evolutionarily stable strategies across a nitrogen gradient. Arrows show gradient of increasing  $N_{\text{avail}}$  for model predictions. Five data are omitted from B ([1,710, 900], [1,720, 1,078], [1,314, 989], [1,333, 931], [1,711, 1,299]) to increase resolution. See figure 4 legend for additional details. These empirical data neither informed model parameters nor constrained the predictions and thus represent an independent test of the model.

We believe this explanation falls short for two reasons. First, the most competitive strategies may not optimize growth rates in monoculture (“Result 5”). For example, in our model the ESS fine root and wood allocation strategies are the most competitive, in the sense that no other strategy can invade a monoculture that uses them. But they do not optimize growth rates in monoculture; strategies that allocate less to fine roots will lead to greater growth rates (“Result 5”). This objection is not specific to our model, closed-canopy forests, or even the plant kingdom (Falster and Westoby 2003): what matters is not that

an ESS monoculture resident maximizes its own growth rate but that it creates conditions in which no other strategy can maintain a greater growth rate (or more accurately, greater fitness) than the ESS resident.

Second, the explanation focuses on fractional allocation, which can be a useful way to understand both within-individual carbon budgeting and responses to multiple resource limitations. Nevertheless, it is absolute allocation that determines resource acquisition for both trees and other types of vegetation. It is the absolute size (or density or area) of a root system that determines its ability to capture nitrogen, not its size relative to the rest of the plant. Similarly, it is the absolute size and height of the light intercepting organs that determine carbon capture, not their size or height relative to the rest of the plant. Moreover, there is no necessary trade-off between absolute allocation to roots and shoots in competition; greater absolute investment in roots may indirectly lead to greater absolute investment in shoots (e.g., by acquiring greater amounts of limiting nutrients that allow greater overall productivity) and vice versa.

#### *The Ecology of ESS Allocational Strategies*

It is easy to understand why the amount of foliage increases with nitrogen availability under nitrogen-limited conditions: because foliage is stoichiometrically constrained by nitrogen availability, greater nitrogen availability allows for more foliage, which leads to greater carbon fixation. Greater carbon fixation leads to greater growth rates. This is true not just of the trees that we have modeled but of any nitrogen-limited vegetation. Self-shading diminishes the relative worth of lower leaves without an equal reduction in their carbon build cost, and a plant should not build or maintain lower leaves with negative carbon balance (Givnish 1988; Anten and Poorter 2009; Reich et al. 2009). In our model, this point is described by  $L_X^{\text{sat}}$  (eq. [13]; app. G), the most competitive LAI of a nitrogen-saturated tree. Although we have neglected it in our model, trees also modify within-canopy physiology and morphology, building a continuum between “sun leaves” and “shade leaves,” which serves to increase  $L_X^{\text{sat}}$ . But there exist light levels below which even the best-adapted and acclimated shade leaf will fail to be productive, indicating that  $L_X^{\text{sat}}$  must exist, even allowing for within-canopy changes in physiology and morphology. Because increasing productivity due to, for instance, longer growing season length or less water limitation allows a given leaf to increase its photosynthetic gain without appreciably affecting its build cost, our model predicts greater  $L_X^{\text{sat}}$  for trees with greater maximum annual net photosynthetic rate (s).

The reason for the decrease in fine root mass with increasing nitrogen availability (fig. 3; eq. [15]; app. G) is

important, nonobvious, and, we believe, likely to underpin competitive interactions in any plant community in which individuals are dual limited by nitrogen and light. Simply put, better nitrogen competitors (strategies of greater fine root mass) are able to build more leaves than a resident that is a poorer nitrogen competitor, but they receive less payoff for their greater fine root investment when the only “extra” leaves they can build relative to the resident are light limited. That payoff becomes smaller as the “extra” leaves become progressively more light limited, and as a consequence, ESS fine root allocation declines with increasing nitrogen availability.

As we discuss below, our model’s prediction of decreasing fine root mass with increasing nitrogen availability is contradicted by the FLUXNET data (fig. 5C), and many empirical papers that have been published on this topic (Brassard et al. 2009). But the prediction is also supported by an approximately equal number of empirical papers, reflecting a well-known paradox of generality that awaits resolution (Brassard et al. 2009). We hope that our model may provide a path forward in this debate and that relaxing the universe of parameters that we currently hold constant (e.g., fine root turnover, annual net photosynthetic rate) with appropriate trade-offs will reveal the conditions under which to expect one or the other response. Our model makes the obviously wrong prediction that fine root mass should actually go to 0 (and not just some small but positive value) at the point of nitrogen saturation. This is a consequence of our assumptions that all other resources (including water) are abundant, independent of allocation, and that nitrogen does not leach from the system. This obvious disagreement with observation argues for a full water-nitrogen-light model.

There are interesting biological reasons for the result that ESS allocation to foliage maximizes growth rates in monoculture (i.e., is “optimal”), whereas ESS allocations to fine roots and wood do not (“Result 5”). It is easy to observe that individual tree crowns in closed-canopy forests overlap very little (Putz et al. 1984; Purves et al. 2007), such that each individual holds an independent light-intercepting “territory” for the strong vertical component of sunlight, presumably because interdigitating branches with neighbors leads to damage in wind storms. It is much less easy to observe but nonetheless true that individual tree roots overlap substantially (Gilman 1988; Stone and Kalisz 1991; Casper et al. 2003; Gottlicher et al. 2008) presumably because, in the conspicuous absence of underground wind storms, it is better to situate a new fine root in the nitrogen diffusion zone of a neighbor’s fine root to “steal” nitrogen that would have otherwise gone to the neighbor (O’Brien et al. 2007). This “mean field” nature of root competition effectively forces competitive plants to divert carbon that could have gone to growth

(or fecundity) in order to maintain an environment that prevents would-be usurpers from deriving any net benefit by playing a different strategy.

In contrast to models that assume that the most competitive strategies are those that maximize growth rates in monoculture, our analysis reveals that low-nitrogen systems, in which all of the closed-canopy foliage is light saturated, will always be invisable by strategies that invest so heavily in fine roots that when they become residents, their growth rates, relative to mortality rates, are too slow to close the canopy (app. C). Thus, at low nitrogen availability, our model predicts that extant closed-canopy forests must necessarily be dual limited by nitrogen and light. At high nitrogen availability, a closed-canopy forest eventually becomes nitrogen saturated, where there exists no reason, either competitive or optimal, for trees to take up the additional nitrogen. If trees can avoid luxury consumption of nitrogen (which incurs costs for conversion from mineral form and storage), we expect nitrogen-saturated forests to leach nitrogen until what remains just meets the nitrogen-saturated demand. Such a forest would be solely light limited but balanced at the brink of dual limitation with nitrogen as well. An extensive study of 50 stands of various compositions in the middle United States revealed no evidence of nitrogen saturation (Reich et al. 1997). In a forest nitrogen addition experiment, Perakis et al. (2005) found a threshold nitrogen addition rate that stimulated leaching, consistent with our conjecture.

#### *Empirical Patterns in Allocation*

With changes in nitrogen availability alone, our model predicts the major quantitative trends in fractional allocation to foliage, wood, and fine roots in the data of FLUXNET (Luyssaert et al. 2007) and Santantonio (1989). The fractional allocations in both the data and our predictions reveal a strong structural trade-off between carbon allocated to fine roots and wood (fig. 4A) but very little structural trade-off between foliage and either fine roots (fig. 4B) or wood (fig. 4C). Our model provides an explanation for this.

The model predicts that trees should allocate carbon to foliage in proportion to the nitrogen they acquire, up to the point at which the lowest and most shaded leaves would fail to pay for themselves in carbon (eq. [14]). Because almost all mineralized nitrogen (net after microbial immobilization) is taken up quickly by nitrogen-limited trees, independent of fine root mass (Raynaud and Leadley 2004), our model predicts that allocation to fine root and foliage should be independent. Because that foliage more than pays for itself, such a “decision” is beneficial, fixing more net carbon to pay for fine roots, fecundity, or growth at the timescale of a season than would

have been available if the initial carbon had originally been invested directly in fine roots, fecundity, or growth. Note that this may not be true of other plant forms, such as annuals, that are incapable of storing enough labile carbon to deploy a full leaf complement at the onset of the growing season. In contrast to foliage, our model predicts that carbon allocation to fine roots and wood, both of which are solely carbon sinks, should negatively covary. Because fecundity is almost entirely a carbon sink, albeit often small, the full trade-off is likely between fine roots, wood, and fecundity.

Santantonio's (1989) analysis of his smaller subset of the data included site conditions, and he found that stands with greater fractional fine root allocation were associated with sites that were less favorable for growth, consistent with our model predictions (notice  $N_{\text{avail}}$  arrow in fig. 4A). Similarly, among 14 oak woodlands, Reich (2002) observed greater fractional fine root allocation associated with sites with lower soil N availability. In contrast to optimization models, which predict that plants should increase allocation to capture the more limiting resource (e.g., Reynolds and Pacala 1993; Poorter and Nagel 2000; Aikio and Markkola 2002), our model predicts that increased shade should decrease allocation to foliage, if anything (consider  $I_x^0$  in eq. [14]; app. G). Consistent with our model prediction, Reich (2002) summarized a number of studies in which experimental shading resulted not in greater leaf mass fraction but rather increased allocation to stem at the expense of roots. We suggest that a casual interpretation of the "root-shoot" trade-off as involving foliage should be more rigorously characterized as a "root-stem" trade-off, or more rigorously still as a "fine root-wood" trade-off, at least for long-lived trees.

The model's ability to predict patterns in absolute allocation of foliage and wood (fig. 5) is, on the one hand, remarkable for a model that is simple enough to yield analytical solutions and that by design ignores some well-known and often highly influential processes (e.g., variations in physiology, water availability, and season length). With earlier analytical models (e.g., Reynolds and Pacala 1993), one could not have even attempted a quantitative prediction of this nature, let alone come close to succeeding. On the other hand, as parameterized, the model does not predict closed-canopy forests of either low or high total NPP (fig. 5); it makes predictions that appear far from the empirical relationships (i.e., fit regression lines, not shown) for both foliage NPP (fig. 5A) and above-ground wood NPP (fig. 5B); and it predicts decreasing fine root NPP with increasing total NPP, in opposition to the dominant increasing trend (fig. 5C). Clearly, shifts in allocation along nitrogen gradients explain some of the variation in the data, but their failure to account for much of it is consistent with the notion that competitive shifts

in physiology and within-organ morphology, as well as limitation by other resources (none of which we have considered here) are of great importance.

The data contain stands with lower productivity than even our lowest predicted closed-canopy stand ( $\sim 300 \text{ g C m}^{-2} \text{ year}^{-1}$ ), but all of those stands are dominated by conifers. Our model is parameterized for temperate deciduous broadleaf species (table 1), and thus our inability to predict those low-productivity conifer sites highlights the important differences between the two taxa. Several of our predictions fall outside the range of observed allocations because our model makes the wrong prediction that fine root mass should fall to 0 at high nitrogen availability. In reality, fine root mass should be low, but not 0, at high nitrogen availability because even abundant nitrogen requires a mechanism of uptake and, in addition, fine roots are responsible for the uptake of other resources. Raising the high nitrogen availability predictions of fine root mass would bring the predictions into better agreement with the data, which highlights the importance of incorporating potential limitation by other resources into the model.

It is curious that the model predicts decreasing fine root NPP with increasing total NPP, whereas the data show a positive correlation between fine root NPP and total NPP, at least for total NPP  $< 700 \text{ g C m}^{-2} \text{ year}^{-1}$ . As mentioned above, there are echoes of such radically divergent patterns in the literature. Brassard et al. (2009) summarized numerous studies across soil nitrogen gradients that reported either significantly increasing or significantly decreasing fine root production, turnover, and biomass. By inspection of the equation for the ESS fine root allocation (eq. [15]), it is clear that several parameters would increase or decrease its value, holding nitrogen availability constant. However,  $s$ , the parameter that scales measured net photosynthesis per second to a yearly rate, stands out as one that is likely to shift along important gradients. We expect  $s$  to be positively correlated with growing season length and negatively correlated with nonnitrogen resource limitation (e.g., water). Among taxa, the parameters that describe fine root and foliage turnover, respiration, and construction costs will vary and thus affect ESS fine root allocation. Our results suggest that studies that effectively hold these parameters, including  $s$ , constant by controlling growing season length, taxa, and other resource limitations should observe decreasing fine root production and biomass, whereas those that allow them to vary might observe any relationship. Since soil texture, water availability, and nitrogen mineralization rates are frequently correlated (Reich et al. 1997), it may be easy to find many naturally occurring nitrogen availability gradients that are also potentially correlated gradients in these other parameters.

We simplified our model by assuming old-growth con-

ditions, but it is likely that many extant forests are still recovering from anthropogenic and natural stand-level disturbances. Indeed, the FLUXNET data set contains 62 and 24 stands that were characterized as “managed” and “recently disturbed,” respectively. Nevertheless, the general allocational patterns between these and the other stands are not substantively different (app. D), suggesting that the strategies of canopy trees, which the data overwhelmingly represent, differ little across disturbance gradients. However, we do expect other aspects, including leaf physiology, wood morphology, and the importance of the understory stage, to vary between early successional and old-growth stands.

#### Unanswered Questions

Much remains to be understood, of course. For example, real forests are often quite diverse. Our model, like others that involve light competition (e.g., Tilman 1988; Reynolds and Pacala 1993; Rees and Bergelson 1997), does not explain this diversity without invoking exogenous mechanisms (e.g., Tilman and Pacala 1993; Fargione and Tilman 2002; Wright 2002) because it admits no local coexistence (app. F). We note that without changing our model structure, the physiological parameters that we currently treat as constants (e.g.,  $A_{\max}$ ,  $M$ ,  $\delta_l$ , etc.) may also be analyzed as ESSs to reveal the competitive mechanisms that underlie physiological shifts and, potentially, local coexistence across gradients under nitrogen and light limitation.

Beyond this, the approach that we have outlined may be viewed as a special case of a more general model that will also accommodate and predict ESS traits for open-canopy conditions and plant growth forms that differ from those of trees. Unlike other approaches, ours permits smooth transitions from, for example, desert to grassland to forest, and holds the promise of a mechanistic understanding of the forces that determine the large-scale, repeatable patterns in global vegetation (and hence their mechanistically based response to global change). More broadly, we believe our formal scaling of individual-level processes and interactions to their community-, ecosystem-, and evolutionary-level consequences, may, with modifications, shed light on open questions in ecology for which the small-scale physiology and large-scale patterns are understood but for which the link between the two scales has so far lacked rigor (Givnish 2002).

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