Appendix G from R. Dybzinski et al., "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., vol. 177, no. 2, p. 153)

Full Model Derivation and Description and Derivation of Analytical Results

Model Overview

Figure 1 in the main text provides a conceptual depiction of our model. In it, individuals in either a canopy stage or an understory stage compete for nitrogen as a function of their fine root mass. We assume an old-growth monoculture of resident individuals and invader individuals of negligible population density. Because of stoichiometric constraints on the construction of foliage, better competitors for nitrogen are able to build more foliage and worse competitors for nitrogen are able to build less foliage. Given a complement of foliage, individuals photosynthesize. At the top of the canopy, leaves photosynthesize at the maximum rate, but that rate diminishes in lower leaves due to self-shading. In addition to self-shading, the photosynthesis of understory individuals is reduced by the shade of the canopy individuals above them. Individuals allocate fixed carbon to support foliage, fine roots, and, if they are in the canopy, reproductive structures. Whatever carbon remains is allocated to structural wood (branches, stem, and coarse roots), which determines stem diameter growth rate, and, via allometry, height growth rate.

By reasonable approximation, our model predicts two diameter-independent growth rates, one for the canopy and another for the understory (see below for details), which are directly used in the perfect plasticity approximation (PPA) macroscopic equations (Strigul et al. 2008). The PPA scales the individual-level ecology to the community level, where we use adaptive dynamics (McGill and Brown 2007) to determine the most competitive allocations to foliage, wood, and fine roots for a given nitrogen availability. We use the term "strategy" to refer to a particular suite of such allocations. All other resources, including water and phosphorus, are assumed to be nonlimiting regardless of allocation.

We use the terms "nitrogen limited," "light limited," and "dual limited" to reflect their empirical interpretations, where adding nitrogen, light, or either nitrogen or light would increase growth rates, respectively. To be clear, a "dual-limited" individual would benefit from the addition of nitrogen by itself, light by itself, or both together. We use the term "dual limited" and not "colimited" to remain uncommitted as to whether the addition of both nitrogen and light would result in interactive or (merely) additive effects, only the former of which is currently defined as "colimitation" (Harpole and Goldstein 2007).

Nomenclature for Parameters and Subscripts

Table G1 lists all model parameters and variables along with the values used to produce figures. Wherever appropriate, the subscript X is a placeholder and indicates that canopy individuals (subscript C) may have a different value (e.g., $R_{C,x}$) than understory individuals (subscript U; e.g., $R_{U,x}$). The subscript x is also a placeholder and indicates that a resident value (subscript r; e.g., $R_{X,r}$) may differ from an invader value (subscript m; e.g., $R_{X,m}$). Together, we write, for example, $R_{C,r}$ when we specifically refer to the variable R for resident individuals (r) in the canopy stage (C). In contrast, we write $R_{X,x}$ when we generically refer to the variable R for either invaders or residents (x) of either the canopy or understory stages (X). To determine the adaptive dynamics of the system, we assume the resident dominates the habitat and that the population size of the invader is negligible. Thus, the resident affects the invader by setting resource availabilities, but the invader does not affect the resident. Evolutionarily stable strategies (ESSs) have asterisks (e.g., R_X^*).

Tree Allometry

All trees share a "toolkit" of organs: leaves to fix carbon, fine roots to capture nutrients and water (either alone or via symbionts), wood to connect and support leaves and fine roots, and reproductive structures. Foresters have successfully described the size of these organs for individuals as functions of stem diameter at breast height (D; e.g., Le Goff and Ottorini 2001; Lambert et al. 2005), and we do as well:

$$A(D) = \pi \alpha^\theta D^\theta,$$
$$Q_{X,x}(D) = R_{X,x} \pi \alpha^\theta D^\varphi,$$
$$B(D) = aD^b, \tag{G1}$$
$$Z(D) = hD^\beta,$$

where $A(D)$ is projected crown area, $Q_{X,x}(D)$ is living fine root carbon, $B(D)$ is wood carbon, and $Z(D)$ is height. The remaining parameters scale the relationships. A virtue of our approach with respect to projected crown area is that we are not committed to any particular geometry, consistent with the variable crown shapes that canopy trees assume when assembled in a closed canopy. Using forestry data, we show in appendix A that

$$\theta \approx \varphi \approx b - 1. \tag{G2}$$

As in earlier versions of the PPA (Strigul et al. 2008), we assume that fecundity is proportional to $A(D)$ for canopy individuals and 0 for understory individuals.

Nitrogen and Light Availability

The purpose of our model is to understand the community dynamics of nitrogen-limited forests, which play out at timescales of decades to centuries and during which total system nitrogen is approximately constant (Bond-Lamberty et al. 2006), with relatively small inputs balanced by comparable losses (Menge et al. 2009). Consequently, total nitrogen, N_T, is effectively conserved within the system:

$$N_T \equiv N_P + N_M + N_H + N_L, \tag{G3}$$

where the nitrogen pools, N, are subscripted for plant (P), soil mineral (M), high-quality organic soil (H), and low-quality organic soil (L).

In the short term, nitrogen availability to plants is determined by the size of the nitrogen pool that is bound to organic molecules (the "organic pool") and the rate at which microbes mineralize that organic pool to plant-available forms (net after microbial immobilization). In addition to temperature and moisture, plant litter quality determines the rate at which microbes can mineralize organic nitrogen. Although the range of plant litter quality forms a continuum from slowly decomposed to quickly decomposed, values of particular compounds across this range are bimodally distributed. Cellulose, lignin, tannins, and materials rich in secondary compounds decompose relatively slowly; amino acids, phenols, and simple carbohydrates decompose relatively quickly (Plante and Parton 2007). It is for this reason that we separate the soil organic pool into N_L and N_H, with associated decomposition rates d_L and d_H (Berndt 2008). Moreover, in a nitrogen-limited system, plant uptake of soil mineral nitrogen is orders of magnitude faster (minutes to days) than turnover times in the plant and organic soil pools (months to decades), and thus can be approximated as instantaneous. As a result, the standing pool of mineral nitrogen, N_M, is approximately 0 relative to the other pools:

$$N_T \approx N_P + N_H + N_L. \tag{G4}$$

We define the following system, where nitrogen cycles between N_H and N_P and between N_L and N_P, and N_P loses

nitrogen at rate γ via senescence, mortality, and disturbance, with fraction ψ returning to N_H and fraction $1 - \psi$ returning to N_L:

$$\frac{dN_P}{dt} = d_H N_H + d_L N_L + \gamma N_P, \tag{G5}$$

$$\frac{dN_H}{dt} = -d_H N_H + \psi \gamma N_P, \tag{G6}$$

$$\frac{dN_L}{dt} = -d_L N_L + (1 - \psi)\gamma N_P. \tag{G7}$$

It is because we assume that plants take up all mineralized nitrogen that d_H and d_L appear as uptake rates in equation (G5).

At equilibrium,

$$\hat{N}_P = N_T \frac{d_L d_H}{\psi(1 - \psi)\gamma^2} \left/ \left[\frac{d_L d_H}{\psi(1 - \psi)\gamma^2} + \frac{d_L}{(1 - \psi)\gamma} + \frac{d_H}{\psi\gamma} \right], \right. \tag{G8}$$

$$\hat{N}_H = N_T \frac{d_L}{(1 - \psi)\gamma} \left/ \left[\frac{d_L d_H}{\psi(1 - \psi)\gamma^2} + \frac{d_L}{(1 - \psi)\gamma} + \frac{d_H}{\psi\gamma} \right], \right. \tag{G9}$$

$$\hat{N}_L = N_T \frac{d_H}{\psi\gamma} \left/ \left[\frac{d_L d_H}{\psi(1 - \psi)\gamma^2} + \frac{d_L}{(1 - \psi)\gamma} + \frac{d_H}{\psi\gamma} \right]. \right. \tag{G10}$$

The equations for $\hat{N}_P$, $\hat{N}_H$, and $\hat{N}_L$ describe the concentration of nitrogen residing in each of the three pools at equilibrium and sum to N_T. From a plant's perspective, the equilibrial nitrogen mineralization rate (net after microbial immobilization), N_{avail}, is the sum of the rates from the slow and fast pools:

$$N_{avail} = d_H \hat{N}_H + d_L \hat{N}_L. \tag{G11}$$

Because d_L is smaller than both d_H and γ, and is frequently much smaller (e.g., Alvarez-Sanchez and Enriquez 1996), we can approximate N_{avail} using a Taylor series, expanding N_{avail} around $d_L \approx 0$:

$$N_{avail} \approx \frac{d_L}{1 - \psi} N_T. \tag{G12}$$

Here we have derived an approximation of N_{avail} for a monoculture at equilibrium that depends only on total nitrogen in the system, the decomposition rate of low-quality soil organic material, and the fractional composition of litter in terms of high and low quality. The importance of these three terms is based on the fact that a given nitrogen molecule will spend only a relatively brief time in N_P and N_H before returning to N_L for a relatively long time. Thus, d_L directly controls the fate of nitrogen molecules in the very large slow pool itself and indirectly controls the sizes of $\hat{N}_P$ and $\hat{N}_H$ by controlling how much nitrogen is in "circulation" outside of $\hat{N}_L$.

Equation (G12) greatly simplifies our equilibrial forest model without seriously compromising its realism by allowing us to replace a dynamical nitrogen cycling model with just one value. The approximation retains the parts of the cycle that have large effects on the results, while omitting features that greatly complicate the analysis despite their small impacts. The analysis of our model spans a gradient in N_{avail} that, given the physical and physiological constraints on the ranges of possible values for d_L and ψ, is perhaps best thought of as arising from a gradient in N_T. Such gradients abound (Post et al. 1985) and are the legacies of processes at large timescales (Menge et al. 2009).

Light is a directional resource that creates fundamentally different competitive interactions than those of soil resources (Weiner 1990; Dybzinski and Tilman 2007). Taller individuals receive more light than individuals below them. Within an individual, higher leaves receive more light than lower leaves. Our model deals with both the between- and within-individual asymmetries explicitly using Beer's law light extinction through crowns of leaf area index $L_{X,x}$. Note that in contrast to empirical measures of LAI, which are made at the ecosystem level, we define LAI at the individual level as the total one-sided leaf area of an individual divided by its projected

crown area. 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.

If I_C^0 is the light intensity at the top of the canopy, $L_{C,r}$ is the uniform canopy LAI in a monoculture, and k is the light extinction coefficient, then the light intensity of a canopy individual's lowest leaves is

$$I_{C,x}^{bottom} = I_C^0 e^{-kL_{C,x}}, \tag{G13}$$

the light intensity at the top of the understory is

$$I_U^0 = I_C^0 e^{-kL_{C,r}\zeta}, \tag{G14}$$

and the light intensity of an understory individual's lowest leaves is

$$I_{U,x}^{bottom} = I_U^0 e^{-kL_{U,x}}. \tag{G15}$$

The parameter ζ is between 0 and 1 and scales $L_{C,r}$ and/or k to phenomenologically account 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. We include within-individual light extinction in our calculations of photosynthesis in the next section.

Nitrogen and Carbon Capture via Root Competition and Photosynthesis

Root competition is a complex and incompletely understood phenomenon (Schenk 2006). Nevertheless, a few things are clear. The rate-limiting step in nitrogen uptake in most natural systems is diffusion through the soil (Chapin 1980; Raynaud and Leadley 2004; Craine et al. 2005; Lambers et al. 2008), suggesting that despite important differences in root physiology and morphology (Eissenstat 1997; Eissenstat and Yanai 1997), to a first approximation, fine root mass is the greatest determinant of uptake rate and thus competitive ability (Casper and Jackson 1997; Raynaud and Leadley 2004; Lambers et al. 2008). We parameterize fine root mass, $R_{X,x}$, in units of living fine root carbon per crown area, which is positively correlated with the strength of the nitrogen diffusion gradient (Casper and Jackson 1997). We recognize that mycorrhizal associations have the potential to change both nitrogen diffusion gradients and the "exchange rate" of nitrogen acquired per carbon expended, but this important area of ecology is not yet well enough quantified to allow us to incorporate it into our model.

As in earlier models of mean field competition for belowground resources (e.g., Tilman 1988; Reynolds and Pacala 1993; Rees and Bergelson 1997), we assume that the roots of competing plants overlap completely and are uniformly distributed throughout the soil. There are compelling game theoretic reasons to expect plant roots to overlap (e.g., O'Brien et al. 2007), and harvests and tracer studies have demonstrated that the roots of tree species extend well past the drip line (Gilman 1988; Stone and Kalisz 1991; Casper et al. 2003) and are extensively commingled (Gottlicher et al. 2008). We assume that, at minimum, nitrogen-limited plants in closed-canopy forests will possess enough fine root density so that no mineral nitrogen is leached from the system when they are active (i.e., that they can, at minimum, "outcompete gravity"). Consistent with this assumption, studies of unpolluted temperate forests show very low levels of leached mineral nitrogen (e.g., Hedin et al. 1995).

Assuming the same physiology and morphology among strategies (as we do here), the total nitrogen captured by an individual j of stage X and strategy x per unit time, $K_{X,x,j}$, is simply equal to its share (numerator) of the total stand fine root mass (denominator) multiplied by the total amount of nitrogen available per unit time (Berendse and Elberse 1990):

$$K_{X,x,j} = \frac{Q_{X,x,j}(D_j)}{\sum\limits_{i=1}^{n_{C,m}} Q_{C,m}(D_i) + \sum\limits_{i=1}^{n_{C,r}} Q_{C,r}(D_i) + \sum\limits_{i=1}^{n_{U,m}} Q_{U,m}(D_i) + \sum\limits_{i=1}^{n_{U,r}} Q_{U,r}(D_i)} N_{avail}T, \tag{G16}$$

where D_j is the stem diameter of individual j, T is the total habitat area, i indexes individuals, and $n_{X,x}$ counts individuals. Note that equation (G16) is the result of competition for nitrogen; mineralized nitrogen is divided

among the plants in proportion to their relative fine root mass. Given the allometry of fine root mass (eqq. [G1], [G2]), dividing both sides by crown area yields $N_{X,x}$, nitrogen uptake on a per crown area basis:

$$N_{X,x} = \frac{R_{X,x}}{R_{C,m}\sum_{i=1}^{n_{C,m}}A(D_i) + R_{C,r}\sum_{i=1}^{n_{C,r}}A(D_i) + R_{U,m}\sum_{i=1}^{n_{U,m}}A(D_i) + R_{U,r}\sum_{i=1}^{n_{U,r}}A(D_i)}N_{avail}T, \tag{G17}$$

In anticipation of the adaptive dynamics problems that follow, we assume that strategy r is common and strategy m is rare. This means that

$$\sum_{i=1}^{n_{C,m}}A(D_i) + \sum_{i=1}^{n_{U,m}}A(D_i) \ll \sum_{i=1}^{n_{C,r}}A(D_i) + \sum_{i=1}^{n_{U,r}}A(D_i). \tag{G18}$$

If we further assume that the sum of the canopy crown areas is equal to the total habitat area (i.e., the canopy is closed),

$$\sum_{i=1}^{n_{C,r}}A(D_i) \approx T, \tag{G19}$$

and that the total fine root contribution of understory individuals is small relative to the canopy (Le Goff and Ottorini 2001),

$$R_{U,r}\sum_{i=1}^{n_{U,r}}A(D_i) \ll R_{C,r}\sum_{i=1}^{n_{C,r}}A(D_i), \tag{G20}$$

then nitrogen uptake per projected crown area (eq. [G17]) may be approximated as

$$N_{X,x} \approx \frac{R_{X,x}}{R_{C,r}}N_{avail}. \tag{G21}$$

Note that equation (G21) 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 or C and x with either r or m.

Annual carbon gain of an individual is determined by the light at the top of its crown, the light extinction through its crown, the relationship between light and photosynthesis, and the duration of the growing season. As shown in figure 2 in the main text, we use a simplified model of photosynthesis in which A_{max} is a leaf's maximum rate of net carbon fixation per area (gross carbon capture minus leaf maintenance respiration) under light saturation, q is the leaf respiration rate, and Φ is the quantum yield. Note that empirically, greater A_{max} typically comes at the expense of proportionately greater q, though for the sake of generality we do not explicitly model that relationship here. To convert to a yearly timescale, net carbon gain is multiplied by s, which will be positively correlated with growing season length and negatively correlated with factors that decrease annual carbon capture, such as water limitation. Annual net photosynthesis measured on a per crown area basis, $E_{X,x}$, is the integral of photosynthesis through an individual's crown (i.e., for all layers from the top of the crown to $L_{X,x}$), assuming Beer's law light extinction due to self-shading, multiplied by s.

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 $\tilde{I} = (A_{max} + q)/\Phi$ (fig. 2 in the main text). In case 1, the entire $L_{X,x}$ is light saturated, such that $I_X^0 > \tilde{I}$ and $I_{X,x}^{bottom} \geq \tilde{I}$:

$$E_{X,x} = s\left(\int_0^{L_{X,x}} A_{max}dy\right) = sA_{max}L_{X,x}. \tag{G22}$$

In the case 2, part of the $L_{X,x}$ is light saturated and part is light limited, such that $I_X^0 > \tilde{I}$ and $I_{X,x}^{bottom} < \tilde{I}$. Here, we must define and solve for $\tilde{L}_X$, the leaf layer at which light saturation switches to light limitation:

$$\frac{A_{max} + q}{\Phi} = I_X^0 e^{-k\tilde{L}_X} \Rightarrow \tilde{L}_X = \frac{1}{k}\ln\left(\frac{\Phi I_X^0}{A_{max} + q}\right). \tag{G23}$$

Its value will be the same for invaders and residents, which is why no x subscript appears. With this, we can calculate $E_{X,x}$:

$$
E_{X,x} = s\left[\int_0^{\tilde{L}_X} A_{max}\,dy + \int_{\tilde{L}_X}^{L_{X,x}} (\Phi I_X^0 e^{-ky} - q)\,dy\right]
$$

$$
= s\left\{\frac{A_{max} + q}{k}\left[1 + \ln\left(\frac{\Phi I_X^0}{A_{max} + q}\right)\right] - \frac{\Phi I_X^0}{k}e^{-kL_{X,x}} - qL_{X,x}\right\}. \tag{G24}
$$

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

$$
E_{X,x} = s\left[\int_0^{L_{X,x}} (\Phi I_X^0 e^{-ky} - q)\,dy\right] = s\left[\frac{\Phi I_X^0}{k}(1 - e^{-kL_{X,x}}) - qL_{X,x}\right]. \tag{G25}
$$

We note that in our treatment, we always assume that $I_C^0 > \tilde{I}$, and thus canopy trees are never in case 3. In contrast, because light at the top of understory individuals is reduced by the canopy's shade, understory individuals are often in case 2 or 3.

Nitrogen and Carbon Allocation

Because leaves contain the nitrogen-demanding enzyme rubisco used to fix carbon, nitrogen concentration is clearly related to function (e.g., maximum photosynthetic rate; Evans 1989). Moreover, leaves represent the dominant nitrogen demand in trees and have higher nitrogen concentrations than any other organ (Whittaker et al. 1979; Reich et al. 2008). Trees respond to increased nitrogen primarily through increases in leaf number, and only secondarily through increases in leaf nitrogen concentration (Chapin 1980; Farquhar et al. 2002). The role of nitrogen in fine roots and living wood is less clear; certainly some of the nitrogen is used to maintain basic cell metabolism and ion gradients; some may be used to process compounds for use in the leaves and elsewhere; and some may be in transit. Because diffusion through the soil, not transport across the fine root cell membrane, is the rate-limiting step in nitrogen-limited systems (Chapin 1980; Raynaud and Leadley 2004; Lambers et al. 2008), the total amount of nitrogen used for the transport machinery need not scale with fine root system size and a simple consideration of kinetics would suggest that higher fine root nitrogen concentrations should decrease nitrogen uptake rates per root (Bloom et al. 1985).

For the purposes of this model, we sidestep these important but poorly understood relationships by focusing only on the fraction of total nitrogen uptake that is committed to leaves, with the remainder going to an unspecified black box of fine roots, living wood, reproductive structures, and symbionts. We impose a stoichiometric constraint on an individual's ability to build LAI:

$$
L_{X,x} \le \frac{N_{X,x}\rho}{\delta_L\gamma_L f}, \tag{G26}
$$

where nitrogen uptake per projected crown area, $N_{X,x}$, is defined by equation (G21), ρ is the fraction of nitrogen taken up that is allocated to foliage; δ_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 δ_L); f is the fraction of nitrogen lost from senesced foliage; and γ_L is leaf turnover.

Fixed carbon is allocated to plant organs and the growth of those organs:

$$
\begin{aligned}
A(D)E_{X,x} = \ &A(D)(1 + \kappa_L)\gamma_L ML_{X,x} \\
&+ A(D)[(1 + \kappa_R)\gamma_R + \Omega]R_{X,x} \\
&+ \frac{dA(D)}{dt}(1 + \kappa_L)ML_{X,x} \\
&+ \frac{dA(D)}{dt}(1 + \kappa_R)R_{X,x} \\
&+ A(D)(1 + \kappa_L)M\frac{dL_{X,x}}{dt} \\
&+ A(D)(1 + \kappa_R)\frac{dR_{X,x}}{dt} \\
&+ A(D)\omega_C \\
&+ \frac{dB(D)}{dt},
\end{aligned}
\tag{G27}
$$

where $A(D)$ is projected crown area as a function of stem diameter, $E_{X,x}$ is the net photosynthetic rate (eqq. [G22], [G24], [G25]), γ_L is leaf turnover, M is leaf carbon per one-sided leaf area, κ_L is the respiratory cost of building leaves, γ_R is fine root turnover, κ_R is the respiratory cost of building fine roots, Ω is the maintenance respiration rate of fine roots, ω_C is the annual build and maintenance cost of fecundity per projected crown area, and $B(D)$ is wood mass as a function of stem diameter. The equation does not include foliage maintenance respiration, as this is already subsumed in the calculation of net photosynthetic rate. The first two terms on the right-hand side (RHS) describe the carbon costs of existing foliage and fine roots. The third and fourth terms describe the costs incurred by an expanding annulus of new growth. The fifth and sixth terms describe the costs incurred by changing per projected crown area foliage and fine root investments. The seventh term describes the cost of fecundity. The final term describes the change in wood mass, which includes stems, branches, and twigs aboveground and coarse roots of all sizes belowground. We assume negligible wood turnover and respiration.

We show in appendix B that terms associated with a new annulus of growth and changed per crown area $L_{X,x}$ and $R_{X,x}$ are small and do not impact the implications of the model. Thus, this conservation equation may be greatly simplified and reordered,

$$
\frac{1}{A(D)}\frac{dB(D)}{dt} = E_{X,x} - (1 + \kappa_L)\gamma_L ML_{X,x} - [(1 + \kappa_R)\gamma_R + \Omega]R_{X,x} - \omega_C,
\tag{G28}
$$

to emphasize that carbon allocated to wood increment (left-hand side) is defined by what remains from net photosynthesis (RHS, first term) after allocating to foliage construction (RHS, second term), fine root construction and respiration (RHS, third term), and reproductive structure construction and respiration (RHS, fourth term). Wythers et al. (2005) developed an ecosystem model that allocates carbon in this manner and showed that it accurately predicted both short-term carbon fluxes and long-term forest production of well-measured forests. We can convert equation (G28) into stem diameter growth rate, $G_{X,x} \equiv dD/dt$, using the allometric equations (eqq. [G1], [G2]):

$$
\frac{dB(D)}{dt} = \frac{dB(D)}{dD}\frac{dD}{dt} = (\theta + 1)aD^\theta\frac{dD}{dt},
\tag{G29}
$$

and thus,

$$
G_{X,x} \approx g\{E_{X,x} - (1 + \kappa_L)\gamma_L ML_{X,x} - [(1 + \kappa_R)\gamma_R + \Omega]R_{X,x} - \omega_C\},
\tag{G30}
$$

where

$$
g = \frac{\pi\alpha^\theta}{(\theta + 1)a}.
\tag{G31}
$$

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Notice that as a consequence of the allometric equations that we use (eqq. [G1], [G2]) and justify in appendix A, stem diameter growth rates $G_{X,x}$ are constant and independent of D, provided that $L_{X,x}$ and I_x^0 are constant. Different strategies will have different $G_{X,x}$ because they have different $L_{X,x}$, $E_{X,x}$, and $R_{X,x}$.

By omitting carbon consumed by respiration, our simplified carbon allocation equation (eq. [G30]) lends itself to comparison with empirical net primary productivity (NPP) measurements:

$$NPP_{foliage} \equiv \gamma_L M L_{X,x},$$

$$NPP_{wood} \equiv G_{X,x}/g,$$

$$NPP_{fine\ root} \equiv \gamma_R R_{X,x}, \qquad\qquad (G32)$$

$$NPP_{aboveground\ wood} = \Lambda \cdot NPP_{wood}$$

$$NPP_{belowground\ wood} = (1 - \Lambda) \cdot NPP_{wood},$$

where Λ is the fraction of wood allocated aboveground. Note that all five values are expressed in common units (g_{carbon} m^{-2} year^{-1} for our parameterization; table G1). Relative NPP of any component is found by dividing it by the sum of $NPP_{foliage}$, NPP_{wood}, and $NPP_{fine\ root}$.

Stem Growth Rate and the Perfect Plasticity Approximation of Height-Structured Competition

To understand the concept underlying the PPA, it is useful to first consider a forest simulator such as SORTIE (Pacala et al. 1996; Strigul et al. 2008), in which each simulated tree situates its crown symmetrically above its perfectly vertical stem. In SORTIE, the crowns of neighbors may interdigitate, and a tree that is half shaded and half exposed will build leaves equally in both regions. Neither phenomenon is observed in real forests because real trees proliferate branches in empty space, maintain growth toward empty space and away from neighbors, and drop branches that become overtopped (Putz et al. 1984; Purves et al. 2007). As more crown plasticity and phototropism is allowed in a simulator, horizontal canopy space fills more completely (Strigul et al. 2008). The PPA takes this to its asymptotic limit, where the canopy becomes totally filled, with no overlap among the crowns of canopy trees, and the canopy crown join height $\tilde{Z}_r$ is uniform across a stand. With the PPA, it becomes possible to classify individual trees as being in the canopy (as tall as or taller than the minimum canopy crown height $\tilde{Z}_r$) or in the understory (shorter than $\tilde{Z}_r$) without knowing their spatial locations.

The mathematics of the PPA are fully described elsewhere (Adams et al. 2007; Strigul et al. 2008), but we briefly review their essential features here. We note that these previous publications had assumed a value of 2 for θ and do not include it as an explicit parameter. Thus, some formulas appear slightly differently here. The PPA is nonspatial (horizontally) and includes no explicit gaps. In the simplest and analytically tractable version, growth and death rates do not depend on size either in the understory or overstory but do change from understory to overstory. Understory individuals grow stems at rate $G_{U,x}$ and die at rate μ_U. They transition to the canopy when their stems equal $\tilde{D}_r$, the diameter that is allometrically (eq. [G1]) related to $\tilde{Z}_r$ rate $G_{C,x}$, whereupon they die at rate μ_C and produce new understory individuals at rate F per crown area. In a stable-size-distribution (i.e., equilibrial), closed-canopy monoculture, the total canopy crown area is fixed (and equal to the habitat area), and thus the influx of new understory individuals is fixed.

Notice that, in contrast to previous publications (Adams et al. 2007; Strigul et al. 2008), we now explicitly calculate $G_{C,x}$ and $G_{U,x}$ as functions of resource availability, as described in the previous sections. Specifically, given values of $L_{X,x}$ and $R_{X,x}$, one can calculate both $G_{C,x}$ and $G_{U,x}$ using equation (G30), with equations (G22), (G24), or (G25) providing the $E_{X,x}$ term. To be congruent with the simplest version of the PPA, $G_{C,x}$ and $G_{U,x}$ must be constant, which will be true provided individuals maintain their allocational strategies through time and that the allocational shifts between understory and canopy stages are fast relative to the lifetimes of average individuals (and hence negligible). We assume for the moment that allocational strategies are constant for a given stage, but our ESS analysis below reveals that deviations from constant ESSs (for a particular soil nitrogen availability) are less competitive. In appendix B, we show that ignoring the full carbon accounting required to change from $L_{U,x}$ to $L_{C,x}$ and from $R_{U,x}$ to $R_{C,x}$ as individuals transition from the understory stage to the canopy stage has a negligible effect on our calculation of lifetime reproductive success. Thus, our model of individual

trees competing for light and nitrogen generates constant $G_{U,x}$ and constant $G_{C,x}$, consistent with the analytically tractable version of the PPA as described in Strigul et al. (2008).

With the PPA, we calculate an individual's expected lifetime reproductive success (or fitness, W_x) by summing its total fecundity over its lifetime. To do this for an average individual, we must calculate the average fraction of understory individuals that will survive to the canopy, assuming their initial diameter is negligible:

$$\exp\left(-\frac{\mu_U}{G_{U,x}}\tilde{D}_r\right) \tag{G33}$$

where $\tilde{D}_r$ is the diameter of strategy r individuals at the transition from understory to canopy (the diameter corresponding to height $\tilde{Z}_r$; eq. [G1]). The fraction of individuals that entered the canopy and then survived for τ years is

$$\exp\left(-\mu_C\tau\right), \tag{G34}$$

and the fecundity of an individual that has survived τ years in the canopy is

$$FA(D) = F\pi\alpha^\theta(\tilde{D}_r + G_{C,x}\tau)^\theta. \tag{G35}$$

Combining these three equations, we integrate over all time to calculate fitness:

$$W_x = \exp\left(-\frac{\mu_U}{G_{U,x}}\tilde{D}_r\right)\int_0^\infty \exp(-\mu_C\tau)F\pi\alpha^\theta(\tilde{D}_r + G_{C,x}\tau)^\theta d\tau. \tag{G36}$$

By changing variables twice, the solution is an incomplete gamma, which we can reasonably approximate as a complete gamma:

$$W_x \approx F\pi\alpha^\theta\Gamma(\theta + 1)\frac{G_{C,x}^\theta}{\mu_C^{\theta+1}}\exp\left[-\left(\frac{\mu_U}{G_{U,x}} - \frac{\mu_C}{G_{C,x}}\right)\tilde{D}_r\right], \tag{G37}$$

where $\Gamma(\ldots)$ represents the gamma function. The equation for W_x embodies the combined effects of interspecific (or interstrategic) competition for both nitrogen and light through its effects on both the canopy and understory stages of residents and invaders. The resident influences itself and the invader through its effects on nitrogen competition, light availability in the understory, and, by setting $\tilde{D}_r$, the length of time that individuals spend in the understory.

At equilibrium, each individual exactly replaces itself over its lifetime, that is, $W_r = 1$, and we are able to solve for $\tilde{D}_r$ in a monoculture:

$$\tilde{D}_r \approx \left(\frac{\mu_U}{G_{U,r}} - \frac{\mu_C}{G_{C,r}}\right)^{-1}\ln\left[F\pi\alpha^\theta\Gamma(\theta + 1)\frac{G_{C,r}^\theta}{\mu_C^{\theta+1}}\right]. \tag{G38}$$

For closed-canopy forests, $\tilde{D}_r$ is always greater than or equal to 0. When this condition is not true, the canopy will open, and a different set of tools and assumptions are needed to evaluate dynamics. Here, we restrict our analysis to allocation strategies that are capable of sustaining closed-canopy conditions in monoculture.

Because $\mu_U > \mu_C$ and $G_{U,x} \leq G_{C,x}$, it will frequently be the case that $\mu_U/G_{U,x} \gg \mu_C/G_{C,x}$ and thus that

$$\tilde{D}_r \approx \frac{G_{U,r}}{\mu_U}\ln\left[F\pi\alpha^\theta\Gamma(\theta + 1)\frac{G_{C,r}^\theta}{\mu_C^{\theta+1}}\right] \tag{G39}$$

and

$$W_x \approx F\pi\alpha^\theta\Gamma(\theta + 1)\frac{G_{C,x}^\theta}{\mu_C^{\theta+1}}\exp\left(-\tilde{D}_r\frac{\mu_U}{G_{U,x}}\right). \tag{G40}$$

For numerical work, we use the more complete expressions (eqq. [G37], [G38]). For analytical work we use the simplified expressions (eqq. [G39], [G40]).

Determining Evolutionary Stable Strategies

We analyze our model to determine the change in ESS allocations to foliage, wood, and fine roots with N_{avail}. We can use the equation for the fitness of a rare invader W_{m} in the equilibrium conditions created by a resident r (eq. [G40]) to find the ESS, if it exists. See Strigul et al. (2008) for a proof that an equilibrial monoculture of the PPA model is locally stable for reasonable parameter values, as is required of this analysis. By definition, the expected W_{r} of a resident individual in an equilibrial monoculture is 1; that is, it will exactly replace itself in its lifetime. Consistent with the assumptions of standard adaptive dynamics analyses (McGill and Brown 2007), we model a stand of infinite size and an invasion process of potentially infinite duration, such that any invader with W_{m} greater than 1 will successfully invade the resident. We use the term ESS to describe a strategy that, once established as a monoculture, cannot be invaded by any rare mutant strategy (McGill and Brown 2007). In other words, the ESS is a strategy r for which no W_{m} is greater than 1.

For a particular trait v, we find the ESS, v^*, by finding the maxima of W_{m} for v:

$$\left. \frac{dW_{\text{m}}(v_{\text{m}}, v_{\text{r}})}{dv_{\text{m}}} \right|_{v_{\text{m}}=v_{\text{r}}, v_{\text{r}}=v^*} = 0,$$

$$\left. \frac{dW_{\text{m}}^2(v_{\text{m}}, v_{\text{r}})}{d^2 v_{\text{m}}} \right|_{v_{\text{m}}=v_{\text{r}}, v_{\text{r}}=v^*} < 0, \tag{G41}$$

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. Because of their functional connection to $G_{\text{X,x}}$ (eq. [G30]), solutions for L_{X}^* and R_{X}^* uniquely determine G_{X}^*. We determine that the ESS values that we find are both global and convergence stable in appendix F.

Derivation of Theoretical Results

Result 1

Increasing ESS foliage with increasing nitrogen availability. Across a fertility gradient, as N_{avail} increases, the most competitive LAI in both the canopy L_{C}^* and the understory L_{U}^* increase up to the point of nitrogen saturation (fig. 3). The canopy light environment is unaffected by $L_{\text{U,r}}^*$, but the reverse is not true, so we begin by solving for L_{C}^*. We solve the ESS condition (eq. [G41]) using the growth rate equation (eq. [G30]) together with either light-saturated or dual-limited net photosynthesis (eqq. [G22], [G24]), assuming for the moment unlimited nitrogen availability to build foliage:

$$L_{\text{C}}^{*\text{sat}} = \frac{1}{k} \ln\left[\frac{s\Phi I_{\text{C}}^0}{(1 + \kappa_{\text{L}})\gamma_{\text{L}}M + sq} \right], \tag{G42}$$

where "sat" indicates that this is the nitrogen-saturated result. Interpretation of this equation is straightforward. The $L_{\text{C}}^{*\text{sat}}$ depends strongly on k, the light extinction coefficient; smaller k leads to greater $L_{\text{C}}^{*\text{sat}}$ because it decreases self-shading. Of those variables that may vary appreciably among species or habitats, increased $L_{\text{C}}^{*\text{sat}}$ occurs with increasing extrapolated net photosynthetic rate s or decreasing leaf turnover rate γ_{L}, leaf carbon per area M, or leaf dark respiration rate q. Because A_{max} and q are often positively correlated, decreasing A_{max} will likely increase $L_{\text{C}}^{*\text{sat}}$. At $L_{\text{C}}^{*\text{sat}}$, 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 (i.e., $N_{\text{C,r}}\rho/\delta_{\text{L}}\gamma_{\text{L}}f < L_{\text{C}}^{*\text{sat}}$; eq. [G26]), a strategy that builds as much foliage as it can (i.e., $N_{\text{C,r}}\rho/\delta_{\text{L}}\gamma_{\text{L}}f$) will invade a strategy that builds $L_{\text{C,r}}$ less than that (see "Result 5"). Thus,

$$L_{\text{C}}^* = \min\left(\frac{N_{\text{avail}}\rho}{\delta_L\gamma_{\text{L}}f}, L_{\text{C}}^{*\text{sat}} \right), \tag{G43}$$

where $N_{C,r}$ has been replaced (eq. [G21]; $m = r$ at the ESS) and L_C^{*sat} is defined by equation (G42).

Having calculated L_C^* and thus I_U^0 (via eq. [G14]) in a monoculture composed of competitively dominant canopy individuals, we are now in a position to determine L_U^*. In an analysis that parallels that of the canopy, we find

$$L_U^{*sat} = \frac{1}{k}\ln\left[\frac{s\Phi I_U^0}{(1 + \kappa_L)\gamma_L M + sq}\right] \tag{G44}$$

and

$$L_U^* = \min\left(\frac{N_{avail}\rho}{\delta_L\gamma_L f}\frac{R_U^*}{R_C^*}, L_U^{*sat}\right). \tag{G45}$$

After solving for R_U^* below (eq. [G47]) and substituting, one can show that the nitrogen-limited form of L_U^* is monotonically increasing with L_C^*/R_C^* and thus with N_{avail}.

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. This result provides constant $G_{C,x}$ and $G_{U,x}$ as assumed in the simple version of the PPA used here.

Result 2

Decreasing ESS fine root mass with increasing nitrogen availability. Across a soil fertility gradient as N_{avail} increases, the most competitive fine root mass R_X^* decreases monotonically. No closed-canopy R_X^* exists at low N_{avail} because successful invaders with greater $R_{C,m}$ drive the system into open-canopy, nonforest conditions (see app. C). For all N_{avail} sufficiently large, a stable R_X^* exists up to the point at which the canopy becomes nitrogen saturated (fig. 3).

The effects of $R_{U,r}$ on the canopy nitrogen environment are negligible, but the reverse is not true, so we begin by solving for R_C^*. We solve the ESS condition (eq. [G41]) using the simplified carbon conservation equation (eq. [G30]) together with $E_{C,m}$ case 2 (eq. [G24]; in app. C we show that no R_C^* exists for $E_{C,m}$ case 1):

$$R_C^* = \frac{s\Phi I_C^0 e^{-kL_C^*} - sq - (1 + \kappa_L)\gamma_L M}{(1 + \kappa_R)\gamma_R + \Omega}L_C^*. \tag{G46}$$

For reasonable parameter values, R_C^* decreases with N_{avail} for all values of R_C^* that generate closed-canopy forest (L_C^* is an increasing function of N_{avail}; eq. [G43]). Root mass R_C^* is both a global ESS and convergent stable (app. F). It is easy to show that R_C^* goes to 0 as L_C^* goes to L_C^{*sat} (eq. [G42]), 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).

Equation (G46) is a ratio. The quantum yield, Φ, 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_{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_{avail}. Simply put, R_C^* decreases with N_{avail} because the marginal benefit to greater root investment decreases while the cost remains fixed.

By reasonable approximation, resident understory individuals will have a negligible effect on the light environment and nitrogen availability for resident canopy individuals or invaders. We need not consider the case of a light-saturated understory, $E_{U,r}$ case 1 (eq. [G22]), because no R_C^* exists for closed-canopy, light-saturated

conditions. The answers for a partially light-limited understory, $E_{U,r}$ case 2 (eq. [G24]), or totally light-limited understory, $E_{U,r}$ case 3 (eq. [G25]), are the same:

$$R_U^* = \frac{1}{k}\frac{R_C^*}{L_C^*}\ln\left\{\frac{s\Phi I_U^0 L_C^*}{[sq + (1 + \kappa_L)\gamma_L M]L_C^* + [(1 + \kappa_R)\gamma_R + \Omega]R_C^*}\right\}. \tag{G47}$$

Root mass R_U^* is most sensitive to the variables outside the natural log, which reflect the dominant nitrogen (R_C^*) and light environments (L_C^*). It is both a global ESS and convergent stable (app. F).

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_{avail}. Having solved for L_C^* (eq. [G43]) and R_C^* (eq. [G46]), we need only substitute them into the carbon balance equation (eq. [G30]) to determine G_C^*:

$$G_C^* = \frac{\pi\alpha^\theta}{(\theta + 1)a}\left\{\frac{(A_{max} + q)s}{k}\left[1 + \ln\left(\frac{\Phi I_C^0}{A_{max} + q}\right)\right] - (kL_C^* + 1)\frac{s\Phi I_C^0}{k}e^{-kL_C^*} - \omega_C\right\}. \tag{G48}$$

Over the range of N_{avail} for which the model predicts closed-canopy forest, the term involving the exponent becomes less negative with increasing N_{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 (G48) differs from the equation for net photosynthesis (eq. [G24]) 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_{avail}.

It is also possible to solve analytically for G_U^* by a similar substitution. However, the resulting expression is neither simple nor illuminating. We omit it here.

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_{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 (app. C). Only after the canopy becomes dual limited with increasing N_{avail} does the possibility exist for an ESS closed-canopy forest. As N_{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^{*sat} (eqq. [G42], [G44]).

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 "optimal"). By design, our method for determining ESSs (eq. [G41]) finds those strategies that are uninvadible 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, that is, 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 R_C^* and growth rate G_C^* are not. This can be seen by asking whether any perturbation, ε, of the ESS leads to greater growth rate of the resident, $G_{C,r}$. If it does, the strategy is not optimal in this sense.

Under nitrogen-limited conditions, plants use all of the nitrogen they acquire with a particular $R_{C,m}$ to build $L_{C,m}$ (eqq. [G43], [G45]), so the only stoichiometrically possible perturbation in $L_{C,m}$ itself (independent of $R_{C,m}$) is a decrease (see inequality in eq. [G26]). Using equations (G24) and (G30) to calculate $G_{C,m}$ (eq. [G30]) with the perturbation term $L_C^*(1 - \varepsilon)$ and a Taylor series expanding the result around $\varepsilon \sim 0$, we find the change in the resident growth rate, $\Delta G_{C,r}$, for a perturbation that decreases $L_{C,r}$:

$$\Delta G_{C,r} = [-s\Phi I_C^0 e^{-kL_C^*} + sq + (1 + \kappa_L)\gamma_L M]L_C^*. \tag{G49}$$

This will be negative provided $L_C^* < L_C^{*sat}$, which is true here by assumption.

Under nitrogen-saturated conditions, plants can build $L_{C,m}$ greater than L_C^{*sat}. A parallel analysis to that above shows that a perturbation of increased $L_{C,m}$ under nitrogen-saturated conditions leads to lower growth rates provided $L_C^* = L_C^{*sat}$, which is true here by assumption. Taking the nitrogen-limited and nitrogen-saturated results together, it follows that L_C^* maximizes growth rates in monoculture, that is, is "optimal."

In contrast, any perturbation that reduces R_C^*, that is, $R_C^*(1 - \varepsilon)$, invariably leaves more carbon to allocate to wood and thus increases $\Delta G_{C,r}$:

$$\Delta G_{C,r} = (1 + \kappa_R)\gamma_R R_C^* + \Omega R_C^* > 0. \tag{G50}$$

Thus, R_C^* and G_C^* (via its functional relationship with R_C^*) do not maximize growth rates in monoculture, that is, are not "optimal."

Table G1. Traits subject to evolutionarily stable strategy analysis: model parameters and subscripts

Symbol	Value	Units	Description
$L_{X,x}$	Any	$m^2\ m^{-2}$	Leaf area index; one-sided area of leaves per ground surface area of an individual, proportional to carbon allocation to foliage
$G_{X,x}$	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; coefficient relating D to $R_{X,x}$, proportional to carbon allocation to fine roots
Allometric relationships:			
D	Any	cm	Stem diameter
A	Any	m^2	Individual tree crown area (projected)
α	.1	$m^{2/\theta}\ cm^{-1}$	Power law coefficient relating D to A
θ	1.4	None	Power law coefficient relating D to A
$Q_{X,x}$	Any	g_{carbon}	Individual tree fine root mass
φ	1.4	None	Power law exponent relating D to $R_{X,x}$
B	Any	g_{carbon}	Individual tree mass
a	81.5	$g_{carbon}\ cm^{-(\theta+1)}$	Power law coefficient relating D to B
b	2.4	None	Power law exponent relating D to B
Z	Any	m	Individual tree height
h	3.58	$m\ cm^{-\beta}$	Power law coefficient relating D to H
β	.5	None	Power law exponent relating D to H
Nitrogen:			
T	Any	m^2	Total habitat area
N_T, N_M, N_P, N_H, N_L	Any	$g_N\ m^{-2}$	Nitrogen pools: total habitat, soil mineral, plant, high-quality soil organic, low-quality soil organic, respectively
γ	...	$year^{-1}$	Whole-plant nitrogen loss rate
d_H, d_L	...	$year^{-1}$	High- and low-quality soil organic decomposition rates, respectively
ψ	0–1	Fraction	Fraction of plant nitrogen that goes to the high-quality soil organic pool
N_{avail}	Any	$g_N\ m^{-2}\ year^{-1}$	Available nitrogen per area
$K_{X,x}$	Any	g_N	Total nitrogen uptake of an individual
$N_{X,x}$	Any	$g_N\ m^{-2}$	Nitrogen uptake of an individual per crown area
ρ	.5	None	Fraction of total plant nitrogen uptake allocated to leaves
δ_L	1.595	$g_N\ m^{-2}$	Nitrogen per unit leaf area
f	.5	None	Fraction of nitrogen lost from senesced foliage
γ_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}	9.9×10^{-5}	$g_{carbon}\ LAI^{-1}\ m^{-2}\ s^{-1}$	Maximum net carbon assimilation rate (see fig. 2)
q	9.9×10^{-6}	$g_{carbon}\ LAI^{-1}\ m^{-2}\ s^{-1}$	Dark respiration rate (see fig. 2)
Φ	3.27×10^{-4}	$g_{carbon}\ LAI^{-1}\ m^{-2}\ s^{-1}$ $PAR^{-1}\ PAR_0$	Quantum yield of light-limited net photosynthesis (see fig. 2)
s	2.26×10^6	$s\ year^{-1}$	Scale conversion between measured (s^{-1}) and yearly net photosynthesis
k	.5	LAI^{-1}	Light extinction coefficient per crown depth
ζ	.75	None	Scales k and $LAI_{C,r}$ in Beer's law light extinction to calculate I_U^0
$\tilde{L}_X$	Any	LAI	Crown depth at which photosynthesis transitions from light saturated to light limited

Table G1 (*Continued*)

Symbol	Value	Units	Description
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
κ_L	.25	None	Foliage construction respiration, expressed as a fraction of leaf carbon
γ_R	.3	$year^{-1}$	Fine root turnover
κ_R	.25	None	Fine root construction respiration, expressed as a fraction of fine root carbon
Ω	.35	g_{carbon} g_{carbon}^{-1} $year^{-1}$	Fine root respiration rate
ω_C	34.6, 0	g_{carbon} m^{-2} $year^{-1}$	Carbon cost of producing seeds; 0 for understory individuals
g	8.14E^{-4}	cm $(g_{carbon}/m^2)^{-1}$	Scale conversion between net carbon per canopy area and diameter growth rate (eq. [G31])
Λ	.78	None	Fraction aboveground of the carbon allocated to wood
Perfect plasticity approximation:			
W_x	Any	individuals	Fitness or lifetime reproductive success of strategy x
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 as determined from height allometry (eq. [G1])
τ	Any	year	Years spent in the canopy stage
μ_X	.013, .038	$year^{-1}$	Mortality rate for 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. 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.

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