**Increased forest carbon storage with increased atmospheric CO2 despite nitrogen limitation: A game-theoretic allocation model for trees in competition for nitrogen and light**

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# Appendix S1 – Detailed model description and analysis

This paper relies on a mathematical model of forest dynamics and competitive optimization methods developed in a series of previous papers. The underlying model is a mechanistic individual-based spatial forest simulator, the Perfect Plasticity Approximation (PPA), from which we derive a series of integro-‐partial differential equations that govern the size-structured dynamics of each tree species at stand‐level (Strigul *et al.*, 2008). When calibrated with data on individual tree vital rates, the equations predict observed successional dynamics (Purves *et al.*, 2008).

Two critical derivations of the PPA motivate our analysis. First, the lifetime reproductive success (i.e. fitness) of an individual tree is calculated by summing over its growth rates and mortality rates during its understory and canopy stages and by assuming it has a constant fecundity per unit crown area while in the canopy. Its solution is:

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|  | (S1) |

where *LRS* is lifetime reproductive success; and are constants that scale crown area by stem diameter; *D* is the allometrically-related stem diameter at which a tree transitions from the understory to the canopy; and *G* are the mortality and growth rates (for the understory, subscript *U*, and canopy, subscript *C*); and is the Gamma Function.

The second critical derivation of the PPA that motivates our analysis recognizes that for a stand in dynamic equilibrium, each canopy tree will exactly replace itself in its lifetime, i.e. . With this, we can solve for , the allometrically-related stem diameter at which trees transition from the understory to the canopy (assuming they survive that long) in a stand in dynamic equilibrium:

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|  | (S2) |

This shows that increasing the canopy stem growth rate, , increases the canopy height and thus increases height-structured competition for light.

Although these more general features of the PPA model should not be forgotten, as they provide the rigorous justification for scaling from individual-level strategies to stand-level properties, our focus now narrows to describe how canopy growth rates depend on light, nitrogen, CO2, and competition. The special case that we study here makes the canopy growth rate a function of the individual’s physiology and allocation strategy, as well as the physiology and allocation strategies of its neighbors in the context of light and nitrogen limitation. We focus on canopy trees only because they dominate the land carbon sink. All other vital rates and parameters are held constant.

Dybzinski et al. (2011) coupled these equations to a dynamic nitrogen model, disallowed changes in litter chemistry that affect the decomposition rate of recalcitrant organic matter, and focused on times scales over which inputs and losses of total ecosystem nitrogen are small. These restrictions simplified the problem by making the rate of nitrogen mineralization approximately constant. Dybzinski et al. (2011) then developed competitive optimization methods to predict the winning foliage-wood-fine root allocation strategy as a function of the nitrogen mineralization rate and showed that the predictions match patterns of biomass allocation along natural productivity gradients (their Fig. 4).

A competitively optimal allocation strategy (i.e. the Evolutionarily Stable Strategy or ESS) is found by introducing a rare “challenger” strategy into a monoculture of a “resident” strategy, and then solving for the strategy that – as a resident – resists challenges by all other strategies and that – as a challenger – can invade any nearby resident strategy (Geritz *et al.*, 1998, McGill & Brown, 2007). Previous papers have shown that the most competitive challenger foliage-wood-fine root allocation strategy for trees while they are in the canopy is approximately the strategy that maximizes the stem growth rate of that challenger against a given resident in either early-successional or old growth forests (Purves *et al.*, 2008, Dybzinski *et al.*, 2011, Farrior *et al.*, 2013a). This is not surprising because canopy trees that are overtopped suffer greatly reduced fitness and because fecundity increases with crown size, which increases with stem size. Although lifetime reproductive success (i.e. fitness) is an increasing function of stem growth rate in the canopy, it is also a complicated function of investment in seed, the density-independent death rate in the canopy, and parameters governing understory growth and survival (Strigul *et al.*, 2008). However, allocation to fecundity can be neglected here because it is a small component of the carbon and nitrogen budgets (Whittaker *et al.*, 1979, Ladeau & Clark, 2006, McCarthy *et al.*, 2010).

The fact that trees change allocation dramatically when moving from the understory to the canopy argues that we may separately optimize understory and canopy allocation. We focus on the optimal canopy allocation in this paper, because we are interested in the size of the carbon sink, which is dominated by canopy trees (Farrior *et al.*, 2013a). Finally, we assume that the density-independent death rate of canopy trees (i.e. from wind throw) is independent of the foliage-wood-fine root allocation strategy. Although this is obviously debatable, we offer it as a useful beginning because the death rate in the canopy is probably affected most by factors other than those considered here, such as wood density and height-diameter allometry. As in Dybzinski et al. (2011), we consider three carbon pools: foliage, wood, and fine roots. However, we have expanded the number of nitrogen pools from three to four. Foliage and wood N:C is fixed at *λ* (0.057 gN gC-1) and *ω* (0.0024 gN gC-1, mean value in Kattge et al. 2011), respectively. Unlike Dybzinski et al. (2011), we divide the nitrogen in fine roots into “structural” and “metabolic” pools, with N:C ratios *σ* (0.001934 gN gC-1, mean value in Kattge et al. 2011 divided by 10) and *ρ* (gN gC-1), respectively. The structural pool is primarily the nitrogen in plant cell walls. The metabolic pool includes the nitrogen in proteins responsible for active transport of nitrate and ammonium and the metabolism that supports and fuels this activity. In a nitrogen-limited forest, nitrogen uptake by fine roots is obviously a critical component of fitness. Trees should invest in the metabolic pool so as to maximize net nitrogen gains. We assume that the rate of uptake of nitrate and ammonium by fine roots is proportional both to fine root biomass (*R*) and an increasing and concave-down function: *f*(*ρ*). This function equals zero at *ρ* = 0 simply because the root has no active transport proteins if it has no nitrogen in its metabolic pool. It is an increasing function of *ρ* because we assume that the density of active transport sites on a root hair increases with *ρ*, and it is a concave‐down function for two reasons. First, the probability that an active transport site will capture a nitrate or ammonium molecule once it touches the surface of a root hair must saturate at one as the density of active transport sites becomes large. Second, the density of transport sites on the surface of a root hair might saturate as *ρ* becomes large. If the nitrogen mineralization rate is a constant and all mineralized nitrogen is ultimately captured by canopy trees, then *N* gN m-2 yr-1 will be captured by a closed canopy forest (see Appendix G in Dybzinski *et al.* (2011) for a full derivation from a nitrogen cycle model).

**Model structure**

The nitrogen capture strategy of the resident strategy is given by its fine root mass per unit crown area, *R*r (gC m-2), and metabolic root stoichiometry *ρ*r, where the subscript “r” denotes a resident variable. The resident’s one-sided canopy leaf area index, *L*r (m2 m-2) and annual wood production rate *W*r (gC m-2 yr-1) are the solutions of the following two equations, the first of which closes a resident tree’s nitrogen budget and the second of which closes its carbon budget:

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|  | (S3) |

and

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| . | (S4) |

In addition to the parameters and variables described above, *p* is the fraction of nitrogen that is resorbed before senescence (0.5 unitless); *γ* is the leaf turnover rate (1 yr-1); *M* is the leaf mass per area (28 gC m-2); *t* is the turnover rate of fine roots (0.3 yr-1); *E*(*L*r) is the canopy-level gross photosynthetic rate as a function of *L*r (gC m-2 yr-1); *a* is the annual cost of leaves per leaf layer (57.37 gC m-2 yr-1); *b* is the annual cost of fine roots per root mass (1.6 gC gC-1 yr-1); *c* is the cost of wood per new wood mass (1 gC gC-1); and *F* is the NPP associated with reproduction (34.6 gC m-2 yr-1). Included within *a*, *b*, and *c* are the carbon costs of respiration and construction. See Dybzinski et al. (2011) for a detailed description of these parameters and their derivations (e.g. *a* and *b* are composed of other physiological parameters such as respiration rates and turnover times that we simply summarize here).

Belowground competition for nitrogen is assumed to be well-mixed, where all roots have access to the same resource pool, consistent with observational (Gilman, 1988, Stone & Kalisz, 1991, Casper *et al.*, 2003), tracer (Gottlicher *et al.*, 2008), and molecular-identification (Frank *et al.*, 2010, Jones *et al.*, 2011) studies of root systems, which show extensive comingling of individual root systems. This implies that to a first approximation, a challenger’s nitrogen uptake per ground area is proportional to the nitrogen mineralization rate and its *relative* uptake capacity (i.e. *R*m *f*(*ρ*m)/[*R*r *f*(*ρ*r)]) (Berendse & Elberse, 1990, Raynaud & Leadley, 2004, Craine *et al.*, 2005). Thus, a challenger strategy has a similar set of equations that closes its nitrogen and carbon budgets that takes this into account:

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|  | (S5) |

and

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| , | (S6) |

where “m” subscripts challenger strategies. Note that the resident equations above (Eqs. S3, S4) are simply a special case of the challenger equations (Eqs. S5, S6) when m = r.

We can solve Eq. (S5) for *L*m,

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| , | (S7) |

substitute the result into Eq. (S6), and set the result equal to zero:

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| . | (S8) |

We have defined a new function, *G*, that is an implicit function of *W*m, *R*m, and *ρ*m and which will become useful in a moment. Because *G* defines *W*m as an implicit function of *R*m, and *ρ*m, we may also write *W*m as *W*m(*R*m, *ρ*m).

To find the ESS strategy (denoted by “\*”) we need to maximize *W*m(*R*m, *ρ*m) with respect to *R*mand *ρ*m when evaluated at the resident strategy (Geritz *et al.*, 1998, McGill & Brown, 2007),

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| , | (S9) |

and verify that such a maximum is convergence-stable,

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| . | (S10) |

Using the implicit function theorem, we know that

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|  | (S11) |

and

|  |  |
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| . | (S12) |

The LHS of both Eq. (S11) and Eq. (S12) will be zero at the ESS according to Eq. (S9), which implies that the numerators on the RHS of both Eq. (S11) and Eq. (S12) will also be zero at the ESS, i.e.:

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|  | (S13) |

and

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| . | (S14) |

First, we will use Eq. (S14) to solve for *ρ*\*, which we will then use together with Eq. S13 to solve for *R\**.

**Solution for *ρ*\***

Together, Eqs. (S14) and (S8) yield the solution for *ρ\**:

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| . | (S15) |

The term in parentheses will be zero when the marginal return of gross photosynthesis on a marginal increase in LAI exactly equals the total costs of that marginal increase. In other words, this is the stopping point beyond which trees should not increase LAI and by which we define nitrogen saturation (see Eq. 13 in Dybzinski et al. 2011). Since we are here interested in solutions within the nitrogen-limited regime, where the term in parentheses will necessarily be positive, the ESS solution is found by

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| . | (S16) |

Using this together with Eq. (S7) yields

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| . | (S17) |

A simple function for *f*(*ρ*) that has the right properties (increasing, concave-down, and approaches zero at *ρ* = 0) is a power law: *zρu*, where 0 < *u* < 1. Using this functional form and the equation above,

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| . | (S18) |

This states that for competitively optimized trees, the total metabolic nitrogen in the fine root system (*R\*ρ*\*) is a simple fraction (*u*/*t*) of the nitrogen mineralization rate (*N*). This is a pleasing result because it provides a competitive optimization argument for the assumption in Dybzinski et al. (2011) that a roughly constant fraction of nitrogen is allocated to foliage, with the remainder going to other tissues in an unspecified way. As we describe below, the small wood N:C (*ω*) and structural fine root N:C (*σ*) are a small perturbation on this result. In what follows, we will use the result from *f*(*ρ*) = *zρu* because it offers the simplest algebraic results and is consistent with Dybzinski et al. (2011). Other functions that are tractable and yield similar results include: *f*(*ρ*) = *c*1*ρ*/(*c*2 + *ρ*) and *f*(*ρ*) = *c*1(1 – exp(*c*2*ρ*)), where *c*1 and *c*2 are constants.

Using the power law functional form, it can be verified that *ρ*\* is a fitness maximum according to Eq. (S9):

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|  | (S19) |

or

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| . | (S20) |

Everything outside the parentheses is necessarily positive, and because 0 < *u* < 1, the term in parentheses is necessarily negative. Similarly, *ρ*\* is convergence-stable according to Eq. (S10):

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| --- | --- |
|  | (S21) |

or

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| . | (S22) |

Again, because 0 < *u* < 1, the LHS is necessarily positive and the RHS is necessarily negative, making the inequality true.

**Solution for *R\****

Together, Eqs. (S13) and (S8) yield the solution:

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| . | (S23) |

or, using Eq. (S7) for *L*m and the result for *R\*ρ\** (Eq. S18),

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|  | (S24) |

where

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| . | (S25) |

Once a functional form for *E*(*L*) is chosen, this expression may be solved numerically. However, note that *ε*R is the ratio of fine root *structural* N:C to *total* foliage N:C, which is a small number, on the order of 0.1 or less, multiplied by the ratio of the turnover time of nitrogen in fine roots to the turnover time of nitrogen in foliage, which is close to unity. We can find a close approximation to the above expression by letting *ε*R = 0,

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| , | (S26) |

where we have subscripted *R*0\* to indicate that it is the solution when *ε*R is approximated as zero. The term outside the parentheses is necessarily positive, and the term inside the parentheses is positive if the marginal return of gross photosynthesis on a marginal increase in LAI is greater than the total costs of that marginal increase, i.e. if the tree is by definition nitrogen-limited (as discussed above in reference to Eq. (S15)). It is here, incidentally, that the careful reader is directed to note the goofy smiley face in Fig. 6m of the main text.

We verify that *R*0\* is a fitness maximum by taking the second derivative of Eq. (S8) with respect to *R*m (assuming *ε*R = 0) and then evaluating the result at *R*m = *R*r = *R*0\*. Using Eq. (S7) for *L*m (for which the second derivative with respect to *R*m is zero), the result is

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| . | (S27) |

The term in parentheses is squared and thus necessarily positive. The term outside the parentheses is the second derivative of the gross photosynthesis function, *E*(*L*) with respect to *L*. In the nitrogen-limited regime, the *first* derivative of *E*(*L*) with respect to *L* must be positive, i.e. gross photosynthesis must increase with LAI. However, a reasonable function for *E*(*L*) should saturate with increasing LAI because of self-shading, which means that the *second* derivative of *E*(*L*) with respect to *L* must be negative. Thus the second derivative is necessarily negative, indicating that *R*0\* is a fitness maximum (Eq. S9).

We verify that *R*0\* is convergence-stable according to (Eq. S10) (assuming *ε*R = 0) . Again, using Eq. (S7) for *L*m (for which the second derivative with respect to *R*m is zero), the condition for convergence stability becomes

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| , | (S28) |

where we have omitted the functional notation of *L*m to save space. At the equilibrium point, *R*m = *R*r = *R*0\*, the first term on the LHS is equal to the RHS, which reduces the expression to

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| . | (S29) |

As discussed in the analyses above, the term in the parentheses is necessarily positive in a nitrogen-limited stand. It is easy to show that the second derivative of *L*m (Eq. S7) with respect to *R*r is necessarily positive, and thus the condition for convergence stability is met. We verify this for the exact model graphically in Fig. S2.

**Solution for *L\****

We can revisit the nitrogen conservation equation for a challenger strategy in light of the solution for *R\*ρ\** (Eq. S18). At the ESS, Eq. (S7) becomes:

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| , | (S30) |

where

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| . | (S31) |

Analogous to *ε*R, *ε*W is the ratio of wood N:C to (total) foliage N:C, which is also a small number, on the order of 0.1 or less, multiplied by the inverse of the turnover time of nitrogen in foliage, which is on the order of unity. If *ε*Rand *ε*W are approximated as zero, then we recover, with the change of a few symbols and parameters, the solution for *L\** found in Dybzinski et al. (2011):

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| , | (S32) |

which is their Eq. 14 for nitrogen-limited stands. Note that we have subscripted *L*0\* to indicate that it is the solution when *ε*R and *ε*W are approximated as zero.

**ESS solutions using the simplified Farquhar model of photosynthesis used in Dybzinski et al. (2011)**

Dybzinski et al. (2011) use a simplified model of whole-crown photosynthesis in which the top leaves of a canopy tree fix carbon at a light-saturated rate, light extinguishes through the crown exponentially (Beer’s Law), and at some point in the crown leaves become light-limited and fix carbon at a light-limited rate. See Dybzinski et al. (2011) for a derivation:

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| , | (S33) |

where *A*(CO2) is the maximum net photosynthetic rate as a function of atmospheric CO2 (9.9•10-5 or 14.553•10-5 gC m-2 s-1 for CO2 = 350ppm or 550ppm respectively, a 47% increase consistent with the mean of trees in Ainsworth and Long (2005)); *q* is the leaf respiration rate (9.9•10-6 gC m-2 s-1), *φ*(CO2) is the quantum yield of photosynthesis (3.27•10-4 or 3.66•10-4 gC m-2 s-1 fPAR-1 for CO2 = 350ppm or 550ppm respectively, a 12% increase consistent with the mean in Ainsworth and Long (2005) and where fPAR is the fraction of total photosynthetically active radiation at a particular leaf), *I* is relative light at the top of the canopy (1 fPAR), *k* is the light extinction coefficient (0.5 m2 m-2), and *s* scales per-second measurements to annual measurements (2.26•106 s yr-1).

With this functional form for *E*(*L*), we can solve Eq. (S24) for *R\** and, together with the solution for *L\** (Eq. S30), use the carbon conservation equation (Eq. S4) to find *W*\*. Together, we find this system of equations that implicitly defines the ESS allocation strategy:

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| . | (S34) |

These are the equations that we solve numerically to produce the figures in the main text, after converting to NPP values:

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| . | (S35) |

All NPP values are in units of gC m-2 yr-1. Total NPP sums these values, and fractional allocation for a given organ is its NPP divided by total NPP. We use the parameter values indicated in the text above, which are exactly as in Dybzinski et al. (2011) except where new parameters have been introduced (we flagged those parameters by citing the sources and/or derivations of their values above as they were introduced; all other parameter values are described in Dybzinski et al. (2011)). We obtained numerical solutions using Mathematica’s FindRoot function (Wolfram Research, 2008) with the approximation of *ε*R = *ε*W = 0 as starting values:

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| . | (S36) |

Note that, with the change of a few symbols and parameters, these approximations correspond exactly to Eqs. (14), (16), and (15) in Dybzinski et al. (2011).

**Closed-form approximations of carbon storage in wood using a Michaelis–Menten model of whole canopy carbon gain**

The simple Farquhar model of whole-crown photosynthesis (Eq. S33) is mechanistically-based and yields reasonable closed-form organ ESS solutions when *ε*R = *ε*W = 0. However, it does not permit closed-form solutions of absolute or relative carbon storage in living wood, which are potentially useful expressions. Because Eq. (S33) saturates with increasing *L* due to self-shading, it may be approximated by a phenomenological Michaelis-Menten model of whole-crown carbon gain,

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| . | (S37) |

This function saturates at *h* (gC m-2 yr-1) for large *L*, obtains half that value at *L* = *y* (m2 m-2), and has an initial slope *h*/*y* at *L* = 0. With this functional form for *E*(*L*), we can solve Eq. (S24) for *R\** and, together with the solution for *L\** (Eq. S30), use the carbon conservation equation (Eq. S4) to find *W*\*. Jumping straight to the approximation of *ε*R = *ε*W = 0, we find:

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| . | (S38) |

Because they are measurable physiological parameters, we understand how *A*(CO2) and *φ*(CO2) depend on atmospheric CO2, but the same cannot be said for *h* and *y*. To gain that insight, we fit the phenomenological Michaelis-Menten model to the simple Farquhar model at both CO2 = 350 and CO2 = 550 over the range of LAI predicted by the full model (2.25 to 5.25 m2 m-2). The best fit is shown in Fig. S1 and gives

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| , | (S39) |

where “550” and “350” subscripts values at atmospheric CO2 = 550ppm and 350ppm, respectively, and *η* and *ψ* represent the ratios of *h* and *y* at elevated relative to ambient CO2.

Because the carbon residence time of wood is approximately two orders of magnitude greater than its residence time in either foliage or fine roots, the carbon storage in living forest biomass is dominated by wood. Thus, we can approximate *storage*difference (Eq. 3) and *storage*ratio (Eq. 4) by focusing on approximate ESS wood allocation, *W*0\* at atmospheric CO2 = 550ppm and 350ppm.

First, *storage*difference (Eq. 3) is approximately

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| , | (S40) |

where *μ* is the canopy tree mortality rate (0.013 yr-1) and *L*0\* is an increasing function of *N* (Eq. S38).

By taking the derivative of the above expression with respect to *N*, we can show that *storage*difference will increase with *N* if the following condition is true:

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| . | (S41) |

The numerator and denominator are necessarily positive, which simplifies the analysis. At the limit of *N* 🡪 0, the condition becomes

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| , | (S42) |

which is true given the numbers above (Eq. S39). At the opposite limit of *N* 🡪 ∞, the condition becomes

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| , | (S43) |

which is false given the numbers above (Eq. S39). Together, this suggests that *storage*difference will increase with *N* at low *N* and decrease with *N* at high *N*, but it does not suggest how these mathematical limits correspond to biologically “low” and “high” *N*. Numerically, the exact solution shows that *storage*difference increases with *N* across the range of *N* that supports closed-canopy, nitrogen-limited forests (Fig. 4f).

*storage*ratio (Eq. 4) is approximately

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| . | (S44) |

We can simplify this expression by neglecting the fecundity term, *F*, which is much smaller than the positive term:

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| . | (S45) |

By taking the derivative of the above expression with respect to *N*, we can show that *storage*ratio will increase with *N* if the following condition is true:

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| . | (S46) |

Given the value determined in Eq. (S39), this condition is not true. Thus, *storage*ratio is expected to decrease with increasing *N*, as confirmed numerically for the exact model (Fig. 5).

**Down-regulation of carbon fixation**

Finally, the nitrogen and carbon conservation equations (Eqs. S3, S4, S5, S6) assume that trees use all of the nitrogen and carbon that they can capture to make tissues. It is easy to show that no strategy that down-regulates is competitively optimal in a nitrogen-limited ecosystem. That is, strategies that release or voluntarily forgo capture of any carbon or nitrogen rather than making tissue of it are never competitively optimal. For example, we can introduce *δ*, a carbon gain “down-regulation factor,” in front of the challenger’s LAI function (Eq. S7), allowing it to decrease both its carbon capture and the costs associated with that carbon capture

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| . | (S47) |

The parameter *δ* varies from zero (complete shutdown of carbon gain) to one (no down-regulation). The derivative of *W* (Eq. S8) with respect to *δ* is

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| . | (S48) |

As we saw above, the term in parentheses will be zero when the marginal return of gross photosynthesis on a marginal increase in LAI exactly equals the total costs of that marginal increase. Since we are here interested in solutions within the nitrogen-limited regime, the term in parentheses will necessarily be positive. The term outside the parentheses is simply LAI, which is also necessarily positive. Together, the whole expression is necessarily positive in a nitrogen-limited stand. Thus, the competitively optimal down-regulation factor takes on the boundary value of one (i.e. no down-regulation); *δ*\* = 1. In contrast, models that down-regulate assume that trees voluntarily forgo capture of some of either one or the other, so as to keep in stoichiometric balance. Our analysis allows competitively optimal strategies to keep in stoichiometric balance both by shifting allocation among organs (which differ in their mean stoichiometry) and by adjusting tissue stoichiometry itself.

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Figure S1. Model fit of the simple Farquhar model of whole-crown carbon gain (black, Eq. S33 and parameter values in text) by the phenomenological Michaelis-Menten model (gray, Eq. S37), yielding parameter values for *h*, *y*, *η*, and *ψ* (Eq. S39).

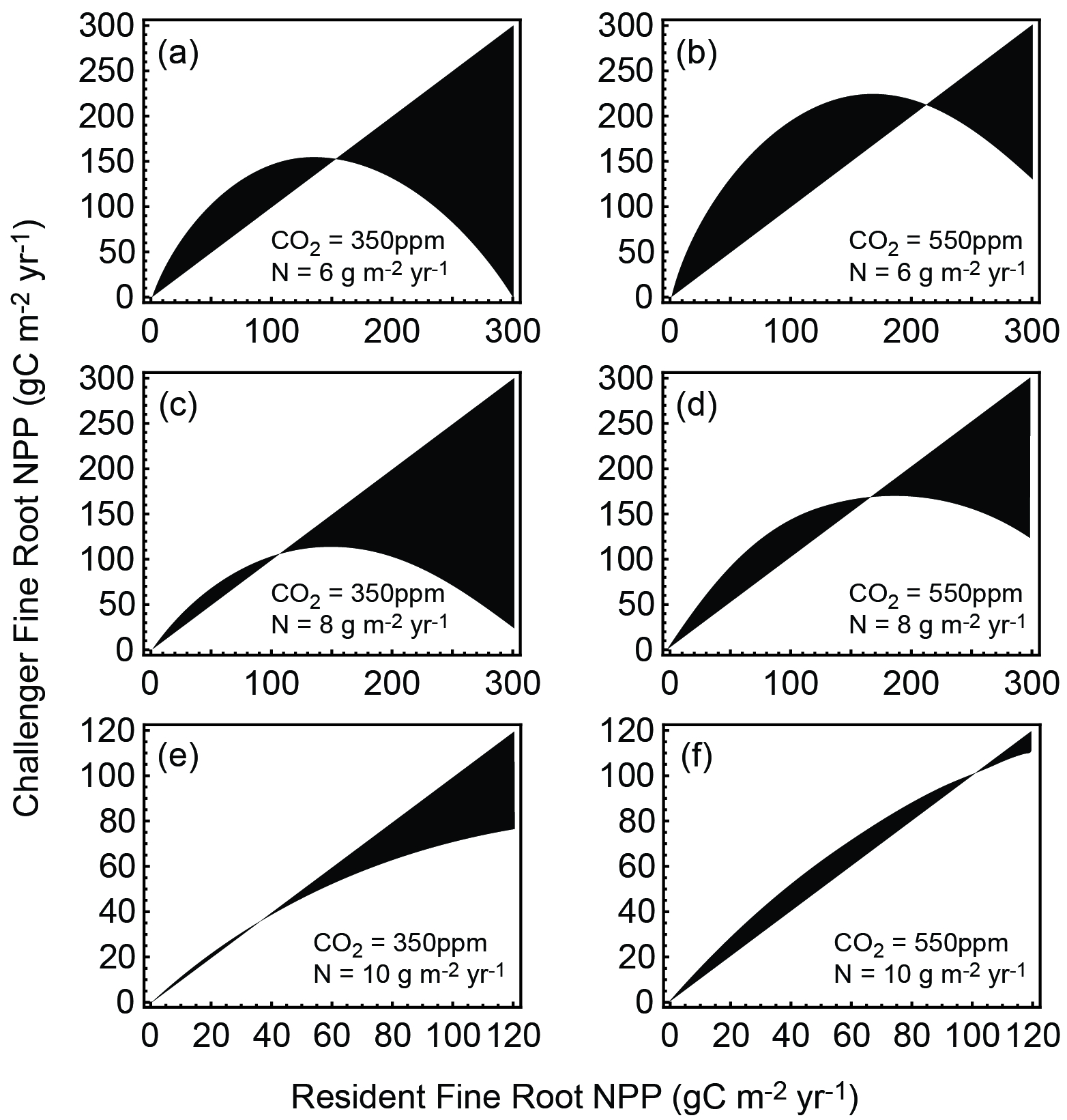


Figure S2. Pairwise invasion plots of the exact model (Eq. S34) at three different nitrogen mineralization rates and two different CO2 concentrations. Black indicates areas where a challenger (vertical axis) would be successful against a resident (horizontal axis). Note the different scale in e & f. Like the approximate solutions, the exact solutions are convergence-stable: against residents below the ESS, challengers with relatively greater fine root NPP succeed, and against residents above the ESS, challengers with relatively smaller fine root NPP succeed.