Competition alters predicted forest carbon cycle responses to nitrogen availability and elevated CO_2: simulations using an explicitly competitive, game-theoretic vegetation demographic model

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Abstract: Competition is a major driver of carbon allocation to different plant tissues (e.g. wood, leaves, fine roots), and allocation, in turn, shapes vegetation structure. To improve their modeling of the terrestrial carbon cycle, many Earth system models now incorporate vegetation demographic models (VDMs) that explicitly simulate the processes of individual-based competition for light and soil resources. Here, in order to understand how these competition processes affect predictions of the terrestrial carbon cycle, we simulate forest responses to elevated atmospheric CO_2 concentration [CO_2] along a nitrogen availability gradient using a VDM that allows us to compare fixed allocation strategies versus competitively-optimal allocation strategies. Our results show that competitive and fixed strategies predict opposite fractional allocation to fine roots and wood, though they predict similar changes in total NPP along the nitrogen gradient. The competitively-optimal allocation strategy predicts decreasing fine root and increasing wood allocation with increasing nitrogen, whereas the fixed strategy predicts the opposite. Although simulated plant biomass at equilibrium increases with nitrogen due to increases in photosynthesis for both allocation strategies, the increase in biomass with nitrogen is much steeper for competitively-optimal allocation due to its increased allocation to wood. The qualitatively opposite fractional allocation to fine roots and wood of the two strategies also impacts the effects of elevated [CO_2] on plant biomass. Whereas the fixed allocation strategy predicts an increase in plant biomass under elevated [CO_2] that is approximately independent of nitrogen availability, competition leads to higher plant biomass response to elevated [CO_2] with increasing nitrogen availability. Our results indicate that the VDMs that explicitly include the effects of competition for light and soil resources on allocation may generate significantly different ecosystem-level predictions of carbon storage than those that use fixed strategies.

1 Introduction

Allocation of assimilated carbon to different plant tissues is a fundamental aspect of plant growth and profoundly affects terrestrial ecosystem biogeochemical cycles (Cannell and Dewar, 1994; Lacointe, 2000). Ecologically, allocation represents an evolutionarily-honed "strategy" of plants that use limited resources and compete with other individuals and consequently drives successional dynamics and vegetation structure (De Kauwe et al., 2014; DeAngelis et al., 2012; Haverd et al., 2016; Tilman, 1988). Biogeochemically, allocation links plant physiological processes, such as photosynthesis and respiration, to biogeochemical cycles and carbon storage of ecosystems (Bloom et al., 2016; De Kauwe et al., 2014). Thus, correctly modeling allocation patterns is critical for correctly predicting terrestrial carbon cycles and Earth system dynamics.

In current Earth System Models (ESMs), the terrestrial carbon cycle is usually simulated by pool-based compartment models that simulate ecosystem biogeochemical cycles as lumped pools and fluxes of plant tissues and soil organic matter (Fig. 1: A) (Emanuel and Killough, 1984; Eriksson, 1971; Parton et al., 1987; Randerson et al., 1997; Sitch et al., 2003). In these models, the dynamics of carbon can be described by a linear system of equations (Koven et al., 2015; Luo et al., 2001; Luo and Weng, 2011; Sierra and Mueller, 2015; Xia et al., 2013):

$$\frac{dX}{dt} = AX + BU \qquad \text{(Eq. 1)}$$

where X is a vector of ecosystem carbon pools, U is carbon input (i.e., Gross Primary Production, GPP), B is the vector of allocation parameters to autotrophic respiration and plant carbon pools (e.g., leaves, stems, and fine roots), and A is a matrix of carbon transfer and turnover. In this system, carbon dynamics are defined by carbon input (U), allocation (B), and residence time and transfer coefficients (A). The allocation schemes (B) are thus embedded in a linear system, or

quasi-linear system if the allocation parameters in B are a function of carbon input (U) or plant carbon pools (X).

The modeling of allocation in this system (i.e., the parameters in vector B) is usually based on plant allometry, biomass partitioning, and resource limitation (De Kauwe et al., 2014; Montané et al., 2017). The allocation parameters are either fixed ratios to leaves, stems, and roots, which may vary among plant functional types (e.g., CENTURY, Parton et al., 1987; TEM, Raich et al., 1991; CASA, Randerson et al., 1997) or are responsive to climate and soil conditions as a way to phenomenologically mimic the shifts in allocation that are empirically observed or hypothesized (e.g., CTEM, Arora and Boer, 2005; ORCHIDEE, Krinner et al., 2005; LPJ, Sitch et al., 2003). These modeling approaches either assume that vegetation is equilibrated (fixed ratios) or average the responses of plant types to changes in environmental conditions as a collective behavior. Thus, the carbon dynamics in these models can be constrained by selecting appropriate parameters of allocation, turnover rates, and transfer coefficients to fit the observations (Friend et al., 2007; Hoffman et al., 2017; Keenan et al., 2013).

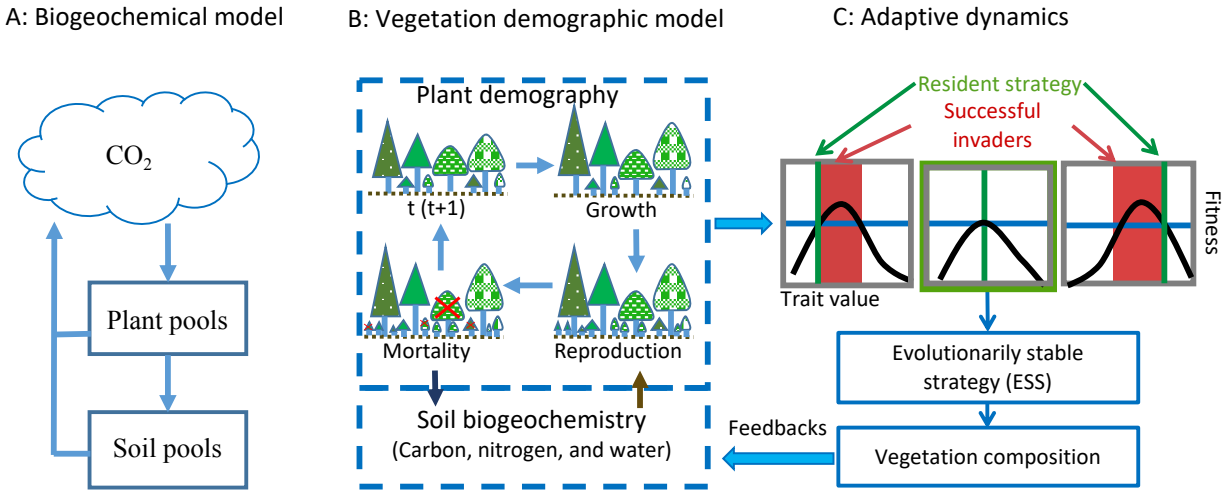


Figure 1 Hierarchical structure of vegetation models

To predict transient changes in vegetation structure and composition in response to climate change, vegetation demographic models (VDMs) that are able to simulate transient population dynamics are being incorporated into ESMs (Fisher et al., 2018; Scheiter and Higgins, 2009). Generally, VDMs explicitly simulate demographic processes, such as plant reproduction, growth, and mortality, to generate the dynamics of populations (Fig. 1: B). To speed computations and minimize complexity, groups of individuals are usually modeled as cohorts. With multiple cohorts and PFTs, VDMs can bring plant functional diversity and adaptive dynamics into the system when explicitly simulating individual-based competition for different resources and vegetation succession and thus predict dominant plant traits changes with environmental conditions and ecosystem development (Scheiter et al., 2013; Scheiter and Higgins, 2009; Weng et al., 2015).

The combinations of plant traits represent the competition strategies at different stages of ecosystem development. Evolutionarily, a strategy that can outcompete all other strategies in the environment created by itself will be dominant. This strategy is called an evolutionarily stable strategy or a competitively-optimal strategy (McGill and Brown, 2007). In VDMs, competitively-optimal strategies can therefore be reasonably predicted based on the costs and benefits of different strategies (i.e., combinations of plant traits) through their effects on demographic processes (i.e., fitness) and ecosystem biogeochemical cycles (Fig. 1:C) (e.g., Farrior et al., 2015; Weng et al., 2015).

The dynamics of plant traits can substantially change predictions of ecosystem biogeochemical dynamics since they change the key parameters of vegetation physiological processes and soil organic matter decomposition (e.g., Dybzinski et al., 2015; Farrior et al., 2015; Weng et al., 2017). Therefore, the key parameters that are used to estimate carbon

dynamics in the linear system model (Eq. 1), such as allocation (B) and residence times in different carbon pools (matrix A, which includes coefficients of carbon transfer and turnover time) become functions of competition strategies that vary with environment and carbon input. In addition, the turnover of vegetation carbon pools becomes a function of allocation, leaf longevity, fine root turnover, and tree mortality rates, which change with vegetation succession and the most competitive plant traits. These changes make the system nonlinear and can lead to large biases within the framework of the compartmental pool-based models as represented by Eq. (1) (Sierra et al., 2017; Sierra and Mueller, 2015). Because of the high complexity associated with demographic and competition processes, the model predictions are usually sensitive to the parameters in these processes and are of high uncertainty (e.g., Pappas et al., 2016).

In contrast to their implementation in the more complicated VDMs discussed above, models of competitively-dominant plant strategies using much simpler model structures and assumptions can sometimes be solved analytically (Dybzinski et al., 2011, 2015; Farrior et al., 2013, 2015). Although simplified, such models can pin-point the key processes that improve the predictive power of simulation models (Dybzinski et al., 2011; Farrior et al., 2013, 2015), allowing them to help researchers formulate model processes and understand the simulated ecosystem dynamics in ESMs. For example, the analytical model derived by Farrior et al. (2013) that links interactions between ecosystem carbon storage, allocation, and water stress at elevated atmospheric CO_2 concentration [CO_2] sheds light on the otherwise inscrutable processes leading to varied soil water dynamics in a land model coupled with an VDM (Weng et al., 2015). Recognizing the benefit, Weng et al. (2017) included both a simplified analytical model and a more complicated VDM to understand competitively optimal leaf mass per area, competition between evergreen and deciduous plant functional types, and the resulting successional patterns.

126 In this study, we use a stand-alone simulator derived from the LM3-PPA model (Weng et
127 al., 2017, 2015) to show how forests respond to elevated [CO_2] and nitrogen availability via
128 different competitively-optimal allocation strategies. The demographic processes of this model
129 have been coupled into the land model of the Geophysical Fluid Dynamical Laboratory's Earth
130 System Model (Shevliakova et al., 2009; Weng et al., 2015) and are being added to NASA
131 Goddard Institute for Space Study's Earth system model, ModelE (Schmidt et al., 2014). Using
132 this model, we simulate the shifts in competitively optimal allocation strategies in response to
133 elevated [CO_2] at different nitrogen levels based on insights from the analytical model derived by
134 Dybzinski et al. (2015). Dybzinski et al.'s (2015) model predicts that increases in carbon storage
135 at elevated [CO_2] relative to storage at ambient [CO_2] are largely independent of total nitrogen
136 because of an increasing shift in carbon allocation from long-lived, low-nitrogen wood to short-
137 lived, high-nitrogen fine roots under elevated [CO_2] with increasing nitrogen availability. Here,
138 we analyze the simulated ecosystem carbon cycle variables (gross and net primary production,
139 allocation, and biomass) of separate mono- and polyculture model runs. In the monoculture runs,
140 ecosystem properties are the result of the prescribed allocation strategies of a given PFT. In the
141 polyculture runs, competition between the different allocation strategies results in succession and
142 the eventual dominance of the most competitive allocation strategy for a given nitrogen
143 availability and [CO_2] level. Since everything else in the model is identical, we are able to
144 compare the predictions of single **fixed strategies** with **competitively-optimal allocation**
145 **strategies** by comparing the ecosystem properties of these two types of runs.

2 Methods and Materials

2.1 BiomeE model overview

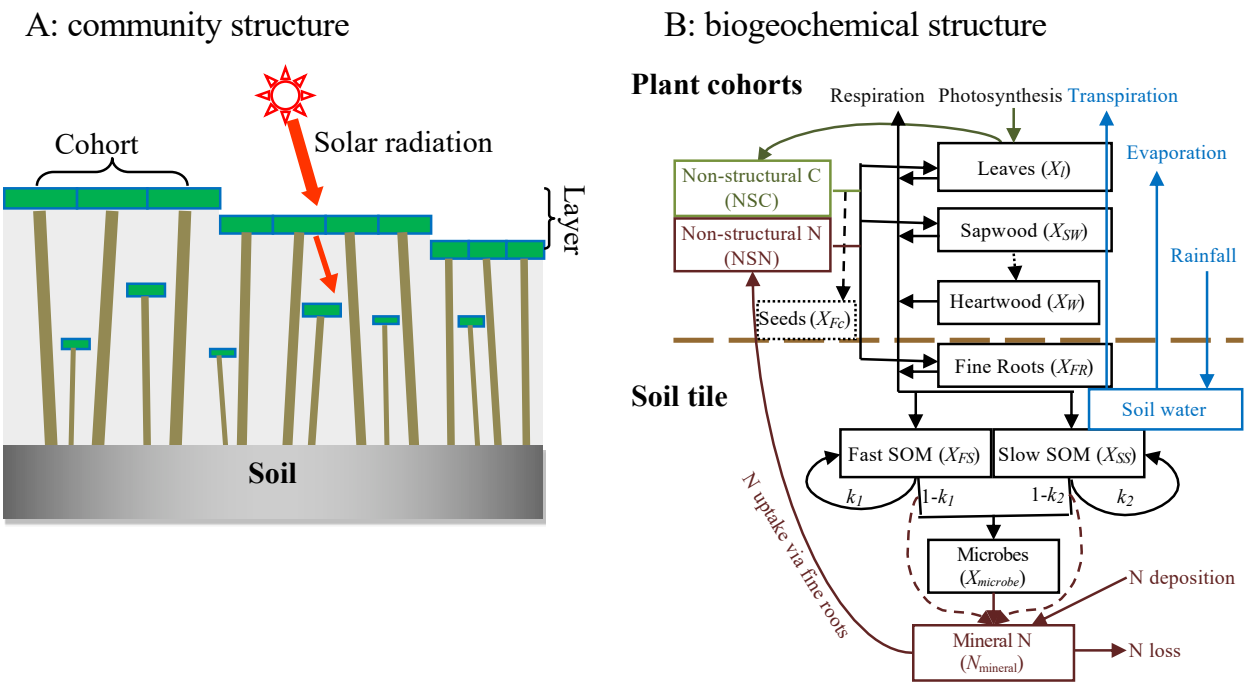


Figure 2. Structure of BiomeE

Panel A: vegetation structure: trees organize their crowns into canopy layers according to both their height and their crown area following the rules of the PPA model, which mechanistically models light competition. Panel B: Biogeochemical structure and compartmental pools. The green, brown, and black lines are the flows of carbon, nitrogen, and coupled carbon and nitrogen, respectively. The green box is for carbon only. The brown boxes are nitrogen pools. The black boxes are for both carbon and nitrogen pools, where *X* can be C (carbon) and N (nitrogen). The C:N ratios of leaves, fine roots, seeds, and microbes are fixed. The C:N ratios of woody tissues, fast soil organic matter (SOM), and slow SOM are flexible. Only one tree's C and N pools are shown in this figure. The blue box and arrows are for water storage in soil and fluxes of rainfall, evaporation, and transpiration. The model can have multiple cohorts of trees, which share the same pool structure. The dashed line separates the aboveground and belowground processes.

We used a stand-alone ecosystem simulator (Biome Ecological strategy simulator, BiomeE) to conduct simulation experiments. BiomeE is derived from the version of LM3-PPA used in Weng *et al*. (2017), and its code is available at Github (https://github.com/wengensheng/BiomeESS). In this version, we simplified the processes of energy transfer and soil water dynamics of LM3-PPA (Weng et al., 2015) but still retained the key features of plant physiology and individual-based competition for light, soil water, and, via the decomposition of soil organic matter, nitrogen (Fig. 2 and Supplementary Information I for details). In this model, individual trees are represented as sets of cohorts of similar size trees and are arranged in different vertical canopy layers according to their height and crown area following the rules of the Perfect Plasticity Approximation (PPA) model (Strigul et al., 2008). Sunlight is partitioned into these canopy layers according to Beer's law. Thus, a key parameter for light competition, critical height, is defined; all the trees above this context-dependent height get full sunlight and all trees below this height are shaded by the upper layer trees.

Each tree consists of seven pools: leaves, fine roots, sapwood, heartwood, fecundity (seeds), and non-structural carbohydrates and nitrogen (NSC and NSN, respectively) (Fig. 2: b). The carbon and nitrogen in plant pools enter the soil pools with the mortality of individual trees and the turnover of leaves and fine roots. There are three soil organic matter (SOM) pools for carbon and nitrogen: fast-turnover, slow-turnover, and microbial pools, along with a mineral nitrogen pool for mineralized nitrogen in soil. The simulation of SOM decomposition and nitrogen mineralization is based on the models of Gerber *et al*. (2010) and Manzoni *et al*. (2010) and described in detail in Weng et al. (2017). The decomposition rate of a SOM pool is determined by the basal turnover rate together with soil temperature and moisture. The nitrogen mineralization rate is a function of decomposition rate and the C:N ratio of the SOM. Microbes

must consume more carbon in the high C:N ratio SOM pools to get enough nitrogen and must release excessive nitrogen in the low C:N ratio SOM pools to get enough carbon for energy (Weng *et al*. 2017).

Table 1 Model parameters

Symbol	Definition	Unit	Default value	Reference
α_Z	Parameter of tree height	m $m^{-0.5}$	36	Farrior et al., 2013
θ_Z	Diameter exponent of tree height	-	0.5	Farrior et al., 2013
Λ	Taper factor	-	0.75	Weng et al. 2015
ρ_W	Wood density	Kg C m^{-3}	300	Jenkins et al., 2003
α_C	Parameter of crown area	m $m^{-1.5}$	150	Farrior et al., 2013
θ_C	Diameter exponent of crown area	-	1.5	Farrior et al., 2013
l^*	Target crown leaf area layers (crown leaf area index)	m^2 m^{-2}	3.5	-
σ	Leaf mass per unit area	kg C m^{-2}	0.14	Wright et al., 2004
γ	Specific root area, calculated from root radius and density	m^2 kg C^{-1}	34.5	Pregitzer et al., 2002
φ_{RL}	Ratio of target fine root area to target leaf area	m^2 m^{-2}	Varied with PFTs	-
α_{CSA}	ratio of target sapwood cross-sectional area to target leaf area	m^2 m^{-2}	$0.2x10^{-4}$	McDowell et al., 2002
$f_{U,max}$	Maximum mineral nitrogen absorption rate	$hour^{-1}$	0.5	-
K_{FR}	Root biomass at which the N-uptake rate is half of the maximum	kg C m^{-2}	0.3	-
$CN_{L,0}$	Target C:N ratio of leaves	kg C kgN^{-1}	76.5 (Function of LMA)	Wright et al., 2004
$CN_{FR,0}$	Target C:N ratio of fine roots	kg C kgN^{-1}	60	Magill et al., 2004
$CN_{W,0}$	Target C:N ratio of wood	kg C kgN^{-1}	350	Martin et al., 2015
$CN_{F,0}$	Target C:N ratio of seeds	kg C kgN^{-1}	20	Soriano et al., 2011
f_1	Supply rate of NSC and NSN at normal growth	-	1/(3*365)	-
f_2	Maximum fraction of NSC and NSN used for growth in a day	-	0.02	-
$f_{LFR,max}$	Maximum fraction of available carbon allocated to leaves and fine roots	-	0.85	-
v	Fraction of carbon converted to seeds	-	0.1	-

$r_{D/S}$	Nitrogen-limiting factor	-	Solved by the model (Eqs 9 and 10)	-

Plant growth and reproduction are driven by the carbon assimilation of leaves via photosynthesis, which is in turn dependent on water and nitrogen uptake by fine roots. The photosynthesis model is identical to that of LM3-PPA (Weng et al., 2015), which is a simplified version of Leuning model (Leuning et al., 1995). This model first calculates photosynthesis rate, stomatal conductance, and water demand of the leaves of each tree (cohort) in the absence of soil water limitation. Then, it calculates available water supply as a function of fine root surface area and soil water content. The demand-based assimilation rate and stomatal conductance are adjusted if soil water supply is less than plant water demand. Soil water content is calculated based on the fluxes of precipitation, soil surface evaporation, and plant water update (transpiration) in three layers of soil to a depth of 2 meters. (Please see Supplementary Information I for details).

Assimilated carbon enters into the NSC pool and is subsequently used for respiration, growth, and reproduction. Empirical allometric equations relate woody biomass (including coarse roots, bole, and branches), crown area, and stem diameter. The individual-level dimensions of a tree, *i.e.*, height (Z), biomass (S), and crown area (A_{CR}) are given by empirical allometries (Dybzinski et al., 2011; Farrior et al., 2013):

$$\begin{aligned} Z(D) &= \alpha_Z D^{\theta_Z} \\ S(D) &= 0.25\pi\Lambda\rho_W\alpha_Z D^{2+\theta_Z} \\ A_{CR}(D) &= \alpha_c D^{\theta_c} \end{aligned} \qquad \text{(Eq. 2)}$$

where Z is tree height, D is tree diameter, S is total woody biomass carbon (including bole, coarse roots, and branches) of a tree, α_c and α_Z are PFT-specific constants, θ_c=1.5 and θ_Z=0.5

(Farrior et al., 2013) (although they could be made PFT-specific if necessary), π is the circular constant, Λ is a PFT-specific taper constant, and ρ_W is PFT-specific wood density (kg C m^{-3}) (Table 1).

We set *targets* for leaf (L^*), fine root (FR^*), and sapwood cross-sectional area (A_{SW}^*) that govern plant allocation of non-structural carbon and nitrogen during growth. These *targets* are related by the following equations based on the assumption of the pipe model (Shinozaki, Kichiro et al., 1964):

$$\begin{aligned} L^*(D,p) &= l^* \cdot A_{CR}(D) \cdot \sigma \cdot p(t) \\ FR^*(D) &= \varphi_{RL} \cdot l^* \cdot \frac{A_{CR}(D)}{\gamma} \\ A_{SW}^*(D) &= \alpha_{CSA} \cdot l^* \cdot A_{CR}(D) \end{aligned} \qquad \text{(Eq. 3)}$$

where L^* (D, p), $FR^*(D)$, and $A_{SW}^*(D)$ are the targets of leaf mass (kg C/tree), fine root biomass (kg C/tree), and sapwood cross sectional area (m^2/tree), respectively, at tree diameter D; l^* is the target leaf area per unit crown area of a given PFT; A_{CR}(D) is the crown area of a tree with diameter D; σ is PFT-specific leaf mass per unit area (LMA); and $p(t)$ is a PFT-specific function ranging from zero to one that governs leaf phenology (Weng et al., 2015); φ_{RL} is the target ratio of total root surface area to the total leaf area; γ is specific root area; and α_{CSA} is an empirical constant (the ratio of sapwood cross-sectional area to target leaf area). The phenology function p(t) takes values 0 (non-growing season) or 1 (growing season) following the phenology model of LM3-PPA (Weng et al., 2015). The onset of a growing season is controlled by two variables, growing degree days (GDD), and a weighted mean daily temperature (T_{pheno}), while the end of a growing season is controlled by T_{pheno}. (Please see Supplementary Information I for details of the phenology model)

Nitrogen uptake

The rate of nitrogen uptake (U, g N m^{-2} hour^{-1}) from the soil mineral nitrogen pool is an asymptotically increasing function of fine root biomass density ($C_{FR,total}$, kg C m^{-2}), following McMurtrie *et al*. (2012)

$$U = f_{U,max} \cdot N_{mineral} \cdot \frac{C_{FR,total}}{C_{FR,total}+K_{FR}}, \quad \text{(Eq. 4)}$$

where, $N_{mineral}$ is the mineral nitrogen in soil (g N m^{-2}), $f_{U,max}$ is the maximum rate of nitrogen absorption per hour when $C_{FR,total}$ approaches infinity, K_{FR} is a shape parameter (kg C m^{-2}) at which the nitrogen uptake rate is half of the parameter f_U,max. The nitrogen uptake rate of an individual tree (U_{tree}, kg N hour^{-1} tree^{-1}) is calculated as follows:

$$U_{tree} = U \cdot \frac{C_{FR,tree}}{C_{FR,total}}, \quad \text{(Eq. 5)}$$

where, $C_{FR,tree}$ is the fine root biomass of a tree (kg C tree^{-1}). The nitrogen absorbed by roots enters into the NSN pool and then is allocated to plant tissues through plant growth.

Allocation and plant growth

The partitioning of carbon and nitrogen into the plant pools (*i.e.*, leaves, fine roots, and sapwood) is limited by the allometric equations, targets of leaves, fine roots, and sapwood cross-sectional area, and the stoichiometry (i.e., C:N ratios) of these plant tissues. At a daily time step, the model calculates the amount of carbon and nitrogen that are available for growth according to the total NSC and NSN and current leaf and fine root biomass. Basically, the available NSC (G_C) is the summation of a small fraction (f_1) of the total NSC in an individual plant and the differences between the targets of leaf and fine roots and their current biomass capped by a larger fraction (f_2) of NSC (Eq. 6.1). The available NSN (G_N) is analogous to that of the NSC and meets approximately the stoichiometrical requirement of plant tissues (Eq. 6.2).

$$G_C = \min\left(f_1 NSC + L^* + FR^* - L - FR, f_2 NSC\right) \quad \text{(Eq. 6.1)}$$

$$G_N = \min\left(f_1 NSN + N_L^* + N_{FR}^* - N_L - N_{FR}, f_2 NSN\right) \quad \text{(Eq. 6.2)}$$

where L^* and FR^* are the targets of leaves and fine roots, respectively (see Eq. 3); L and FR are current leaf and fine roots biomass, respectively; N_L^* and N_{FR}^* are nitrogen of leaves and fine roots at their targets according to their target C:N ratios. The parameter f_1 is the fraction of NSC (or NSN) for normal growth after leaves and fine roots approach their targets and f_2 caps the maximum daily availability of NSC (or NSN) during the period of leaf flush at the beginning of a growing season. The parameter f_1 is much smaller than f_2. We let f_1= 1/(365x3) and f_2=0.02 in this study.

The allocation of the available NSC (i.e., G_C) to wood (G_W), leaves (G_L), fine roots (G_{FR}), and seeds (G_F) follows the equations below (Eq. 7). These equations describe the mass growth of plant tissues with nitrogen effects on the carbon allocation between high-nitrogen tissues and low-nitrogen tissues (wood) for maximizing leaves and fine roots growth (G_L and G_{FR}, respectively), optimizing carbon usage at given nitrogen supply (G_N), and keeping the tissues at their target C:N ratios.

$$G_C \geq G_W + G_L + G_{FR} + G_F \quad \text{(Eq. 7.1)}$$

$$G_N \geq \frac{G_L}{CN_{L,0}} + \frac{G_{FR}}{CN_{FR,0}} + \frac{G_F}{CN_{F,0}} + \frac{G_W}{CN_{W,0}} \quad \text{(Eq. 7.2)}$$

$$\frac{(FR+G_{FR})\gamma}{(L+G_L)/\sigma} = \varphi_{RL} \quad \text{(Eq. 7.3)}$$

$$G_L + G_{FR} = Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix} \cdot r_{S/D} \quad \text{(Eq. 7.4)}$$

$$G_F = \left[G_C - Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix} r_{S/D}\right] \cdot v \cdot r_{S/D} \quad \text{(Eq. 7.5)}$$

$$G_W = \left[G_C - Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix} r_{S/D}\right] \cdot (1 - v \cdot r_{S/D}) \quad \text{(Eq. 7.6)}$$

where, $CN_{L,0}$, $CN_{FR,0}$, $CN_{F,0}$, and $CN_{W,0}$ are the target C:N ratios of leaves, fine roots, seeds, and sapwood, respectively; γ is specific root area (m^2 kg C^{-1}); σ is leaf mass per unit area (kg C m^{-2}); $f_{LFR,max}$ is the maximum fraction of G_C for leaves and fine roots (0.85 in this study); v is the fraction of left carbon for seeds (0.1 in this study); $r_{S/D}$ is a nitrogen-limiting factor ranging from 0 (no nitrogen for leaves, fine roots, and seeds) to 1 (nitrogen available for full growth of leaves, fine roots, and seeds). The parameter $r_{S/D}$ controls the allocation of G_C and G_N to the four plant pools (Eq. 7.1). It can be analytically solved (Eqs. 8 and 9).

$$r_{S/D} = Min\left[1, Max\left(0, \frac{G_N - G_C/CN_W}{N' - G_C/CN_W}\right)\right], \quad \text{(Eq. 8)}$$

where, N' is defined as the potential nitrogen demand for plant growth at $r_{S/D}$=1 (i.e., no nitrogen limitation).

$$N' \equiv \frac{\gamma\sigma\left[FR + Min\begin{pmatrix} L^*+FR^*-L-FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right] - \varphi_{RL} L}{(\gamma\sigma + \varphi_{RL}) CN_L} + \frac{\varphi_{RL}\left[L + Min\begin{pmatrix} L^*+FR^*-L-FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right] - \gamma\sigma L}{(\gamma\sigma + \varphi_{RL}) CN_{FR}} + \frac{v\left[G_C - Min\begin{pmatrix} L^*+FR^*-L-FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right]}{CN_F} + \frac{(1-v)\left[G_C - Min\begin{pmatrix} L^*+FR^*-L-FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right]}{CN_W}. \quad \text{(Eq. 9)}$$

When $G_N \geq N'$ ($r_{S/D}$ = 1), there is no nitrogen limitation, and all the G_C will be used for plant growth and the allocation follows the rules of the carbon only model (Eqs 7.4~7.6 as $r_{S/D}$ = 1). The excessive nitrogen ($G_N - N'$) will be returned to the NSN pool (as if they were never taken out). When $G_C/CN_{W,0} < G_N < N'$ (i.e., $0 < r_{S/D} < 1$), all G_C and G_N will be used in new tissue growth; however, the leaves and fine roots cannot reach their targets at this step (i.e. they are down-

regulated). When $G_N \leq G_C/CN_{W,0}$ ($r_{S/D} = 0$), all the G_N will be allocated to sapwood and the excessive carbon ($G_C - G_N CN_{W,0)}$ will be returned to NSC pool. This is a very rare case since a low G_N leads to low leaf growth, reducing G_C before the case $G_N < G_C/CN_{W,0}$ happens. Therefore, in most cases, Eq. 7.1 is: $G_C = G_W + G_L + G_{FR} + G_F$. Overall, this strategy down-regulates leaf production under low nitrogen conditions while making use of assimilated carbon in height-structured competition for light.

Allocation to wood tissues (G_W) drives the growth of tree diameter, height, and crown area and thus increases the targets of leaves and fine roots (Eq. 3). By differentiating the stem biomass allometry in Eq. 2 with respect to time, using the fact that dS/dt equals the carbon allocated for wood growth (G_W), we have the diameter growth:

$$\frac{dD}{dt} = \frac{G_W}{0.25\pi\Lambda\rho_W\alpha_Z(2+\theta_Z)D^{1+\theta_Z}} \quad \text{(Eq. 10)}$$

This equation transforms the mass growth to structural changes in tree architecture. With an updated tree diameter, we can calculate the new tree height and crown area using allometry equations (Eq. 2) and targets of leaf and fine root biomass (Eq. 3) for the next growth step.

Overall, this is a flexible allocation scheme and still follows the major assumptions in the previous version of LM3-PPA (Weng, et al., 2015, 2017). This allocation scheme prioritizes the allocation to leaves and fine roots, maintains a minimum growth rate of stems, and keeps the constant area ratio of fine roots to leaves. Based on these allocation rules, the average allocation of carbon and nitrogen to leaves, fine roots, and wood over a growing season are governed by the targets for the leaf area per unit crown area (i.e., crown leaf area index, l^*) and fine root area per unit leaf area (φ_{RL}). Since the crown leaf area index, l^*, is fixed in this study, φ_{RL} is the key parameter determining the relative allocation of carbon to fine roots and stems. A high φ_{RL}

means a high relative allocation to fine roots and therefore low relative allocation to stems, and *vice versa*. Note, here φ_{RL} is fixed for each PFT and will remain so for all the model runs.

The process of choosing a context-dependent competitively dominant φ_{RL} will take place after finding the fitness of each φ_{RL} in monoculture and in competition with other PFTs (*i.e.*, different values of φ_{RL}). The competitively optimal strategy is the one that can successfully exclude all others in the processes of competition and succession, but it is not necessarily the one that maximizes production in monoculture. For example, each φ_{RL} creates an environment of light profile and soil nitrogen in its monoculture. Other φ_{RL} PFTs may have higher fitness in this environment than the one that creates it. Only the competitively dominant strategy has the highest fitness in the environment it creates (Fig. 1: C).

2.2 Site and Data

Data pertaining to vegetation, climate, and soil at Harvard Forest (Aber et al., 1993; Hibbs, 1983; Urbanski et al., 2007) were used to design the plant functional types (PFTs) and ecosystem nitrogen levels used in the simulation experiments, to drive the model, and to calibrate model parameters. Harvard Forest is located in Massachusetts, USA (42.54°, -72.17°). The climate of Harvard Forest is cool temperate with annual precipitation 1050 mm, distributed fairly evenly throughout the year. The annual mean temperature is 8.5 °C with a high monthly mean temperature of 20°C in July and a low of -7°C in January. The soils are mainly sandy loam with average depth around 1 m and are moderately well drained in most areas. In forest sites, soil carbon is around 8 kg C m^{-2} and nitrogen 300 g N m^{-2} (Compton and Boone, 2000). The vegetation is deciduous broadleaf/mixed forest with major species red oak (*Quercus rubra*), red maple (*Acer rubrum*), black birch (*Betula lenta*), white pine (*Pinus strobus*), and hemlock (*Tsuga canadensis*) (Compton and Boone, 2000; Savage et al., 2013). The data used to drive our model

319 runs are gap-filled hourly meteorological data at Harvard Forest from 1991 to 2006, obtained
320 from North American Carbon Program (NACP) Site-Level Synthesis datasets (Barr et al., 2013).
321
322 **2.3 Simulation experiments**
323 We set two atmospheric CO_2 concentration ($[CO_2]$) levels: 380 ppm and 580 ppm, and
324 eight ecosystem total nitrogen levels (ranging from 114.5 g N m^{-2} to 552 g N m^{-2} at the interval
325 of 62.5 g N m^{-2}) by assigning the initial content of the slow SOM pool for our simulation
326 experiments (Table 2). This range covers the soil nitrogen contents across the plots at Harvard
327 Forest with different species compositions and land use history (200~300 g N m^{-2}) (Compton and
328 Boone, 2000; Melillo et al., 2011), and represents the range from infertile to fertile soils in
329 temperate forests (Post et al., 1985; Yang et al., 2011). The nitrogen cycles through the plant and
330 soil pools and is redistributed among them via plant demographic processes, soil carbon
331 transfers, and plant uptake. In all the simulation experiments, we assume the ecosystem has no
332 nitrogen inputs and no outputs for convenience since we already have eight total nitrogen levels
333 to represent the consequences of different nitrogen input and output processes at an equilibrium
334 state. The PFTs were based on an evergreen needle-leaved tree PFT with different leaf to fine
335 root area ratios, φ_{RL}, in the range from 1 to 8 (Table 2). Simply stated, the PFTs we investigate
336 only differ in parameter φ_{RL}.
337 We define the model runs started with only one fixed-φ_{RL} PFT as "monoculture runs"
338 although the actual allocation of carbon to different plant tissues varies with $[CO_2]$ and
339 ecosystem nitrogen availability. The model runs started with multiple PFTs are called
340 "polyculture runs" (eight PFTs with different φ_{RL} at the beginning, although many are driven to

extinction during a given model run). We conducted one set of monoculture runs and two sets of polyculture runs (Table 2).

Table 2 Simulation experiments

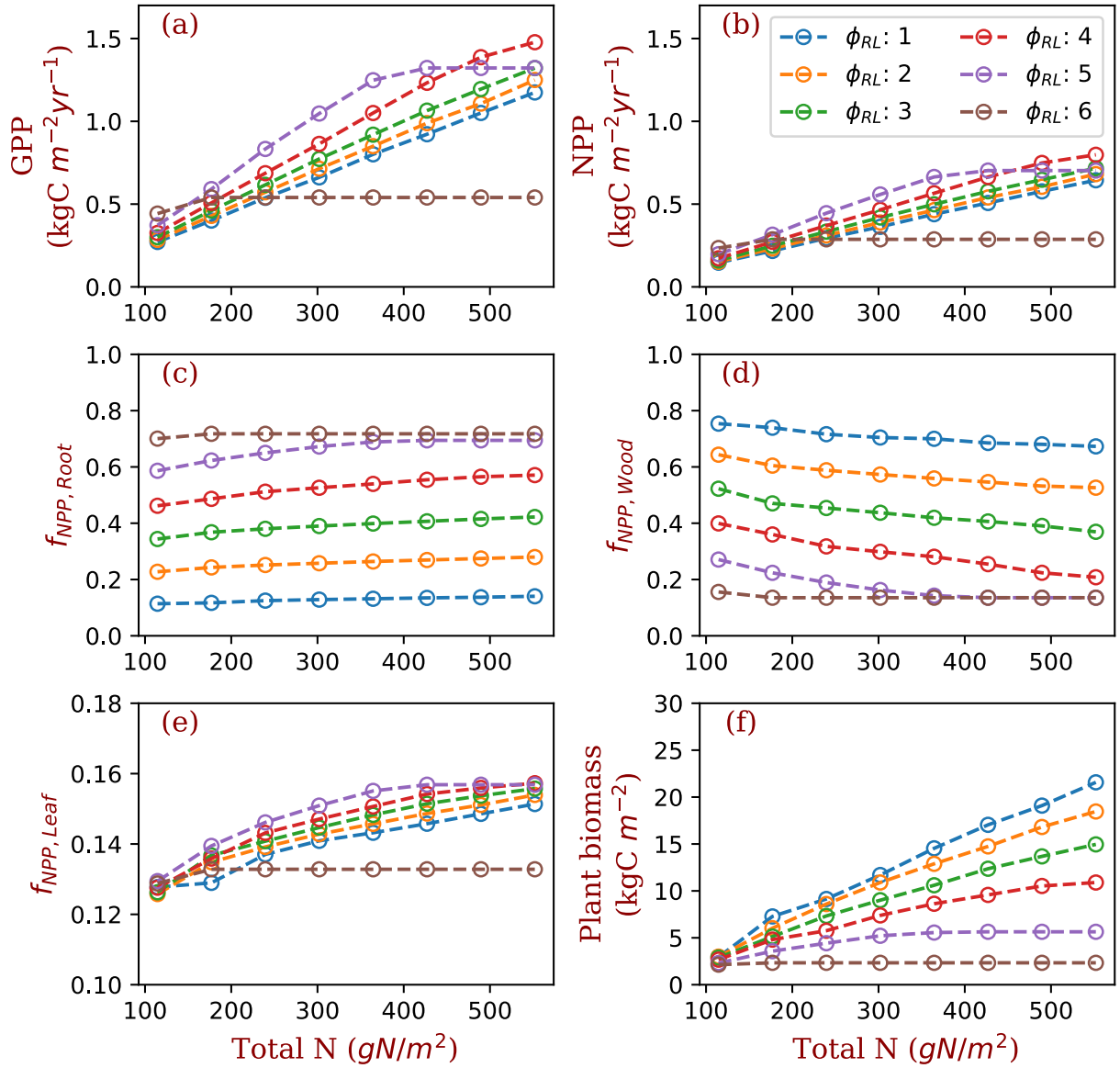
Type	Model runs	Initial PFT(s) φ_{RL}	Ecosystem total nitrogen levels	CO_2 concentration [CO_2]
Monoculture runs	One model run per combination of PFT (φ_{RL}), nitrogen level, and CO_2 concentration	One of the following PFTs: φ_{RL}= 1, 2, 3, 4, 5, 6, 7, or 8	Eight levels ranging from 114.5 g N m^{-2} to 552 g N m^{-2} at the interval of 62.5 g N m^{-2}: (i.e., 114.5, 177, 239.5, 302, 364.5, 427, 489.5, and 552 g N m^{-2})	Ambient: 380 ppm Elevated: 580 ppm
Polyculture runs I	One model run per combination of nitrogen level and CO_2 concentration	All the PFTs (φ_{RL}= 1~ 8) used in the monoculture runs		
Polyculture runs II	One model run per combination of nitrogen level and CO_2 concentration	Eight PFTs with φ_{RL} ranging from 4.5-0.5*i* to 8.5-0.5*i* at the interval of 0.5, where *i* denotes the eight nitrogen levels from 114.5 to 552 gN m^{-2}.		

In the monoculture runs, we run the full combinations of eight PFTs with root/leaf area ratios (φ_{RL}) from 1 to 8, eight ecosystem total nitrogen levels, and two CO_2 concentrations (380 ppm and 580 ppm) (Table 2). For the eight PFTs, only those with φ_{RL} <=6 survived at ambient [CO_2] (380 ppm) because the carbon assimilated by leaves could not meet the demand by plant tissues at φ_{RL}>6. The monoculture runs are for exploring the model predictions of gross primary production (GPP), net primary production (NPP), allocation, and biomass at equilibrium with fixed φ_{RL} at different total nitrogen levels.

353 In polyculture runs I, we used the same PFTs as in those monoculture runs, where their φ_{RL}
354 varied from 1 to 8 at the interval of 1.0 and the ecosystem total nitrogen levels were the same as
355 those used in the monoculture runs (Table 2). This set of polyculture runs was used to explore
356 successional patterns at both ambient and elevated [CO_2] (380 ppm and 580 ppm, respectively).
357 However, this set of model runs could not show the details of equilibrium plant biomass and
358 allocation patterns along the nitrogen gradient because of the large intervals between the φ_{RL}
359 values.
360 To achieve greater resolution in our competition predictions, we designed the polyculture
361 runs II using a dynamic PFT combination scheme according to the ranges of φ_{RL} obtained from
362 the polyculture runs I that could survive at a particular nitrogen level at both CO_2 concentrations.
363 For each nitrogen level, we set eight PFTs with φ_{RL} that varied in a range 3.5 (e.g., $x \sim x+3.5$) at
364 the interval of 0.5, starting with the highest φ_{RL} of 8.0 at the lowest N level (114.5 g N m^{-2}) and
365 decreasing 0.5 per level of increase in ecosystem total N. We used i=1, 2, …, 8 to denote the
366 eight N levels from 114.5 to 552 g N m^{-2}. The φ_{RL} of the eight PFTs at each level were 5.0-0.5i,
367 5.5-0.5i, …, 8.5-0.5i (Table 2). For example, at the nitrogen of 114.5 g N m^{-2} (i = 1), the φ_{RL} of
368 the eight PFTs were 4.5, 5.0, …, 8.0 and at 177 g N m^{-2} (i = 2), they were 4.0, 4.5, …, 7.5.
369 For both monoculture and polyculture runs, visual inspection indicated that stands had
370 reached equilibrium after ~1200 years. To be conservative, we present equilibrium data by
371 averaging model properties between years 1400 and 1800. We compared simulated equilibrium
372 GPP, NPP, allocation (both absolute amount of carbon and fractions of the total NPP), and plant
373 biomass of the polyculture runs II with those from the monoculture runs. We used the results
374 from one PFT (φ_{RL}=4) to highlight the differences of plant responses with competitively optimal
375 allocation strategies obtained from the polyculture runs II.

3 Results

In the monoculture runs, GPP and NPP increase by a factor of three along the gradient of nitrogen used in this study (114.5 - 552 g N m^{-2}) at both ambient (Fig. 3) and elevated [CO_2] (Figs. S1). The magnitude of differences in GPP and NPP due to differences in fixed allocation within a given nitrogen level is comparable to the magnitude of differences in GPP and NPP due to nitrogen level within a given fixed allocation strategy (Fig. 3: a and b) when φ_{RL} is in the range that allows plants to grow normally (1~5 in the case of ambient [CO_2]). As prescribed by the definition of φ_{RL}, allocation of NPP to fine roots increases with φ_{RL} in monoculture runs (Fig. 3: c). As a consequence, allocation of NPP to wood decreases as φ_{RL} increases (Fig. 3: d). Allocation to leaves does not change much with φ_{RL}. (Fig. 3: e, note differences in scale). Correspondingly, plant biomass at equilibrium decreases with φ_{RL} (Fig. 3: f). The effects of nitrogen on the allocation of carbon to fine roots and wood follow our allocation model assumptions because more carbon is allocated to low-nitrogen woody tissues in our model when nitrogen is limited. However, the amplitude of changes in GPP and NPP induced by nitrogen availability is lower than the amplitude of changes resulting from different values of φ_{RL} in the monoculture runs.



393

394 **Figure 3. GPP, NPP, Allocation and Plant biomass at equilibrium state simulated by**

395 **monoculture runs**. GPP: Gross primary production; NPP: Net primary production; $f_{\mathrm{NPP},x}$: the

396 fraction of NPP allocated to x, where x is Root (fine roots), Leaf (leaves in crown), or Wood

397 (including tree trunk, stems, and coarse roots). The data are from the averages of the model run

398 years from 1400 and 1800. Each model run is initiated with one PFT with fixed ratio of fine root

399 area to leaf area (φ_{RL}).

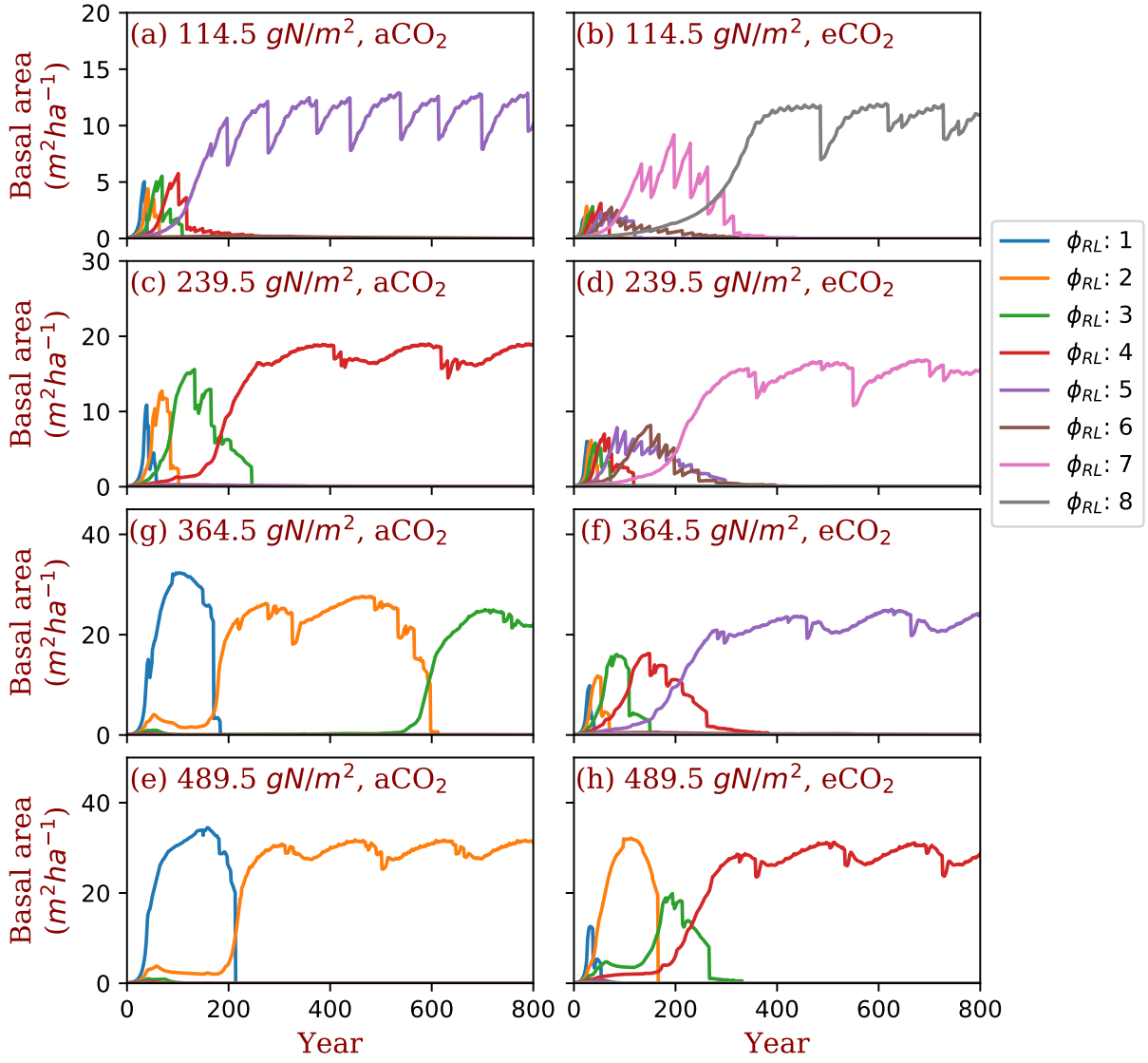
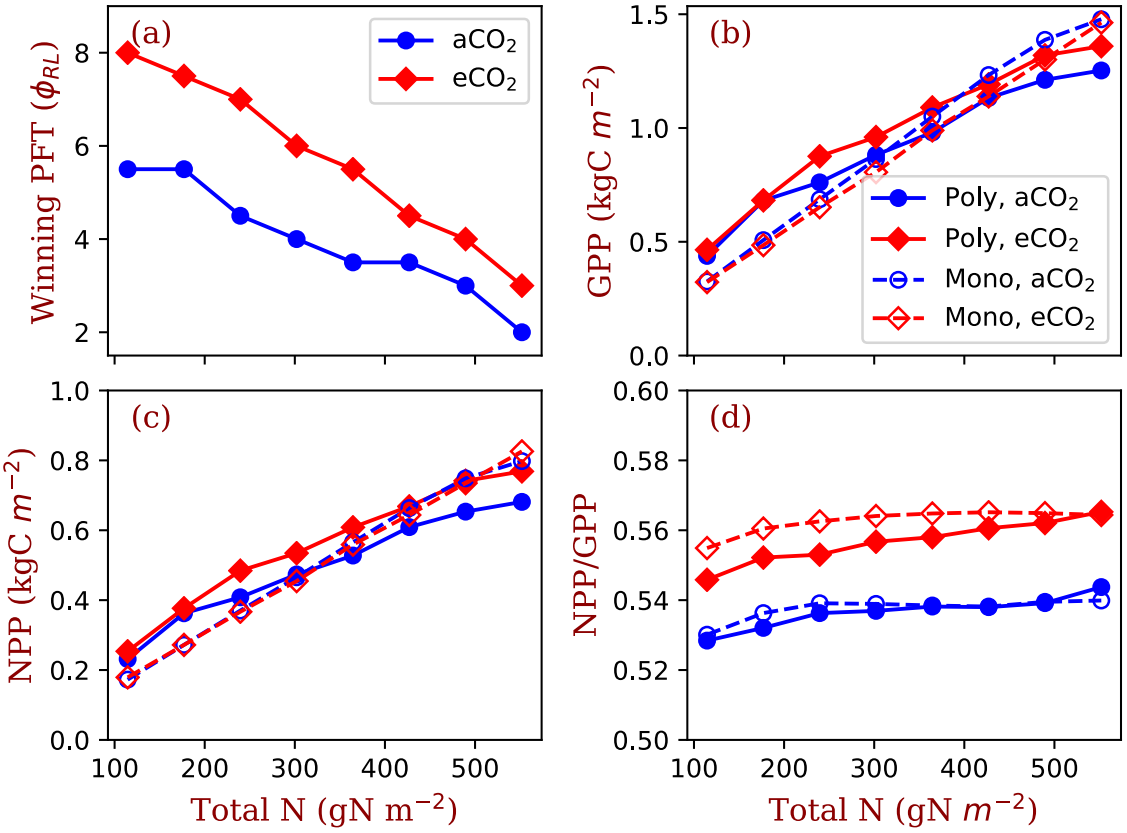


Figure 4 Successional patterns of polyculture runs I at ambient and elevated [CO_2] concentrations. φ_{RL} is the fixed ratio of fine root area to leaf area of a particular strategy.

We used two sets of polyculture runs to look for the φ_{RL} that is closest to competitively optimal. In the polyculture runs I, where φ_{RL} ranges from 1 to 8 at all nitrogen levels, the winning strategy (φ_{RL}) increases from 5 to 2 as the total nitrogen increases from 114.5 g N m^{-2} to 489.5 g N m^{-2} at ambient [CO_2] (380 ppm) (Fig. 4: a, c, g, e). Elevated [CO_2] (580 ppm) shifts

409 the winning strategy to higher (φ_{RL}) at all the total nitrogen levels. As shown in Fig. 4, the
410 winning strategy shifts from φ_{RL}=5 to φ_{RL}=8 at 114.5 g N m^{-2} and from φ_{RL} =2 to φ_{RL}=4 at 489.5
411 g N m^{-2}. In some situations (e.g., Fig. 4: g and Figs. S2 and S3), it takes a long time for the most
412 competitive PFTs to out-compete the previously dominant PFTs because of the sequential
413 replacement of dominant PFTs during the course of succession and the slow growth rate of trees
414 in understory.

415



416

417 **Figure 5 Winning PFTs (φ_{RL}, a) in polyculture runs II and equilibrium Gross Primary**
418 **Production (GPP, b), Net Primary Production (NPP, c), and Carbon Use Efficiency**
419 **(NPP/GPP, d) at two CO_2 concentrations (aCO_2: 380 ppm; eCO_2: 580 ppm).** The closed
420 symbols with solid line represent polyculture runs. The open symbols with dashed lines represent

monoculture runs (only φ_{RL}=4 shown in this figure). φ_{RL} is the fixed ratio of fine root area to leaf area of a particular strategy.

Based on the shifts of the winning φ_{RL} from ambient [CO_2] to elevated [CO_2] at the eight nitrogen levels, we designed the polyculture runs II with high resolution of φ_{RL} and calculated their GPP, NPP, allocation, and plant biomass at equilibrium state. The of φ_{RL} of the winning PFTs decreases from 5.5 to 2 at ambient [CO_2] and from 8.0 to 3.0 at elevated [CO_2] as total nitrogen increases from 114.5 g N m^{-2} to 552.0 g N m^{-2}. The equilibrium GPP and NPP increase with total nitrogen at values similar to those of the monoculture runs (Fig. 5: b and c). However, the CO_2 stimulation of NPP increases with total nitrogen in the polyculture runs more than it in the monoculture runs. Elevated [CO_2] increases carbon use efficiency (defined as the ratio of NPP to GPP in this study, NPP/GPP) in both the monoculture and polyculture runs (Fig. 5: d). Also, the dependence of NPP:GPP ratio on nitrogen is higher in the polyculture runs than it in the monoculture runs (Fig. 5:c).

Allocation of NPP to leaves increases with nitrogen in all conditions, i.e. both competition and monoculture at both ambient [CO_2] and elevated [CO_2] (Fig. 6: a). Foliage NPP is similar in these four model runs when nitrogen is low. At high nitrogen (>400 g N m^{-2}), polyculture runs have higher foliage NPP than the monoculture runs generally. Allocation to leaves is relatively stable across the nitrogen gradient at the two [CO_2] levels (Fig. 6: b). The fraction of NPP allocated to leaves changes little with nitrogen (Fig. 6: b) and it is universally higher at ambient [CO_2] than it at elevated [CO_2].

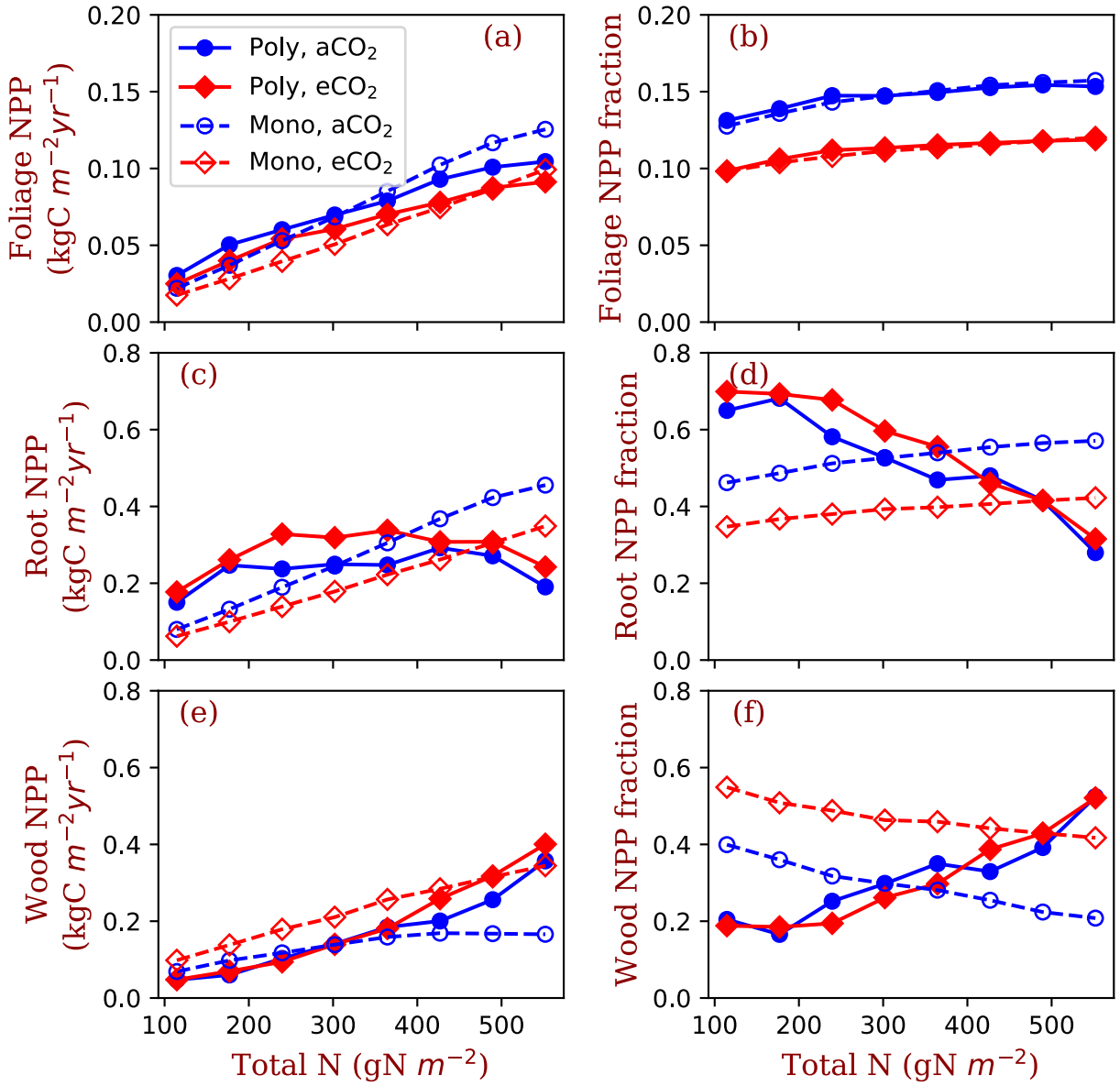
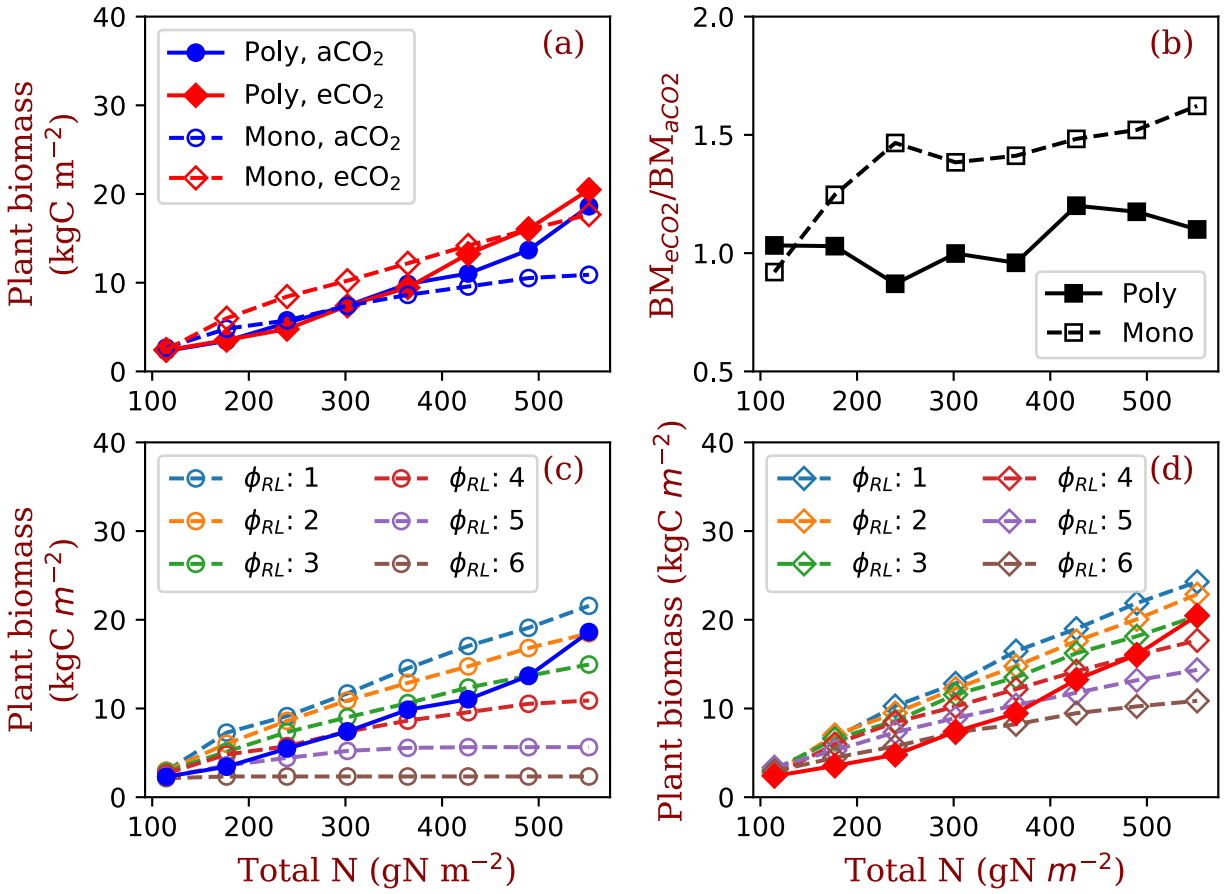


Figure 6 Allocation to leaves, fine roots, and wood tissues of the competition and monoculture runs at the eight total nitrogen levels and two CO_2 concentrations (aCO_2: 380 ppm; eCO_2: 580 ppm). The panels a, c, and e show the NPP allocated to the tissues and the panels b, d, and f show the fractions of the allocation in total NPP. The closed symbols with solid line represent polyculture runs (Poly). The open symbols with dashed lines represent monoculture runs (only φ_{RL}=4 shown in this figure, Mono). φ_{RL} is the fixed ratio of fine root area to leaf area of a particular strategy.

Fine root NPP does not significantly change with ecosystem total nitrogen in polyculture runs, whereas it increases monotonically with increasing nitrogen in monoculture runs (Fig. 6: c). Elevated [CO_2] increases fine root allocation at low nitrogen in polyculture runs but decreases root allocation irrespective of nitrogen in monoculture runs (Fig. 6: c). The fraction of NPP allocated to fine roots decreases with nitrogen at both CO_2 concentrations in polyculture runs but it increases slightly in monoculture runs (Fig. 6: d). In monoculture runs, elevated [CO_2] reduces the fraction of NPP allocated to fine roots at all nitrogen levels. In polyculture runs, fractional allocation to fine roots increases at elevated [CO_2] when nitrogen is low (e.g., 114.5-302 g N m^{-2}) and decrease at elevated [CO_2] when nitrogen is high (e.g., 364-552 g N m^{-2}).

In the reverse of the fine root response, NPP allocation to woody tissues increases with total nitrogen in both competition and monoculture runs (Fig. 6: e). In polyculture runs, the fraction of allocation to woody tissues decreases at elevated [CO_2] when ecosystem total nitrogen is low (e.g., 114 – 245 g N m^{-2}) and increases at elevated [CO_2] when ecosystem total nitrogen is high (e.g., 302 – 552 g N m^{-2}).

As a result of the changes in competitively-optimal φ_{RL}, plant biomass increases dramatically with ecosystem total nitrogen in polyculture runs compared with that in monoculture runs (Fig. 7: a). The effects of elevated [CO_2] on plant biomass increase with nitrogen in polyculture runs but are constant overall in monoculture runs (Fig. 7: b). Compared with the full spread of monoculture runs with φ_{RL} ranging from 1 to 6, polyculture runs have high root allocation at low nitrogen and low root allocation at high nitrogen due to changes in the dominant competitive allocation strategy, which amplifies plant biomass responses to elevated [CO_2] with increasing nitrogen (Fig. 7: c and d).



475

476 **Figure 7 Plant biomass responses to elevated [CO_2] and nitrogen**

477 Panel a shows the equilibrium plant biomass (means of simulated plant biomass from model run
478 year 1400 to 1800) in polyculture runs and monoculture runs (only φ_{RL}=4 shown as an example).
479 Panel b shows the ratio of simulated plant biomass at elevated [CO_2] to ambient [CO_2] for both
480 competition and monoculture runs. Panels c and d show the comparisons with monoculture runs
481 with φ_{RL} increasing from 1 to 6 at ambient (c) and elevated [CO_2] (d). The closed symbols with
482 solid line represent polyculture runs. The open symbols with dashed lines represent monoculture
483 runs (φ_{RL} ranges from 1 to 6). φ_{RL} is the fixed ratio of fine root area to leaf area of a particular
484 strategy. aCO_2: 380 ppm; eCO_2: 580 ppm.

485

4 Discussion

Our simulations show that the predicted responses of individual plants to elevated [CO_2] can be significantly changed by explicit inclusion of competition processes. Here, the major tradeoff for light- and N-limited trees is the relative allocation between stems and fine roots (Dybzinski et al. 2011). Although the wood allocation (and thus carbon sequestration potential) of every PFT used in this study increases under elevated [CO_2] at all nitrogen levels (e.g. Fig. 6: e dashed lines), only those PFTs that allocate more to fine roots (with lower carbon sequestration potential) can survive competition under elevated [CO_2] (Fig. 6: c solid lines). Put together, explicit inclusion of competition processes reduces the expected increase in biomass (and thus carbon sequestration potential) under elevated [CO_2] compared with simulations that do not include competition processes (Fig. 7: b).

Since there is a lack of direct observations or experiments to quantitatively validate the long-term patterns predicted by our model, we did not calibrate it to fit observations at Harvard Forest. In the following section, we analyze the model processes in detail and validate our modeling approach by comparing the general patterns from observations and experiments with model predictions. These comparisons also shed light on the modeling of allocation and vegetation responses to elevated [CO_2].

4.1 Mechanisms of game-theoretic allocation modeling and simulation results validation

In our model, the allocation of carbon and nitrogen within an individual tree is based on allometric scaling (Eq. 2), functional relationships (Eq. 3), and optimization of resource usage

508 (Eq. 7). Generally, the allometric scaling relationships define the maximum leaf and fine root
509 surface area at a given tree size, and the functional relationships define the ratios of leaf area to
510 sapwood cross-sectional area and fine root surface area. These rules are commonly used in
511 ecosystem models (Franklin et al., 2012) and have been shown to generate reasonable
512 predictions (De Kauwe et al., 2014; Valentine and Mäkelä, 2012). These rules implicitly define
513 the priority of allocation to leaves and fine roots but allow for structurally-unlimited stem growth
514 when resources (carbon and nitrogen in this study) are available (i.e., the remainder goes to
515 stems after leaf and fine root growth) and NSC is not accumulated exaggeratedly when
516 ecosystem nitrogen is limited (Fig. S6).

517 We used a tuning parameter, maximum leaf and fine root allocation, $f_{LFR,max}$, to constrain
518 the maximum allocation to leaves and fine roots in order to maintain a minimum growth rate of
519 wood in years of low productivity. This is consistent with wood growth patterns in temperate
520 trees, where new wood tissues must be continuously produced (especially early in the growing
521 season) to maintain the functions of tree trunks and branches (Cuny et al., 2012; Michelot et al.,
522 2012; Plomion et al., 2001). This parameter does not change the fact that leaves and fine roots
523 are the priority in allocation, since allocation ratios to stems are around 0.4~0.7 in temperate
524 forests (Curtis et al., 2002; Litton et al., 2007). With a value of 0.85, parameter $f_{LFR,max}$ seldom
525 affects the overall carbon allocation ratios of leaves, fine roots, and stems. If $f_{LFR,max} = 1$ (i.e., the
526 highest priority for leaf and fine root growth), simulated trunk radial growth would have
527 unreasonably high interannual variation because leaf and fine root growth would use all carbon
528 to approach to their targets, leaving nothing for stems in some years of low productivity.

529 The simulation of competition for light and soil resources is based on two fundamental
530 mechanisms: 1) competition for light is based on the height of trees according to the PPA model,

which assumes trees have perfectly plastic crown to capture light via stem (trunk) and branch phototropism (Strigul et al., 2008); and 2) individual soil N uptake is linearly dependent on the fine root surface area of an individual tree relative to that of its neighbors (Dybzinski et al., 2019; McMurtrie et al., 2012; Weng et al., 2017). These two mechanisms define an allocational tradeoff between wood and fine roots for carbon and nitrogen investment in different CO_2 concentrations and nitrogen environments. Including explicit competition for these resources to determine the dominant strategies results in very different predicted allocation patterns – and thus ecosystem level responses – than those of strategies in the absence of competition. For example, fractional wood allocation increases with increasing nitrogen availability under competitive allocation but decreases – *the opposite qualitative response* – under a fixed strategy (Fig. 6: f). Consequently, equilibrium plant biomass is predicted to increase much more with increasing nitrogen availability under a competitive strategy (Fig. 4: c, d). In nature, the effects of competition on dominant plant traits may occur through species replacement or community assembly (akin to the mechanism in our model) (e.g., Douma et al., 2012), but it may also occur through adaptive plastic responses or in-place sub-population evolution of ecotypes (Grams and Andersen, 2007; McNickle and Dybzinski, 2013; Smith et al., 2013).

Generally, the predictions from competitively-optimal allocation strategies predicted by our model can be found in large scale forest censuses and site-level experiments, such as: 1) high nitrogen environments (i.e., productive environments) favor high wood allocation and low root allocation (Litton et al., 2003; Poorter et al., 2012); 2) elevated [CO_2] increases root allocation (Drake et al., 2011; Iversen, 2010; Jackson et al., 2009; Nie et al., 2013; Smith et al., 2013); 3) low nitrogen availability limits vegetation biomass responses to elevated [CO_2] as a result of high root allocation or root exudation (Jiang et al., 2019a; Norby and Zak, 2011); and 4)

554 increases in vegetation biomass at elevated [CO_2] are largely due to high wood allocation (Norby
555 and Zak, 2011; Walker et al., 2019). These predictions emerge from the fundamental
556 assumptions of our model without tuning parameters to fit the data, providing some confidence
557 in the robustness of our approach.

558 The literature on experimental responses of plant community to elevated [CO_2] shows
559 that the responses vary with site characteristics, forest composition, stand age, plant
560 physiological responses, and soil microbial feedbacks (Norby and Zak, 2011; Terrer et al., 2016,
561 2018). For example, in Duke Free Air CO_2 Enhancement (FACE) experiment, where the major
562 trees are loblolly pine (*Pinus taeda*), increases in root production at elevated [CO_2] stimulated
563 increased nitrogen supply that allowed the forest to sustain higher productivity (Drake et al.,
564 2011). However, in Oak Ridge FACE, where the major trees are sweetgum (*Liquidambar*
565 *styraciflua*), increased fine-root production under elevated [CO_2] did not result in increased net
566 nitrogen mineralization and increases in root production declined after eight years of CO_2
567 enhancement (Iversen, 2010; Norby and Zak, 2011). In EucFACE (Jiang et al., 2019a), where the
568 major trees are *Eucalyptus tereticornis* and the soil is infertile, trees significantly increased their
569 root exudation under limited nutrient supplies but had no significant increase in biomass in
570 response to elevated [CO_2]. The BangorFACE experiment (Smith et al., 2013) found that
571 interspecific competition (*Alnus glutinosa*, *Betula pendula* and *Fagus sylvatica*) resulted in
572 greater increases in root biomass at elevated [CO_2]. Leaf area index (LAI) responses to elevated
573 [CO_2] are also highly varied. As summarized by Norby and Zak (2011), low LAI (in this case,
574 open canopy) sites showed significant increases in LAI and high LAI (in this case, closed
575 canopy) sites showed low increases or even decreases in LAI. They concluded that LAI in

576 closed-canopy forests is not responsive to elevated [CO_2] (Norby et al., 2003; Norby and Zak,
577 2011).

578 The nature of developing a model with generic assumptions and balanced processes
579 reduces its capability to predict all of these responses. For example, plants have a variety of
580 physiological mechanisms to deal with excessive carbon supply when plant demand (i.e., "sink")
581 is relatively low (Fatichi et al., 2019; Körner, 2006), such as down-regulating leaf photosynthesis
582 rate by the accumulated assimilates (Goldschmidt and Huber, 1992) or respiring excessive
583 carbohydrates to regenerate substrates for photosynthesis (Atkin and Macherel, 2009). But these
584 mechanisms are short-term physiological responses (minutes to hours, sometimes days) for
585 plants in situations of temporary nitrogen shortage, high irradiation, or drought stress. It is not
586 "economically" sustainable in an infertile environment to maintain highly productive leaves but
587 often suppress their photosynthesis or respire a large portion of their assimilated carbon.

588 Root exudation is a critical process for plants. It can stimulate soil organic matter
589 decomposition and nitrogen mineralization to facilitate soil nitrogen supply at the expense of
590 carbon (Cheng, 2009; Cheng et al., 2014; Drake et al., 2011; Phillips et al., 2011). The process of
591 root exudation has been adopted by many models to couple with microbial processes in the
592 determination of soil organic matter decomposition (Sulman et al., 2014; Wieder et al., 2014,
593 2015). Some carbon-only models, e.g., LM3 (Shevliakova et al., 2009), the parent model of this
594 one, and TECO (Luo et al., 2001), incorporate root exudation to put extra carbon into the soil in
595 order to avoid down-regulating canopy photosynthesis or overestimating vegetation biomass,
596 both of which had been tuned against data. However, in a demographic competition model like
597 this one, individual plants cannot reap a reward from root exudation as they do in nature when
598 the microbial activities are not fully coupled and the nitrogen in soil is assumed fully accessible

by roots of all individuals. Therefore, root exudation is not a competitive strategy in the system defined by the assumptions of this model.

Since the purpose of this study is to explore long-term ecological strategies in different but relatively stable environments, we did not include these processes, especially since they present additional challenges in balancing the complexity of the tradeoffs between modeled demographic processes and plant traits. However, the lack of these processes does limit the predictions of instantaneous responses to variation in environmental conditions or resource supply and possibly of some long-term vegetation characteristics as well. For example, our model predicts reduced LAI under nitrogen limitation (Fig. S7) based on first principles, but it is incidentally the only mechanism that reduces the whole-canopy photosynthesis rate in our model. There are mechanisms that increase nitrogen use efficiency at the expense of carbon by increasing LMA and therefore leaf longevity to maintain high LAI and high canopy-level photosynthesis rates (Aerts, 1995, 1999; Aerts and Chapin, 1999; Givnish, 2002). We did not include these mechanisms in our simulations, although they are well-developed in this model (Weng et al. 2017), because we wished to focus on the strategy of allocation. The clear descriptions of our model's assumptions, its traceable processes, and inclusion of the tradeoffs involved in aboveground and belowground competition provide a useful benchmark from which to incorporate additional mechanisms and tradeoffs.

4.2 Root overproliferation vs. wood allocation

The allocation strategy that maximizes site vegetation biomass allocates very little to fine roots (Figs. 3 and S1). In contrast, the competitively optimal strategy allocates more carbon to fine roots, termed "fine-root overproliferation" in the literature (Gersani et al., 2001; McNickle

622 and Dybzinski, 2013; O'Brien et al., 2005). It is the result of a competitive "arms race": while
623 increasing fine root area under elevated [CO_2] does not result in more nitrogen for an individual,
624 failing to do so would cede some of that individual's nitrogen to its neighbors. Because most
625 nitrogen uptake is via mass flow and diffusion (Oyewole et al., 2017) and because both of these
626 mechanisms depend on sink strength, individuals with *relatively* greater fine root mass than their
627 neighbors take a greater share of nitrogen, as was recently demonstrated empirically (Dybzinski
628 et al., 2019; Kulmatiski et al., 2017). Thus, fine roots may overproliferate for competitive
629 reasons relative to lower optimal fine root mass in the hypothetical absence of an evolutionary
630 history of competition (Craine, 2006; McNickle and Dybzinski, 2013). This may also explain
631 why root C:N ratio is highly variable (Dybzinski et al., 2015; Luo et al., 2006; Nie et al., 2013): a
632 high density of fine roots in soil may be more important than the high absorption ability of a
633 single root in competing for soil nitrogen in the usually low mineral nitrogen soils.

634 Root overproliferation is still controversial in experiments. For example, Gersani et al.
635 (2001) and O'Brien (2005) found that competing plants generated more roots than those
636 growing in isolation; whereas McNickle and Brown (2014) found that competing plants
637 generated comparable roots to those growing in isolation. Compared to modeled roots, real roots
638 are far more adaptive and complex at modifying their growth patterns in response to soil nutrient
639 and water dynamics (Hodge, 2009). The root growth strategies in response to competition also
640 vary with species (Belter and Cahill, 2015). The mechanisms of self-recognition of inter- and
641 intra- roots also can lead to varied behavior of root growth (Chen et al., 2012). However, all of
642 the aforementioned studies considered only *plastic* root overproliferation, where individuals
643 produce more roots in the presence of other individuals than they do in isolation, analogous to
644 stem elongation of crowded seedlings (Dudley and Schmitt, 1996). A portion of root

overproliferation may also be *fixed*, analogous to trees that still grow tall even when grown in isolation. Dybzinski et al. (2019) showed that plant community nitrogen uptake rate was independent of fine root mass in seedlings of numerous species, suggesting a high degree of fixed fine root overproliferation. To improve root competition models, more detailed experiments that control root growth should be conducted to quantify the marginal benefits of roots in isolated, monoculture, and polyculture environments.

At high soil nitrogen, height-structured competition for light (also a game-theoretic response, Falster and Westoby, 2003; Givnish, 1982) prevails, and trees with greater *relative* allocation to trunks prevail. The balance between these two competitive priorities (fine roots vs. stems) can be observed in our model predictions as a shift from fine root allocation to wood allocation as soil nitrogen increases. The increases in the critical height (i.e. the context-dependent height of the shortest tree in canopy layer in the PPA) from low nitrogen to high nitrogen indicates a shift from the importance of competition for soil nitrogen to the importance of competition for light as ecosystem nitrogen increases (Fig. S8). Because the most competitive type shifts from high fine root allocation to low fine root allocation as ecosystem total nitrogen increases, increases in NPP and plant biomass across the nitrogen gradient are greater than the increases in NPP and plant biomass assuming allocational strategies in the absence of competition (Fig. 3). This greatly reduces the carbon cost of belowground competition as ecosystem total nitrogen increases. The decrease in the fraction of NPP allocated to leaves at elevated [CO_2] (Fig. 6: b) occurs because of increases in total NPP and nearly constant absolute NPP allocation to foliage (Fig. 6: a).

4.3 Model complexity and uncertainty

668 Compared with the conventional pool-based vegetation models that use pools and fluxes
669 to represent plant demographic processes at a land simulation unit (e.g., grid or patch), VDMs
670 add two more layers of complexity. The first is the inclusion of stochastic birth and mortality
671 processes of individuals (i.e., demographic processes). These processes allow the models to
672 predict population dynamics and transient vegetation structure, such as size-structured
673 distribution and crown organization (e.g., Moorcroft et al., 2001; Strigul et al., 2008). With
674 changes in vegetation structure, allocation and mortality rates can change, generating a different
675 carbon storage accumulation curve compared with those predicted by pool-based models where
676 vegetation structure is not explicitly represented (e.g., Weng et al., 2015). The second is the
677 simulated shift in dominant plant traits during succession due to the shifting of competitive
678 outcomes among different PFTs, which changes the allocation between fast- and slow-turnover
679 pools and thus the parameters of allocation and the residence time of carbon in the ecosystem.
680 Together, these mechanisms may alter long-term predictions of terrestrial carbon cycl due
681 to changes in PFT-based parameters (Dybzinski et al., 2011; Farrior et al., 2013; Weng et al.,
682 2015). As described in Introduction, current pool-based models can be described by a linear
683 system of equations characterized by the key parameters of allocation, residence time, and
684 transfer coefficients (Eq. 1) with the rigid assumption of unchangeable plant types (Luo et al.,
685 2012; Xia et al., 2013). In VDMs however, allocation, residence time, leaf traits, phenology,
686 mortality, plant forms, and their responses to climate change are all strategies of competition
687 whose success varies with the environmental conditions and the traits of the individuals they are
688 competing against.
689 Many tradeoffs between plant traits can shift in response to environmental and biotic
690 changes, limiting the applicability of varying a single trait, as we have in this study. For example,

allocation, leaf traits, mycorrhizal types, and nitrogen fixation can all change with ecosystem nitrogen availability (Menge et al., 2017; Ordoñez et al., 2009; Phillips et al., 2013; Vitousek et al., 2013). The unrealistic effects of model simplification can be corrected by adding important tradeoffs that are missing. For example, the positive feedback between root allocation and SOM decomposition plays a role in mitigating the effects of tragedies of the commons of root over-proliferation (e.g., Gersani et al., 2001; Zea-Cabrera et al., 2006) due to a negative feedback induced by root turnover. High root allocation increases the decomposition rate of SOM and the supply of mineral nitrogen because of the high turnover rate of root litter, which favors a strategy of high wood allocation and reduces the competitive optimal fine root allocation. This negative feedback indicates that the model structure is flexible and that we can incorporate correct mechanisms step by step to improve model prediction skills. Testing single strategies is still a necessary step to improving our understanding of the system and prediction skills of the models, though it could lead to unrealistic responses sometimes.

We found that model predictions can differ significantly in response to seemingly-small variations in basic assumptions or quantitative relationships. For example, our model predicts that the ratio of plant biomass under elevated [CO_2] relative to plant biomass under ambient [CO_2] should increase with increasing nitrogen due to the shift of carbon allocation from fine roots to woody tissues. In contrast, the analytic model of Dybzinski *et al*. (2015) predicts that the ratio of plant biomass under elevated [CO_2] relative to plant biomass under ambient [CO_2] should be largely independent of total nitrogen because of an increasing shift in carbon allocation from long-lived, low-nitrogen wood to short-lived, high-nitrogen fine roots under elevated [CO_2] and with increasing nitrogen. This significant difference between these two predictions traces back to differences in how fine root stoichiometry is handled in the two models. In the model of

714 Dybzinski *et al*. (2015), the fine root C:N ratio is flexible and the marginal nitrogen uptake
715 capacity per unit of carbon allocated to fine roots depends on its nitrogen concentration. Like the
716 model presented here, the model of Dybzinski *et al*. (2015) predicts decreasing fine root mass
717 with increasing nitrogen availability. *Unlike* the model presented here (which has constant fine
718 root nitrogen concentration), the model of Dybzinski et al. (2015) predicts increasing fine root
719 nitrogen concentration with increasing nitrogen availability. As a result, there is less nitrogen to
720 allocate to wood as nitrogen increases in the model of Dybzinski *et al*. (2015) than there is in the
721 model presented here. These countervailing factors even out the ratio of plant biomass under
722 elevated [CO_2] relative to plant biomass under ambient [CO_2] across the nitrogen gradient in
723 Dybzinski *et al*. (2015), whereas their absence amplifies this ratio with increasing nitrogen in the
724 model presented here. Our ability to diagnose and understand this discrepancy highlights the
725 utility of deploying closely-related analytical and simulation models (Weng et al., 2017).

726 We conducted simulations only at one site for the purpose of exploring the general
727 patterns of competitively optimal allocation strategies and their responses to elevated [CO_2] at
728 different nitrogen availabilities. We can speculate about shifts in the competitively optimal
729 allocation strategy in different forest biomes by considering the effects of temperature on soil
730 nitrogen supply via the SOM's decomposition rate and its positive effect on net nitrogen
731 mineralization. For example, the SOM decomposition rate is usually high in warm regions and
732 low in cold regions (Davidson and Janssens, 2006) assuming there are no water limitations and
733 SOM is equilibrated with carbon input. According to our model, allocation to roots is high in low
734 nitrogen supply conditions (cold regions) and low in high nitrogen supply conditions (warm
735 regions). This pattern can be found from temperate to boreal forest zones (Cairns et al., 1997;
736 Gower et al., 2001; Reich et al., 2014; Zadworny et al., 2016). Temperature also alters NPP, i.e.,

carbon supply: as temperature goes down, NPP decreases and nitrogen demand decreases, alleviating nitrogen limitation and leading to shifts of allocation to stems. So, the differences in temperature effects on photosynthesis and SOM decomposition will determine competitive allocation strategy. Since SOM decomposition is more sensitive to temperature than gross primary production is at long-temporal and large-spatial scales (Beer et al., 2010; Carey et al., 2016; Crowther et al., 2016), our model suggests that allocation will shift to wood in a warming world. Whether the carbon stored in that wood is enough to offset the carbon released from increasing soil respiration is a critical question.

Water is also a critical factor affecting allocation and its responses to elevated [CO_2]. Low soil moisture usually leads to high allocation to roots (Poorter et al., 2012). Elevated CO_2 can reduce transpiration (as found in our study as well, Figs. S9~S11) and therefore increase soil moisture, resulting in increases in allocation to stems and aboveground biomass (Walker et al., 2019). A game-theoretic modeling study using the PPA framework shows that the competitively optimal allocation strategy shifts to high wood allocation at elevated [CO_2] in environments with water limitation (Farrior et al., 2015). This is opposite to the elevated [CO_2] effects on allocation in nitrogen-limited environments as simulated in this study. According to field experiments, fine root allocation is more responsive to nitrogen changes than it to soil moisture changes (Canham et al., 1996; Poorter et al., 2012). Poorter et al. (2012) attribute the mechanisms to the optimal strategies in response to the relative stable nitrogen supply and stochastic water input in soil. The vertical distribution of roots and the contributions of roots in different layers to water and nitrogen uptake also suggest that the uptake of soil nutrients are dominant in shaping root system architecture (Chapman et al., 2012; Morris et al., 2017), though root growth and turnover are

759 flexible and sensitive to nitrogen and water supply (Deak and Malamy, 2005; Linkohr et al.,
760 2002; Pregitzer et al., 1993).

761

762 **4.4 Common principles for allocation modeling and implications**

763 As shown in model inter-comparison studies, the mechanisms of modeling allocation
764 differ very much, leading to high variation in their predictions (e.g., De Kauwe et al. 2014).
765 Calibrating model parameters to fit data may not increase model predictive skill because data are
766 often also highly variable. Franklin et al. (20`12) suggest that in order to build realistic and
767 predictive allocation models, we should correctly identify and implement fundamental principles.
768 Our model predicts similar patterns to those predicted by the model of Valentine and Mäkelä
769 (2012), which has very different processes of plant growth and allocation. However, these two
770 models share fundamental principles, including 1) evolutionary- or competitive-optimization, 2)
771 capped leaves and fine roots at given tree sizes, 3) structurally unlimited stem allocation (i.e.,
772 optimizing carbon use) because the woody tissues can serve as unlimited sink for surplus carbon,
773 and 4) height-structure competition for light and root-mass-based competition for soil resources.
774 The principles 2 and 3 are commonly used in models (De Kauwe et al., 2014; Jiang et al.,
775 2019b). However, the different rules of implementing them (e.g., allometric equation, functional
776 relationships, etc.) lead to highly varied predictions (as shown in De Kauwe et al., 2014), though
777 model formulations may be very similar.

778 In competitively-optimal models, such as this study and also Valentine and Mäkelä (2012),
779 the competition processes generate similar emergent patterns by selecting those that can survive
780 in competition, regardless the details of those differences. The competition processes also make
781 the details of allocation settings for a single PFT and their direct responses to elevated [CO_2] less

782 important, because competition processes will select out the most competitive strategy from
783 diverse strategies in response to changes in [CO_2] and nitrogen. Our study and Valentine and
784 Mäkelä (2012), posit a fundamental tradeoff between light competition and nitrogen competition
785 via allocation based on insights gained from simpler models (e.g., Dybzinski et al., 2015; Mäkelä
786 et al., 2008) for predicting allocation as an emergent property of competition. One advantage of
787 building a model in this way is that the vegetation dynamics are predicted from first principles,
788 rather than based on the correlations between vegetation properties and environmental
789 conditions. With these first principles, the models can produce reasonable predictions, though the
790 details of physiological and demographic processes vary among models.

791 For vegetation models designed to predict the effects of climate change, the important
792 operational distinction is that the fundamental rules cannot or will not change as climate changes.
793 Nor, presumably, will the underlying ecological and evolutionary processes change as climate
794 changes. The emergent properties can change as climate changes however, and the models built
795 on the "scale-appropriate" unbreakable constraints and ecological and evolutionary processes
796 will be able to accurately predict changes in emergent ecosystem properties (Weng et al., 2017).
797 In our opinion, the scientific effort to build better models is better served by understanding
798 unrealistic predictions than by "fixing" them with unreliable mechanisms when there is a lack of
799 data or theory to make them consistent with observations. Validating assumptions and initial
800 responses are critical, and the long-term responses can be validated via spatial patterns.

801 This modeling approach also demands improvement in model validation and benchmarking
802 systems (Collier et al., 2018; Hoffman et al., 2017). As shown in this study, allocation responses
803 to elevated CO_2 at different nitrogen levels in monoculture runs are opposite to those in
804 competitive-allocation runs. For example, in monoculture runs, elevated [CO_2] increases wood

allocation and decreases fine root allocation at low nitrogen; whereas in competitive-allocation runs elevated [CO_2] leads to low wood allocation and high fine root allocation. Simply calibrating our model against short-term observational data may improve the agreement with observations but would not change the model's predictions because the model's predictions emerge from its fundamental assumptions.

5 Conclusions

Our study illustrates that including the competition processes for light and soil resources in a game-theoretic vegetation demographic model can substantially change the prediction of the contribution of ecosystems to the global carbon cycle. Allowing the model to explicitly track the competitive allocation strategies can generate significantly different ecosystem-level predictions (e.g., biomass and ecosystem carbon storage) than those of strategies in the absence of explicit competition. Building such a model requires differentiating between the unbreakable tradeoffs of plant traits and ecological processes from the emergent properties of ecosystems. Drawing on insights from closely-related analytical models to develop and understand more complicated simulation models seems, to us, indispensable. Evaluating these models also requires an updated model benchmarking system that includes the metrics of competitive plant traits during the development of ecosystems and their responses to global change factors.

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Codes and data availability

The model codes used in this study, simulated data, and Python scripts used in this study are in Github (https://github.com/wengensheng/BiomeE-Allocation).

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1296