Dear Dr. Zaehle,

Thanks for your suggestions on addressing reviewers' concerns. We have revised our manuscript thoroughly according to the comments from Dr. De Kauwe and reviewer #1.
We have added more evidences and experimental results to support our modeling approach and simulation results in section Discussion, described the details of modeling water dynamics in this model (BiomeE) and added the figures of simulated transpiration and soil water dynamics in supplementary information II, discussed possible effects of changes in temperature and water on model predictions. For addressing reviewer #1's concerns on "the fate of excessive carbon", we discussed three possible options and explained why we chose this one. We also discussed the uncertainty of our model in predicting short-term physiological responses and long-term ecological responses based on the fundamental assumptions of this model.

Please see the detailed responses to reviewers' comments and revised manuscript with tracking changes enclosed in this letter. Review comments are in italics and our responses are in normal. The line numbers of manuscript are referred to the tracking change version enclosed in this letter.

Your sincerely,
Ensheng Weng, Ray Dybzinski, Caroline E. Farrior, and Stephen W. Pacala

Submitted on 09 Jul 2019
Referee #4: Martin De Kauwe, mdekauwe@gmail.com

In this study, Weng et al. explore the important question of how competition alters the responses of the vegetation to elevated CO2. They simulated forest responses to eCO2 along a N availability gradient using fixed and "competitively-optimal" allocation strategies. For such an important plant response (i.e. change in allocation) to global change, the detail afforded in most global models is troubling, so a study like this is very timely. Overall, I found this study interesting and one that I would like to see published in Biogeosciences. Nevertheless, I think this study will require some further revisions, particularly focusing issues of clarity (hopefully I've helped outline a few places).

My main suggestion would be to think a bit more about the discussion ...

- ***What do the authors want the reader to take from this study?*** *For example, the authors open their discussion by saying: "Our model predicts increased root allocation at all nitrogen levels in response to elevated [CO2] in the competition runs." This is fine, but why not tell the reader why this happens mechanistically? What about your approach leads to this? Is it simply a consequence of what you assumed, or something more emergent? Also, what magnitude of change do you predict? And how does this vary with N availability? This seems more insightful than root allocation increased and this is broadly what you see in FACE experiments.*

We have rewritten this paragraph and re-organized the section of Discussion following Dr. De Kauwe's comments. The first two paragraphs (Lines 517~532) are copied below:
"Our simulations show that the 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. 6e dashed lines), only those PFTs that allocate more to fine roots (with lower carbon sequestration potential) can survive competition under elevated [CO_2] (Fig. 6c 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. 7b).

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].”

- *Exploring this further, in the discussion about increased "fine-root overproliferation" being an emergent outcome of your simulations, could you talk a bit more about how this happens? As I understand it, you use a saturating N uptake function of root mass. In my experience, this does what it says on the tin, so there is only limited benefit in terms of increasing N with greater root investment. So, how does this differ in this study? One logical way would be if root allocation was very low to begin with, is this true here? I would suggest that the saturating root function is consistent with some of the FACE results, i.e. there is a benefit in increased N uptake, but this saturates. So, this leads me to ask how this leads to such a strong response in your experiments, over such a long time period ... This is interesting and worthy of discussion.*

The fine-root overproliferation is resulted from competition with other individuals, instead of the saturation uptake rate of roots. It is like an arm race: when your neighbor increases its investment in roots, you must follow. Otherwise, your neighbor will get more resources, grow faster, and overtop you. Even if fine roots are saturated at the stand level (i.e., adding new roots does not increase the total N uptake rate of all the trees in this site), individual plants still benefit from increased root investment, because this gives them more nitrogen than their neighbors. Yet, these competitive games lead to a tragedy of the commons in the form of lowered allocation to stems by the competitive-dominant strategies when they are resident.

We reorganized this paragraph to make explanations clearer (Lines: 663~677):

“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 and

Dybzinski, 2013; O’Brien et al., 2005). It is the result of a competitive “arms race”: while increasing fine root area under elevated [CO2] does not result in more nitrogen for an individual, failing to do so would cede some of that individual’s nitrogen to its neighbors. Because most nitrogen uptake is via mass flow and diffusion (Oyewole et al., 2017) and because both of these mechanisms depend on sink strength, individuals with relatively greater fine root mass than their neighbors take a greater share of nitrogen, as was recently demonstrated empirically (Dybzinski et al., 2019; Kulmatiski et al., 2017). Thus, fine roots may overproliferate for competitive reasons relative to lower optimal fine root mass in the hypothetical absence of an evolutionary history of competition (Craine, 2006; McNickle and Dybzinski, 2013). This may also explain why root C:N ratio is highly variable (Dybzinski et al., 2015; Luo et al., 2006; Nie et al., 2013): a high density of fine roots in soil may be more important than the high absorption ability of a single root in competing for soil nitrogen in the usually low mineral nitrogen soils.”

- ***It would be good to talk about competition for water and explore how both this and climate might change your model predictions.*** *I make this point below so I won't repeat it. Particularly when you make the link to the shift to competition for light (paragraph ln 725 onwards).* ***Those cited studies that your model result are consistent with, don't as I recall****, consider an explicit role for water either ...*

We have added a paragraph discussing water effects in section “**4.3 Model complexity and uncertainty**” (Lines: 768~783):

“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, Fig S7) 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. 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 flexible and sensitive to nitrogen and water supply (Deak and Malamy, 2005; Linkohr et al., 2002; Pregitzer et al., 1993)."

Since it would require additional simulations across two dimensions of environmental variables to determine how water limitation influences the effects of CO_2 in this model, we prefer leave this work for future. We have investigated the effects of water limitation in the absence of nitrogen limitation (Weng et al. 2015). In that study, the results show changes in φ_{RL} ranging from 0.5~0.9.

As for the comment "***Those cited studies that your model result are consistent with, don't as I recall***", we reorganized the validation section and discussed the various responses in FACE experiments and the rationale of model development (Lines 603~621).
"The literature on experimental responses of plant community to elevated [CO_2] shows that the responses vary with site characteristics, forest composition, stand age, plant physiological responses, and soil microbial feedbacks. For example, in Duke Free Air CO_2 Enhancement (FACE) experiment, where the major trees are loblolly pine (*Pinus taeda*), increases in root production at elevated [CO_2] stimulated increased nitrogen supply that allowed the forest to sustain higher productivity (Drake et al., 2011). However, in Oak Ridge FACE, where the major trees are sweetgum (*Liquidambar styraciflua*), increased fine-root production under elevated [CO2] did not result in increased net nitrogen mineralization and increases in root production declined after eight years of CO_2 enhancement (Iversen, 2010; Norby and Zak, 2011). In EucFACE, where the major trees are *Eucalyptus tereticornis* and the soil is infertile, trees significantly increased their root exudation under limited nutrient supplies but had no significant increase in biomass in response to elevated [CO2] (Jiang et al., 2019a). The BangorFACE experiment (Smith et al., 2013) found that interspecific competition (*Alnus glutinosa, Betula pendula and Fagus sylvatica*) resulted in greater increases in root biomass at elevated [CO_2]. Leaf area index (LAI) responses to elevated [CO_2] are also highly varied. As summarized by Norby and Zak (2011), low LAI (in this case, open canopy) sites showed significant increases in LAI and high LAI (in this case, closed canopy) sites showed low increases or even decreases in

LAI. They concluded that LAI in closed-canopy forests is not responsive to elevated [CO_2] (Norby et al., 2003; Norby and Zak, 2011)."

- Line 791: This argument is completely true, but it also stands to reason that such approaches also need to be tested against data too! Just because something has the potential to predict more variable responses to climate, does not mean the predictions are more sound! This point is developed on line 848 by calling for an improvement in model validation/benchmarking. I don't follow this argument, to be honest. There is surely plenty of data available with which you could test core elements of the predictions of your model? For example, you could use the BAAD allometry databases, or similar, you need not just focus on CO2. Moreover, asserting that because your model predicts different responses over > 1000 years than those from short term experimental responses, and so, little can (may) be learned by tested against such data is ill thought through in my opinion. You are never going to have the types of data your model will need to "validate" it. The point of manipulation experiments, or comparisons across natural gradients (e.g. N availability, aridity, temperature), is to test core elements of (what should be emergent) model behaviour. In doing so, you are or trying to ensure that the underlying principles are sound. There are a number of studies that also have competition experiments (e.g. BIOCON, PHACE, etc) admittedly in grassland ecosystems, but there are data. It is, of course, true that simply assuming the response in a short term manipulation experiment is the "truth" would be fanciful, but these are one of our best ways to ground models in data. With this paragraph, why not think a bit more creatively about what kinds of existing datasets could be used to test elements of your model predictions? You will never have the data to replicate this experiment, so one either discusses the state of data, or one appreciates quite how much data we actually have and try to make use of it.

We agree with Martin that we should have tested our model with data. Since this research was designed to explore the rules of allocation and roles of allocation schemes in the competition outputs of a vegetation dynamics model with full demographic processes, we didn't run experiments in FACE sites and didn't tune parameters according observations. We analyzed BAAD data and the data from Luyssaert et al. (2007), but found they could not be helpful in presenting the patterns along with nitrogen gradient. However, we analyzed our results with the meta-analyses of Poorter et al. (2012), Litton et al. (2003), and many FACE results (Duke, ORNL, EucFACE, BangorFACE, etc.)

We reorganized the discussion section with more results from field observations, data synthesis, FACE experiments throughout this section. Particularly, we added more evidences in sections "**4.1 Mechanisms of game-theoretic allocation modeling and simulation results validation**" and "**4.3 Model complexity and uncertainty**".

We copy the validation paragraph in section "4.1" below (Lines: 592~602. Please see more in these two sections):

"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 [CO2] 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 [CO2] as a result of high root allocation or root exudation (Jiang et al., 2019a; Norby and Zak, 2011); and 4) increases in vegetation biomass at elevated [CO2] are largely due to high wood allocation (Norby and Zak, 2011; Walker et al., 2019). These predictions emerged from the fundamental assumptions of our model without tuning parameters to fit the data, providing some confidence in the robustness of our approach."

We removed the "*completely true*" argument ("To make predictions of carbon cycle responses to the novel conditions of climate change, we must understand what determines the most competitive strategy, how the most competitive strategy changes with conditions, and how the most competitive strategy impacts the carbon cycle.") because our detailed discussion has shown these. We also removed the arguments related to "model benchmarking". It is too far from our results. We have discussed what this model can and cannot do, and explained why in sections "**4.1 Mechanisms of game-theoretic allocation modeling and simulation results validation**" and "**4.4 Common principles for allocation modeling and implications**".

Specific things:

- In the methods, I do not really follow the simplification from LM3-PPA to BiomeE. After reading section 2.1, I'm really unclear what the key differences are, all that is presented for guidance is: "simplified the processes of energy transfer and soil water dynamics". This could mean a wide range of things! Does that mean otherwise the models are the same? So what is gained by this simplification? Does the model perform similarly? Could this be shown?

As a model embedded in the land model of GFDL's ESMs, LM3-PPA has the modules that calculate the energy balances of raindrops, leaves/vegetation, and soil in detail, particularly for providing boundary conditions of land surface to atmosphere. For example, it requires a raindrop's temperature, energy content, mixture with leaves and soil. These calculations take lot computation time, making the model runs very slow. We simplified these processes with the soil water dynamics module used in TECO (Weng & Luo 2008).

We added a section "**F. Root Water Uptake and Soil Water Dynamic**s" in supplementary material I (model description). The root water uptake processes is the same as it in LM3-PPA (Eqs. F1~F9). The soil water dynamics and the energy budget associated with water fluxes are simplified using the algorithms in the TECO model. This model performs the same as LM3-PPA (the version used in Weng et al., 2017) does in plant growth and soil organic matter decomposition because the codes for these processes are almost identical.

We added three figures in supplementary information (II) to show water budget and soil water dynamics. Since this is study is not to explore the questions about water-carbon cycle interactions, we didn't particularly tune parameters to fit observations at Harvard Forest.

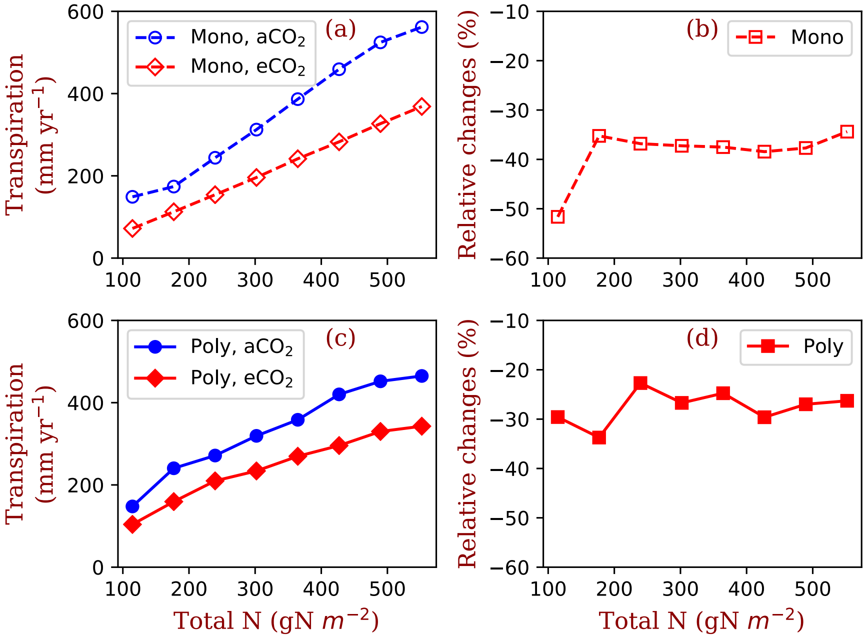


Figure S7 Responses of transpiration to elevated [CO2] in monoculture and in polyculture runs. The open symbols with dashed lines represent monoculture runs (panels a and b, only φ_{RL}=4 shown here.). The closed symbols with solid line represent polyculture runs (panels c and d). The relative changes of transpiration at eCO$_2$ are calculated as: 100x (Transp$_{eCO2}$-Trans$_{aCO2}$)/ Transp$_{aCO2}$.

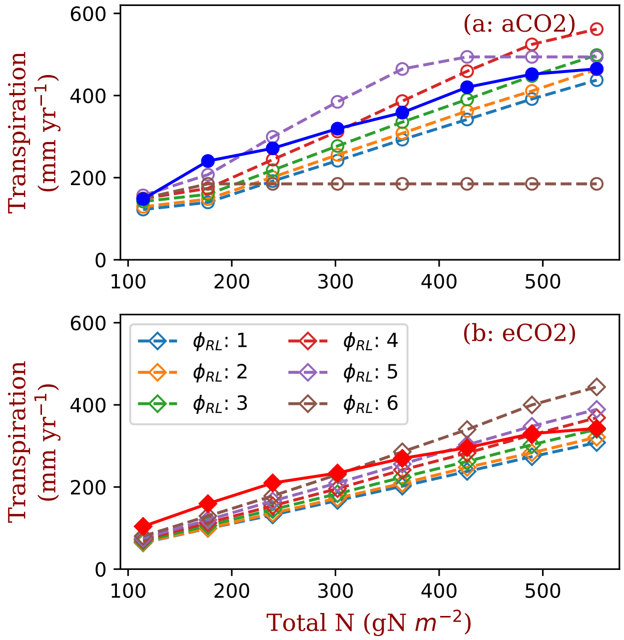


Figure S8 Mean annual transpiration in monoculture and in polyculture runs at equilibrium state. Panel a is for ambient CO_2 and panel b is elevated CO_2. The open symbols with dashed lines represent monoculture runs The closed symbols with solid line represent polyculture runs (blue-closed circles are for transpiration at aCO_2 and red-closed diamonds eCO_2).

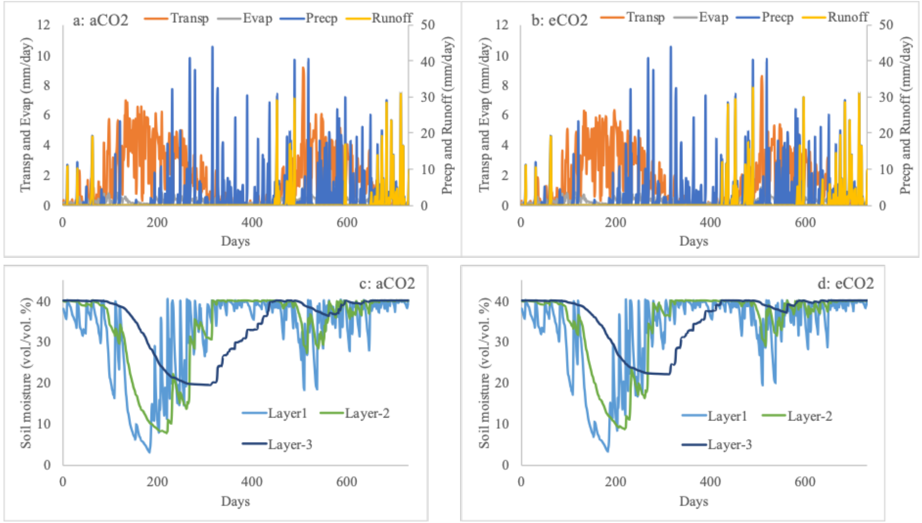


Figure S9 Water fluxes and soil water dynamics. Two years' daily water dynamics at ambient and elevated [CO2], respectively, are shown in this figure, including daily precipitation (Precp), transpiration (Transp), soil surface evaporation (Evap), runoff, soil water content (vol./vol.) in layers 1 (0~0.05 m), 2 (0.05~0.5), and 3 (0.5~1.5 m).

- Following on from this...the description of how water stress affects productivity is completely unclear to me, even after reading the text on lines 212-215. From digging through the supplementary, it seems like individuals could have different levels of water stress, but do they? Do you assume different slope terms "m" in your Leuning stomatal model? Do individuals have different rooting depths?

We added the details of root water uptake and soil water dynamics modeling in SI – 1 (model description). We assume the roots follow the same vertical distribution (Eq. F9) and the slope "m" is also the same for individuals that differ in their sizes. However, the individuals with different sizes may still have different water stress when soil water is limiting because these individuals have different absolute roots in each soil layer and their water demand is dependent on the radiation they are getting (i.e., the canopy layers they are in). As shown in the figures in SI-2, lower soil layers have low water variation.

- Following up on this point, where would an interested reader find the equations? Does Weng et al. (2017) contain all the equations? If so, can the authors more clearly indicate this at the top? My understanding is that the code is freely available, why not tell the reader of this in the methods? I know if I was reading this paper in my free time that would immediately make me more interested...

The equations can be found in Weng et al. 2015 and Weng & Luo 2008. We have added a section (F) in the supplementary material I: model description. We also move the codes availability description to the Method section (Lines 170~172).

"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)."

- Eqn 3 ... could the authors provide rough ranges for the targets that emerge from these equations? I would have found this very helpful as I was reading the paper. I'm anticipating that the authors will respond by saying the range could be huge given the possible combinations, so consider this an optional request. I just wanted to get a sense of how much each target varied by and over what kinds of numbers.

The range is huge, as Martin said, because tree size can vary from centimeters to tens of meters, but it follows the same allometry equations. The idea of targets of leaves and fine roots is to define a fully developed tree based on the structural relationships between tree diameter, height, and crown area, and the functional relationships between leaves, fine roots, and sapwood. In this model, the structural relationships define the tree sizes in height and spread (i.e., crown area), and the functional relationships define how many leaves and fine roots can potentially be attached to this tree.

- where does the empirical constant representing the ratio of sapwood cross-sectional area to target leaf area come from? Is this based on measurements in any way? It presumably comes by given that leaf area and sapwood cross-sectional area are measured.

It is described in Weng et al. 2015. This parameter is estimated from the observed ratios of cross sectional area of sapwood to leaves (i.e., Huber values, McDowell et al. 2002) times crown leaf area index. However, since we don't have a plant hydraulic model here, it is just used to separate wood into sapwood and heartwood for reasonably fitting these two pools that have been defined in LM3, and this parameter does not affect any plant physiological processes, though it is very important for plant hydraulics.

- *In instances where the plant doesn't have the resources to grow, if I follow the text, then C and N are returned to the storage pools for later. How large do these pools get? How much respiration takes place? In other models applied to eCO2 experiments (e.g. CABLE, CLM), the inability to grow in response to eCO2 led to a need to up-regulate respiration to make things balance (Zaehle et al. 2014, New Phyt). There is arguably very little experimental support for this kind of behaviour, in fact the data from the EucFACE experiment would show no support at all (paper in press).* ***This could be a worthwhile thing to comment on in the discussion of the manuscript. Does the model assumptions lead to large builds up of these stores? If it doesn't, then can the models make a mechanistic link to explain how they achieve this seems more realistic behaviour compared to other models applied to eCO2 experiments...***

The case of carbon returning to NSC pool due to short of N is very rare, because leaf growth has been slowed down long before it happens and therefore reducing carbon supply.

Three cases: 1) N_supply >= N', C_supply is allocated according to the carbon-only scheme (full growth of leaves and fine roots as defined by their targets);

2) C_supply/CN_Wood <=N_supply< N', allocation follows the equations (7);

3) N_supply< C_supply/CN_Wood, part of C in C_supply return to NSC pool. However, the case (2) has reduced leaf growth and therefore C_supply (i.e., negative feedback by reducing leaves) before the condition "N_supply< C_supply/CN_Wood" is met.

We slightly revised this section to make it clearer (lines: 274~293).

"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).

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

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**. ”

This allocation scheme does not lead to high non-structural carbon (NSC) accumulation at low nitrogen environments (see the figure below and also in SI-II).

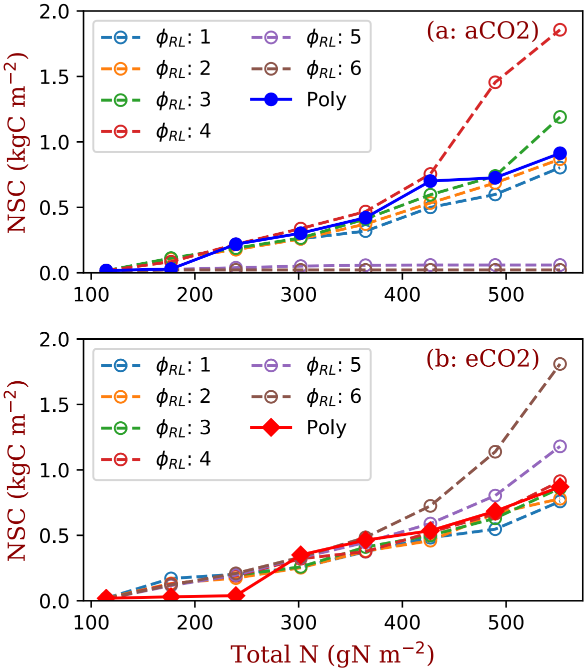


Figure S10 Non-structural carbon storage in monoculture and in polyculture runs at equilibrium state. Panel a is for ambient [CO_2] and panel b is elevated [CO_2]. The open symbols with dashed lines represent monoculture runs The closed symbols with solid line represent polyculture runs (blue-closed circles are for transpiration at aCO_2 and red-closed diamonds eCO_2).

As for respiration, we did not increase respiration at the short of nitrogen, but reduced leaf and root growth to reduce carbon supply and therefore nitrogen demand (i.e., negative feedback). The idea of this allocation scheme is to down-regulate photosynthesis by reducing LAI and make the most efficient use of available resources (particularly assimilated carbon). Increasing wood growth and reducing leaves and root growth is an optimal strategy at the limitation of nitrogen. This strategy would not compensate the decreases in plant growth induced by limiting nitrogen (i.e., no overgrowth of wood at limited nitrogen). It also does not waste the assimilated carbon by

respiration (which is shown not true in many studies, as the study mentioned by Martin, the research of Jiang et al. 2019. We cited this paper according to the version in bioRxiv).
We added a paragraph in section "4.1 Mechanisms of game-theoretic allocation modeling and simulation results validation" discussing this strategy (Lines: 622~631):
"The nature of developing a model with generic assumptions and balanced processes reduces its capability to predict all of these responses. For example, plants have a variety of physiological mechanisms to deal with excessive carbon supply when plant demand (i.e., "sink") is relatively low (Fatichi et al., 2019; Körner, 2006), such as down-regulating leaf photosynthesis rate by the accumulated assimilates (Goldschmidt and Huber, 1992) or respiring excessive carbohydrates to regenerate substrates for photosynthesis (Atkin and Macherel, 2009). But these mechanisms are short-term physiological responses (minutes to hours, sometimes days) for plants in situations of temporary nitrogen shortage, high irradiation, or drought stress. It is not "economically" sustainable in an infertile environment to maintain highly productive leaves but to often suppress their photosynthesis or respire a large portion of their assimilated carbon."

- *I note that the other reviewers mentioned it and it is a theme I've noticed across a few of the papers from this set of authors...**there are datasets that are *freely* available to test the behaviour of this and other models from this group. I don't immediately see the what is stopping these authors testing their approaches on eCO2 data?** Is it because those studies don't have competition (not true of all FACE sites), but then please say so. The lead author was involved in a number of these studies and so would have access to all the data required. I realise they've added a further paragraph about the broad responses being consistent, but I find this a bit unsatisfactory to be honest. For years, modelling groups have been able to pass off general statements that their models were consistent with eCO2 experiments when they were explicitly tested, this clearly wasn't the case! Despite my reservations on this issue, this isn't a sticking point for me, the authors designed their experiment and it is not my place to tell them the paper I would have written (even if I might just have done that :P). It would be great in future work if the authors found a way to make use of the experimental data.*
Thanks for these suggestions. We do have access to the data of Oak Ridge and Duke FACE experiments. We really want to use these data to calibrate our model quantitatively at different sites and explore the key parameters (mechanisms) leading to different responses to elevated

[CO2] in these sits. I have joined a FACE-MIP proposal led by Dr. Walker for model inter-comparison with demographic vegetation models. Hopefully, we can do it together with Dr. De Kauwe in the near future. In the revised text (Lines: 645~660), we clearly described what this model cannot do and hopefully to be solved in the future with careful calibration of this model with data from those FACE sites.

"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. S11) 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. "

- *With the competition angle (this could be me not quite following), you effectively have 8 PFTs competing? But you've only tested one fairly specific ecosystem (i.e. the meteorology found at Harvard forest). Presumably, your results would vary with climate? If I've followed, then I'm somewhat surprised this wasn't also a consideration? At the very least, can this be explored as a discussion point? Temperature and changing water availability (if properly parameterised, see earlier question), could conceivably change your conclusions...*

The overall pattern would be the same, though the quantity would change. We did a likely research in Weng et al. 2017 for the strategy of LMA at three sites (Oak Ridge, Harvard forest, and a Northern Old Black Spruce site in Manitoba, Canada) but not in this study. We added two paragraphs to discuss possible responses in different climates, combined with water effects (Lines: 748~783).

“We conducted simulations only at one site for the purpose of exploring the general patterns of competitively optimal allocation strategies and their responses to elevated [CO2] at different nitrogen availabilities. We can speculate about shifts in the competitively optimal allocation strategy in different forest biomes by considering the effects of temperature on soil nitrogen supply via the SOM’s decomposition rate and its positive effect on net nitrogen mineralization. For example, the SOM decomposition rate is usually high in warm regions and low in cold regions (Davidson and Janssens, 2006) assuming there are no water limitations and SOM is equilibrated with carbon input. According to our model, allocation to roots is high in low nitrogen supply conditions (cold regions) and low in high nitrogen supply conditions (warm regions). This pattern can be found from temperate to boreal forest zones (Cairns et al., 1997; 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 [CO2]. Low soil moisture usually leads to high allocation to roots (Poorter et al., 2012). Elevated CO2 can reduce transpiration (as found in our study as well, Fig S7) 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 [CO2] in environments with water limitation (Farrior et al., 2015). This is opposite to the elevated [CO2] effects on allocation in nitrogen-limited environments as simulated in this study. 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 flexible and sensitive to nitrogen and water supply (Deak and Malamy, 2005; Linkohr et al., 2002; Pregitzer et al., 1993)."

- *With Fig 3, would it be useful to make the allocation changes relative? It is a little hard to see the changes because of the span of different fractions on the c and d panels. Similarly, instead of showing one of either GPP or NPP, why not show the response ratio?*

We tried a couple of ways to show the relative changes and response ratio and found this is the best way to show the spreads of allocation along the gradient of nitrogen and root: leaf area ratio (RL). It is difficult to use a case (e.g., RL=6 and N = 114.5) as base to calculate relative changes and response ratio because they vary too much when RL changes from 6 to 1 and N from 114.5 to 552. The purpose of this figure is to show the predictions for monoculture runs are consistent with our predictions of the rules of allocation.

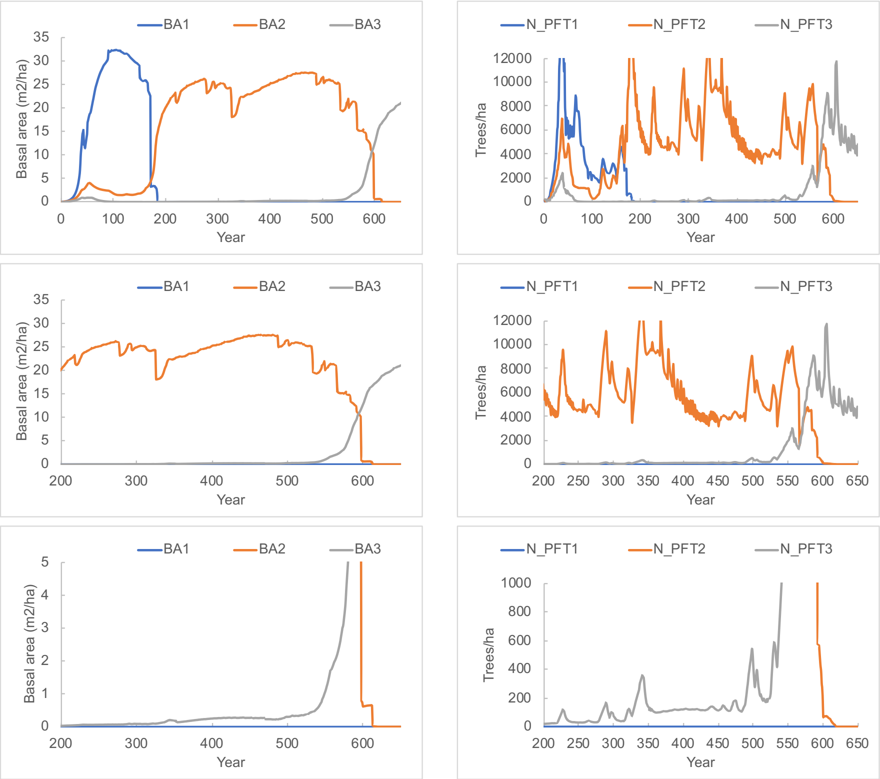
We changed the span of panels c and d in this figure, making it the same with it in the Fig. S1 (monoculture runs at elevate [CO]). The relative changes in response to elevated [CO2] can be found in Figures 5~7 (with the case of RL=4).

- *Is there a reason you don't show a figure more like Fig 3 for the polyculture simulations? You seem to jump straight to the changes for basal area, I was certainly expecting a similar plot first to orientate myself.*

For polyculture runs, there is only one PFT left at equilibrium state (this PFT outcompetes all others). So, the lines in each panel (variable) of Fig.3 become one for the polyculture runs. We used Fig. 4 to show how this happens through succession by showing the temporal changes in basal area of each PFT. For polyculture runs, all the panels (variables) in Fig. 1 are shown in Figs. 5, 6 and 7 with comparison with a monoculture case (RL=4) and responses to elevated [CO_2]. Fig. 7 c and d are specifically for comparison with all cases of the polyculture runs (Fig. 3f).

- In fig 4g, I don't follow why the orange (RL=2) ends up being succeeded by (RL=3) after 600 years? This seems pretty abrupt and I don't see it commented on. Could the mechanism be explained further in the text? In every other panel, there seems to be a clear winner and then that is it. Similarly, across all panels, the transition between the dominance of one strategy and replacement by another looks quite abrupt. My expectation was that this would be more gradual than these plots are showing? Could the authors explain why I've got this concept so wrong! Or perhaps it is the compression of time on the x-axis that makes it seem like this visually?

A successful invasion is slow because the invader (RL=3) only has a little advantage over the resident (RL=2) and it must start from a very low density of population. I zoomed in this figure at two levels (time and tree density) to show the details of changes in basal area and tree density (See the figure below).



The winning PFT must wait for an environment that will be generated by a dominant PFT that favors them. In our simulations, it took almost 200 years and the density of the winning PFT was very low after 200 years waiting (around 7 individuals/ha). Then, these individuals had to grow slowly in dark understory, though a little bit faster than the seedlings of current dominant PFT (RL=2). At the same time, the individuals of current dominant PFTs in understory kept replacing the trees in the top layer. After the winning PFT approached the top layer, they could generate seeds to increase its density finally. These new seedlings also need time to grow and approach the top layer with mortality of top layer trees. However, once there were enough individuals of the winning PFT in the top layer and plenty of new seedlings were generated, individuals of RL=2 will have no chance to get to the top layer and the replacing processes will be accelerated. We only showed 4 nitrogen levels in this figure (Fig. 4). There are some more such cases (slow invasion) shown in the supplementary material II Figs. S2 and S3, especially in the case of eCO_2 and N=427 g/m^2, where PFT4 takes around 1200 years to win.
We added a brief explanation of the succession processes in Lines 430~433.
"In some situations (e.g., Fig. 4g and Figs. S2 and S3), it takes a long time for the most competitive PFTs to out-compete the previously dominant PFTs because of the sequential replacement of dominant PFTs during the course of succession and the slow growth rate of trees in understory."

Small things:

- This could be my ignorance of the difference (or lack of) but when the authors refer to "vegetation demographic models" do they simply mean dynamic vegetation model (DVMs) or DGVMs (with "global" thrown in)? If they do, would it make sense to maintain the far more common (ubiquitous?) usage? I'm usually not pedantic over such things, but to be honest I didn't see the need to redefine a very common catch-all term. It is up to the authors what they do with this point.

We follow the community’s term (e.g., Fisher et al. 2018). I agree with Martin that this is a type of dynamic vegetation model (DVM) and this term should be replaced by DGVM eventually and become a description of model mechanisms.

- How many ESMs actually have VDMs in them? It would be good to cite a few if there are, I can't think of many off the top of my head! Aren't most run offline, rather than interactively with climate? The papers cited are certainly not examples of DGVMs embedded within ESMs.
There are a couple of teams working on incorporating demographic processes into DGVMs (e.g., FATES of DOE, LM4 of NOAA GFDL, and Ent of NASA GISS). However, no one is successful in their coupled ESMs (as I know). We replaced “ESMs” with “the system” in this sentence to avoid confusion (Lines 84~89):
“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 citations of this sentence are all standalone vegetation models.

- In the methods when the authors refer to "monoculture" runs as having allocation schemes as "analogous to the fixed allocation", I have a bit of trouble with this description. To me, this says fixed fraction, i.e. X, Y and Z% to difference plant pools. But, in which DGVM is that true? Some land surface models perhaps, but DGVMs? I feel like there is a lot of space for interpretation by the reader in with the authors mean here and the "see above" would send the reader back to ~line 60 from line 150. Why not be explicit in the methods exactly what is meant? I think the clarity will only help the readability of the paper.

We removed this phrase because it cannot be explained well in one sentence and it is not the place to compare the single PFT’s allocation strategy with other models’. Here, we actually meant it is a fixed strategy, instead of fixed allocation (or fixed fraction), as defined in De

Kauwe et al. 2014, based on allometry, functional relationships, and abiotic conditions. In this paper, there are two steps in determining allocation scheme: individual strategy and competitively optimal strategy as a result of competition. We have added a paragraph to discuss our modeling approach (Lines: 827~839).

"In competitively-optimal models, such as this study and also Valentine and Mäkelä (2012), the competition processes generate similar emergent patterns by selecting those that can survive in competition, regardless the details of those differences. The competition processes also make the details of allocation settings for a single PFT and their direct responses to elevated CO2 less important, because competition processes will select out the most competitive strategy from diverse strategies in response to changes in [CO2] and nitrogen. Our study and Valentine and Mäkelä (2012), posit a fundamental tradeoff between light competition and nitrogen competition via allocation based on insights gained from simpler models (e.g., Dybzinski et al., 2015; Mäkelä et al., 2008) for predicting allocation as an emergent property of competition. One advantage of building a model in this way is that the vegetation dynamics are predicted from first principles, rather than based on the correlations between vegetation properties and environmental conditions. With these first principles, the models can produce reasonable predictions, though the details of physiological and demographic processes vary among models."

- The CN target of leaves seems pretty high? Where do these targets come from? Table 1 would be great with an additional column with "references". If the value isn't literature based then that column should be left empty.

There are two measurements in GLOPNET data: 58.8 and 74.1. So, ours is a little bit higher than them (76.5). This value is from the eq. 2 of Weng et al. 2017 (leaf N per unit area = A+B*LMA, where parameters A and B are obtained by fitting the GLOPNET data. We didn't specifically tune these parameters in this study. We added a column for references in Table 1 following Martin's suggestion,

- "This range covers the soil nitrogen content at Harvard Forest" - in space (across the forest?)? In time (i.e. over what time periods?)? Could the authors attempt to characterise what this range reflects in terms of N availability in the wider context of availability found globally? I suspect

this would be helpful for the general reader, I don't personally have an intuitive SOM value in my head and I would have found this helpful.
We changed this sentence as (Lines 339~342):
“This range covers the soil nitrogen contents across the plots at Harvard Forest with different species compositions and land use history (200~300 gN m^{-2}) (Compton and Boone, 2000; Melillo et al., 2011), and represents the range from infertile to fertile soils in temperate forests (Post et al., 1985; Yang et al., 2011).”

- Line 344: You said that the PFT was based on an evergreen needle-leaved tree, but you’re modelling a deciduous ecosystem? Is this to avoid phenology issues, then why not pick a different ecosystem!?
Harvard forest is a mixed forest with evergreen and deciduous trees. the reason we chose “Evergreen” is to simplify model processes by skipping phenology, which could complicate our simulations.

- Line 547 - presumably you meant to replace "significantly" and forgot to, please check.
Corrected. Thanks!

Martin De Kauwe
Thank you, Martin. Your comments are so helpful!

Submitted on 18 Jul 2019

Anonymous Referee #1

This paper is a revision of a previous discussion paper looking at the interaction of competition and dynamic biomass allocation in response to N availability and elevated CO2 within a vegetation model. While the authors have expanded and clarified the methods, as well as clarifying their terms and extending the discussion, ***I find that there is one fundamental issue raised by all three reviewers which has not been addressed satisfactorily, namely the allocation of carbon to sapwood under nitrogen limitation.*** *The brief text description has been replaced by a series of detailed equations (Eq. 7), but the conceptual problem remains. Under N limitation, so a low r_S/D, the C allocated to leaves and roots decreases (Eq. 7.4), while the C allocated to sapwood increases (Eq. 7.6). This is not merely a 'numerical step' as the authors claim in one of their replies but a fundamental assumption of the model. The implications of this assumption are that under N limitation, the tree size increases, with the C:N ratio of wood increasing and the leaf area moving away from its target value.*

This is actually a strategy of down-regulating LAI to reduce photosynthesis rate (carbon supply) at limited nitrogen supply. Woody tissue is an economic and efficient place to accept the extra carbon. We clarified it in the main text (Lines: 291~293).

"this strategy down-regulates leaf production under low nitrogen conditions while making use of assimilated carbon in height-structured competition for light."

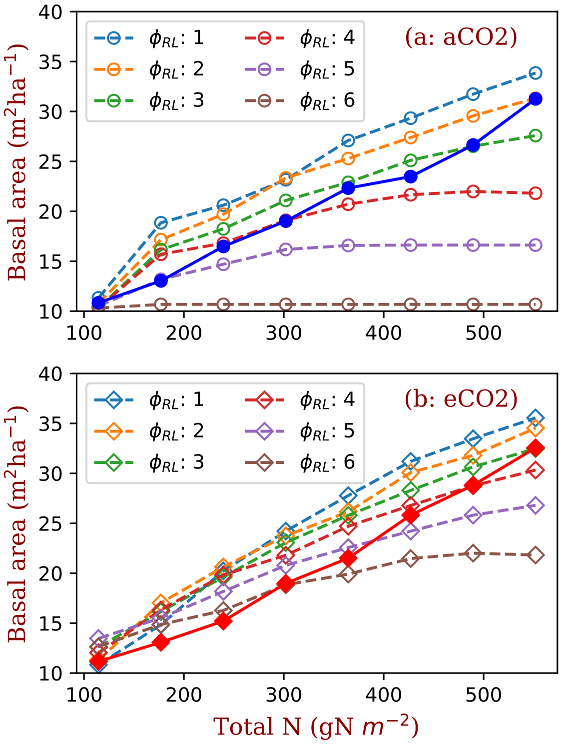
The tree size does not increase at limited nitrogen (see the figure blow for simulated basal area, which can be an index of tree size). Please also see detailed responses to the last question.

The effects of this assumption can be seen clearly for the monoculture model version, with increased allocation to sapwood but decreased allocation to roots under elevated CO2 (Fig. 6), as well as a sharp decrease in tree height at high N availability (Fig. S6) The implied variation in tree height must also have some implications for the PPA and competition part of the model. This is in contradiction with observations, where, while a stoichiometric change is observed under nutrient limitation, this is limited in range and often accompanied by a reduction in growth e.g (Norby et al., 2010).

Overall, the critical height (an index of PPA model that separates canopy and understory layers, defined as the height of the shortest tree in canopy layer) increases with N levels. Only in one case, it decreases because of the oscillation of size structure. This problem can be attenuated by tuning parameters to fit the actual growth and mortality rates (as we did in Weng et al. 2015 with a U-shaped mortality curve with tree size), but cannot be fully resolved within a patch.

The tree size is increasing generally as N increases. Please see the figure of biomass changes vs. ecosystem total nitrogen. Biomass increases with nitrogen at equilibrium state. The biomass per unit ground it proportional to tree diameter because each single tree's biomass is proportional to $D^{2.5}$ and crown area is proportional to $D^{1.5}$, so biomass per unit crown area is proportional to $D^{2.5}/D^{1.5} = D$ approximately.

Please see the basal area figure above (an index of the size of all trees, proportional to $D^{2.0}/D^{1.5} = D^{0.5}$ approximately) at equilibrium in different nitrogen levels below:



While prioritising the growth of leaves and roots under resource limitation is supported by other studies, the allocation of excess C to wood is not. The question of the fate of excess C under nutrient limitation is of course still a very important problem (Fatichi et al., 2014), and proposed solutions cover increased storage, root exudates or ecosystem respiration but I cannot think of any studies that support unlimited wood growth.

Our allocation scheme is a leaf (and root, because of the fixed R/L) priority strategy. We have made it clear in the revised manuscript.

(Lines: 302~304) "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})."

(Lines: 291~293) "Overall, this strategy down-regulates leaf production under low nitrogen conditions while making use of assimilated carbon in height-structured competition for light."

Following editor's suggestions, "*including one or two paragraphs in the discussion that thoroughly discusses the implications of the evolutionary principles behind the allocation assumption in PPA, and whether or not these assumptions adequately reflect the short-term vegetation responses to instantaneous environmental changes rather than gradual changes of vegetation dynamics under gradually changing environmental boundary conditions*", we have added three paragraphs to discuss the fate of excess C and explain why we choose this one based on the differences between physiological responses and long-term ecological strategies (Lines 622~660).

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

Root exudation is a critical process for plants. It can stimulate soil organic matter decomposition and nitrogen mineralization to facilitate soil nitrogen supply at the expense of carbon (Cheng, 2009; Cheng et al., 2014; Drake et al., 2011; Phillips et al., 2011). The process of root exudation has been adopted by many models to couple with microbial processes in the determination of soil organic matter decomposition (Sulman et al., 2014; Wieder et al., 2014, 2015). Some carbon-only models, e.g., LM3 (Shevliakova et al., 2009), the parent model of this one, and TECO (Luo et al., 2001), incorporate root exudation to put extra carbon into the soil in order to avoid down-regulating canopy photosynthesis or overestimating vegetation biomass, both of which had been tuned against data. However, in a demographic competition model like this one, when the microbial activities are not fully coupled and the nitrogen in soil is assumed fully accessible by roots of all individuals, individual plants cannot reap a reward from root exudation as they do in nature. 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. S11) 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."

Given that all reviewers have asked the authors to justify and discuss their wood allocation assumption and I do not find that they have done so in a satisfactory manner, I cannot recommend this paper for publication.

Hope our explanations and revisions in the main text addressed the concerns of you and the reader of this paper who raised the same concerns.

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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Key words: Allocation; Biome Ecological strategy simulator (BiomeE); Competitively-optimal strategy; Game theory; Nitrogen cycle

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 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 allocation 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).

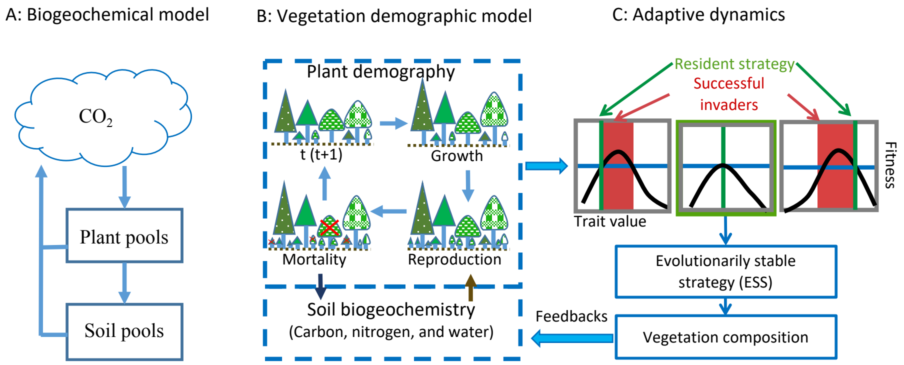

Figure 1 Hierarchical structure of vegetation models

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 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).

Deleted: ESMs

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 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.

In this study, we use a stand-alone simulator derived from the LM3-PPA model (Weng et al., 2017, 2015) to show how forests respond to elevated CO_2 and nitrogen availability via different competitively-optimal allocation strategies. The model is an individual-based vegetation demographic model, whose vegetation demographic scheme has been coupled into the land model of the Geophysical Fluid Dynamical Laboratory's Earth System Model (Shevliakova et al., 2009; Weng et al., 2015) and NASA Goddard Institute for Space Study's Earth system model, ModelE (Schmidt et al., 2014). Using this model, we simulate the shifts in competitively optimal allocation strategies in response to elevated CO_2 at different nitrogen levels based on insights from the analytical model derived by Dybzinski et al. (2015). Dybzinski et al.'s (2015) model predicts that increases in carbon storage at elevated CO_2 relative to storage at ambient CO_2 are 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 with increasing nitrogen availability. Here, we analyze the simulated ecosystem carbon cycle variables (gross and net primary production, allocation, and biomass) of separate mono- and polyculture model runs. In the monoculture runs, ecosystem properties are the result of the prescribed allocation strategies of a given PFT. In the polyculture runs, competition between the different allocation strategies results in succession and the eventual dominance of the most competitive allocation strategy for a given nitrogen availability and CO_2 level. Since everything else in the model is identical, we are able to compare the predictions of single **fixed strategies** with **competitively-optimal allocation strategies** by comparing the ecosystem properties of these two types of runs.

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2 Methods and Materials

2.1 BiomeE model overview

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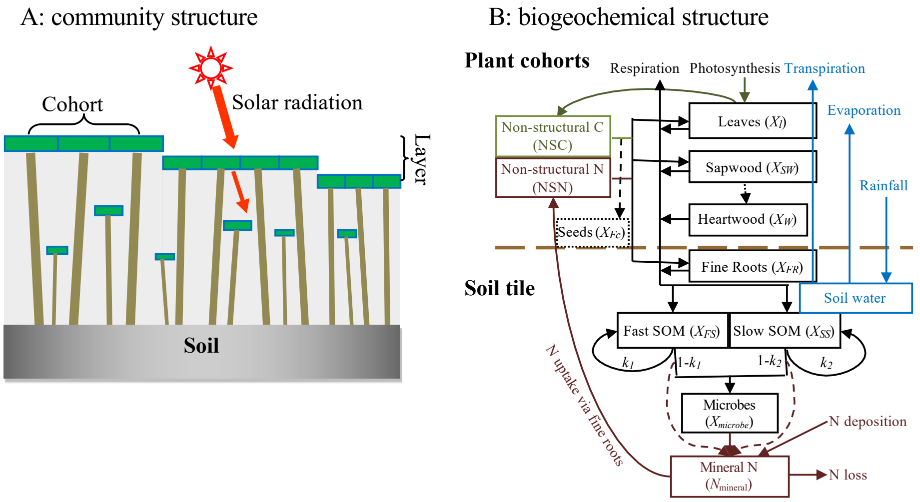

Figure 2. Structure of BiomeE

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.

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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.

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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 pool to get enough nitrogen and must release excessive nitrogen in the low C:N ratio SOM pool 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	$kgC\ m^{-3}$	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	$kgC\ m^{-2}$	0.14	(Wright et al., 2004)
γ	Specific root area, calculated from root radius and density	$m^2\ kgC^{-1}$	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	$kgC\ m^{-2}$	0.3	-
$CN_{L,0}$	Target C:N ratio of leaves	$kgC\ kgN^{-1}$	76.5 (Function of LMA)	(Wright et al., 2004)
$CN_{FR,0}$	Target C:N ratio of fine roots	$kgC\ kgN^{-1}$	60	(Magill et al., 2004)
$CN_{W,0}$	Target C:N ratio of wood	$kgC\ kgN^{-1}$	350	(Martin et al., 2015)
$CN_{F,0}$	Target C:N ratio of seeds	$kgC\ kgN^{-1}$	20	(Soriano et al., 2011)
f_1	Supply rate of NSC and NSN	-	1/(3*365)	-
f_2	Maximum fraction of NSC and NSN used for growth in a day	-	0.02	-

$f_{\mathrm{LFR,max}}$	Maximum fraction of available carbon allocated to leaves and fine roots	-	0.85	-
v	Fraction of carbon converted to seeds	-	0.1	-
$r_{\mathrm{D/S}}$	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, $\theta_c=1.5$ and $\theta_Z=0.5$ (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):

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

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 ($C_{\mathrm{FR,total}}$, kg C m^{-2}), following McMurtrie *et al*. (2012)

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

where, N_{mineral} is the mineral nitrogen in soil (g N m^{-2}), $f_{\mathrm{U,max}}$ is the maximum rate of nitrogen absorption per hour when $C_{\mathrm{FR,total}}$ 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:

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

where, $C_{\mathrm{FR,tree}}$ is the fine root biomass of a tree (kgC 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_{l}) 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_2 gives the daily availability of NSC during periods of leaf flush at the beginning of a growing season and f_1 normal growth of stems after plant leaves and fine roots approach their targets. Usually, parameter f_1 is much greater than f_2. We let f_1=0.02 and f_2= 1/(365x3) 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.

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

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

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

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

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

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

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 ($m^2\ kgC^{-1}$); 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).

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

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

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

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

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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:

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

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 runs are gap-filled hourly meteorological data at Harvard Forest from 1991 to 2006, obtained from North American Carbon Program (NACP) Site-Level Synthesis datasets (Barr et al., 2013).

2.3 Simulation experiments

We set two atmospheric CO_2 concentration ($[CO_2]$) levels: 380 ppm and 580 ppm, and eight ecosystem total nitrogen 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}) by assigning the initial content of the slow SOM pool for our simulation experiments (Table 2). This range covers the soil nitrogen contents across the plots at Harvard Forest with different species compositions and land use history (200~300 gN m^{-2}) (Compton and Boone, 2000; Melillo et al., 2011), and represents the range from infertile to fertile soils in temperate forests (Post et al., 1985; Yang et al., 2011). The nitrogen cycles through the plant and soil pools and is redistributed among them via plant demographic processes, soil carbon transfers, and plant uptake. In all the simulation experiments, we assume the ecosystem has no nitrogen inputs and no outputs for convenience since we already have eight total nitrogen levels to represent the consequences of different nitrogen input and output processes at an equilibrium state. The PFTs were based on an evergreen needle-leaved tree PFT with different leaf to fine root area ratios, φ_{RL}, in the range from 1 to 8 (Table 2). Simply stated, the PFTs we investigate only differ in parameter φ_{RL}.

We define the model runs started with only one fixed-φ_{RL} PFT as "monoculture runs" although the actual allocation of carbon to different plant tissues varies with $[CO_2]$ concentration and ecosystem nitrogen availability. The model runs started with multiple PFTs are called "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}: 114.5 g N m^{-2}, 177 g N m^{-2}, 239.5 g N m^{-2}, 302 g N m^{-2}, 364.5 g N m^{-2}, 427 g N m^{-2}, 489.5 g N m^{-2}, 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 $[CO_2]$ (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 consumed by fine roots exceeded what leaves provided 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} and ecosystem total nitrogen levels, analogous to the functional relationship schemes used in many ecosystem models (e.g., De Kauwe et al., 2014).

In polyculture runs I, we used the same PFTs as in the monoculture runs, where their φ_{RL} varies from 1 to 8 at the interval of 1.0 and the ecosystem total nitrogen levels are the same as those used in the monoculture runs (Table 2). This set of polyculture runs was used to explore successional patterns at both ambient and elevated [CO_2] concentrations (380 ppm and 580 ppm, respectively). However, this set of model runs could not show the details of equilibrium plant biomass and allocation patterns along the nitrogen gradient because of the large intervals between the φ_{RL} values.

To achieve greater resolution in our competition predictions, we designed the polyculture runs II using a dynamic PFT combination scheme according to the ranges of φ_{RL} obtained from the polyculture runs I that could survive at a particular nitrogen level at both CO_2 concentrations. 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 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 decreasing 0.5 per level of increase in ecosystem total N. We use i=1, 2, …, 8 to denote the eight N levels from 114.5 to 552 g N m^{-2}. The φ_{RL} of the eight PFTs at each level are 5.0-0.5i, 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 the eight PFTs are 4.5, 5.0, …, 8.0 and at 177 g N m^{-2} (i = 2), they are 4.0, 4.5, …, 7.5.

For both monoculture and polyculture runs, visual inspection indicated that stands had reached equilibrium after ~1200 years. To be conservative, we present equilibrium data by averaging model properties between years 1400 and 1800. We compared simulated equilibrium gross primary production (GPP), net primary production (NPP), allocation (both absolute amount of carbon and fractions of the total NPP), and plant biomass of the polyculture runs II with those from the monoculture runs. We used the results from one PFT (φ_{RL}=4) to highlight the differences of plant responses with competitively optimal 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. c: 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 *proportionally* 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.

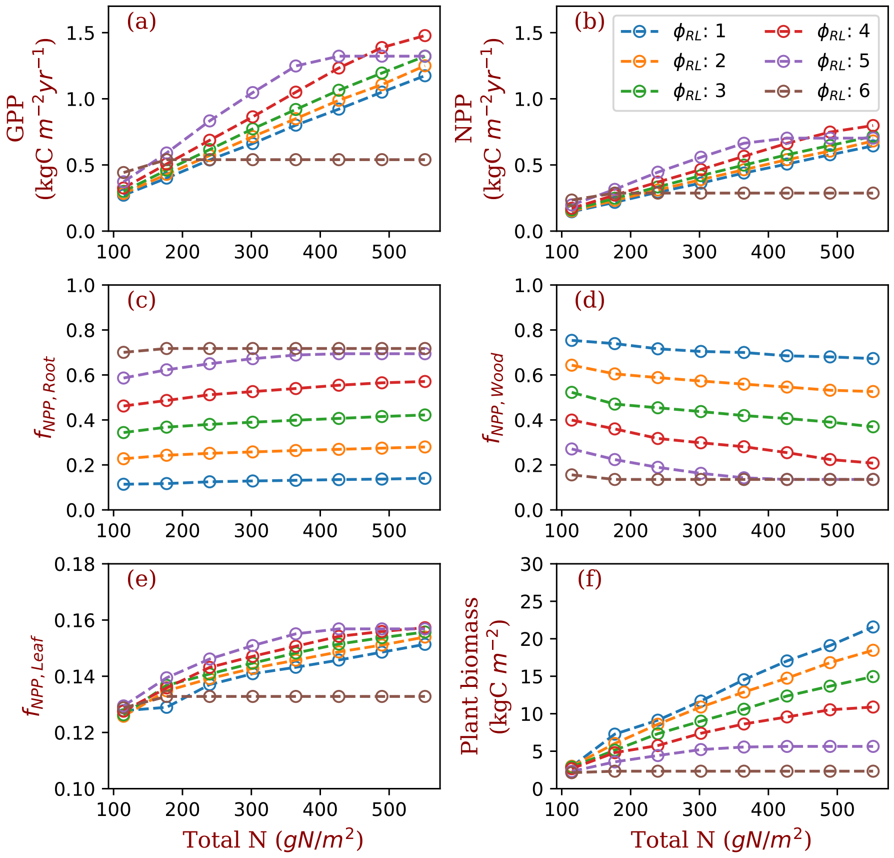

Figure 3. GPP, NPP, Allocation and Plant biomass at equilibrium state simulated by monoculture runs. GPP: Gross primary production; NPP: Net primary production; $f_{\mathrm{NPP},x}$: the fraction of NPP allocated to x, where x is Root (fine roots), Leaf (leaves in crown), or Wood (including tree trunk, stems, and coarse roots). The data are from the averages of the model run years from 1400 and 1800. Each model run is initiated with one PFT with fixed ratio of fine root area to leaf area (φ_{RL}).

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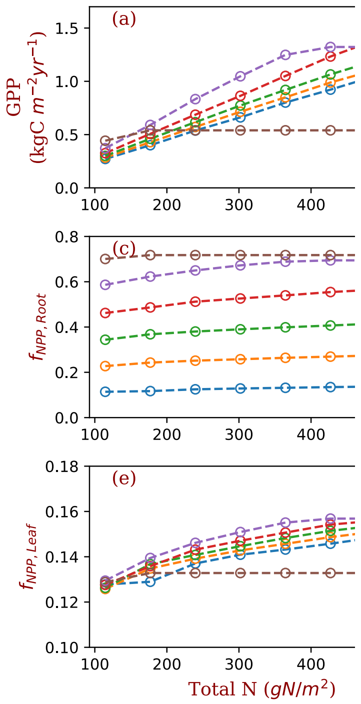

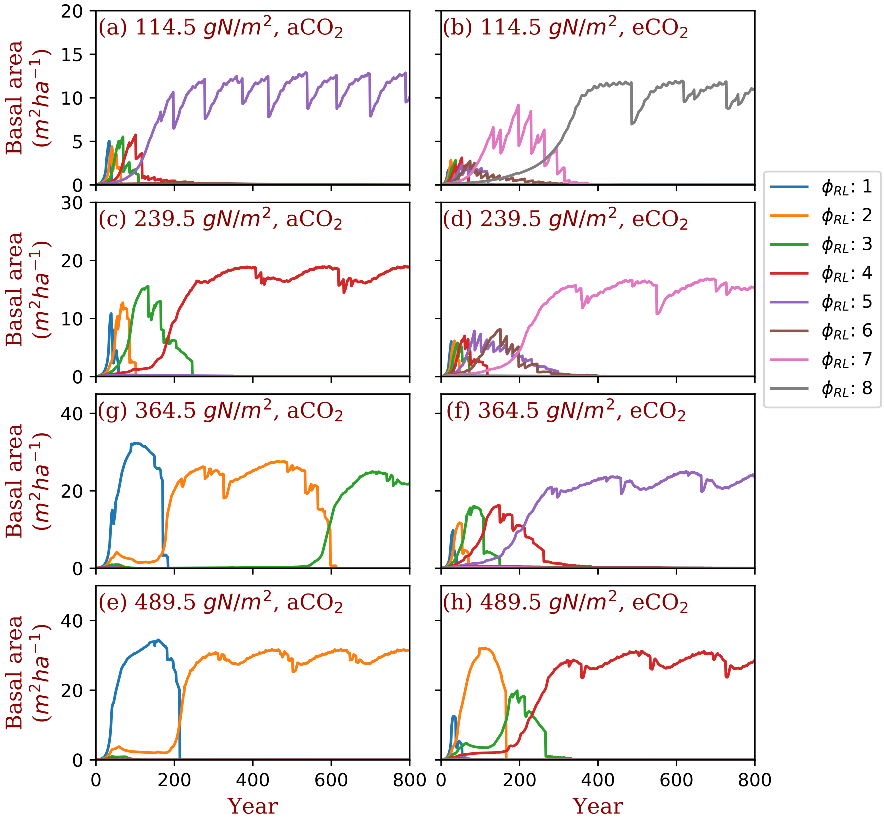

Figure 4 Successional patterns of polyculture runs I at ambient and elevated CO2 concentrations. φ_{RL} is the fixed ratio of fine root area to leaf area of a particular strategy.

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We used two sets of polyculture runs to look for the φ_{RL} that is closest to competitively optimal (i.e., the evolutionarily stable strategy). 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).

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Elevated [CO_2] (580 ppm) shifts the winning strategy to higher (φ_{RL}) at all the total nitrogen levels. As shown in Fig. 4, the 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 g N m^{-2}. In some situations (e.g., Fig. 4g and Figs. S2 and S3), it takes a long time for the most competitive PFTs to out-compete the previously dominant PFTs because of the sequential replacement of dominant PFTs during the course of succession and the slow growth rate of trees in understory.

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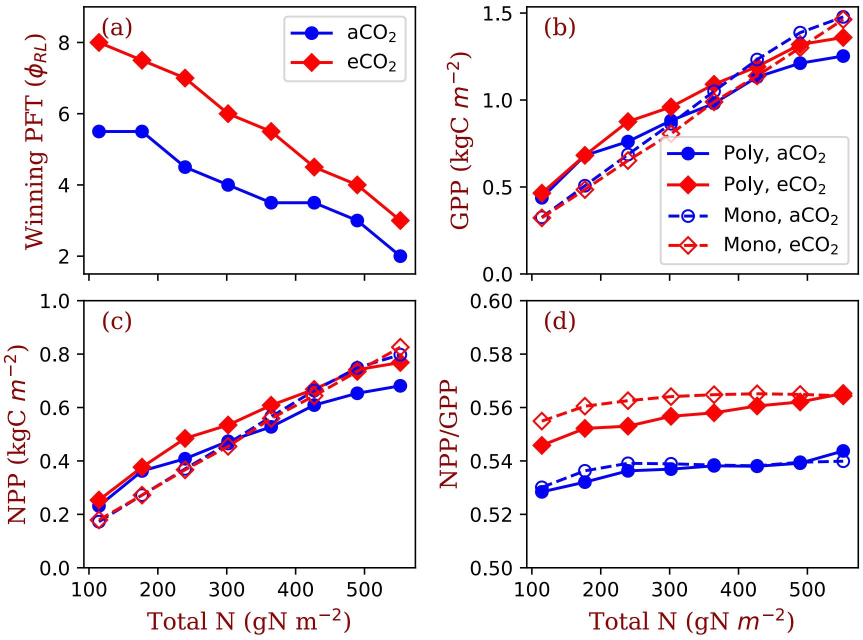

Figure 5 Winning PFTs (φ_{RL}, a) in polyculture runs II and equilibrium Gross Primary Production (GPP, b), Net Primary Production (NPP, c), and Carbon Use Efficiency (NPP/GPP, d) at two CO_2 concentrations (aCO_2: 380 ppm; eCO_2: 580 ppm). The closed symbols with solid line represent polyculture runs. 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 gN m^{-2} to 552.0 gN 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).

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Allocation of NPP to leaves increases with total 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 at elevated [CO_2].

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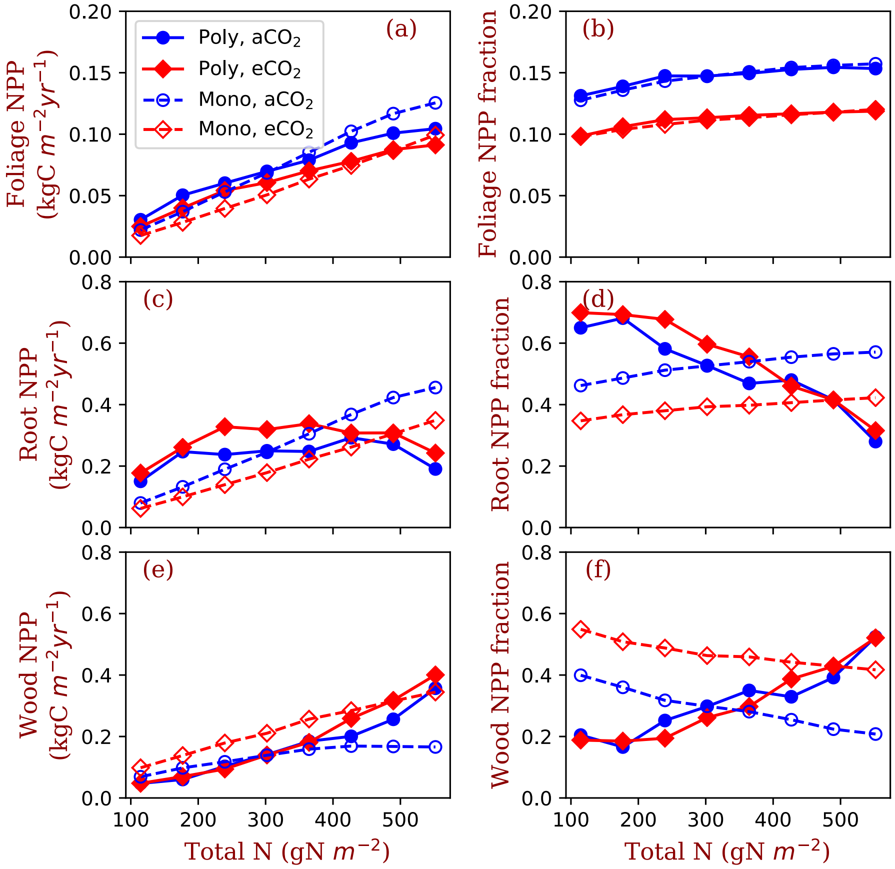

Figure 6 Allocation to leaves, fine roots, and wood tissues of the competition and monoculture runs at the eight total nitrogen levels and two CO$_2$ concentrations (aCO$_2$: 380 ppm; eCO$_2$: 580 ppm). The panels a, c, and e show the NPP allocated to the tissues and the panels b, d, and f show the fractions 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). 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 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 ecosystem total nitrogen is low (e.g., 114.5 - 302 g N m^{-2}) and decrease at elevated [CO_2] when ecosystem total 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}).

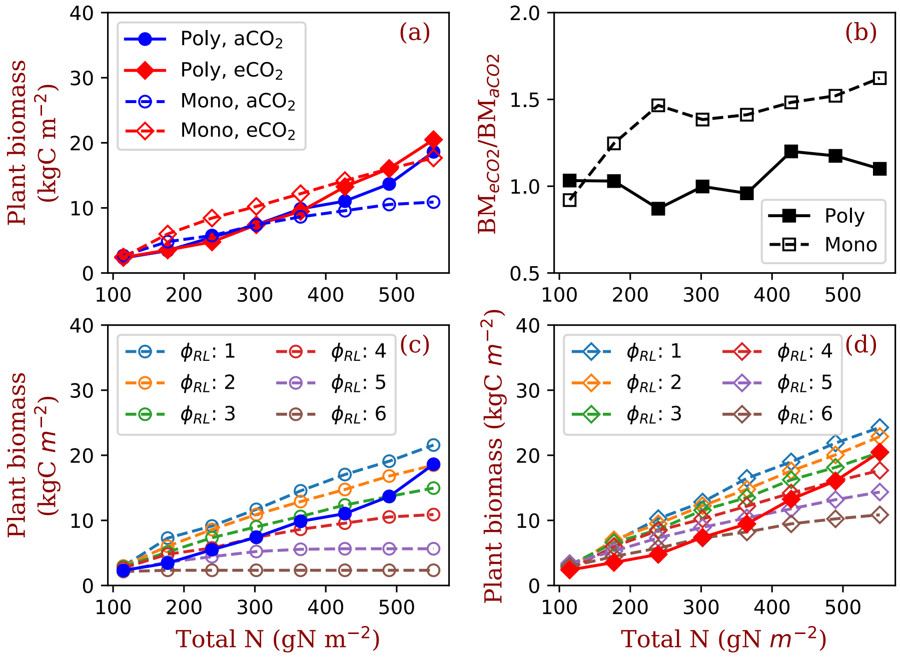

Figure 7 Plant biomass responses to elevated [CO$_2$] and nitrogen

Panel a shows the equilibrium plant biomass (means of simulated plant biomass from model run year 1400 to 1800) in polyculture runs and monoculture runs (only φ_{RL}=4 shown as an example). Panel b shows the ratio of simulated plant biomass at elevated [CO$_2$] to ambient [CO$_2$] for both competition and monoculture runs. Panels c and d show the comparisons with monoculture runs with φ_{RL} increasing from 1 to 6 at ambient (c) and elevated [CO$_2$] (d). The closed symbols with solid line represent polyculture runs. The open symbols with dashed lines represent monoculture runs (φ_{RL} ranges from 1 to 6). φ_{RL} is the fixed ratio of fine root area to leaf area of a particular strategy. aCO$_2$: 380 ppm; eCO$_2$: 580 ppm.

As a result of the changes in competitively-optimal φ_{RL}, plant biomass increases dramatically with ecosystem 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).

4 Discussion

Our simulations show that the 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. 6e dashed lines), only those PFTs that allocate more to fine roots (with lower carbon sequestration potential) can survive competition under elevated [CO_2] (Fig. 6c 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. 7b).

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 (Eqs. 6 and 7). Generally, the allometric scaling relationships define the maximum leaf and fine root surface area at a given tree size, and the functional relationships define the ratios of leaf area to sapwood cross-sectional area and fine root surface area. These rules are commonly used in ecosystem models (Franklin et al., 2012) and have been shown to generate reasonable predictions (De Kauwe et al., 2014; Valentine and Mäkelä, 2012). These rules implicitly define the priority of allocation to leaves and fine roots but allow for structurally-unlimited stem growth when resources (carbon and nitrogen in this study) are available (i.e., the remainder goes to stems after leaf and fine root growth).

We used a tuning parameter, maximum leaf and fine root allocation, $f_{\mathrm{LFR,max}}$, to constrain the maximum allocation to leaves and fine roots in order to maintain a minimum growth rate of wood in years of low productivity. This is consistent with wood growth patterns in temperate trees, where new wood tissues must be continuously produced (especially early in the growing season) to maintain the functions of tree trunks and branches (Cuny et al., 2012; Michelot et al., 2012; Plomion et al., 2001). This parameter does not change the fact that leaves and fine roots are the priority in allocation, since allocation ratios to stems are around 0.4~0.7 in temperate forests (Curtis et al., 2002; Litton et al., 2007). With a value of 0.85, $f_{\mathrm{LFR,max}}$ only seldom affects

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the overall carbon allocation ratios of leaves, fine roots, and stems and still maintains wood grow in years of low productivity. If $f_{\mathrm{LFR,max}} = 1$ (i.e., the highest priority for leaf and fine root growth), simulated trunk radial growth would have unreasonably high interannual variation because leaf and fine root growth would use all carbon to approach to their targets, leaving nothing for stems in some years of low productivity.

The simulation of competition for light and soil resources is based on two fundamental 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 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 N 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) increases in vegetation biomass at elevated [CO_2] are largely due to high wood allocation (Norby and Zak, 2011; Walker et al., 2019). These predictions emerged from the fundamental assumptions of our model without tuning parameters to fit the data, providing some confidence in the robustness of our approach.

The literature on experimental responses of plant community to elevated [CO_2] shows that the responses vary with site characteristics, forest composition, stand age, plant physiological responses, and soil microbial feedbacks. For example, in Duke Free Air CO_2 Enhancement (FACE) experiment, where the major trees are loblolly pine (*Pinus taeda*), increases in root production at elevated [CO_2] stimulated increased nitrogen supply that allowed the forest to sustain higher productivity (Drake et al., 2011). However, in Oak Ridge FACE, where the major trees are sweetgum (*Liquidambar styraciflua*), increased fine-root production under elevated [CO_2] did not result in increased net nitrogen mineralization and increases in root production declined after eight years of CO_2 enhancement (Iversen, 2010; Norby and Zak, 2011). In EucFACE, where the major trees are *Eucalyptus tereticornis* and the soil is infertile, trees significantly increased their root exudation under limited nutrient supplies but had no significant increase in biomass in response to elevated [CO_2] (Jiang et al., 2019a). The BangorFACE experiment (Smith et al., 2013) found that interspecific competition (*Alnus glutinosa*, *Betula pendula* and *Fagus sylvatica*) resulted in greater increases in root biomass at elevated [CO_2]. Leaf area index (LAI) responses to elevated [CO_2] are also highly varied. As summarized by Norby and Zak (2011), low LAI (in this case, open canopy) sites showed significant increases in LAI and high LAI (in this case, closed canopy) sites showed low increases or even decreases in LAI. They concluded that LAI in closed-canopy forests is not responsive to elevated [CO_2] (Norby et al., 2003; Norby and Zak, 2011).

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

Root exudation is a critical process for plants. It can stimulate soil organic matter decomposition and nitrogen mineralization to facilitate soil nitrogen supply at the expense of carbon (Cheng, 2009; Cheng et al., 2014; Drake et al., 2011; Phillips et al., 2011). The process of root exudation has been adopted by many models to couple with microbial processes in the determination of soil organic matter decomposition (Sulman et al., 2014; Wieder et al., 2014, 2015). Some carbon-only models, e.g., LM3 (Shevliakova et al., 2009), the parent model of this one, and TECO (Luo et al., 2001), incorporate root exudation to put extra carbon into the soil in order to avoid down-regulating canopy photosynthesis or overestimating vegetation biomass, both of which had been tuned against data. However, in a demographic competition model like this one, when the microbial activities are not fully coupled and the nitrogen in soil is assumed fully accessible by roots of all individuals, individual plants cannot reap a reward from root exudation as they do in nature. 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. S11) 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 and Dybzinski, 2013; O'Brien et al., 2005). It is the result of a competitive "arms race": while increasing fine root area under elevated [CO_2] does not result in more nitrogen for an individual, failing to do so would cede some of that individual's nitrogen to its neighbors. Because most nitrogen uptake is via mass flow and diffusion (Oyewole et al., 2017) and because both of these mechanisms depend on sink strength, individuals with *relatively* greater fine root mass than their neighbors take a greater share of nitrogen, as was recently demonstrated empirically (Dybzinski et al., 2019; Kulmatiski et al., 2017). Thus, fine roots may overproliferate for competitive reasons relative to lower optimal fine root mass in the hypothetical absence of an evolutionary history of competition (Craine, 2006; McNickle and Dybzinski, 2013). This may also explain why root C:N ratio is highly variable (Dybzinski et al., 2015; Luo et al., 2006; Nie et al., 2013): a high density of fine roots in soil may be more important than the high absorption ability of a single root in competing for soil nitrogen in the usually low mineral nitrogen soils.

Root overproliferation is still controversial in experiments. For example, Gersani et al. (2001) and O'Brien (2005) found that competing plants generated more roots than those growing in isolation; whereas McNickle and Brown (2014) found that competing plants generated comparable roots to those growing in isolation. Compared to modeled roots, real roots are far more adaptive and complex at modifying their growth patterns in response to soil nutrient and water dynamics (Hodge, 2009). The root growth strategies in response to competition also vary with species (Belter and Cahill, 2015). The mechanisms of self-recognition of inter- and intra- roots also can lead to varied behavior of root growth (Chen et al., 2012). However, all of the aforementioned studies considered only *plastic* root overproliferation, where individuals produce more roots in the presence of other individuals than they do in isolation, analogous to 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. S6). 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

Compared with the conventional pool-based vegetation models that use pools and fluxes to represent plant demographic processes at a land simulation unit (e.g., grid or patch), VDMs add two more layers of complexity. The first is the inclusion of stochastic birth and mortality processes of individuals (i.e., demographic processes). These processes allow the models to predict population dynamics and transient vegetation structure, such as size-structured distribution and crown organization (e.g., Moorcroft et al., 2001; Strigul et al., 2008). With changes in vegetation structure, allocation and mortality rates can change, generating a different carbon storage accumulation curve compared with those predicted by pool-based models where vegetation structure is not explicitly represented (e.g., Weng et al., 2015). The second is the simulated shift in dominant plant traits during succession due to the shifting of competitive outcomes among different PFTs, which changes the allocation between fast- and slow-turnover pools and thus the parameters of allocation and the residence time of carbon in the ecosystem.

Together, these mechanisms may alter long-term predictions of terrestrial carbon cycling due to changes in PFT-based parameters (Dybzinski et al., 2011; Farrior et al., 2013; Weng et al., 2015). As described in Introduction, current pool-based models can be described by a linear system of equations characterized by the key parameters of allocation, residence time, and transfer coefficients (Eq. 1) with the rigid assumption of unchangeable plant types (Luo et al., 2012; Xia et al., 2013). In VDMs however, allocation, residence time, leaf traits, phenology, mortality, plant forms, and their responses to climate change are all strategies of competition whose success varies with the environmental conditions and the traits of the individuals they are competing against.

Many tradeoffs between plant traits can shift in response to environmental and biotic 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.

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We conducted simulations only at one site for the purpose of exploring the general patterns of competitively optimal allocation strategies and their responses to elevated [CO_2] at different nitrogen availabilities. We can speculate about shifts in the competitively optimal allocation strategy in different forest biomes by considering the effects of temperature on soil nitrogen supply via the SOM’s decomposition rate and its positive effect on net nitrogen mineralization. For example, the SOM decomposition rate is usually high in warm regions and low in cold regions (Davidson and Janssens, 2006) assuming there are no water limitations and SOM is equilibrated with carbon input. According to our model, allocation to roots is high in low nitrogen supply conditions (cold regions) and low in high nitrogen supply conditions (warm regions). This pattern can be found from temperate to boreal forest zones (Cairns et al., 1997; 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, Fig S7) 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 flexible and sensitive to nitrogen and water supply (Deak and Malamy, 2005; Linkohr et al., 2002; Pregitzer et al., 1993).

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

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4.4 Common principles for allocation modeling and implications

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

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In competitively-optimal models, such as this study and also Valentine and Mäkelä (2012), the competition processes generate similar emergent patterns by selecting those that can survive in competition, regardless the details of those differences. The competition processes also make the details of allocation settings for a single PFT and their direct responses to elevated [CO_2] less important, because competition processes will select out the most competitive strategy from diverse strategies in response to changes in [CO_2] and nitrogen. Our study and Valentine and Mäkelä (2012), posit a fundamental tradeoff between light competition and nitrogen competition via allocation based on insights gained from simpler models (e.g., Dybzinski et al., 2015; Mäkelä et al., 2008) for predicting allocation as an emergent property of competition. One advantage of building a model in this way is that the vegetation dynamics are predicted from first principles, rather than based on the correlations between vegetation properties and environmental conditions. With these first principles, the models can produce reasonable predictions, though the details of physiological and demographic processes vary among models.

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

This modeling approach also demands improvement in model validation and benchmarking systems (Collier et al., 2018; Hoffman et al., 2017). As shown in this study, allocation responses to elevated CO_2 at different nitrogen levels in monoculture runs are opposite to those in 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.

Deleted: To make predictions of carbon cycle responses to the novel conditions of climate change, we must understand what determines the most competitive strategy, how the most competitive strategy changes with conditions, and how the most competitive strategy impacts the carbon cycle. ¶
An updated model benchmarking system should have the metrics of competitive plant traits during the development of ecosystems and their responses to changes in climate.

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 codes of the BiomeE model are available at GitHub:

https://github.com/wengensheng/BiomeESS

The simulated data from simulation experiments and Python scripts used in this study will be made publicly available at the publish of this paper.

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