Tropical Dry Forest Response to Nutrient Fertilization: A Model Validation and Sensitivity Analysis

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Abstract. Soil nutrients, especially nitrogen (N) and phosphorus (P), regulate plant growth and hence influence carbon fluxes between the land surface and atmosphere. However, how forests adjust biomass partitioning to leaves, wood, and fine roots in response to N and/or P fertilization remains puzzling. Recent work in tropical forests suggests that trees increase fine root production under P fertilization, but it is unclear whether mechanistic models can reproduce this dynamic. In order to better understand mechanisms governing nutrient effects on plant allocation and improve models, we used the nutrient enabled ED2 model to simulate a fertilization experiment being conducted in a secondary tropical dry forest in Costa Rica. We evaluated how different allocation parameterizations affected model performance. These parameterizations prescribed a linear relationship between relative allocation to fine roots and soil P concentrations. The slope of the linear relationship was allowed to be positive, negative, or zero. Some parameterizations realistically simulated leaf, wood and fine root production, and these parameterizations all assumed a positive relationship between relative allocation to fine roots and soil P concentration. Model simulations of a 30-year timeframe indicated strong sensitivity to parameterization and fertilization treatment. Without P fertilization, On a thirty-year timescale, under unfertilized conditions, our model predicted the largest amounts of aboveground biomass (AGB) accumulation were attainable under a range of parameterizations of when relative allocation to fine roots was positively related to independent to soil P concentration. However, this result was mostly driven by increased water use optimal relative acquisition of C and P rather than decreased nutrient limitation. On a thirty-year timescale w With P fertilization, the greatest AGB accumulation occurred when relative allocation to fine roots was independent of soil P. the assumption of a positive correlation between relative allocation to fine roots and soil P concentration led to over-investment to fine roots and reductions in vegetation biomass. Our study demonstrates the need of simultaneous measurements of leaf, wood, and fine root production in nutrient fertilization experiments, and for longer-term experiments. Models that do not accurately represent allocation to fine roots may be highly biased in their simulations of AGB, especially on multidecadal time scales when simulating a range of sites with significantly different soil P concentrations.

1 Introduction

Primary production in many terrestrial ecosystems is likely to be limited by nitrogen (N), phosphorus (P), or both (LeBauer and Treseder 2008; Hou et al. 2020). Because nutrient availability modulates plant growth and death, it can determine terrestrial carbon storage (Oren et al., 2001), affect tree mortality and recovery after disturbance events (Gessler et al., 2016), and even alter the sign and magnitude of land carbon sink in response to climate change (Wieder et al., 2015). The balance between N and P availability also influences terrestrial vegetation functioning, as shifts in N:P ratios are related to the changes in plant performance and species composition (Güsewell, 2004). Nutrient limitation is essential for reliable prediction on the primary production of terrestrial ecosystem under future environmental change, as demonstrated by Free-Air CO2 Enrichment (FACE) experiments have demonstrated that insufficient N and/or P can eventually halt the initial stimulation of aboveground growth by increased CO2 (e.g. Norby et al., 2010; Reich and Hobbie, 2013; Terrer et al., 2019) and nutrient-accounted. Earth System Models (ESMs) also highlight the effects of nutrient limitation. The C4MIP CMIP6 models that account for N cycling exhibit a 25-30% lower CO2 fertilization effect on land carbon storage than models that do not (Canadell et al., 2021). However, in nutrient-enabled Earth System Models, there is significant variation across model predictionss (Arora et al., 2020), suggesting the need for increased process-level understanding. A fundamental aspect of these models is the allocation of total production to production of leaves, wood, and fine roots. If the effects of nutrient limitation on allocation are not correctly simulated by models, simulation of total production and its sensitivity to climate change may be biased.

Nutrient fertilization field experiments in the field can be used to assess the effects of nutrient limitation on terrestrial ecosystems and to improve model simulations of production and allocation. Global meta-analysis has shown that both aboveground (Hou et al. 2020) and belowground production (Yuan and Chen 2012) increases with P addition. Further, Li et al. (2016) also reported aboveground production increased more than belowground production with P addition. The increase in aboveground production relative to belowground production is consistent with resource limitation theory (Bloom et al., 1985; Chapin et al., 1987). Resource limitation theory stipulates that trees should grow the tissue type (leaves, wood, fine roots) that would increase uptake rates of the most limiting resource to achieve optimal partitioning. Thus, if fine root biomass is the limiting factor for nutrient acquisition, then resource limitation theory would predict fine root production to decrease as soil nutrients increased.

However, there is also evidence that the story in tropical forests may be more complex. These global meta-analyses have pointed out large variation across sites and as well as dependence on the amount of fertilizer applied (Li et al. 2016; Hou et al., 2020). Furthermore, concerns have been raised by Wright (2019) about the tropical forest plot selection in Li et al. (2016). In a meta-analysis focusing on tropical forests, Wright (2019) concluded that P addition increased fine litter and wood production. No effect was found on fine root biomass, but it was cautioned that the number of studies was small and also that fine root production was not analysed due to lack of data. More recently, fertilization experiments in central Amazonia indicated increased fine root production with P fertilization (Lugli et al. 2021; Cunha et al. 2022). Intriguingly, Cunha et al.

(2022) also reported increases in fine root production relative to aboveground production, in contrast to Li et al. (2016). Relative fine root production was not reported in Lugli et al. (2021).

However, little stand level effect was found in existing experiments but large variability appeared across studies. In tropical moist forests, several studies found little effect of nutrient fertilization had insignificant effect on stand level carbon accumulation but relatively strong effects on the productivity of particular species and size classes (Wright et al., 2011; Alvarez-Clare et al., 2013; Schulte-Uebbing and de Vries, 2018; Wright et al. 2018; Báez and Homeier, 2018), but relatively strong effects on the productivity of particular species and size classes. In Panama, the addition of N and K was associated with increased growth rates of sapling and pole-sized trees but not of larger size classes (Wright et al., 2011). A fertilization experiment in central Amazonia reported increased NPP with P fertilization but not N fertilization; in particular, fine root production increased under P addition but slightly decreased under N addition (Lugli et al., 2021; Cunha et al., 2022). In Costa Rica, the addition of P led to faster wood growth for smaller stems but this effect was not significant for all size classes (Alvarez-Clare et al., 2013). Basal area growth was found to vary between species depending on their traits in a nutrient fertilization experiment in an Ecuadorian tropical montane forest (Báez and Homeier, 2018). At this forest, common species with acquisitive traits (traits supporting fast resource acquisition and growth rates, including high stem conductivity, high specific leaf area, high foliar N and P concentrations, and low wood density) generally had stronger responses to nutrient addition (mainly N+P) than trees without acquisitive traits. At the community level, nutrient fertilization did not have a statistically significant effect on aboveground biomass productivity. A fertilization experiment in central Amazonia reported increased NPP with P fertilization but not N fertilization; in particular, fine root production increased under P addition but slightly decreased under N addition (Lugli et al., 2021; Cunha et al., 2022).

Compared to tropical moist forests, fewer fertilization experiments have been done in tropical dry forests (Wright 2019). In a Mexico, P fertilization led to strongly increased basal area increments (Campo and Vázquez Yanes, 2004). However, after three years of fertilization in a Costa Rican forest, wood aboveground production was unchanged following either N or P fertilization (Waring et al., 2019). Instead, Waring et al. (2019) found that fine root production increased in response to P fertilization, but not following N fertilization. This increase in relative allocation to fine roots under P fertilization is consistent with the response observed by Cunha et al. (2022) in the Amazon. SeveralThese observed increases in relative allocation to fine roots with P fertilization are also consistent with several studies that have shown that roots proliferate in nutrient-rich patches (Pregitzer et al., 1993; Robinson, 1994; Zhang and Forde, 1998; Robinson et al., 1999; Fransen et al., 1999; Hodge et al., 1999; Jing et al., 2010; Li et al., 2012). This proliferation may be related to enhanced root morphological plasticity with increasing soil P, which increases nutrient uptake per unit construction cost (Fitter, 1994; Eissenstat and Yanai, 2002; Zhang et al., 2016). It may also be physiologically adaptive if it allows for faster uptake of nutrients from the soil (Jackson et al., 1990; Hodge et al., 2004). In addition, plant fine root production could also be independent of soil P. In this case, relative allocation to fine roots would depends more on water or N and thereby not be directly sensitive to soil P.

~~The mechanism underlying fine root allocation with increasing soil P is particularly impressive for distinct observations and corresponding explanations across existing studies. One premise is that plants decrease fine root production with increasing soil P, which is in accordance with~~ Increases in fine root production in response to P fertilization are surprising in light of resource limitation theory (Bloom et al., 1985; Chapin et al., 1987). This theory stipulates that trees should grow the tissue type (leaves, wood, fine roots) that would increase uptake rates of the most limiting resource to achieve optimal partitioning. For example, plants should allocate relatively more biomass to leaves when light is limiting, and relatively more to roots when nutrients or water are limiting. According to this theory, if fine root biomass is the limiting factor for nutrient acquisition, then we would expect fine root production to decrease as soil nutrients increased, and vice versa.

Some temperate forests have responded in this way to N fertilization (George & Seith, 1998; Wang et al., 2017; Lugli et al., 2021) and this response has also been observed in herbaceous species (Shipley and Meziane 2002). ~~The second premise is that plants increase fine root production with increasing soil P, as the first premise does~~But these ideas do not fully account for construction costs of new tissues. For example, ~~if soil nutrient supply is relatively low,~~ allocation to fine roots may ~~would be likely~~ not be favored ~~when~~if the potential gains in nutrient uptake resulting from increased fine root biomass are less than the nutrient cost of constructing that biomass. ~~Several studies have shown that roots proliferate in nutrient-rich patches (Pregitzer et al., 1993; Robinson, 1994; Zhang and Forde, 1998; Robinson et al., 1999; Fransen et al., 1999; Hodge et al., 1999; Jing et al., 2010; Li et al., 2012). This proliferation may be related to enhanced root morphological plasticity with increasing soil P, which increases nutrient uptake per unit construction cost (Fitter, 1994; Eissenstat and Yanai, 2002; Zhang et al., 2016). It may also be physiologically adaptive if it allows for faster uptake of nutrients from the soil (Jackson et al., 1990; Hodge et al., 2004). In addition, plant fine root production could also be independent of soil P. In this case, relative allocation to fine roots would depends more on water or N and thereby not be directly sensitive to soil P. Such a situation would be more likely to occur if soil nutrient supply is relatively low.~~

Given that several of the most recent tropical forest fertilization experiments show increases in absolute (and even relative) fine root production in response to P fertilization, models should be tested as to whether they simulate this dynamic~~Models that simulate the terrestrial carbon sink must correctly simulate the effects of P availability on biomass allocation. I~~Otherwise, ~~if~~ simulated allocation were biased, the simulated carbon sink would likely also be biased because wood residence time is much longer than that of leaves or fine roots. Moreover, as most soil carbon is derived from roots rather than aboveground tissues (Jackson et al., 2017), the soil carbon pool is also likely sensitive to plant biomass allocation. Finally, incorrect allocation would also likely lead to biases in simulations of ecosystem functioning. Despite the number of P-enabled models that now exist (e.g. CASACNP, Wang et al., 2010; JSBACH, Goll et al., 2012; CLM-CNP, Yang et al., 2014; ORCHIDEE-CNP, Goll et al., 2017; QUINCY, Thum et al., 2019; ED2, Medvigy et al., 2019; ELM-CNP, Zhu et al. 2019; JULES-CNP, Nakhavali et al., 2022; FUN-CNP, Braghiere et al. 2022), the simulated effects of P availability on relative allocation to leaves, wood and fine roots ha~~ve rarely~~s not been analyzed. Such analysis is needed, especially because different models use different schemes to determine allocation.

An additional useful application of models is sensitivity analysis, which can be used to generate new hypotheses and suggest new experiments. While most field fertilization experiments have only lasted a few years (Wright 2019), forest responses to fertilization on that time scale may differ from forest responses to longer time scales. For example, ~~Forest age could be an important variable related to relative allocation to fine roots, as~~ forests of different ages would be expected to have different composition, structure, and demographic rates, and tropical forest composition has been shown to affect the response of production to fertilization (Báez and Homeier, 2018). ~~A longer term experimental perspective could be instructive, and A~~ further difficulty is that models of the carbon sink typically simulate decades to centuries, ~~but~~ but most forest nutrient fertilization experiments have only been carried out for a few years (Wright 2019). ~~A longer term experimental perspective could be instructive, especially in~~ ~~Although the pattern seen in the relatively young forest (Waring et al., 2019) could be similar to the pattern seen in the old growth forests (Cunha et al., 2022),~~Responses in secondary forests, as in Waring et al. (2019), could be particularly sensitive to time scales. ~~In these forests,~~ nutrient demand can change rapidly over the course of a few decades (Batterman et al., 2013; Waring et al., 2015), and changing nutrient demand may lead to changes in allocation strategies. ~~While models have rarely be validated on multi~~these time scales~~decadal timescales, models can nevertheless be used for sensitivity analysis.~~Thus, ~~The~~ results from multidecadal sensitivity analyses can then be used to pinpoint potentially important processes and to suggest hypotheses for future field experiments.

The objective of this study was to use both a model and an experiment to better understand how relative allocation varies with nutrient availability~~; specifically, we~~ ~~want to~~ investigated the consequences of three related premises: (a) plants increase relative fine root production with ~~increasing soil~~ P fertilization (Waring et al. 2019; Cunha et al. 2022), (b) plants decrease relative fine root production with increasing soil P (Li et al. 2016), and (c) plant fine root production is independent of soil P. This last type of response would be expected if relative allocation to fine roots depended more on water or N than on P. Our model was the ED2 vegetation demographic model that now includes N and P cycling (Medvigy et al., 2019). The experiment involved N and P fertilization in a secondary tropical dry forest in Guanacaste, Costa Rica at Estación Experimental Forestal Horizontes (https://www.acguanacaste.ac.cr) (Waring et al., 2019). We implemented a new allocation scheme in which root production was made dependent on soil P concentration. We carried out model validation ~~and hypothesized that biomass production would be best simulated under the assumption that relative allocation to fine roots is positively correlated with soil P~~with respect to leaf, wood, and fine root production. We also carried out a sensitivity analysis to determine how allocation parameterization affected simulations on time scales ranging from three to thirty years.

2 Materials and Methods

2.1. Field Site and Observations

A nutrient fertilization experiment has been ongoing since 2015 at Estación Experimental Forestal Horizontes (10.712N, 85.594W) in Guanacaste, Costa Rica. The experimental design is fully described in Waring et al. (2019) and is summarized

here. The site is embedded within an approximately 30-year-old regenerating tropical dry forest, where mean annual temperature is about 25°C and mean annual precipitation is about 1700mm. Precipitation has strong seasonality with most of rain falling between May and November, and seasonal~~intra-annual~~ variability of precipitation does influence plant phenology: new leaves are produced in April and May and shed between January and March; stems d~~oi~~d not grow during the dry season. Precipitation also has high interannual variability typically associated with El Niño Southern Oscillation. Soils are mainly Andic and Typic Haplustepts (Alfaro et al., 2001), with high percentage of clay (38±1%) and a total N:P of 8.3±0.4. The majority of trees in Horizontes are deciduous and arbuscular mycorrhizal (Hayward and Horton, 2014), and the distribution of plant functional groups are analogous to nearby regenerating forests (Powers and Tiffin, 2010). Although it is a secondary forest, this region has notable biodiversity (60 tree species from 23 families within a 1-ha area in the experimental plots), including many nitrogen-fixing legumes (average of 17±4% stand basal area, and range of 1-53%).

The experiment consists of 16 25m×25m plots, each containing approximately 70 stems ≥5 cm diameter at breast height (DBH). Plots were randomly assigned to one of four treatments: control, nitrogen addition (150 kg N ha^{-1} yr^{-1}, urea solution), phosphorus addition (45 kg P ha^{-1} yr^{-1}, phosphoric acid solution), or addition of N and P together. The fertilization was conducted only during wet season. N~~: n~~Nutrient addition started in June 2015, and was carried out by spraying the solutions three times per year (early, middle and late wet season). ~~The measurements of leaf/wood/fine root production were conducted differently to accommodate seasonality:~~ Leaf production was measured monthly using litter traps and summed up from April to March of the following year.~~;~~ ~~W~~wood production ~~(mainly wet season growth)~~ was measured using tree diameter measurements and allometric equations.~~; and~~ ~~F~~fine root production was measured using root in-growth cores in June, August, and November of each year. R~~; r~~oot mycorrhizal colonization was quantified subsequently. ~~Note that our model simulations and the calculation of productivity were in accordance with this experiment.~~ Other measurements included soil NO_3 and NH_4, soil PO_4, and tree mortality.

Results from this study, covering the years 2015-2017, have been reported in Waring et al. (2019). This period experienced large interannual variability in rainfall, with rainfall being 628 mm in 2015, 1754 mm in 2016, and 2050 mm in 2017. In brief, leaf production did not vary by treatment or by year. Wood production varied by year but not by treatment. Fine root production varied by both treatment and year, and was~~with fine root production being~~ about 40% larger in the +P and +NP treatments than in the control or +N treatment. Despite the large variation in rainfall, the ratio of fine root production to leaf production did not exhibit a clear correlation with rainfall. Averaged over all 16 plots, this ratio was 0.37 in 2015, 0.44 in 2016, and 0.24 in 2017. When broken down by treatment, this production ratio was always intermediate in 2015, greatest in 2016, and smallest in 2017. Root colonization by mycorrhizal fungi did not vary among nutrient treatments or across years. ~~This experiment showed that relative allocation to fine roots was impacted by P fertilization but not N fertilization. Furthermore, the experiment spanned years of relatively high and low rainfall, but actual fine root to leaf productivity ratio lacked a clear correlation with rainfall. Therefore, we decided to only focus on the impacts of P on the leaf:fine root productivity ratio.~~

2.2 Model Description

Our model simulations were conducted using the ED2 model (Medvigy et al. 2009, 2019; Longo et al., 2019a). ED2 is a vegetation demographic model that simulates the dynamics of plant cohorts (Fisher et al., 2018). The model has recently been validated in both tropical dry forests (Xu et al., 2016; Medvigy et al., 2019; Schwartz et al., 2022) and tropical moist forests (Levy-Varon et al., 2019; Longo et al., 2019b; Xu et al., 2021). The source code is publicly available on GitHub (https://github.com/EDmodel/ED2).

Each cohort is specified by its plant functional type (PFT), physical dimensions (height and DBH), and stem number density. The model included eight PFTs. Species are assigned to a PFT on the basis of three traits: wood density, specific leaf area, and legume/non-legume status. The binning of species into PFTs is discussed in Xu et al. (2016) and Medvigy et al. (2019). Each cohort's PFT designation is constant, but physical dimensions and stem number density vary over time. The three ~~critical~~ fundamental demographic processes simulated by the model are growth (increases in physical dimensions), mortality (decreases in stem density), and recruitment (creation of new cohorts). Cohort biomass compartments include leaf, wood, fine root, and non-structural biomass. New photosynthate gets added to the non-structural pool, and respiratory costs are also debited from this pool. The non-structural pools do not have any fixed stoichiometry. Growth occurs when C, N, and P move from their respective non-structural pools to the leaf, wood, and fine root pools; all of these pools have fixed C:N and C:P ratios. Wood biomass and maximum leaf biomass are related via an allometric relationship (Longo et al., 2019a). The target leaf biomass is the product of the maximum leaf biomass and a phenology scaling factor, and d~~Drought~~ deciduousness is triggered when leaf water potentials are persistently below the turgor loss point (Xu et al., 2016). In previously published versions of the model, ~~maximum~~ the target fine root biomass was assumed to be directly proportional to ~~maximum~~ the target leaf biomass (Longo et al., 2019a), but here we explore various alternatives, as described below (section 2.3). ~~Phenological variation leads to sub-maximal leaf and fine root biomass as an emergent model outcome instead of pre-assigned processes (Xu et al., 2016).~~

Simulated growth can be constrained by C, N, or P~~nutrients~~ (Medvigy et al., 2019). ~~Structural tissues (leaf, wood and fine root) have fixed C:N:P stoichiometries; however, the non-structural pools do not have a fixed stoichiometry.~~ When C, N, and P are initially acquired, they accumulate in their respective non-structural pool. Allocation to leaves and fine roots is done simultaneously on a daily time step. This allocation consists of the transfer of C, N, and P from the non-structural pools to the leaf and fine root biomass pools until either: (i) one of the non-structural pools is exhausted, or (ii) the leaf and fine root biomass pools reach their target values. Allocation to wood and reproduction is done on a monthly time step. ~~.~~ This allocation step can either be limited by the supply of any of the nonstructural pools (C, N, or P). ~~is diagnosed for C-limitation based on the C : N and C : P ratios of the non-structural pools and water-limitation based on leaf water potential, and root-to-leaf biomass ratio will be adjusted accordingly. It can also be limited by the maximum leaf and fine root biomass as determined by allometric~~

~~equations.~~ Whatever remains in the non-structural pools at the end of each month is used to simultaneously generate new wood and reproductive tissues; this process is only limited by the sizes of the non-structural pools (Medvigy et al., 2019; Longo et al., 2019a). Some PFTs are capable of symbiotic N fixation (Levy-Varon et al., 2019; Medvigy et al., 2019). The model's approach to soil biogeochemistry explicitly includes the dynamics of physically defined soil organic matter pools in microbial-enzyme-mediated decomposition based on the Michaelis-Menten kinetics ~~microbial mechanisms of soil organic matter decomposition (i.e., enzymatic catalysis)~~ (Wang et al., 2013). Nutrient competition between plant and microbes (for N) and between plants, microbes and mineral surfaces (for P) is calculated using an equilibrium chemistry approximation (Zhu et al., 2016). ~~Growth can also be constrained by water (Xu et al., 2016). As leaf water potentials become increasingly negative, photosynthesis and stomatal conductance are down-regulated. Drought deciduousness is triggered when leaf water potentials are persistently below the turgor loss point (Xu et al., 2016).~~

The model implements mortality by reducing cohort stem density (Longo et al., 2019a). Each PFT has a baseline mortality rate that is applied to all corresponding cohorts. In addition, cohort-level mortality rates increase rapidly if respiration persistently exceeds photosynthesis. Finally, recruitment consists of the creation of a new cohort at minimum height (typically set to 1-2 m). Recruitment is driven both by external seed rain and the reproduction investment of local cohorts.

2.3 Model Modifications

We defined a parameter, *r2l*, which specified the target ratio of fine root biomass to leaf biomass. In previously published versions of the model, *r2l* is a constant. Because several fertilization studies found that relative fine root production increase~~s~~d with soil P (Waring et al., 2019; ~~Lugli et al., 2021;~~ Cunha et al., 2022), we modified the code so that *r2l* would be related to soil soluble P (*psol*, unit: gP / kg soil) following:

$$r2l = a + b * psol \tag{1}$$

where *b* could be positive, negative, or zero. Thus, this formulation is flexible enough to also accommodate the situation where relative fine root production decreases with soil soluble P (Li et al., 2016). It can also include the previously-used ED2 parameterization for tropical dry forests which had~~In all situations this value should not exceed a prescribed range (0.2-1.8). In the remainder of the manuscript, we refer to *b* > 0 parameterizations as "pos" parameterizations, *b* < 0 parameterizations as "neg" parameterizations, and *b* = 0 parameterizations as "const" parameterizations. Our initial model parameterization~~ ~~was a "const" parameterization with~~has *a* = 0.3 (unit: (kgC fine root) / (kgC leaf)) and *b* = 0 (unit: (kgC fine root) / (kgC leaf) * (kg soil) / (gP)) (Xu et al., 2016; Medvigy et al., 2019; Schwartz et al., 2022), ~~consistent with previous ED2 simulations of tropical dry forests.~~ We did not consider varying *r2l* with N or with soil water because the observed leaf to fine root production ratio was insensitive to N fertilization and uncorrelated with precipitation in Waring et al. (2019).

2.4 Simulations

The purposes of our simulations were model validation and sensitivity analysis (Table 1). Validation required that we focus on the three years (2015-2017) of previously published observations (Waring et al., 2019). We validated the previously-published baseline (Medvigy et al., 2019) model parameterization, as well as alternative parameterizations. We carried out sensitivity analysis on both three-year and thirty-year timescales. The three-year timescale was chosen to correspond with the field experiment. The thirty-year timescale was chosen to see how model sensitivity varied over the course of forest development. A thirty-year simulation would approximately double the age of the forests and would be one order of magnitude longer than the existing experiment.

Table 1. Description and rationale of model simulations

Simulation set	Number of simulations	Allocation ~~parameterizations~~ schemes	Analysis period	Rationale
Baseline	16, corresponding to 16 plots	~~const2 (~~a=0.3, b=0~~)~~	2015-2017	Validate the baseline model
Alternative parameterizations, short-term	16 plots * 63~~12~~ parameterizations	all ~~neg1, neg2, neg3 pos1, pos2, pos3 const1, const3, const4, const5, const6, const7~~ combinations of a and b, with a=0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, and b=-60, -40, -20, 0, 20, 40, 60.	2015-2017	(1) Determine short-term sensitivity of model to parameterization; (2) validate alternative parameterizations
Alternative parameterizations, long-term	16 plots * 63~~7~~ parameterizations	~~neg1, neg2, neg3, const2, pos1, pos2, pos3;~~ the same as short term	30 years	Determine longer-term sensitivity of model to parameterization

2.4.1 Baseline simulations and validation

We simulated each of the 16 experimental plots using the model's baseline parameterization. Each plot received nutrient inputs in accord with what was done during the fertilization experiment; i.e., there were four control plots, four +N plots, four +P plots, and four +NP plots. We also applied natural deposition rate of 0.13 kgN ha^{-1} yr^{-1} and 0.019 kgP ha^{-1} yr^{-1} in all 16 plots. In each plot, tThe vegetation cohorts in the model were initialized with in situ measurement of DBH and height data for each individual tree. Soil properties of each site were initialized with in situ soil state observations following the procedure of Medvigy et al. (2019). Nutrient additions rates were set to be equivalent to the amount added to each site in the experiment: control, N addition (126 kgN ha-1 yr-1), P addition (50 kgP ha-1 yr-1), or addition of N and P together (Waring et al. 2019). We also applied natural deposition rate of 0.13 kgN ha-1 yr-1 and 0.019 kgP ha-1 yr-1 in all 16 plots. All the simulations were driven by meteorological variables from the ERA5-Land hourly reanalysis datasets (Copernicus Climate Change Service, 2022; Muñoz Sabater, 2019). Simulations ran from January 2013 until April 2018, and we analyzed the same time period as the field measurements, 2015-2017. Since the actual forest is not in equilibrium and we used the observed stand structure and composition and observed soil nutrient status to initialize the model, only soil water neededs to be initialized by spin-up. To this end, we discarded the first two years (Xu et al., 2016)were discarded as spin-up.

Simulations and observations were compared both qualitatively and quantitatively. For qualitative validation, we emphasized (1) production averaged over treatments and/or years and (2) variation in production across treatments and years. For quantitative validation, we were mainly concerned with variation across treatments, so we first averaged all production measures over the three years of measurements. We then used Student's t-tests to assess whether the simulations and the observations had the same means. Linear regression was used to assess whether observed variation in production across treatments and years was accurately simulated. In all statistical tests, we, and applied p < 0.05 as the threshold for statistical significance. Prior to applying t-tests, we confirmed normality with the Shapiro-Wilk test (p < 0.05). We also assessed equality of variances with Welch's test.

We were only able to use Student's t-tests to evaluate leaf and wood production. The reason is that t-tests require multiple replicates that are all assumed to be drawn from the same normal distribution. For leaf production, we had 12 replicates (three years times four treatments). For wood production, previous analysis had shown that data from different years had statistically significant variation; i.e., they cannot be assumed to be drawn from the same distribution (Waring et al., 2019). We therefore averaged wood production over the three years, leaving us with four replicates. These four replicates correspond to the four treatments and they are suitable for our t-test because previous analysis did not identify a statistically significant treatment

2.4.22 Alternative parameterizations, validation and sensitivity analysis

We analyzed the sensitivity of production (leaf, wood, and fine root, wood, total) to allocation parameterization. In Eqn. 1, First, we linked variation in a to variation in b such that all parameter combinations would yield approximately the same r2l for the control (unfertilized) plots. Preliminary simulations suggested that the following constraint would be appropriate:

$$0.3 = a + \frac{b}{psol} \tag{2}$$

Under this constraint, different a-b combinations would yield about the same $r2l$ for the control plots, but different $r2l$ for the P fertilized plots (larger $r2l$ in the fertilized plots for "pos" parametrizations and smaller for "neg" parametrizations). lLarger absolute values of b indicate greater sensitivity of allocation to $psol$. For a, we considered nine values: 0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, and 0.8 (kgC fine root) / (kgC leaf). For b, we considered seven values: -60, -40, -20, 0, 20, 40, and 60 (kgC fine root) / (kgC leaf) * (kg soil) / (gP). Altogether, we tested a total of 63 a-b pairs (Table 1). Given a and b and the dynamically-varying $psol$, the model computes $r2l$ using Eq. (1). To avoid having negative or otherwise unrealistic $r2l$, we also required it to fall between 0.2 and 1.8. The largest value of b that we tested was 60 (kgC fine root) / (kgC leaf) * (kg soil) / (gP), which corresponded to a=0 and also set $r2l$=0 when $psol$=0 (Table 2). We regarded this parameter setting as an end member case. For complementarity, the lowest value of b that we tested was -60 (kgC fine root) / (kgC leaf) * (kg soil) / (gP). The largest value of a was 0.8 (kgC fine root) / (kgC leaf), which corresponded to $r2l$=0.8 (upper boundary in the model) when $psol$=0. We chose 9 values for a: 0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, and 0.8; 7 values for b: -60, -40, -20, 0, 20, 40, and 60. Altogether, we tested a total of 63seven a-b pairs (Table 2), the same number of values used in the sensitivity tests of LeBauer et al. (2013).

We also tested sensitivity to a constant $r2l$ that did not respond to $psol$. That is, we varied a while keeping b fixed at zero. The particular values that we tested ranged from a=0.2 to 0.8 (kgC fine root) / (kgC leaf) (Table 2).

The alternative parameterizations were validated in the same way as the baseline simulationsvalidation focused on differences between plant tissues and fertilization effect. We firstly averaged over years, and then performed statistical tests for leaf, wood, and fine root productivity by treatment, to determine whether there were significant differences between simulations and observations.

Parameter sSensitivity analysis was carried outn three-year and thirty-year timescales. For the three-year simulations, we averaged across years but considered each treatment separately. For each treatment, we calculated the coefficients of variation of leaf, wood and fine root production with respect to the 63 parameter sets. we aggregated across years Seven parameter settings were chosen, and response variables (leaf, wood, fine root production) were plotted against parameter value. Cubic splines were fit through these points, and we alsoand determined coefficients of variation of leaf, wood and fine root production for each treatment. For the thirty-year simulations, we had to prescribe meteorological forcing and fertilization rates for years beyond 2018. For these years, the meteorological forcing was obtained by recycling the 2009-2018 observations. N and P fertilization rates were maintained as they were in all other simulations; thus, these simulations constituted virtual 30-year fertilization experiments. The simulation results were also averaged over years and plotted on a plane of 63 a-b pairs, to visualize the variation across alternative parameterizations.

Table 2. Parameter values for each allocation scheme

Parameterization	Value of a (unit: (kgC fine root) / (kgC leaf))	Value of b (unit: (kgC fine root) / (kgC leaf) * (kg soil) / (gP))
neg1	0.6	−60
neg2	0.5	−40
neg3	0.4	−20
const2	0.3	0
pos1	0.2	20
pos2	0.1	40
pos3	0	60
const1	0.2	0
const3	0.4	0
const4	0.5	0
const5	0.6	0
const6	0.7	0
const7	0.8	0

3 Results

3.1 Baseline simulation validation

We first qualitatively evaluated the baseline model simulation (a=0.3, b=0). Variation across treatments and years is shown in Fig. 1. The magnitude of leaf production was similar in simulations and observations, though the simulations had a larger range of values (Fig. 1aA). The simulations and observations agreed that wood production was smallest in the strong ENSO year of 2015, but disagreed as to whether ~~maximum production occurred~~it was largest in 2016 or 2017 (Fig. 1bB). Overall, the model somewhat overestimated wood production. Fine root production had a much larger bias than leaf or wood production, especially in 2015-2016 (Fig. 1cC). The baseline simulations did not appear to capture the observed treatment effect (higher fine root production in +P and +NP than in the control and +N ~~plots~~).

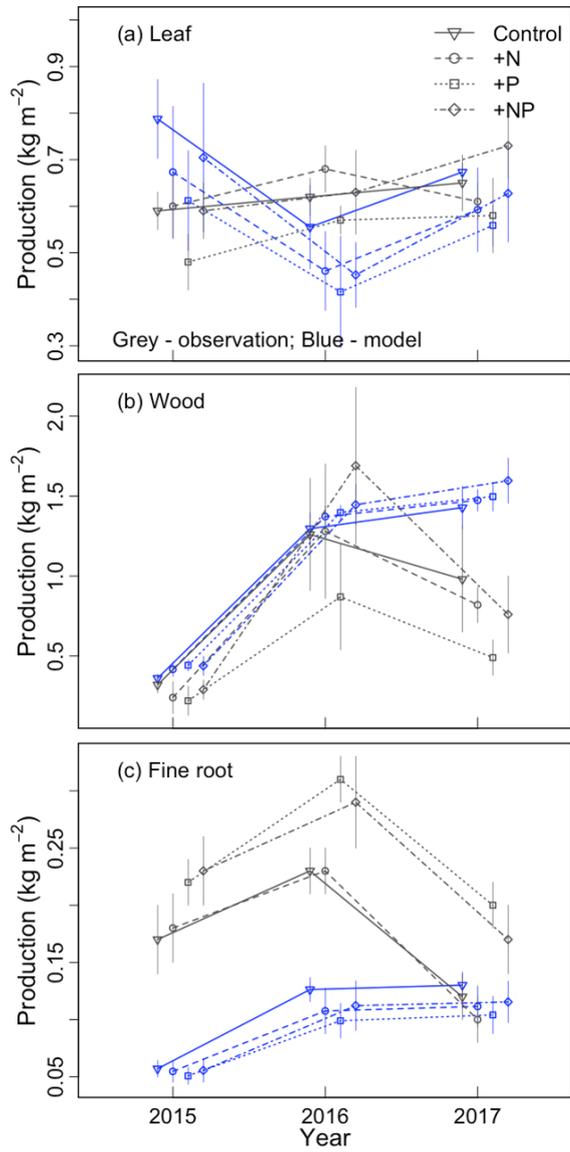
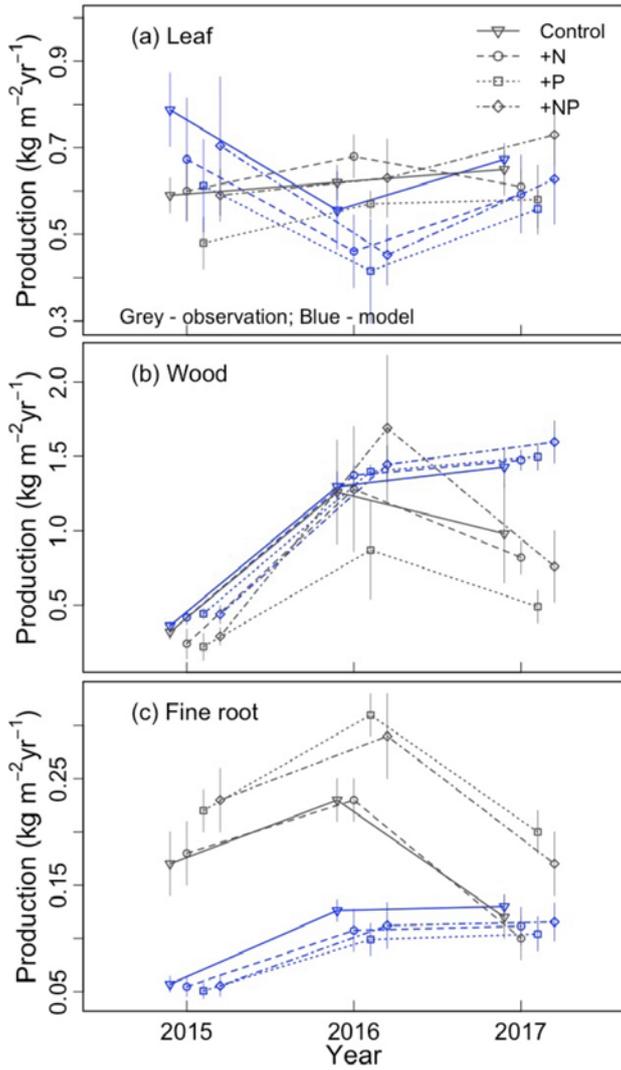
We also compared other simulated values to observations. The simulated stem mortality was close to observations in each of three years, including 2015, when stem mortality was relatively large (Table 23). Over the three years, simulated stem mortality in +NP plots was about 1.5 times larger than the other treatments, consistent with observations. Simulated and (temporally sparse) observations of plant available nutrients are shown in Fig. 22. The observed soluble P, NH_4, and NO_3 fell within the range of what was simulated. Both the simulations and the observations show a strong effect of P fertilization on soluble P. In the simulations, most of the peaks associated with the pulse inputs of P are clearly visible. By contrast, similar peaks are much less apparent in NH_4 and NO_3.~~, and fertilization had a weak impact on their concentrations.~~

355 **Figure 11. Comparison of simulated and observed (a) leaf, (b) wood and (c) fine root production for each year-treatment combination.**

Table 23. Comparison of simulated and observed annual stem mortality. The notation "+NP/others" indicates the ratio of the result from the +NP treatments to the average result from the control, +N, and +P treatments.

Stem mortality	2015	2016	2017	+NP/others
observation	10.6%	6.0%	4.6%	1.3-1.8
neg1	13.5%	6.3%	4.8%	0.9
neg2	12.2%	6.1%	4.8%	1.0
neg3	10.5%	5.8%	4.8%	1.3
baseline modelconst2	10.7%	6.3%	4.7%	1.5
pos1	9.1%	5.7%	4.7%	1.4
pos2	10.3%	5.8%	4.8%	1.4
pos3	11.8%	6.4%	4.7%	1.2
const1	9.3%	6.0%	4.9%	1.4
const3	11.6%	5.9%	4.9%	1.2
const4	13.5%	5.9%	4.8%	1.1
const5	15.4%	5.9%	4.8%	1.0
const6	17.4%	6.3%	4.7%	0.9
const7	19.8%	6.5%	4.6%	0.9

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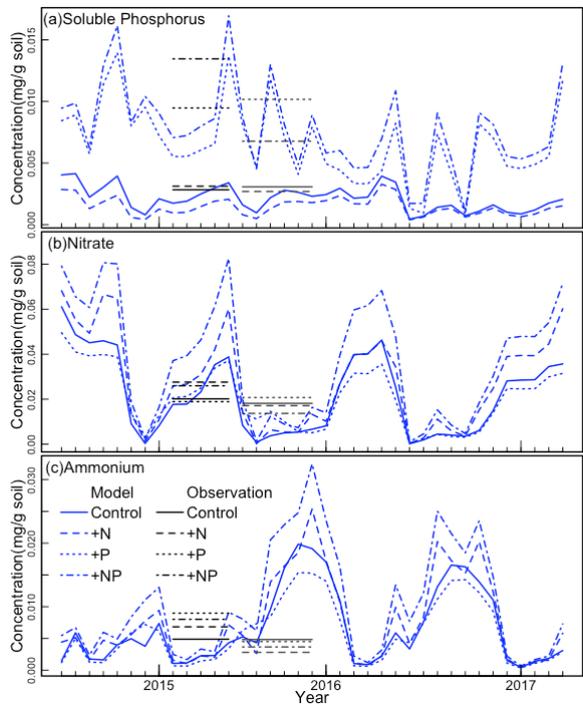
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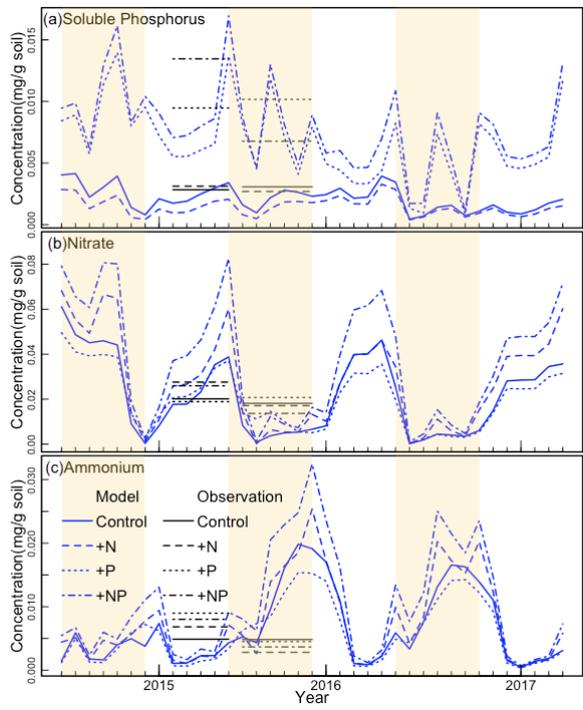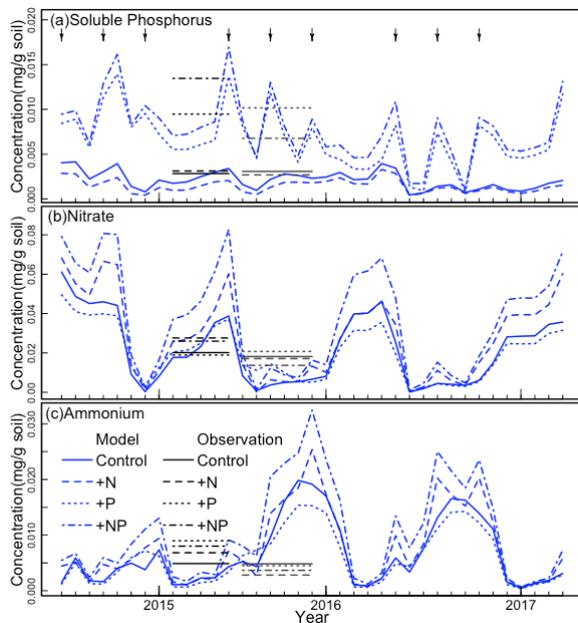
Figure 22. The continuous curves show the model-simulated (a) soil soluble phosphorus, (b) nitrate, and (c) ammonium concentrations. The black horizontal line segments indicate the observed averages from the wet and dry seasons in 2016; observations were not available for other periods. ~~Shaded area indicates fertilization periods.~~The arrows at the top indicate the approximate times of fertilization.

3.2 Alternative Parameterizations: Three Year Sensitivity analysis

~~W~~We then analysed the sensitivity of the simulations to parameterization (Fig. ~~3~~3). Different treatments were analysed separately, but leaf, wood and fine root production had similar variation. ~~In the control and +N treatments, leaf, wood and fine root production was relatively insensitive to parameterization,~~ ~~wood production increased from the "neg" to the "pos" parameterizations, and fine root production decreased from the "neg" to the "pos" parameterizations. The sensitivity of total production was similar to that of wood production.~~ By contrast, in the +P and +NP treatments, ~~the different components of production did not vary monotonically. Rather, leaf and fine root production were minimized and wood production was maximized with the "const" scheme~~the production of all components was more sensitive to parameterization.

~~For absolute CV (coefficient of variation), f~~Fine root production had a larger coefficient of variation~~CV~~ than ~~leaf and~~ wood production, and wood production had a larger coefficient of variation~~CV~~ than leaf production.

Given the temporal variation in soluble P (Fig. 2a), we investigated the temporal variation in $r2l$. High-frequency oscillations in this parameter could indicate inefficient allocation and the need for some smoothing. We found that the variability of $r2l$ depended on treatment and parameterization (Fig. 4). Without P fertilization, there is some seasonal variability in $r2l$, but it is relatively small. The variability is largest under P fertilization with parameterizations having $b > 0$, where $r2l$ ranges mostly from 0.4 to 1.0. Despite this variability, the $b > 0$ parameterizations consistently lead to larger $r2l$ under P fertilization than the $b = 0$ or $b < 0$ parameterizations.

~~also showed substantial variation across treatments. Wood production had a larger CV than leaf production, but the leaf production CV was more sensitive to treatment.~~
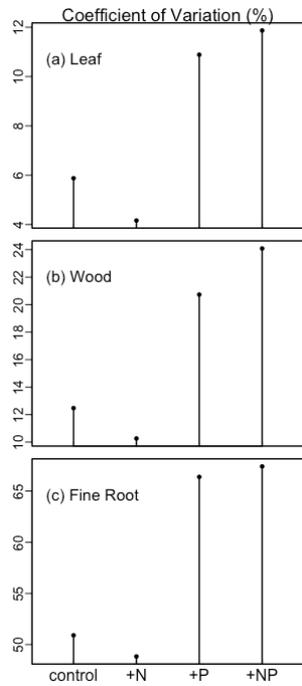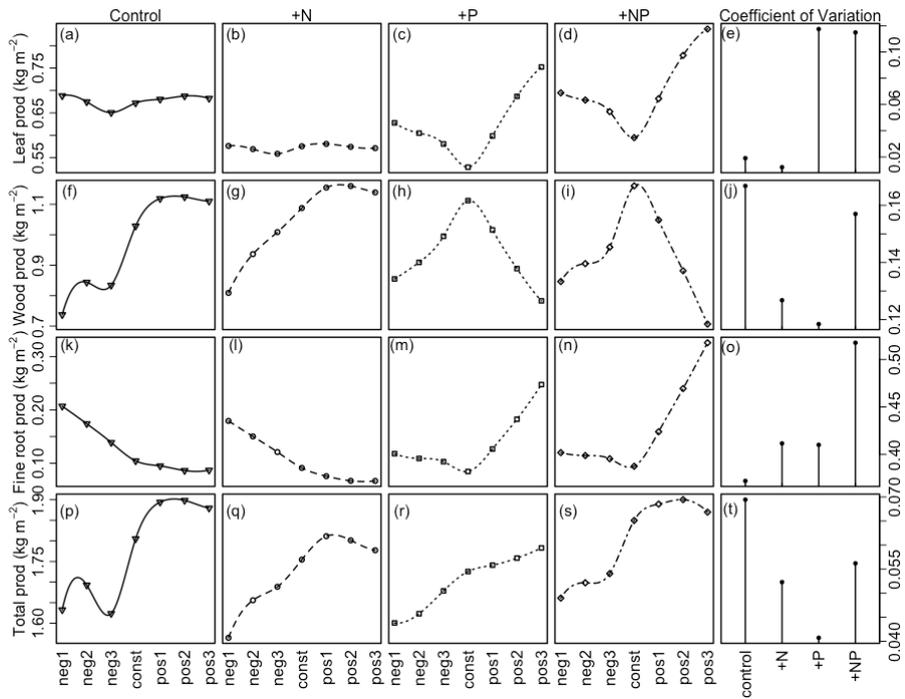
Figure 3~~3~~. The coefficient of v~~V~~ariation of simulated leaf, wood, **and** fine root ~~and total~~ biomass production among treatments under different parameterizations. ~~The lines in left four columns represent fitted cubic spline. Figure (e), (j), (o), (t) represent the coefficient of variation.~~
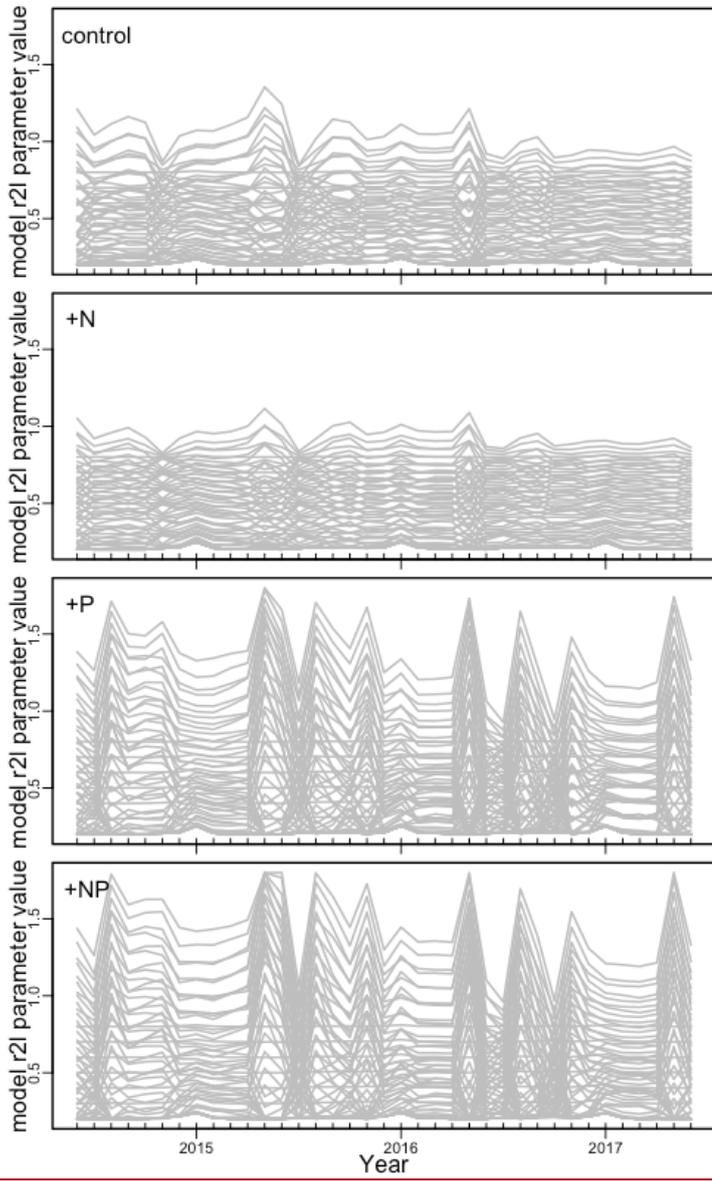
Figure 4. Time series of the r2l parameter for each of the 63 parameterizations. Results are shown separately for the control plots (labelled "control"), the N-fertilized plots (labelled +N), the P-fertilized plots (labelled +P), and plots fertilized with both N and P (labelled +NP).

395

3.3 Alternative Parameterizations: Three-Year Model Validation

We carried out t-tests to determine whether there were significant differences between simulations and observations. For leaf production (Table 3)~~vity~~, almost all model parameterizations were consistent with observations~~successfully predicted leaf productivity~~. For wood production (Table 4)~~vity~~, many parameterizations, especially with $b < 0$, $b = 0$, or relatively small a, did not predict wood production~~vity~~ in the +P treatment. Parameterizations with $b > 0$ were mostly successful in all treatments. For fine root production (Table 5)~~vity~~, only four parameterizations, all with $b = 20$ or $b = 40$, successfully predicted the observations in all treatments~~fine root productivity in all treatments~~. These four parameterizations also successfully predicted leaf and wood production~~vity~~ in all treatments. A drawback of this approach is the small sample size: each t-test was done with only four replicates. As an additional test, we tried aggregating control and +N, and comparing that to the aggregation of +P and +NP. This procedure doubled the number of replicates and gave very similar results (not reported here).

~~For a particular treatment, the observed and simulated means were significantly different ($p < 0.05$), we indicated that in the tables below. "C" means the control plots were significantly different, "N" means the +N plots were significantly different, "P" means the +P plots were significantly different, and "B" indicates that the +NP plots were significantly different. If an entry is empty, it means that no significant differences were found for any treatment. Here are our results for leaf (Table 3), wood (Table 4), and fine root (Table 5) productivity:~~

Table 3. ~~Comparison~~Validation of simulated ~~and observed~~ leaf production for 63 parameter settings~~vity~~. Validation was done separately for each treatment. An entry of ~~For a particular treatment, the observed and simulated means were significantly different ($p < 0.05$), we indicated that in the tables below.~~ "C" indicates statistically significant ($p < 0.05$) differences in the ~~means of the~~ control plots ~~were significantly different~~, "N" means the +N plots were significantly different, "P" means the +P plots were significantly different, and "B" indicates that the +NP plots were significantly different. ~~The notation "P" indicates the simulated +P plots were significantly different from observations~~The notation "-" indicates that ~~If an entry is empty, it means that~~ no significant differences were found for any treatment.

Leaf Production~~vity~~	a=0	a=0.1	a=0.2	a=0.3	a=0.4	a=0.5	a=0.6	a=0.7	a=0.8
b = -60	-	-	-	-	-	-	-	-	-
b = -40	-	-	-	-	-	-	-	-	-
b = -20	-	-	-	-	-	-	-	-	-
b = 0	-	-	-	-	-	-	-	-	-

	a=0	a=0.1	a=0.2	a=0.3	a=0.4	a=0.5	a=0.6	a=0.7	a=0.8
b = 20	-	-	-	-	-	-	-	-	-
b = 40	-	-	-	-	-	-	-	-	-
b = 60	P	P	-	-	-	-	-	-	-

Table 4. ~~Comparison of simulated and observed wood productivity. The notation "P" indicates the simulated +P plots were significantly different from observations~~As for Table 3, but for wood production.

Wood Product~~ivit~~ion	a=0	a=0.1	a=0.2	a=0.3	a=0.4	a=0.5	a=0.6	a=0.7	a=0.8
b = -60	P	P	P	P	P	-	-	-	-
b = -40	P	P	P	P	P	-	-	-	-
b = -20	P	P	P	P	P	P	-	-	-
b = 0	P	P	P	P	P	P	P	-	-
b = 20	P	P	P	-	-	-	-	-	-
b = 40	-	-	-	-	-	-	-	-	-
b = 60	-	-	-	-	-	-	-	-	-

Table 5. As for Table 3, but for fine root production. ~~Comparison of simulated and observed fine root productivity. The notation "C" indicates the simulated control plots were significantly different from observations, "N" means the +N plots were significantly different, "P" means the +P plots were significantly different, and "B" indicates that the +NP plots were significantly different.~~

Fine Root Product~~ivit~~ion	a=0	a=0.1	a=0.2	a=0.3	a=0.4	a=0.5	a=0.6	a=0.7	a=0.8
b = -60	C,N,P,B	C,N,P,B	C,N,P,B	C,N,P,B	C,N,P,B	P,B	P,B	C,P	C,P
b = -40	C,N,P,B	C,N,P,B	C,N,P,B	C,N,P,B	P,B	P,B	P,B	C,P	C
b = -20	C,N,P,B	C,N,P,B	C,N,P,B	C,N,P,B	P,B	P,B	P	C	C
b = 0	C,N,P,B	C,N,P,B	C,N,P,B	C,N,P,B	P,B	P	P	C	C
b = 20	C,N,P,B	C,N,P,B	C,N,P,B	N,P	-	-	C	C	C,B
b = 40	C,N,P,	C,N	N	-	-	C,B	C,P,B	C,P,B	C,N,P,B
b = 60	C,N	N	B	P,B	C,P,B	C,P,B	C,P,B	C,P,B	C,N,P,B

~~For leaf productivity, almost all model parameterizations successfully predicted leaf productivity. For wood productivity, many parameterizations, especially with $b < 0$, $b = 0$, or relatively small a, did not predict wood productivity in the +P treatment. Parameterizations with $b > 0$ were mostly successful in all treatments. For fine root productivity, only four parameterizations,~~

all with $b = 20$ or $b = 40$, successfully predicted fine root productivity in all treatments. These four parameterizations also successfully predicted leaf and wood productivity in all treatments.

Our "neg" and "pos" parameterizations all slightly overestimated the observed leaf production, while the "const" parameterizations underestimated the observed leaf production (Fig. 4a). This result is consistent with our sensitivity analysis, which showed that the "const" parameterization minimized leaf production. Despite these differences, the observed and simulated means were significantly different ($p < 0.05$) in only two cases, pos3 and const6 (Table 4). All simulations showed greater variability than the observations (Fig. 4a). Wood production was generally overestimated by the model (Fig. 4b). For the simulations with $b=0$ and relatively small values of a, the model and observations differed significantly (Table 4). Simulations with larger negative or positive values of b were consistent with observations (Table 4). All "neg" and "pos" parameterizations underestimated fine root production, while "const" parameterizations varied in the sign of their bias (Fig. 4c). We did not compare simulated and observed mean fine root production using t-tests because the different observations are known to be drawn from different distributions (see Methods).
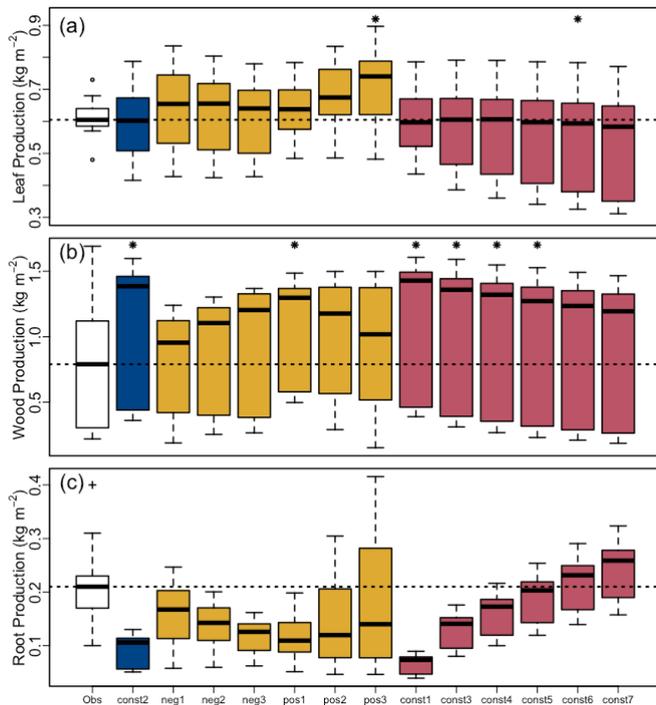
Table 4. P-values of the tests for difference in means between simulated and observed leaf and wood production. Significantly different means are indicated with *. This statistical test was not applied to fine root production.

Parameterization	a	b	Leaf production: t test	Wood production: t test
neg1	0.6	-60	0.403	0.642
neg2	0.5	-40	0.616	0.223
neg3	0.4	-20	0.997	0.102
const2	0.3	0	0.628	0.010*
pos1	0.2	20	0.451	0.013*
pos2	0.1	40	0.053	0.073
pos3	0	60	0.022*	0.279
const1	0.2	0	0.705	0.007*
const3	0.4	0	0.469	0.015*
const4	0.5	0	0.359	0.025*
const5	0.6	0	0.265	0.043*
const6	0.7	0	0.034*	0.216
const7	0.8	0	0.131	0.106

Because fine root production showed both year and treatment effects, we regressed simulated fine root production on the observations. Among all the parameterizations, only pos2 and pos3 had a slope consistent with one and intercept consistent with zero (Fig. 5, Table 5). Simulation pos1 also had an intercept consistent with zero, but it had a slope that was significantly less than one. Other simulations performed more poorly (Table 5). In terms of mortality, the largest biases were found in simulations const5, const6 and const7, which had relatively large values of a combined with $b=0$ (Table 3).

Table 5. Statistics from the fine root regressions.

Parameterization	a	b	Intercept estimate	Intercept standard error	p-value	Slope estimate	Slope standard error	p-value
neg1	0.6	-60	0.25	0.06	0.002	-0.44	0.28	0.145
neg2	0.5	-40	0.20	0.05	0.001	-0.32	0.22	0.170
neg3	0.4	-20	0.15	0.04	0.002	-0.15	0.17	0.374

const2	0.3	0	0.10	0.03	0.011	-0.04	0.15	0.782
pos1	0.2	20	0.04	0.04	0.358	0.37	0.19	0.075
pos2	0.1	40	-0.02	0.07	0.755	0.82	0.34	0.039
pos3	0	60	-0.07	0.11	0.553	1.23	0.53	0.042
const1	0.2	0	0.07	0.02	0.005	-0.02	0.09	0.817
const3	0.4	0	0.14	0.04	0.003	-0.03	0.17	0.841
const4	0.5	0	0.17	0.04	0.003	-0.04	0.2	0.863
const5	0.6	0	0.20	0.05	0.002	-0.03	0.23	0.894
const6	0.7	0	0.22	0.05	0.002	-0.02	0.26	0.936
const7	0.8	0	0.24	0.06	0.002	-0.003	0.27	0.991
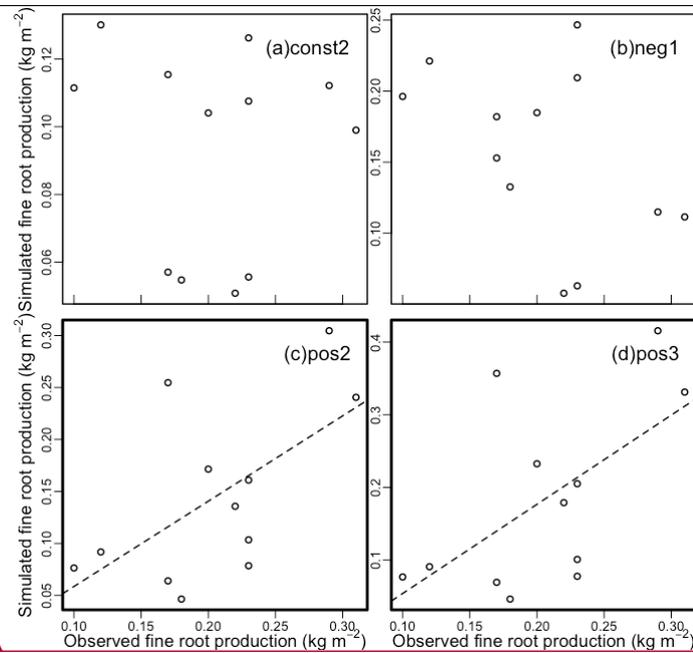
Figure 5. Comparison of simulated and observed fine production for 4 representative parameterizations. (a)const2 and (b)neg1 show typical patterns of "const" and "neg" parameterizations. Only (c)pos2 and (d)pos3 have p-values less than 0.05.

3.4 Alternative Parameterizations: Thirty-Year Sensitivity analysis

Allocation parameters had a large impact on simulated aboveground biomass (AGB) accumulation, as seen in our ~~thirty~~30-year simulations (Fig~~s~~. ~~5~~6a). On a 30-year timescale, the largest AGB occurred when both a and b were relatively small. These parameterizations also led to low fine root biomass (Fig . 5b), high leaf area index (Fig. 5c), and a low ratio of fine root biomass to leaf biomass (Fig. 5d). The overall pattern of AGB was closely related to leaf area index, suggesting that capture of aboveground resources ultimately limited production on the 30-year timescale.

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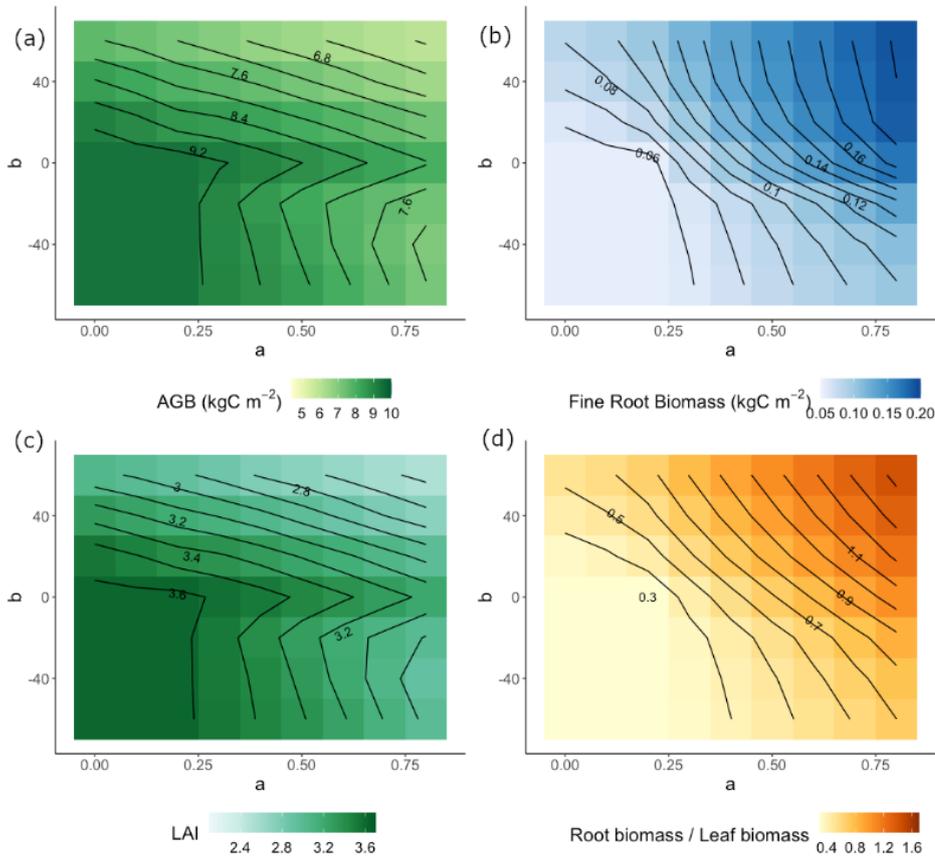


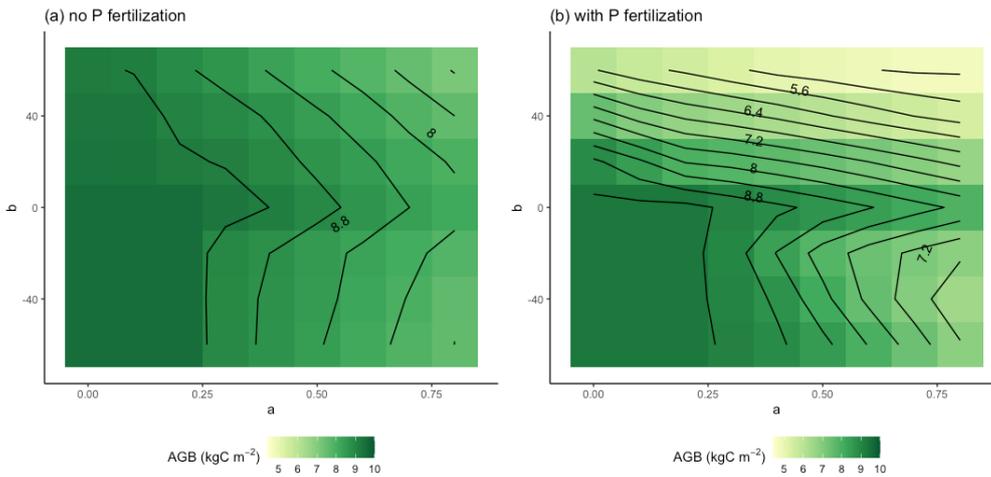
Figure 5. Parameter sensitivity of AGB (a), fine root biomass (b), leaf area index (c), and the ratio of fine root to leaf biomass (d). Results are averaged over the 30 years of simulation and across treatments.

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Figure 6. Parameter sensitivity of AGB in the control and +N plots (a) and in the +N and +NP plots (b). Results are averaged over the 30 years of simulation.

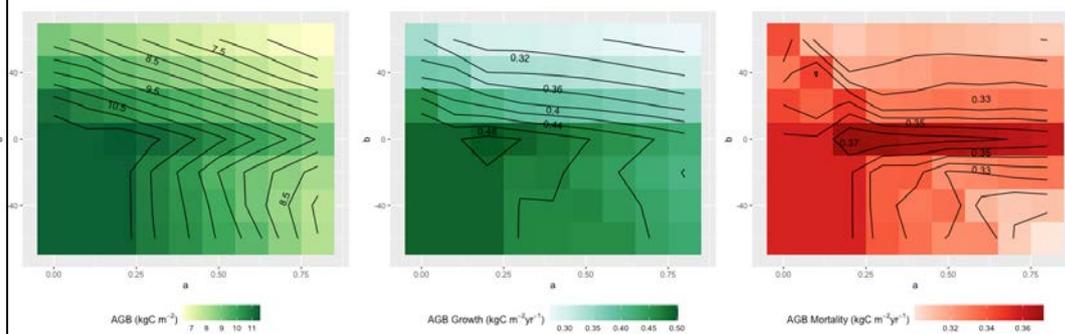
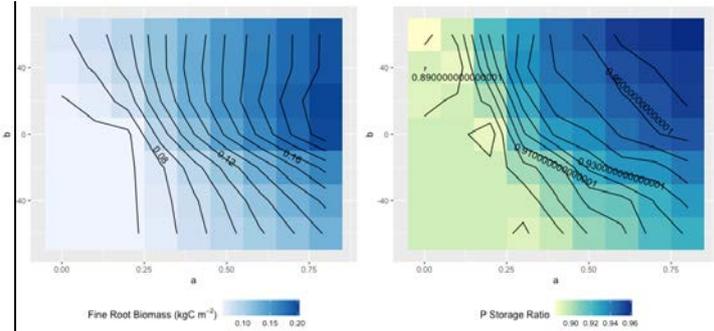
The sensitivity of AGB to a and b depended on the sign of b. When $b \gtrsim 0$, the AGB contours (Fig. 5a) had a negative slope. We can understand this result in light of Eq. (1) and assuming that AGB was a continuous function of $r2l$; when a was increased, decreasing b could maintain same value of $r2l$, and thus AGB. Although the same effect would be expected for $b <$ 0, there are two further complications. First, there is a minimum imposed value of $r2l$ of 0.2. The minimum is never reached when $b \gtrsim 0$ because $r2l$ was an increasing function of $psol$, but was often reached when $b < 0$. In fact, all the simulations with small a and negative b were almost identical because $r2l$ was almost always set to its minimum value. To the extent that $r2l$ is equal to its minimum value, the contours when $b < 0$ would be vertical lines. This constraint on $r2l$ explains why the contours when $b < 0$ are more vertical than the contours when $b > 0$. A second effect likely contributes to the bend in the contours between $b = 0$ and $b = -20$. We saw that $psol$ was reduced at the beginning of the growing season (Fig. 2), likely because trees required relatively large amounts of phosphorus to build new leaves. When $b < 0$, this reduction in $psol$ would lead to an increase in $r2l$. But this relative increase in fine roots would not lead to enhanced productivity because the growing season is wet, and has ample moisture supply, and the construction of wood requires relatively little nutrient input (compared to leaves). These factors collectively result in the bend in the contours immediately below $b = 0$.

These effects were also apparent when we separated the control and +N plots from the +P and +NP plots. For the control and +N plots (Fig. 6a), the $b \gtrsim 0$ AGB contours were more vertical than in the +P and +NP plots (Fig. 6b) or the all-plot average (Fig. 5a). This result occurred because the average $psol$ (and thus $r2l$) values were smaller in the control and +N plots than in the all-plot average or in the +P and +NP plots. As in Fig. 5a, we also see in Fig. 6a-b that the AGB contours have a more vertical orientation when $b < 0$ than when $b \gtrsim 0$. The largest AGB values occurred generally when a is small in the control and +N plots (Fig. 6a), and when both a and b were small in the +P and +NP plots (Fig. 6b). The smallest values of AGB occurred when both a and b are large in the +P and +NP plots (Fig. 6b). This pattern of AGB probably does not result from variation in P limitation. We computed the ratio of non-structural C to the non-structural P ($C:P_{ns}$) in both the control and +N plots (Fig. 7a) and in the +P and +NP plots (Fig. 7b). We interpreted larger values of $C:P_{ns}$ to indicate greater P limitation. However, the largest values of $C:P_{ns}$ occurred when a was relatively small (Fig. 7), similar to where AGB attained its largest values (Fig. 6). The smallest values of $C:P_{ns}$ occurred when both a and b were relatively large (Fig. 7), where AGB attained its smallest values (Fig. 6).

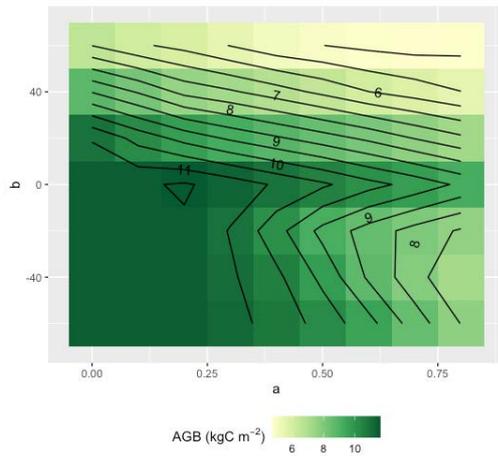
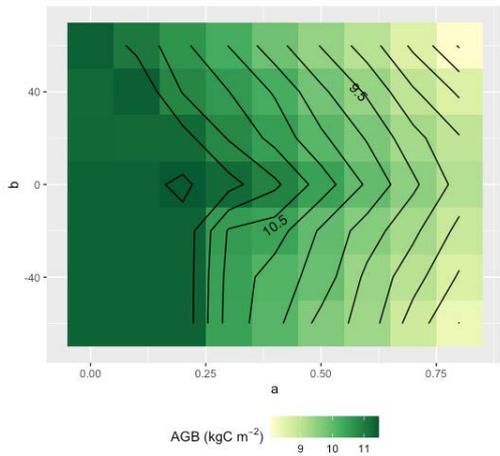
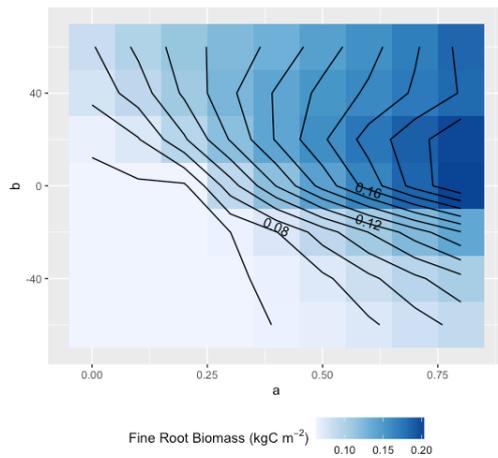
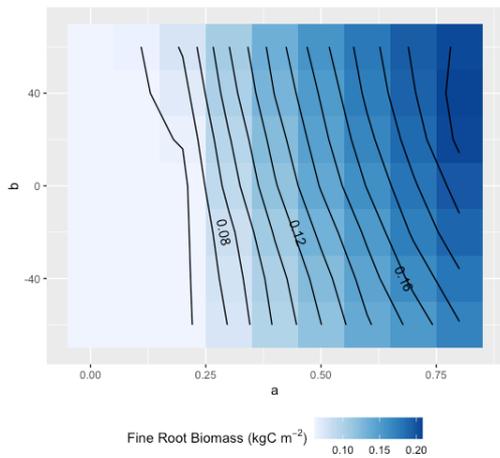
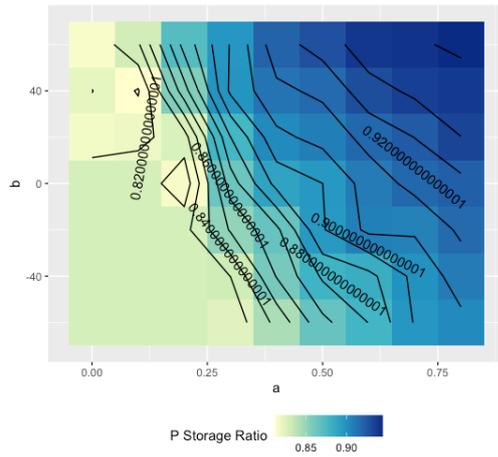
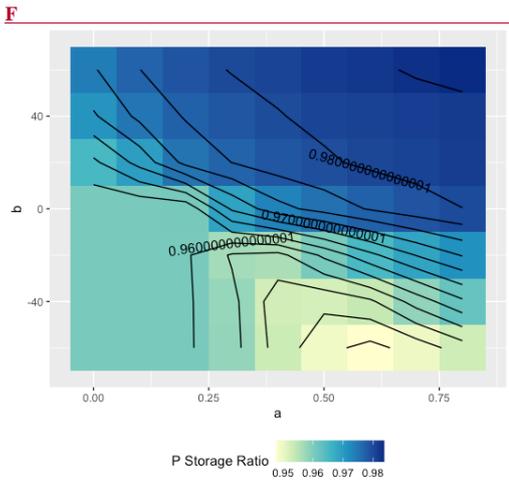
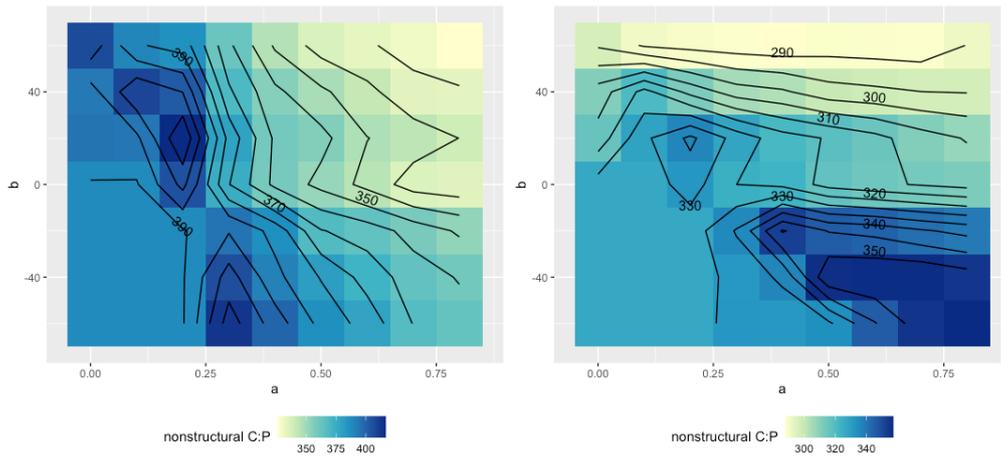
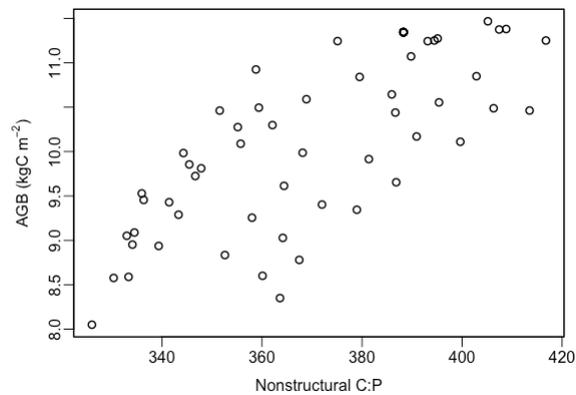
baseline parameterization (a=0.3, b=0) simulated the more AGB than all other parameterizations. This pattern of simulated AGB resulted from the patterns of AGB growth and mortality rate. Fine root biomass shown a very different pattern. P storage ratio (the ratio of nonstructural P to maximum nonstructural P), an indicator of plant P limitation, coincided with simulated fine root biomass, as more fine roots should alleviate P limitation. Allocation parameters had a large impact on simulated AGB accumulation, as seen in our multi-decadal simulations (Fig. 6a, e). Over a 30-year timeframe, the baseline parameterization consistently simulated the more biomass throughout the study period than the "neg" and "pos" parameterizations. This pattern

505 of simulated AGB resulted from the patterns of AGB growth and mortality, as the "neg" and "pos" parametrizations typically led to lower AGB growth (Fig. 6b, f) and higher AGB mortality (Fig. 6c, g) than the baseline parameterization. However, the relative ranking of the "neg" and "pos" parametrizations varied throughout the 30 years. During approximately the first decade, the "neg" parametrizations had the least plant biomass. For the rest of the time period, biomass in the pos3 simulation declined markedly, and this simulation ended up with the least amount of biomass. Also notable in all simulations were the large biomass
510 dips that occurred in approximately years 10 and 20. These biomass dips coincided with the driest year in meteorological forcing.

However, tThe relationship between biomass growthAGB and P limitation was complex.

In our model, we assessed P limitation by considering the non-structural P pool. For each cohort, this pool increased when the cohort took P out of the soil and it decreased when P was deployed to build structural tissue. The pool has a maximum size,
515 dependent on cohort DBH. If the ratio of actual non-structural P to maximum non-structural P were equal to one, then the cohort would be able to rapidly make up for any P used. for growth and there would be no P limitation. Values less than one would indicate P limitation, and a value of zero would represent an extreme case in which a cohort has no P to support growth. There was a clear distinction across simulations, with smaller *a* and *b* corresponding to lower values (stronger P limitation). *with* the "pos" parametrizations having the lowest values (strongest P limitation) and the baseline and "neg" parameterizations
520 having values closer to one (Fig. 6d, h). For all simulations, this ratio exhibited substantial interannual variability, but no long-term trend.

525 **Figure 6. Simulated average AGB, AGB annual growth, AGB annual mortality, fine root biomass and P storage ratio (the ratio of nonstructural P to maximum nonstructural P) over 30 years across treatments under different parameterizations.**

To better understand the results in Fig. 6, and to evaluate the P fertilization effect, we analysed the P-fertilized plots
(+P and +NP) separately from the others (control and +N). In the control and +N treatments, the parameterizations
530 with larger AGB were not the result of there being little P limitation in that simulation. In fact, those parameterizations
tended to have more P limitation than parameterizations with less AGB. To explain why some parameterizations had
larger AGB despite having more P limitation, we explored other aspects of the simulations. We hypothesized that the
highest AGB would occur when the relative acquisition of C:P was optimal, and therefore compared the ratio of
nonstructural C to nonstructural P with AGB (Fig. 8). The highest nonstructural C:P ratios corresponded most closely
535 to leaf C:P (which was fixed at 600 g C (g P)$_N^{-1}$) and to the highest simulated AGB values. This result confirms that such
a scheme would work well in the unfertilized plots; however, it would not capture the P fertilization effect. The +P and
+NP treatments showed much more sensitivity of AGB and fine root biomass to parameterization than the control and
+N treatment. Despite relatively little P limitation for all parameterizations, those with *b*>0 did capture more P
fertilization effect (increased relative fine root production with increased soil P).

F

545 **Figure 77. Parameter sensitivity of~~Effect of P fertilization on~~ the ratio of non-structural C to non-structural P~~AGB in the control and +N plots (a) and in the +N and +NP plots (b). Results are averaged over the 30 years of simulation.~~, fine root biomass, P storage ratio (the ratio of nonstructural P to maximum nonstructural P), and nonstructural C:P over 30 years under different parameterizations. Left panels show the average over the control and +N treatments and right panels shown the average of the +P and +NP treatments.**

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~~Figure 8. The relationship between simulated AGB and C:P in nonstructural pool for different parameterizations.~~
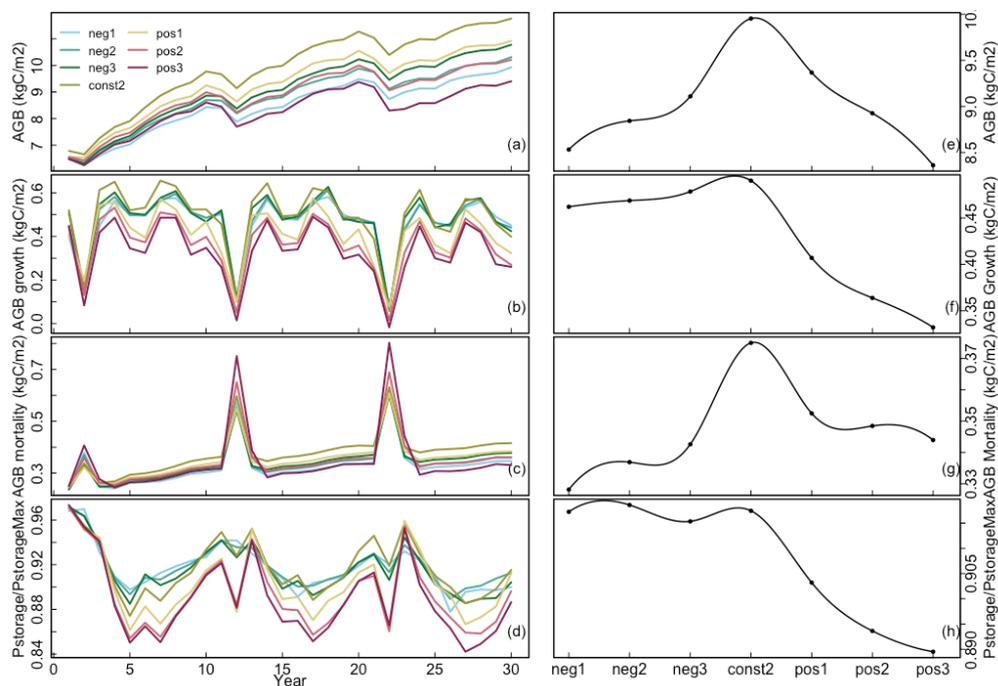
Figure 6. Time series of simulated (a)AGB, (b)AGB growth, and (c)AGB mortality over 30 years under different parameterizations. The ratio of nonstructural P to maximum nonstructural P ("Pstorage/PstorageMax"), an index of P limitation, is shown in panel (d). Also shown are (e)AGB, (f)AGB growth, (g)AGB mortality, and (h) ratio of nonstructural P to maximum nonstructural P at the end of the thirty-year simulation plotted against parameterization. Cubic splines connect the points in (e)-(h).

To better understand the results in Fig. 6, and to evaluate the P fertilization effect, we analyzed the P fertilized plots (+P and +NP) separately from the others (control and +N). In the control and +N treatments, the positive correlation parameterizations had larger AGB than negative correlation parameterizations throughout most of the simulation period (Fig. 7a), and well relatively large AGB growth (Fig. 7b) and intermediate AGB mortality (Fig. 7c). The large AGB growth rates in positive correlation parameterizations were not the result of there being little P limitation in that simulation (Fig. 7d). In fact, positive correlation parameterizations tended to have more P limitation than negative correlation parameterizations. To explain why positive correlation parameterizations had larger AGB growth despite having more P limitation, we explored other aspects of the simulations. In particular, relative allocation to fine roots affected water capture in that the "neg" parameterizations had less transpiration than the others (Fig. 8).

The +P and +NP treatments showed much more sensitivity of AGB to parameterization (Fig. 7e) than the control and +N treatment (Fig. 7a). This difference occurred because P fertilization reduced the AGB growth (Fig. 7f) and increased mortality (Fig. 7g) in the "pos" schemes relative to the other schemes. This result occurred despite there being relatively little P limitation in the P-fertilized plots (Fig. 7h).

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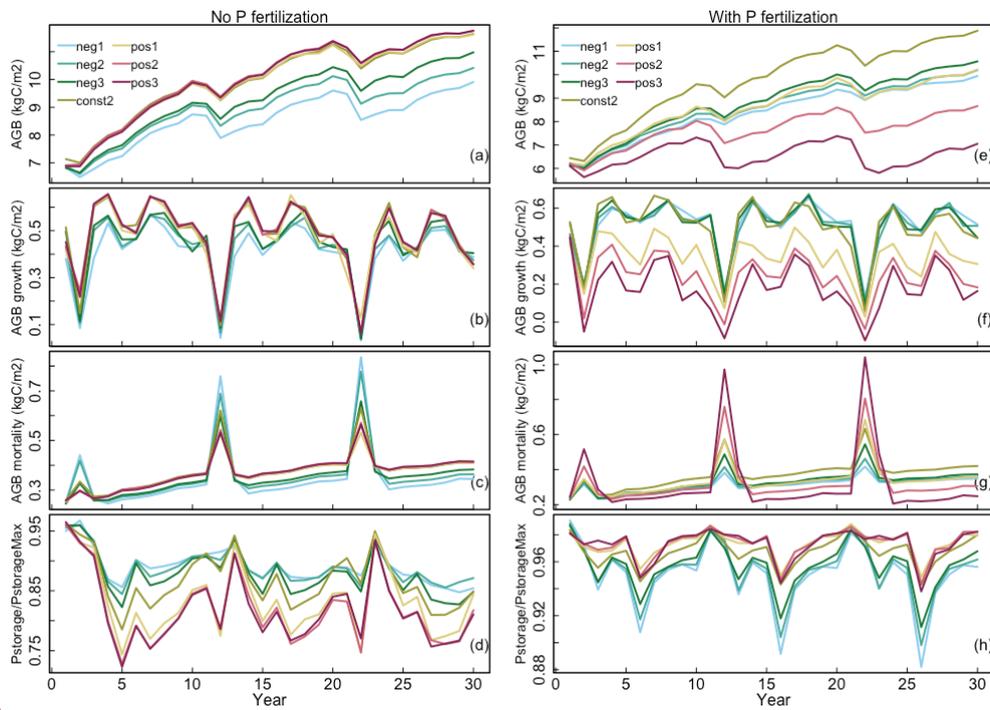
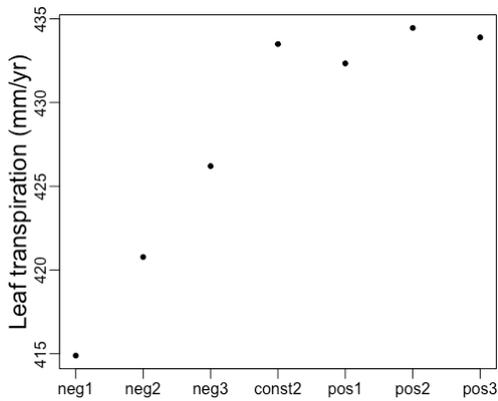


Figure 7. Effect of P fertilization on AGB (a,e), AGB growth (b,f), AGB mortality (c,g) and the ratio of nonstructural P to maximum nonstructural P (Pstorage/PstorageMax) (d,h) during 30-year simulations. Panels (a)-(d) show the average over the control and +N treatments and panels (e)-(h) shown the average of the +P and +NP treatments.

4 Discussion

Soil nutrients can regulate plant biomass production in terrestrial ecosystems (LeBauer and Treseder, 2008; Hou et al., 2020). The control that nutrients exert on carbon partitioning among different types of plant tissues is drawing increasing attention

580   because it can strongly affect long-term ecosystem carbon accumulation and loss (Gessler et al., 2016). This study focused on the effect of soil soluble P on carbon partitioning. We evaluated different parameterizations within the ED2 model, and compared model results to observed carbon partitioning at a fertilization experiment site in Costa Rican tropical dry forest (Waring et al., 2019). We did not set out to identify a single "best" parameter set, but were rather interested in determining the range of parameter values for which the simulation was consistent with observations. The results presented here demonstrate

585   the importance of an allocation parameterization for biomass productionthat sensitive to external nutrient availability nutrient-sensitive allocation parameterization. In particular, we found that the model simulated the most realistic overall partitioning of biomass production when relative allocation to fine roots was positively correlated with soluble soil P, at least on a three-year time scale (a "pos" parameterization). Analysis of multi-decadal simulations suggests that parameterizations havingunder certain circumstances the model assuming relative allocation to fine roots was independent of soil P (thereafter "const"

590   parameterizations), positively correlated with soil P (thereafter "pos" parametrizations), or negatively correlated with soil P (thereafter "neg" parameterizations) these "pos" parametrizations can all lead to comparablegreater aboveground carbon accumulation than parameterizations where relative allocation to fine roots was positively correlated with soil P (thereafter "pos" parametrizations)independent of soil P ("const" parameterizations) or negatively correlated with soil P (thereafter "neg" parameterizations), at least in unfertilized scenarios. However, especially in scenarios with P fertilization, these modelling

595   results also raise issues that could not have easily been foreseen by merely looking at model-data comparisons over three years.

4.1 Model validation

ED2 has long included N dynamics as an option (Moorcroft et al., 2001), but published simulations rarely had this option activated. Recently, Medvigy et al. (2019) introduced a new representation of N and P dynamics into ED2, based on microbial model of Wang et al. (2013) and the nutrient competition model of Zhu et al. (2016). In the Medvigy et al. (2019) parameterization, relative allocation to fine roots was unaffected by nutrients (i.e., the model employed a "const" parameterization). Here, we found that this version of the model simulated reasonable leaf and wood biomass production, especially when averaged over a three-year time frame (Figs. ~~1~~1, 2). These successful predictions of leaf and wood production are consistent with previous ED2 simulations of tropical forests (Xu et al., 2016, 2021; Levy-Varon et al., 2019; Longo et al., 2019a; Longo et al., 2019b). An important feature of our analysis is that we additionally validated the model's simulation of fine root production, which had not been done previously. We found that the baseline parameterization resulted in an underestimate of fine root production and that "const" parameterizations in general could not simulate the observed stimulation of fine root production by P fertilization (Fig. 1c~~1C; Table 5~~). At this point, we cannot say whether ED2 would generate similar biases in fine root production at other tropical forest sites. More observations of biomass partitioning (including fine root production) under P fertilization would be helpful for testing the model, and such observations are becoming increasingly available (Waring et al., 2019; Lugli et al., 2021~~Yuan and Chen, 2012~~; ~~Wright, 2019~~; Cunha et al., 2022). Thus, model validation at additional sites, coupled with validation along soil fertility gradients, would be useful ways of further increasing our understanding.

Besides our baseline parameterization, we evaluated other "const" parameterizations as well as "pos" and "neg" parametrizations. Most parameterizations simulated leaf production consistent with observations and about half simulated wood production consistent with observations (~~Fig. 4,~~ Table 3, 4). However, most parameterizations failed to simulate root production that was consistent with the observations (~~Fig. 5,~~ Table 5). As a result, only 4~~one~~ of the 63~~13~~ parameterizations, all "pos" parameterizations, were~~that we tested was~~ able to simultaneously simulate leaf, wood and fine production consistent with the observations. For future work, it will be interesting to see how these "pos" parameterizations scale in space and time. For example, they can be applied to simulations of the Amazon and compared to the results of Cunha et al. (2022). Also, the fertilization experiment first reported by Waring et al. (2019) is ongoing and the data subsequent to 2017 are currently being analyzed. ~~These~~~~is particular parameterizations were~~~~as a "pos" parametrizations with a moderate sensitivity of fine root relative allocation to soil soluble P. Importantly, it was also reasonably accurate in simulating tree mortality and soil nutrient concentrations (Table 3).~~ Comparison of this longer-term data set to "pos" scheme simulations will be informative. Because ~~our~~~~It will be interesting to see if these~~~~is "pos" parametrizations would be consistent with longer term observations of production,~~ 30-year simulations with "pos" parameterizations and P fertilization yielded much less AGB than simulations with "const" parameterizations (Fig. 6b), we might expect to see some acclimation of the longer-term *r2* response to increased soil P in order to avoid over-allocation to fine roots~~biomass partitioning and mortality. We will soon be able to test that point, as~~ Analysis of fine root production from sites arrayed across a strong natural fertility gradient could also help test this point

because individuals growing on naturally high-P sites should have had sufficient time to acclimate to their local environment.~~the fertilization experiment first reported by Waring et al. (2019) is ongoing and the data are currently being analyzed. It will also be important to test "pos" parametrizations at other tropical forest sites. For example, Lugli et al. (2020) found increasing fine root production with increasing soil P but did not report relative allocation of fine roots to leaves, so we do not know if their relationship was due to an increase in total production (including fine root production) or whether biomass partitioning changed. Cunha et al. (2022) reported strong increase of NPP exclusively with P fertilization, and fine root production was found to have greater response to P increase than canopy production (29% and 19%, respectively). Their findings showed a preferred biomass allocation to root when P availability increases, which is what our model with a "pos" parametrization simulates.~~

But what might explain even the short-term success of ~~These finding~~the "pos" parameterizations?~~s are surprising~~ ~~because~~ ~~in the sense of multiple limitation theory~~Considering multiple limitation theory, we might have expected that~~:~~ when acquisition of P is the most limiting factor for plants, ~~would predict tha~~any~~the~~ increases in soil P would have resulted in decreased allocation to fine roots, contrary to the "pos" parameterizations. Here we offer several potential explanations. First, it could be~~One potential explanation is~~ that soil P supply, not fine root biomass, limited P uptake in the unfertilized plots. In an extreme case ~~For example~~, in the complete absence of soil P, P acquisition would be zero regardless of fine root biomass. The optimal amount of fine root biomass (with respect to P acquisition) would be zero in order to avoid construction and maintenance costs. As soil P increases above zero, the optimal amount of fine root biomass would also increase. An analogy would be "rain roots" that are produced by some species, which occur as lateral branches on established roots after rain events and die during droughts (Nobel et al., 1990). Second, the deciduousness of this forest may be significant. At the beginning of the rainy seasons, trees experience a large P demand to build their P-rich leaves. It may be adaptive for plants to construct these leaves as quickly as possible, and having large fine root production may facilitate that (Jackson et al., 1990; Hodge et al., 2004). Finally, plants may overallocate to fine roots in order to maximize their ability to compete with neighbors (Gersani et al., 2001; Zea-Cabrera et al., 2006; Farrior et al., 2013).

Other processes, not simulated here, may also be relevant to understanding and simulating the observed response of production to fertilization. ~~In addition to direct nutrient acquisition via fine root, other plant mechanisms to increase P uptake could be important as well.~~These includ~~ing~~e phosphatase synthesis (Liu et al. 2015; Kong et al. 2016; Lugli et al. 2020) and symbioses with arbuscular mycorrhizae (Hodge 2004; Comas et al. 2014; Eissenstat et al. 2015; Liu et al. 2015; Kong et al. 2016; Ma et al. 2018). R~~For example, r~~oot phosphatases hydrolyze organic P-containing compounds and releasing inorganic P that is absorbable by roots, while m~~; m~~ycorrhizal associations are~~can be~~ even more effective by enlarging the root absorbing surface per unit cost. B~~; b~~oth mechanisms provide additional P sources. Plants adaptively adjust their traits or metabolic processes in terms of effective P acquisition (Raven et al. 2018; Han et al. 2021; Aoyagi et al. 2022), and diverse P acquisition strategies are being evaluated from observations (Reichert et al. 2022). However, estimates of plant allocation of carbohydrates to mycorrhizae are rare and difficult to obtain, and were not made by Waring et al. (2019). It is possible that, in the Waring et al.

(2019) experiment, P fertilization led to reduced allocation to mycorrhizae and increases in both the number and average diameter of roots, while reducing overall ~~belowground~~ (mycorrhizal plus roots) allocation. ~~It should be noted that these biases and our "supply-limited" hypothesis are not mutually exclusive.~~

665 Because this study is focused largely on model validation and sensitivity, we took the observational data at face value. However, the observational data can also have biases that would impact our interpretations. In particular, fine root production, stock, and loss are difficult to measure accurately in forests (Clark et al., 2001), largely due to highly uncertain spatial and temporal variability in fine root biomass (Finér et al., 2011) and rooting depth (Paz et al., 2015). In tropical forests, maximum root length is often longer than the depth of ingrowth cores in Waring et al. (2019) (Canadell et al. 1996), implying that field

670 measurements underestimate root production. Further, addition of P to the soil surface could have caused roots to proliferate at the surface, at the expense of deeper roots. Further field experiments are necessary to understand potential changes in root vertical distributions. ~~Finally, estimates of plant allocation of carbohydrates to mycorrhizae are rare and difficult to obtain, and were not made by Waring et al. (2019). It is possible that P fertilization led to reduced allocation to mycorrhizae and increases in both the number and average diameter of roots, while reducing overall belowground allocation. It should be noted~~

675 ~~that these biases and our "supply-limited" hypothesis are not mutually exclusive.~~ In addition, we are open to the idea that allocation responses to P fertilization on a three-year time scale might differ from correlation analysis (e.g., correlation of soil P with fine root productivity across a strong fertility gradient). Individuals growing on naturally high-P sites, for example, may have had sufficient time to acclimate to their local environment.

4.2 Three-Year Sensitivity Analysis

680 ~~We~~Our approach to sensitivity analysis was to focused on the sensitivity of several output variables (leaf, wood and fine root production) simultaneously against the two~~one~~ input parameters that determined the fine root to leaf ratio. By contrast, other studies using ED2 have focused on one output variable ~~and multiple inputs~~ (LeBauer et al., 2013; Levy-Varon et al., 2019; Medvigy et al., 2019). Our sensitivity analysis of leaf, wood, fine root and total production showed distinct responses for the different production measures~~, but their patterns across treatments were analogous~~ (Fig. 3~~3~~). Of these, fine root production had

685 the largest CV because its average magnitude was smallest. This suggests that just because one measure of productivity is sensitive to a particular parameter does not mean that the model is generally sensitive to that parameter. Our results also varied considerably depending on whether P fertilization was applied, underscoring the importance of environmental context for sensitivity analysis. Furthermore, we note that the sensitivity on one time scale (three~~3~~ years) can be different from the sensitivity on another time scale (30 years), a~~nd more discussion on this point will be~~s discussed ~~elaborated~~ in the next section.

690 **4.3 Thirty-Year Sensitivity Analysis**

In our 30-year simulations, we found that the effects of fine root allocation parameterization on AGB ~~depended on~~differed across fertilization treatment. In the control and +N plots~~plots not fertilized with P~~, the well-validated "pos" schemes led to

30-year AGB that was comparable to AGB from the other parameterizations. This result is satisfying because it suggests that what is validated in the short term is adaptive in the long term. But in the +P and +NP plots, the well-validated "pos" schemes led to 30-year AGB that was markedly less than some other parameterizations, including the baseline. Evidently, these schemes over-allocated to fine roots on this time scale. It is possible that the low biomass accumulation in these schemes is related to other model parameters. For example, the maximum non-structural P pool size was set equal to the amount of P required to re-construct all leaves and fine roots. This maximum pool size would limit the advantage of having more roots to acquire more P under high P conditions.

Based on our sensitivity analysis, we are able to offer new hypotheses that may be testable with longer-term fertilization experiments. First, it may be that the "pos" simulations, which were validated in the short term, may also be valid on longer time scales. (2) It could be that P fertilization over 30 years would expose trees to soil P concentrations that are well outside the natural range. In such a novel environment, the response may well be maladaptive. Second, some acclimation might occur on decadal to multidecadal time scales. Third, the response of $r2l$ to soil P may be saturating rather than linear. A saturating parameterization would help to prevent over-allocation to fine roots under the very high soil P concentrations associated with P fertilization (but would be a bit more complicated than our parameterization because it would require an additional parameter). Finally, forest demand for P may change as a function of forest age or as species turn over. If the PFT composition changes and different PFTs have different a and b values, the community-level $r2l$ would also be affected. Observations across a soil P gradient would also be useful for testing several of these points.

"const" simulations had more AGB accumulation than either "pos". or "neg" simulations if with the same a. Although higher sensitivity to soil P (larger absolute value of b) could lead to less AGB accumulation, it did not seem that "pos" or "neg" parameterizations had a lot of differences (Fig. 7). To understand why, it is important to consider relative acquisition of C and P. Different allocation parameterizations led to different ratio of nonstructural C and P, and the highest nonstructural C:P ratios corresponded to the highest simulated AGB values (Fig. 8). Based on this result, it could be argued that allocation rule for relative allocation to fine roots should be targeted to the nonstructural C:P ratio. We think that such a scheme would work well in the unfertilized plots.

In plots not fertilized with P, the "neg" simulations had less growth, more mortality and less AGB accumulation than either the "const" or "pos" simulations (Fig. 7). To understand why, it is important to consider that fine roots facilitate the acquisition of water as well as P. Different allocation parameterizations led to different amounts of water uptake and thus transpiration (Fig. 8). Overall, the low AGB accumulation associated with the "neg" simulations provides an explanation for why the observed fine root production was inconsistent with a "neg" parameterization. By contrast, the "const" and "pos" simulations had higher transpiration and had higher aboveground biomass accumulation. Interestingly, the increase in aboveground biomass did not arise from alleviation of P limitation (indeed, P limitation is largest in the "pos" simulations). It is notable that a long time series is helpful for seeing this effect, as it is most prominent during extremely dry years.

725 Long-term simulations under P fertilization were qualitatively different (Fig. 7e-h). Given that the only four "pos" parametrizations were most consistent with the short-term observations, we were surprised to see that the "pos" parametrizations led to much less AGB accumulation in the long term then either the "neg" or "const" parameterizations (with the same *a*). In the "pos" parametrizations, fertilization drove very high P concentrations and thus very high relative allocation to fine roots. This allocation to fine roots was inevitably costly in terms of root respiration and turnover because the models

730 sets both of these processes to be proportion to fine root biomass. In addition, the marginal benefit of increases in fine allocation are smaller when allocation to fine roots is large than when allocation to fine roots is small. Because P limitation was nearly non-existent under P fertilization, the benefits of further increasing fine root biomass to scavenge P declined. Thus, the "pos" parametrizations caused the simulations to overcompensate for high P concentrations. At the same time, the "neg" parametrizations also had less AGB accumulation than "const" parameterizations. In the "neg" parametrizations, very high

735 soil P concentrations led to very low allocation to fine roots. This low allocation to fine roots would impact relative acquisition of C and Pdid not much impact P limitation, but it would impact water acquisition. These dynamics also help to explain why "neg" parametrizations were incompatible with the observations of Waring et al. (2019).

Although some parameterization works well in the short term in the sense that it yields simulation results that are consistent

740 with observations, we do not know how well these parameterizations would work in the long term without long-term observations to compare the simulations to. In our 30-year model simulations, successional changes in forest structure, composition, and function are allowed to occur, but the allocation rule remains fixed (no acclimation). It is interesting that those parameterizations simulated less AGB accumulation than many other parameterizations on 30-year time scales with P fertilization. This model result spurred some thoughts: (1) Some acclimation would occur on decadal to multidecadal time scales. Forest demand for P may change as a function of forest age or as species turn over, and such changes can affect relative

745 allocation. This idea can mathematically be incorporated into the model by having relative fine root allocation be a saturating function of soil P rather than a linear function. Such a rule would help to prevent over-allocation to fine roots under the very high soil P concentrations associated with P fertilization, but may also complicate the parameterization compared to the one we employed. (2) It could be that P fertilization over 30 years would expose trees to soil P concentrations that are well outside the natural range. In such a novel environment, the response may well be maladaptive. (3) There does not appear to be any

750 problem with "pos" parameterizations under "normal" unfertilized conditions, thus a scheme that employed a target nonstructural C:P might yield a similar result (but again, such a scheme is unlikely able to simulate the increase in fine root production observed to occur with P fertilization). Overall, we see a strong need for longer-term experiments exactly in order to make such assessments.

4.4 Towards more sophisticated models

Going forward, it would be interesting to validate the ability of other models to simulate biomass partitioning at tropical forest fertilization sites. Existing models use a variety of allocation schemes, but we are not aware of other models using a scheme analogous to our "pos" parameterizations. For example, CLM-CNP (Yang et al., 2014) and JULES-CNP (Nakhavali et al., 2022) use parameterizations similar to our "const" parameterization to control new growth allocation. Other models use dynamic allocation schemes ~~that we speculate would function like our "neg" parametrizations.~~ ORCHIDEE-CNP (Goll et al., 2017) and QUINCY (Thum et al., 2019) applied a pipe theory to partition leaf and root mass, modulated by the most limiting soil available nutrient (and water, for QUINCY). ELM-CNP (Zhu et al. 2019) and DLEM-CNP (Wang et al., 2020) appl~~yies~~ a method that make allocation co-limited by both N and P (Friedlingstein et al., 1999~~; Wang et al., 2020~~). Braghiere et al. (2022) integrated the most recent version FUN3.0 with ELM, modulating plant nutrient uptake from multiple pathways by optimizing carbon cost, but did not illustrate how this strategy might affect new-growth allocation. Whether any of these approaches would lead to increases in relative allocation to fine roots under P fertilization should be investigated. ~~These models do not use the same equations but are functionally close to our "neg" parameterizations. We are not aware of other models using a scheme analogous to our "pos" parameterizations. Our sensitivity analysis also suggests that it will be important to carry out model validation on time scales longer than three years, as the optimal allocation strategy in the short-term may differ from the optimal allocation strategy in the long term.~~

The effect of nutrients on biomass partitioning also depends on stoichiometry.~~Just as important to models is the balance between N and P availability. Current models approach stoichiometry differently.~~ That is, nutrient limitation might lead to changes in tissue stoichiometry rather than tissue production. ~~Some have fixed stoichiometries (e.g. JSBACH, Goll et al., 2012; CLM-CNP, Yang et al., 2014; JULES-CNP, Nakhavali et al., 2022).~~ Some models account for stoichiometric flexibility by prescribing ranges for each pool based on empirical studies (e.g. CASACNP, Wang et al., 2010; ORCHIDEE-CNP, Goll et al., 2017; QUINCY, Thum et al., 2019). ED2 has fixed stoichiometries in structural pools but non-fixed stoichiometries in non-structural pools. ~~Models adjusting relative allocation of new growth to fine roots mostly apply an idea that new growth is scaled by minimum of N and P stress scaling factor, rendering increased fine root production when P demand exceeds supply (for example, when the ratio of nonstructural C:P greatly exceeds the ratio present in plant tissues). By contrast, we parameterized the model only from the perspective of supply (soil P). We suggest that model intercomparison be carried out, especially at tropical nutrient fertilization sites. Our sensitivity analysis also suggests that it will be important to carry out model validation on time scales longer than three years, as the optimal allocation strategy in the short term may differ from the optimal allocation strategy in the long term.~~

785 When comparing the influence of different allocation schemes, we made some simplifications to make our analyses more straightforward. For example, we did not account for the effect of N limitation on carbon partitioning. However, such an effect was not observed at our study site (Waring et al., 2019). Neither did we account for the effect of water limitation on carbon partitioning. Carbon partitioning may also depend on community composition (Dybzinski et al., 2011) and it may be temporally variable (Farrior et al., 2013). We did not account for either of these effects except for the impact of water limitation on tree

790 phenology (Xu et al., 2016). More sophisticated parameterizations that account for these effects should be investigated in future studies.

5 Conclusion

The partitioning of the new growth in a forest ecosystem between leaf, wood and fine root pools is a critical aspect ecosystem functioning and can strongly affect forest carbon budgets (Litton et al., 2007). We applied the nutrient enabled ED2 model in

795 simulating a fully factorial N and P fertilization experiment conducted in a secondary tropical dry forest in Costa Rica over three years. Some model parameterizations were able to accurately simulate leaf, wood and fine root production, as well as mortality. Surprisingly, these parameterizations all assumed a positive relationship between relative allocation to fine roots and soil P. This result might be expected at relatively low levels of soil P, when increased root growth would lead to larger construction and maintenance costs but only modest increases in P uptake. Further experimentation is needed to test whether

800 this relationship would hold on ~~to~~ longer time scales and at other siteshigh P concentrations. Indeed, our sensitivity analysis suggested that this parameterization would over-allocate to fine roots in P-fertilized plots on multidecadal time scales.other dynamics may be at play on longer time scales. This analysis showed over-allocation to fine roots in long-term, P-fertilized situations. Our findings also suggested the need of more model-data intercomparison, especially with respect to simultaneous measurements of leaf, wood and fine root production. Such analyses will enable us to develop improved model

805 parameterizations and ultimately better simulations of forest carbon balances.

Code and data availability. The most up-to-date source code, post-processing R scripts, and an open discussion forum are available on GitHub at https://github.com/EDmodel/ED2. Field data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mq62g78.

Author contributions. SL ran the simulations, carried out the analysis and wrote the first draft of the manuscript. JSP and BGW

810 provided the field data. DM designed the study. All authors contributed to manuscript revisions.

Competing interests. DM is a member of the Biogeosciences editorial board. The peer-review process was guided by an independent editor, and the authors have no other competing interests to declare.

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815 CAREER Grant DEB-1053237 to JSP. Muñoz Sabater, J. (2019) was downloaded from the Copernicus Climate Change Service (C3S) Climate Data Store (2022). The results contain modified Copernicus Climate Change Service information 2020. Neither the European Commission nor ECMWF is responsible for any use that may be made of the Copernicus information or data it contains.

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