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Key Points:

- Water-phosphorus interactions reduce seasonal variation in gross primary productivity
- Reduced ion mobility during dry season impairs plant's nutritional status
- Phosphorus mineralization is decoupled from decomposition during droughts

Supporting Information:

- Supporting Information S1

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Low Phosphorus Availability Decreases Susceptibility of Tropical Primary Productivity to Droughts

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Abstract Large uncertainties in the susceptibility of tropical forest productivity to precipitation changes hamper climate change projection. Interactions between the availabilities of water and phosphorus could theoretically either increase or decrease the susceptibility of tropical gas exchange to variation of precipitation. The inclusion of phosphorus-water interactions in a land surface model reduces the coefficient of variance, a measure of variability, of biweekly gross primary productivity by a factor of 1.5–2.3 at three tropical forest sites in Brazil, bringing it closer to estimates from eddy covariance measurements and remote sensing. Soil drought conditions are attenuated due to 8–30% lower water consumption during wet periods in presence of phosphorus limitation. When soils are dry, plant phosphorus acquisition is impaired by reduced ion mobility, despite an increase in net phosphorus mineralization. We conclude that water-phosphorus interactions cannot be omitted in analysis of the resilience of tropical ecosystems to precipitation changes.

Plain Language Summary Phosphorus is an essential plant nutrient and limited availability of phosphorus in soils can negatively affect plant growth and photosynthesis. Therefore, a low soil supply of phosphorus can limit the capacity of ecosystems to draw down carbon dioxide emitted by human activities. Using model simulations for three tropical sites, we show that besides the negative effect on plant growth, low phosphorus availability can have a positive effect on photosynthesis during the dry season. The positive effect is caused by lower water consumption of plants during the preceding wet season due to an overall reduced plant growth. As the interactions between water and phosphorus availability are commonly overlooked in climate change assessment, we conclude that the susceptibility of tropical ecosystem to future changes in precipitation, and thereby the risk of a catastrophic die back of tropical vegetation, could be lower than previously estimated.

1. Introduction

The observed decline of the Amazon aboveground carbon sink “diverges markedly from the recent increase in terrestrial carbon uptake at global scale and is contrary to expectations based on models” (Brienen et al., 2015). The sink decline of natural systems is driven by increasing biomass mortality and a leveling of productivity “due either to a relaxation of the growth stimulus itself, or to the onset of a counteracting factor depressing growth rates” (Brienen et al., 2015), like water availability or soil nutrients.

Increased moisture stress is projected for the 21st century for Amazonia, particularly for southern Amazonia, (Cox et al., 2008; Salazar et al., 2007), and there is some evidence that moisture stress is already increasing (Li et al., 2008). The coupling between vegetation and atmosphere could self-amplify forest losses due reductions in rainfall (Zemp et al., 2017), potentially leading to a collapse of the system (Cox et al., 2000; Verbesselt et al., 2016). However, the implications of increased moisture stress for the carbon balance are unclear, primarily due to uncertainties in the plant physiological responses (Huntingford et al., 2013; Powell et al., 2013) and the role of functional diversity (Roman et al., 2015; Skelton et al., 2015; Zemp et al., 2017). While land surface models simulate reductions in net primary productivity (NPP) in response to droughts (Huntingford et al., 2013), plot data from Amazonia indicate that recent droughts, despite their impact on the net carbon balance (Phillips et al., 2009), caused only little immediate reduction in NPP (Lee et al., 2013) but a strong increase in mortality (Doughty et al., 2015; Feldpausch et al., 2016).

Amazon forest structure and functioning are heavily influenced by the diverse soil conditions “reflecting a rich diversity of geologic origins and geomorphic processes” (Quesada et al., 2012). Soil hydraulic properties and soil phosphorus availability are linked to wood production rates and stand level turnover (Malhi et al., 2009; Quesada et al., 2012). Nutrient manipulation experiments in the tropics show effects of phosphorus availability on aboveground biomass production, seed production, and seedling survival as well as nutrient return in litterfall (Alvarez-Clare et al., 2013; Homeier et al., 2012; Wright et al., 2011). While variation in soil hydraulic properties, although somewhat limited (Marthens et al., 2014), is considered in land surface models, variation in soil fertility is usually omitted. The few land surface models that incorporate a phosphorus cycle indicate that low phosphorus availability is limiting tropical productivity and carbon sink capacity (Goll et al., 2012, 2017; Wang et al., 2010; Yang et al., 2014).

Few publications investigated the interaction between drought and plant nutrition, primarily focusing on nitrogen (Gessler et al., 2017; Royo & Knight, 2012; Sergent et al., 2014; Wang et al., 2012) with only one considering phosphorus (He & Dijkstra, 2014). Aggravating this situation is a potential decoupling of nitrogen and phosphorus availability with increasing soil aridity, “because of the different degrees of control exerted on the supply of these elements by biological and geochemical processes” (Delgado-Baquerizo et al., 2013). Therefore, it is unclear to what extent findings about nitrogen can be transferred to phosphorus. Generally, low nutrient availability could decrease the susceptibility to drought due to reduced shoot-to-root ratios and change of other plant traits (Ewers et al., 2000) as well as hypothetically attenuate soil drought conditions due to reduced water consumption during wet periods in the case of nutrients limiting photosynthesis. During a drought event, the plant’s nutritional status can be impaired by reduced soil nutrient availability, which can deteriorate the general functioning and resistance of the plant (Kreuzwieser & Gessler, 2010). As these two effects can either decrease or increase the susceptibility to drought, a basic understanding of the relative importance of these processes is needed but currently missing.

To investigate the role of water-phosphorus interactions on the seasonal variations in the carbon balance of tropical forest ecosystems we use a land surface model that accounts for the major water-phosphorus interactions (Figure 1) at three tropical sites in the Amazon. We hypothesize two mechanisms: (1) Water availability in tropical forest ecosystem increases with phosphorus stress as the resource water is decreasingly exploited (following Liebig’s law of the minimum), and (2) amplification of phosphorus stress by drought due to impaired mineralization and lower ion mobility, that is, the diffusion controlled transport of phosphate ions from soil pores (Barraclough & Tinker, 1981) to the root surface being reduced in dryer soils. These two hypotheses have opposite effects during the dry season; the first one implies that phosphorus limitation during the wet season increases legacy soil moisture available during dry periods, whereas the second one implies that phosphorus limitation further exacerbates a drought-induced reduction of productivity.

2. Methods

2.1. Model

Here we use the coupled carbon, nitrogen, and phosphorus dynamics version (CNP) of the land surface model Organizing Carbon and Hydrology in Dynamic Ecosystems (ORCHIDEE; Goll et al., 2017). The model simulates the terrestrial biogeochemical cycles of carbon, nitrogen, and phosphorus and their interactions as well as the water budget and the exchanges of energy, water, and carbon dioxide and nitrogen between the atmosphere and the biosphere. ORCHIDEE is well evaluated (e.g., Joetzjer et al., 2015; Krinner et al., 2005) and is able to reproduce the shift from nitrogen- to phosphorus-limited plant growth along a soil formation chronosequence in Hawaii, including differences between nitrogen and phosphorus stress in respect to their control on growth compared to leaf level productivity (Goll et al., 2017).

It has a detailed representation of root phosphorus uptake and accounts for root zone depletion of phosphorus as a function of root phosphorus uptake and phosphate ions diffusion controlled transport from the soil pores to the root surface. The major interactions between water and phosphorus cycling (Figure 1) in ORCHIDEE are (1) the positive dependence of phosphate mobility on soil moisture (Equation 23 in Goll et al., 2017), which affects the uptake of phosphate by roots (Equation 4 in Goll et al., 2017) and its availability for plant growth, (2) the positive dependence of microbial mineralization on soil moisture (Section 2.1.3 in Goll et al., 2017), (3) the direct dependence of plant growth on plant internal phosphorus availability (Equation 13 in Goll et al., 2017), and (4) the indirect dependence of the photosynthetic capacity (maximum carboxylation rate) on leaf phosphorus. The latter is a consequence of constraints on the elasticity of the leaf

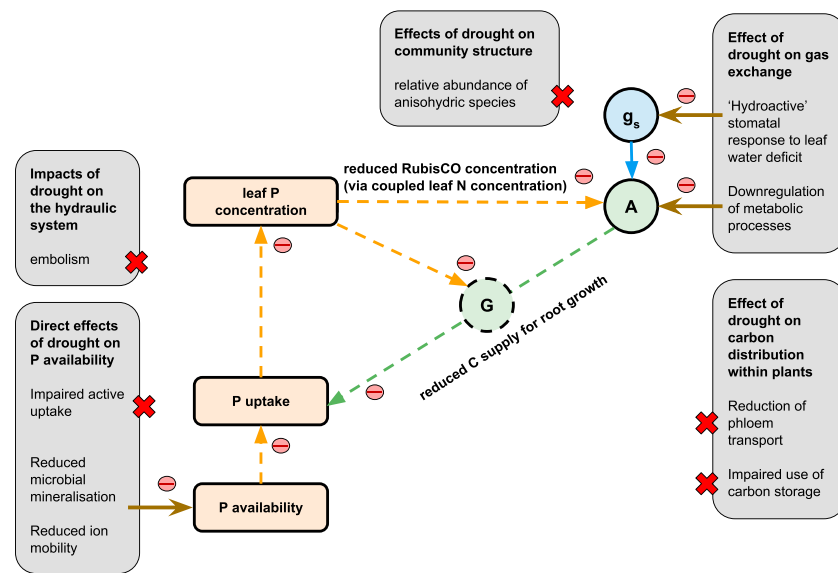


Figure 1. Schematic of major phosphorus-drought interactions in evergreen tropical forests. Drought has a direct effect on stomatal conductance (g_s) and assimilation (A) leading to lower transpiration and to reduced assimilation of carbon as well as uptake and transport of phosphorus. Drought negatively affects labile phosphorus concentration at the root surface as the mobility of ions, and the supply of phosphorus from microbial mineralization are reduced. Reduced tissue P contents directly impairs growth (G) and indirectly affects stomatal conductance and assimilation via stoichiometric constraints on the leaf N:P ratio. Additional major interactions that are omitted in ORCHIDEE are marked with a red cross (scheme inspired by Gessler et al., 2017).

nitrogen:phosphorus ratio (Equation 11 in Goll et al., 2017). Thereby, the maximum nitrogen concentration, which is linked to the photosynthetic capacity, might not be realized under phosphorus scarcity. A detailed model description can be found in Goll et al. (2017).

We exchanged the original two-layer hydrological bucket scheme in Goll et al. (2017) with an 11-layer hydrological scheme (Campoy et al., 2013; de Rosnay et al., 2002), which was shown to better reproduce evapotranspiration for subbasins of the Amazon with marked dry season (Guimberteau et al., 2014). We further account for increased soil resistance to evaporation when the top layers of the soil are dry (Oleson et al., 2008; Sellers et al., 1992).

We exchanged the original formulation of phosphorus sorption, which assumes a fixed fraction of labile phosphorus being dissolved in soil solution (Goll et al., 2017) with a more realistic Freundlich Isotherm, which is parameterized based on a compilation of isotopic dilution data ($n = 379$; Achat et al., 2016; Kvakić et al., 2018). Three different soil classes are distinguished in respect to sorption dynamics, namely, Oxisols, Molisols, and "others." Details are given in supporting information Text S1.

2.2. Simulation Setup

We performed simulations for three forest sites in Brazil (BR-Ma2, BR-Sa1, and BR-Sa3) forced by in situ hourly meteorological measurements, namely, air temperature, net radiation, soil heat flux, incoming solar or photosynthetic photon flux density irradiance, and accumulated precipitation (Da Rocha et al., 2009; see supporting information Table S2). The sites are all tropical terra firme humid forests that have 30- to 40-m-tall closed canopies of evergreen broadleaved trees, with occasional palms and lianas (Da Rocha et al., 2009). For each site we performed simulations in which (a) nitrogen and phosphorus availability was either prescribed as optimal (nonlimiting; C model) or (b) prognostically computed to disentangle the effects of nutrients on plant productivity and transpiration (CNP model). A third set of simulations with the CNP model was performed in which we added nitrogen fertilizer at a high rate (supporting information Text S3). We prescribed site specific soil types according to the U.S. Department of Agriculture soil classification (Araújo et al., 2002; Goulden et al., 2004; Saleska et al., 2003) and specific leaf area (Malhi et al., 2009), as well as atmospheric nitrogen and phosphorus deposition from reconstruction by Wang et al. (2017).

We account for the increase in atmospheric carbon dioxide concentration and changes in atmospheric nitrogen and phosphorus deposition since 1850 by simulating the historical period prior the observation period.

To do so, we first equilibrated the biogeochemical cycles to the carbon dioxide concentration (284.7 ppm) and atmospheric deposition of 1850 using repeated cycles of observed meteorology. Afterward, the simulations were continued till the observation period using reconstructions of atmospheric carbon dioxide and atmospheric deposition (Wang et al., 2017) using repeated cycles of observed meteorology.

2.3. Evaluation Data

At all sites hourly turbulent fluxes were measured using the eddy covariance method. Specific site details can be found elsewhere (Araújo et al., 2002; Goulden et al., 2004; Saleska et al., 2003). For two sites (BR-Ma2 and BR-Sa1) aboveground and belowground biomass, leaf area index and stoichiometry, as well as annual fluxes of NPP and gross primary productivity (GPP) were compiled by Malhi et al. (2009). Here aboveground biomass estimates are derived from measurements of tree diameter using allometric equations, whereas belowground biomass estimates are derived from the aboveground biomass estimates applying a root:shoot ratio of 0.21. Annual GPP is derived from eddy covariance measurements of net ecosystems exchange subtracting bottom up estimates of ecosystem respiration. Malhi et al. (2009) provides average GPP over measurement periods that are somewhat different (2002–2005 for BR-Sa1 and 1999–2000 for BR-Ma2) from the ones we use for the analysis of the temporal dynamics of GPP (see supporting information Table S2). Annual NPP is given by summing up measurements of litterfall, stem growth (tree diameter and recruitment), and root growth (soil core). Nutrient status of leaves was determined by collection of leaves at various heights for 19–30 individuals in each site. Leaf area index is the average of estimates based on different methods (hemipfoto, destructive harvest, leaf area index [LAI] 2000, and allometric relation). Details on the estimation and an uncertainty discussion can be found in Malhi et al. (2009).

For all three locations we extracted biweekly satellite proxy retrievals for GPP (total scene near-infrared reflectance [NIR_t] and NIR of terrestrial vegetation [NIR_v]) and for LAI (normalized difference vegetation index [NDVI] and enhanced vegetation index [EVI]). NIR_t and NIR_v are products from the Advanced Very High Resolution Radiometer sensors, while NDVI and EVI are derived from the third-generation Global Inventory Monitoring and Modeling System NVDI and Moderate Resolution Imaging Spectroradiometer Vegetation Index Product (MOD12A1), respectively. Satellite proxies retrievals of GPP have the advantage of spanning longer periods (1982–2005) than the estimates from the eddy covariance method (3 years). NIR_v was shown to explain a large part (76%) of the monthly variance in GPP derived from eddy covariance measurements across 105 mostly extratropical sites (Badgley et al., 2017). A disadvantage is the coarse spatial resolution (8 km). Details on satellite retrievals can be found in the supporting information Text S2 (Badgley et al., 2017; Huete et al., 2002; Myneni et al., 1997; Pinzon & Tucker, 2014; Rahman et al., 2005).

2.4. Statistical Analysis

We computed root-mean-square error, Pearson correlation (r), Taylor score, and the coefficient of covariance (cv) between simulated and observed fluxes of GPP, net ecosystem exchange (NEE), and latent heat (Da Rocha et al., 2009). The analysis was done on detrended time series of monthly and daily averages of fluxes of GPP, NEE, and latent heat.

We computed the cv of biweekly averages of simulated GPP, NIR_t , and NIR_v , as well as the cv between simulated LAI and corresponding satellite retrievals NDVI and EVI. Due to poor correlation ($r < 0.2$) between satellite proxy retrievals of GPP and eddy covariance-derived GPP we omit a more detailed statistical analysis of simulated GPP versus satellite proxies.

3. Results and Discussion

3.1. Model Evaluation

At all three sites, nutrient availability is suboptimal when computed prognostically, this is indicated by leaf carbon:nitrogen:phosphorus ratios of 744:30:1, 1264:38:1, and 983:36:1 for BR-Ma2, BR-Sa1, and BR-Sa3, respectively, which are elevated compared to the optimal ratio in ORCHIDEE of 267:17:1 (Goll et al., 2017). Furthermore, the nitrogen addition experiment (supporting information Text S3) and the elevated leaf nitrogen:phosphorus ratios indicate that nitrogen availability is not limiting plant productivity at all sites. At BR-Ma2 the simulated leaf carbon:nitrogen:phosphorus stoichiometry is close to the observed ratio of 781:36:1 (Malhi et al., 2009), while at BR-Sa1 the simulated leaf nutrient content is lower than observed (821:31:1; Malhi et al., 2009). For the third sites stoichiometric information is not available. An analysis of site-specific biases in leaf nutrient content is hampered due to the lack of observational data, in particular on soil phosphorus availability and plant phosphorus recycling efficiency and uptake.

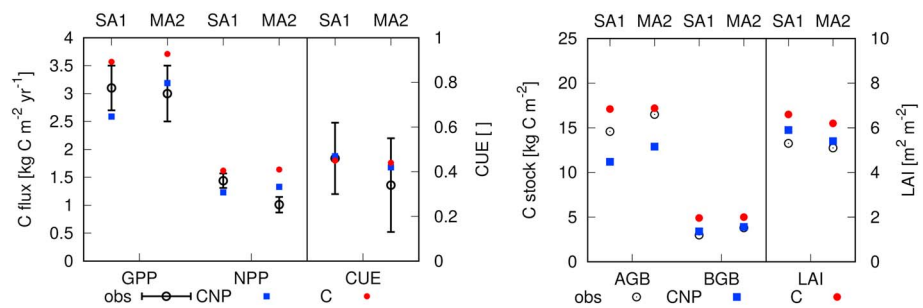


Figure 2. Comparison of simulated and observed gross primary productivity (GPP), net primary productivity (NPP), and carbon use efficiency (CUE) for two sites (BR-Sa1 and BR-Ma2) for which observations are available (Malhi et al., 2009). Comparison of simulated and observed aboveground biomass (AGB), belowground biomass (BGB), and leaf area index (LAI).

The model reproduces well the state of the vegetation carbon cycle at the two sites where observations are available, in particular when nutrient availability is prognostically computed (Figure 2), with the exception of aboveground biomass. The simplistic representation of mortality by constant turnover rates in the model, instead of linking mortality to productivity as observed in forest sites in French Guiana (Grau et al., 2017), can explain the model bias in aboveground biomass.

At all three sites, the observed and simulated fluxes of NEE, GPP, and latent heat correlate rather poorly on daily and monthly basis (supporting information Figure S1), irrespectively of how nutrient availability is handled in the model. Simulated latent heat fluxes and GPP tend to be closer to observations with prognostic nutrient availability. The interpretation of the carbon fluxes comparison is hampered on the one hand, by the high uncertainty in GPP estimates derived from eddy covariance measurements of NEE, which is related to issues in the estimation of nighttime respiration in tropical regions (Aubinet et al., et al., 2012; Malhi et al., 2009), and on the other hand, by the oversimplified phenology of evergreen tropical plant functional types in ORCHIDEE, which cannot capture the seasonal signal in leaf age, associated photosynthetic capacity, and litterfall (Doughty et al., 2015; Wright & Van Schaik, 1994; Wu et al., 2016) and thus in GPP and NEE (see supporting information Text S3). A further improvement of simulated fluxes of GPP and latent heat, in particular in respect to differences between the wet and dry seasons, can be expected when coordinated shifts in canopy leaf demography and leaf photosynthetic capacity depending on demography are accounted for in the model.

There is substantial uncertainty about the coupling of gas exchange to soil water supply, as it is unclear to what extent trees have access to deep soil water reservoirs (Da Rocha et al., 2009; Giardina et al., 2018) in which case evapotranspiration could be primarily controlled by atmospheric evaporative demand. Although the cooccurrence of trees with contrasting water use strategies (for example, stomatal regulation) can result in uncertainties in the coupling strength of canopy scale conductance to soil moisture (Roman et al., 2015), this is less of an issue for evergreen tropical forests that are dominated by trees with strict (isohydric) stomatal regulation (Konings & Gentile, 2016). The implications of the omission of deep soil water reservoirs and functional diversity in ORCHIDEE for the simulated interactions between water and phosphorus availability are discussed in the model limitation section below.

3.2. Hypothesis 1: Water Availability Increases With Phosphorus Stress

Low phosphorus availability attenuates plant water use and consequently the effect of soil drought conditions during dry periods due to (1) water savings during preceding wet periods and (2) overall lower water demand (model result consistent with mechanism 1). During the dry season, soil moisture stress at all three sites is lower in simulations with suboptimal nutrient availability. This is illustrated by differences in the soil moisture stress factor used to downscale photosynthetic capacity and stomatal conductance in ORCHIDEE when soil water availability falls below a threshold of 0.8 for root zone relative soil moisture (Figure 3).

The lowering of dry season water stress is related to a shift of transpiration from wet toward dry season at all sites (Table 1), and an overall lower annual transpiration of 3–17% due to phosphorus constraints on GPP. The lower GPP is a result of reductions in LAI and photosynthetic capacity. The suboptimal phosphorus availability reduces LAI by 11–17% depending on the site (Figure 2). Due to the constraints on the leaf nitrogen to phosphorus concentration, suboptimal phosphorus availability indirectly reduces the maximum rate

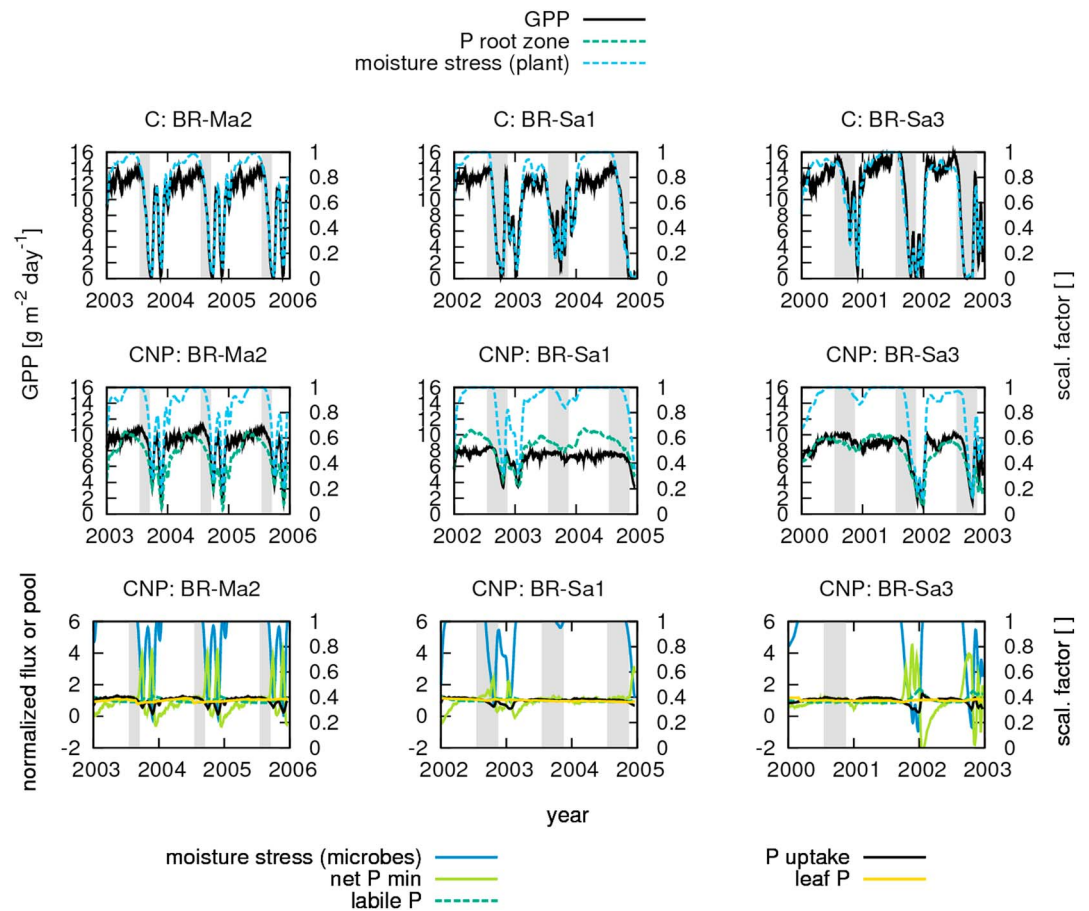


Figure 3. Simulated gross primary productivity (GPP; black), soil moisture stress factor (plant; light blue), and the ratio of phosphorus concentration at the root surface versus surrounding (P root zone; green) in simulation with optimal (top) and prognostic nutrient availability (middle). (Bottom) Leaf phosphorus concentration (yellow), plant phosphorus uptake (black), net mineralization (light green), and labile soil phosphorus concentration (green; broken), as well as absolute soil moisture stress factor (microbes; dark blue). Stress scalars: 1 = no stress; 0 = max stress. Shown are 14 days running averages (normalized). The climatological drought period is shaded in gray.

of carboxylation by 32–53% (not shown). We further find a small reduction in evaporative losses due to the lower LAI, which results in less water being intercepted and evaporated in the canopy.

3.3. Hypothesis 2: Amplification of Phosphorus Stress by Drought Conditions Due to Impaired Mineralization and Ion Mobility

We find that soil drought conditions impair plant phosphorus uptake due to lower ion mobility and do not decrease but increase phosphorus mineralization (partly consistent with mechanism 2). There is no seasonal variation in plant phosphorus stress, as indicated by the stable leaf phosphorus concentration, due to plant

internal storage of nutrients, which is able to buffer seasonal variation in phosphorus uptake (Figure 3). Plant phosphorus uptake tracks the drought-induced declines in labile phosphorus concentration at the root surface, irrespective of changes in net phosphorus mineralization (Figure 3), that is, phosphorus uptake being more limited by the transport from the soil to the root surface than by the supply from mineralization. The simulated increase in phosphorus mineralization is in contrast to the expectations and is caused by the asymmetric effect of drought on microbial decomposition and biochemical mineralization. While drought directly reduces microbial growth, and thus phosphorus immobilization (see below), rates of biochemical phosphorus mineralization (Equation 18 in Goll et al., 2017), mediated by extracellular enzymes (phosphatase)

Table 1
Effect of Suboptimal Nutrient Availability on Transpiration During Dry and Wet Seasons As Well As on Annual Transpiration

Site	Transpiration		
	Wet season (%)	Dry season (%)	All year (%)
BR-Ma2	−8	+26	−3
BR-Sa1	−30	+20	−17
BR-Sa3	−22	+26	−7

Note. Shown is the relative difference between simulations with prognostic and optimal nutrient availability.

Table 2

Coefficient of Covariance of Gross Primary Productivity From EC Measurements, Remote Sensing Proxies (NIR_t and NIR_v) As Well As Simulated Gross Primary Productivity in Simulations With Optimal (C Model) and Prognostic Nutrient Availability (CNP Model)

Site	EC	NIR_t	NIR_v	C model	CNP model
BR-MA2	0.195	0.211	0.242	0.402	0.143
BR-Sa1	0.104	0.189	0.236	0.408	0.267
BR-Sa3	0.165	0.176	0.225	0.482	0.224

Note. EC = eddy covariance; NIR = near-infrared reflectance.

produced by plants and microbes, remain unaffected. This leads to a positive effect of drought on net phosphorus mineralization. Microbial decomposition results on average in a net immobilization of nutrients to compensate for losses that occur when microbial biomass turns over. Immobilization is enhanced under conditions in which soil organic matter is accumulating, for example, as a result of increasing atmospheric carbon dioxide concentration and subsequent plant litter production, like it is here the case.

While the negative effect of soil drought on activity of microbial communities is well documented (Moyano et al., 2012), little information is available about the response of phosphorus mineralization to droughts. The few studies that investigate the links between water availability and phosphorus mineralization support our findings. A meta-analysis did not find any direct effect of annual precipitation on phosphatase activity across globally distributed sites but did not investigate seasonal changes at single sites (Margalef et al., 2017). Drought treatment did not affect phosphatase activity in Mediterranean soils (Sardans et al., 2006), and organic phosphorus mineralization was less affected by seasonal droughts than organic carbon and nitrogen mineralization in a tropical forest in Panama (Turner et al., 2015).

3.4. Susceptibility of Tropical Gas Exchange to Seasonal Changes in Precipitation

As a consequence of elevated water availability during the dry season and the lack of a seasonal amplification of phosphorus stress during droughts, we find that the interactions between water and phosphorus availability lead to reduced seasonal variability in GPP, and thus a lower susceptibility of tropical gas exchange to seasonal changes in precipitation. The statistical measure of variability (coefficient of variation) of monthly GPP is substantially lower at all sites in simulation with prognostic nutrient availability compared to simulations with optimal nutrients and is closer to the coefficient of variation derived from remote sensing and eddy covariance measurements of GPP (Table 2). An underestimation of the seasonal variability in GPP, as found in simulations with suboptimal but not with optimal nutrient availability, has to be expected as the model omits coordinated shifts in canopy leaf demography, which were shown to control seasonal variations in GPP in Amazon evergreen forests (Wu et al., 2016, 2017).

3.5. Model Limitations

The model does not account for embolism, reduction of phloem transport, and impaired use of carbon storage during droughts, which would result in a stronger negative feedback between low phosphorus availability and drought (Figure 1). Embolism and reduction of phloem transport are related to the transport of nutrients within a plant, while impaired use of C storage reduces carbon supply for growth. Observations of canopy rejuvenation (Wu et al., 2016), higher canopy photosynthesis, and overall enhanced plant growth (Rowland et al., 2014) during the dry season in Amazon evergreen forest do not indicate an impaired nutritional status of vegetation during the dry season. Nonetheless, these processes could be partly responsible for the observed increase in tree mortality in years following intense droughts (Doughty et al., 2015; Feldpausch et al., 2016). A better understanding of the role of plant internal storages in sustaining growth during periods of reduced photosynthesis (Hartmann & Trumbore, 2016) and/or soil nutrient availability is needed to evaluate existing models and guide new developments.

Several aspects that might affect acquisition of phosphorus by plants in general and during droughts are not represented in the model. On the one hand, the diversity of foraging strategies of plant roots (Giehl & von Wiren, 2014), for example, targeted root growth, is omitted, which increases the sensitivity of simulated phosphorus uptake to changes in ion mobility. On the other hand, the model omits changes in the soil redox potential in response to drought, which reduce phosphorus availability as more phosphorus is being bound to iron oxide and hydroxide minerals (Wood & Silver, 2012). While the omission of root foraging

should amplify drought-induced declines in plant phosphorus uptake, the omission of changes in the soil redox potential has the opposite effect.

Tropical ecosystems are characterized by variable trait strategies related to water (Apgaua et al., 2015) and nutrient use (Turner et al., 2018), as well as by variability in forest height and age (canopy heterogeneity) (Giardina et al., 2018). Although functional diversity is being discussed as a relevant measure for ecosystem level gas exchange, there is still limited empirical evidence demonstrating the role of functional trait diversity (Reichstein et al., 2014). Nonetheless, it was shown that the relative abundance of contrasting plant strategies regarding water (Roman et al., 2015; Skelton et al., 2015) and phosphorus (Turner et al., 2018) use can shape ecosystem scale responses to drought and phosphorus availability, respectively. Additionally, age and height of trees is affecting water and phosphorus use (Giardina et al., 2018; Sardans et al., 2015; Turner et al., 2018). As ORCHIDEE omits functional diversity and canopy heterogeneity, substantial uncertainty remains about the extent to which interactions between water and phosphorus availability affect the susceptibility of tropical gas exchange to seasonal changes in precipitation.

4. Conclusions

Interactions between water and phosphorus availability reduce seasonal variability in GPP driven by precipitation changes in a model, indicating their importance for accurately simulating ecosystem-scale responses to climate change. This indicates that models omitting water-phosphorus interactions are likely overstating (1) the risk of loss of forest cover due to changes in precipitation and increased evapotranspiration in response to warming and (2) the stimulation of plant growth due to enhanced water use efficiency under increasing carbon dioxide.

Although tropical evergreen forests are dominated by species with strict stomatal control (Konings & Gentine, 2016), mechanisms were identified, which partly uncouple canopy scale gas exchange from seasonal variation in precipitation. Recently, it was demonstrated that coordinated shifts in canopy leaf demography rather than climate variability, control seasonal variation in GPP, and litterfall along a rainfall gradient in Amazonia (Wu et al., 2016). Here we demonstrate an additional mechanism that reduces the sensitivity of tropical gas exchange to precipitation. Both findings point toward a less tight coupling of tropical ecosystem gas exchange to climatic variability than currently implemented in the majority of land surface models, which omit tropical phenology and phosphorus availability.

The sensitivity of land carbon uptake to water availability is expected to decrease as increasing atmospheric carbon dioxide concentration can shift ecosystems toward phosphorus limitation (Goll et al., 2012). This has far reaching implications for the role of tropical forest in the earth system. Further, we find a partly decoupling of phosphorus mineralization from microbial dynamics, which dampens the response to seasonal changes in soil moisture. This is an overlooked aspect in the role of phosphatases in ecosystems, and it deserves more attention. In particular, as it potentially can contribute to the observed effects of aridity on the coupling between nitrogen and phosphorus availability (Delgado-Baquerizo et al., 2013; He & Dijkstra, 2014).

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