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RESEARCH ARTICLE

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Species-specific effects of phosphorus addition on tropical tree seedling response to elevated CO_2

Jennifer B. Thompson[1,2] | Martijn Slot[1] | James W. Dalling[1,3] | Klaus Winter[1] | Benjamin L. Turner[1] | Paul-Camilo Zalamea[1,4]

[1]Smithsonian Tropical Research Institute, Panama City, Republic of Panama

[2]Department of Environmental Science, Policy, and Management, University of California Berkeley, Berkeley, CA, USA

[3]Department of Plant Biology, University of Illinois, Champaign-Urbana, IL, USA

[4]Department of Integrative Biology, University of South Florida, Tampa, FL, USA

Correspondence
Paul-Camilo Zalamea
Email: camilozalamea@gmail.com

Jennifer B. Thompson
Email: jenniferbriana.thompson@gmail.com

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Abstract

1. Tropical forest productivity is often thought to be limited by soil phosphorus (P) availability. Phosphorus availability might therefore constrain potential increases in growth as the atmospheric CO_2 concentration increases, yet there is little experimental evidence with which to evaluate this hypothesis. We hypothesized that while all species would respond more strongly to elevated CO_2 when supplied with extra P, the responses of individual species would also depend on their habitat associations with either high- or low-P soils. We further hypothesized that this effect would be exacerbated by a reduction in transpiration rate under elevated CO_2, as transpiration may aid in P acquisition.
2. We used a pot experiment to test the effects of P addition on the physiological and growth response to elevated CO_2 of eight tropical tree species with contrasting distributions across a soil P gradient in Panamanian lowland forests. Seedlings were grown in an ambient (400 ppm) or elevated (800 ppm) CO_2-controlled glasshouse in either a high- or low-P treatment to quantify the effects of P limitation on relative growth rate (RGR), transpiration, maximum photosynthetic rate and foliar nutrients.
3. We found evidence of limitation by P and CO_2 on growth, photosynthesis, foliar nutrients and transpiration. However, the affinity of a species for P, defined as the species distribution relative to P availability, was not correlated with RGR or transpiration responses to elevated CO_2 in either the low-P or high-P treatments.
4. Transpiration rates decreased under elevated CO_2, but foliar P was greater for some species under elevated CO_2, suggesting a greater capacity for upregulation of P acquisition in species associated with low-P soils.
5. Our results show that tropical forest responses to elevated CO_2 will be species-specific and not necessarily explained by P affinities based on distribution, which poses challenges for predictions of community-wide responses.

KEYWORDS

climate response, CO_2 fertilization, phosphorus limitation, species distributions, tropical forest

Jennifer B. Thompson and Paul-Camilo Zalamea contributed equally to this work.

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1 | INTRODUCTION

Tropical forests store over half of the world's forest carbon stocks (Pan et al., 2011) and have some of the highest rates of net primary productivity of any biome (Cramer et al., 1999). Thus, tropical forests have the potential to strongly impact atmospheric CO_2 concentrations through carbon sequestration. For example, without accounting for emissions due to land conversion, it is estimated that tropical forests sequester 1.4 ± 0.4 Pg C year^{-1} (Schimel, Stephens, & Fisher, 2015), which is equivalent to 15% of global annual anthropogenic C emissions. Nonetheless, the responses of tropical trees to elevated CO_2 are understudied compared to temperate ecosystems (Cernusak et al., 2013; Leakey, Bishop, & Ainsworth, 2012) and, consequently, predictions of sequestration potential for tropical forests under elevated CO_2 vary widely (Cox et al., 2004; Hickler et al., 2008; Yang, Thornton, Ricciuto, & Hoffman, 2016). This highlights uncertainties regarding the future of tropical forests, as well as their potential to mitigate current increases in atmospheric CO_2.

It is expected that by 2100, atmospheric CO_2 concentrations will have increased from the current *c*. 400 ppm to between 538 and 936 ppm, according to the IPCC's RCP4.5 and RCP8.5, respectively (IPCC, 2013). Many plant species have higher photosynthetic rates under elevated CO_2, because photosynthesis is less limited by carbon availability (Ainsworth & Rogers, 2007; Norby et al., 2005; Ziska, Hogan, Smith, & Drake, 1991). This may cause a CO_2 fertilization effect, whereby the stimulated photosynthetic rate leads to increased growth. However, when one physiological limitation is lifted, it is expected that other environmental factors will limit plant responses (Leakey et al., 2012), an idea held by Liebig's law of the minimum in which growth is controlled not by the total resources available but rather by the limiting resource. In temperate ecosystems where soil nitrogen (N) is often the most limiting nutrient (Vitousek & Howarth, 1991), low soil N availability limits plant growth from CO_2 fertilization over time as N becomes depleted by stimulated growth (Norby & Warren, 2010; Oren et al., 2001; Reich et al., 2006). In contrast, the productivity of lowland tropical forests is generally thought to be limited by soil phosphorus (P), rather than by N (Cleveland et al., 2011; Turner, Brenes-Arguedas, & Condit, 2018; Vitousek, 1984). Although N can limit growth in regenerating forests in eastern Amazonia (Davidson et al., 2004) and there is increasing evidence of nutrient colimitation in the tropics (Wright, 2019), the strongly weathered nature of the tropical landscape means that P is more likely to limit growth (Vitousek, 2004). Indeed, recent evidence suggests that such limitation occurs broadly at the species level (Turner et al., 2018).

Phosphorus limitation has strong physiological and ecological effects on vegetation. Quesada et al. (2012) found that wood production in the Amazon was positively correlated with total soil P, while in Panama the majority of tree species grow faster where soil P concentrations are greater (Turner et al., 2018). Phosphorus has also been shown to be important in explaining tree species distributions (Condit, Engelbrecht, Pino, Perez, & Turner, 2013; Prada et al., 2017; Turner et al., 2018; Zalamea et al., 2016). In the Panama Canal watershed, where small-scale heterogeneity in soil P availability is comparable to its variation across the entire Amazon basin, P availability was the most important edaphic predictor of the distribution of over 500 tree species even when comparing other soil nutrients including N and K (Condit et al., 2013). More than half of the species showed strong positive or negative associations with P availability (Condit et al., 2013). While increasing P appears to stimulate growth rates for most tree species in lowland forests in Panama (Turner et al., 2018; Zalamea et al., 2016), low-P levels do not necessarily imply a community-wide limitation on productivity; rather, some species thrive on low-P soils, while others dominate soils with higher P levels (Turner et al., 2018). In fact, Zalamea et al. (2016) showed that the growth of species naturally distributed in sites with high-P availability was stimulated by P addition in a pot experiment, while species from low-P availability sites have little or no change in growth when P was added. Furthermore, species distributional associations with soil P did not predict biomass allocation or foliar P when plants were grown at either low- or high-P (Zalamea et al., 2016). Although it is still unclear how some species maintain high growth rates on low-P sites, this most probably involves mechanisms that promote efficient use or uptake of P (Turner et al., 2018). Transpiration—the rate of water loss per unit leaf area—typically decreases with increasing atmospheric CO_2 concentration (e.g. Winter, Aranda, Garcia, Virgio, & Paton, 2001). Cernusak, Winter, and Turner (2011) found that in response to decreased transpiration at elevated CO_2 foliar P of some tropical tree species may decline. Thus, constraints by nutrient limitation on the CO_2 response may be further exacerbated by negative effects of elevated CO_2 on transpiration rates (Morison & Gifford, 1984; Carlson & Bazzaz, 1980; Winter, Garcia, Gottsberger, & Popp, 2001) given that transpiration may help modulate nutrient acquisition, including P, via mass flow (Cernusak, Winter, & Turner, 2011).

Incorporating P limitation into models of plant response to increases in CO_2 can strongly influence predictions of future forest productivity (Yang et al., 2016). Yang et al. (2016) found that including the natural gradient of soil P across the Amazon basin reduced prior estimates of future forest productivity responses to increased CO_2 by as much as 26%. Despite these model predictions of the importance of P limitation in the context of global climate change, few experimental studies have explored interacting effects of soil P and CO_2 on tropical trees. In a subtropical eucalyptus forest in Australia, Ellsworth et al. (2017) found that increasing the CO_2 concentration 150 ppm above ambient in a Free-Air CO_2 Enrichment (FACE) experiment did not increase tree biomass in P-limited soils. When the plots were fertilized with P at ambient CO_2, however, net primary productivity increased by 35%, suggesting that species response to CO_2 was P limited. In a study in central Panama, two lowland tree species, *Ficus insipida* and *Virola surinamensis*, accumulated 52% more biomass in open-top chambers in the presence of twice-ambient CO_2 when given a NPK+ micronutrient fertilizer than those grown without fertilizer, indicating nutrient limitation of the response to CO_2 fertilization (Winter, Garcia, et al., 2001).

Here we conducted a greenhouse experiment using ambient and twice-ambient CO_2, and low- and high-P soil treatments, to determine whether soil P availability limits growth and physiological responses to elevated CO_2. Because plant responses to P might vary depending on adaptations to the availability of P in their native habitat (Zalamea et al., 2016), we selected species that are naturally associated with habitats that represent a range of soil P availability (Condit et al., 2013). We hypothesized that while all species would respond more strongly to elevated CO_2 when supplied with extra P, the responses of individual species would also depend on their habitat associations with either high- or low-P soils (Figure 1). We predicted four possible scenarios for plant responses to CO_2 in relation to soil P availability, in which species' growth and physiological responses reflect differential allocation to soil P acquisition. First, a CO_2 response would be precluded if species with distributional affinities for low-P soils have conservative resource investment in P uptake under limited P availability. In contrast, species with affinities for high-P soils and higher P needs might be unable to respond to elevated CO_2 on low-P soils due to P limitation, leading to little change in the magnitude of the CO_2 response with P affinity (Figure 1, scenario 1). Second, the inherent ability of species associated with low-P soils to be productive at low-P availability could permit a strong positive CO_2 response, leading to a decline in the response to CO_2 as P affinity increases (Figure 1, scenario 2). Third, a more conservative growth strategy in species associated with low-P may constrain the response to elevated CO_2 relative to species associated with high-P soils, leading to an increasing response to CO_2 as P affinity increases (Figure 1, scenario 3). Finally, in the absence of P limitation, the CO_2 response may be independent of traits associated with P uptake and use, leading to little variation in the increasing response to CO_2 with P affinity (Figure 1, scenario 4). Furthermore, we predicted that elevated CO_2 would reduce transpiration rates per unit of plant biomass, resulting in a reduction in foliar P concentration. For species associated with P rich soils, this predicted reduction in foliar P would further constrain their CO_2 response under low-P conditions.

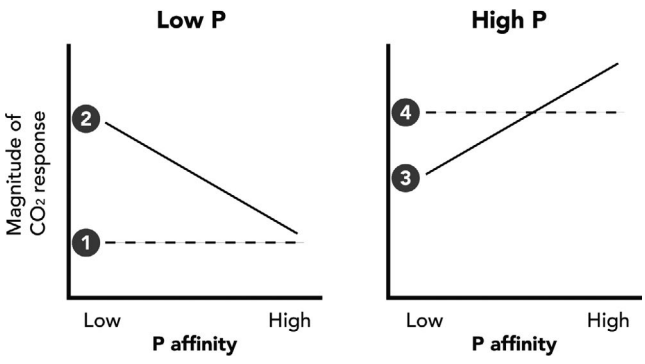

FIGURE 1 Potential responses to elevated CO_2 among species with contrasting distributional affinities for soil P in different soil P environments. The magnitude of CO_2 response indicates the degree of change between the ambient and elevated CO_2 treatments (see text for details)

2 | MATERIALS AND METHODS

2.1 | Study species and growth conditions

Seeds of eight pioneer tree species were collected from the Barro Colorado Nature Monument (BCNM) in central Panama (Table 1). We selected pioneer species because they are ubiquitous in the neotropics, and due to their small seed reserves, they rapidly become dependent on the acquisition of external nutrients. As such, they are ideal for studying seedling nutrient dynamics. Furthermore, pioneers that occur in the BCNM and across the Panama Canal watershed forests have widely ranging soil P associations that predict their growth response to P addition under ambient CO_2 conditions (Zalamea et al., 2016). Using presence/absence data for 550 tree species across the Panama Canal watershed, Condit et al. (2013) implemented Gaussian logistic regression models to determine species' distributional associations with plant-available P. They showed that resin-extractable phosphorus, a measure of plant-available P, was a strong predictor of species distributions, and more than half of the tree species studied had pronounced associations with either high- or low-P soils. Phosphorus associations for each species have been measured as P effect sizes, defined as the first-order parameter of the logistic model for the species distribution relative to P, which reflect the change in the probability of occurrence of a species across the gradient in P availability in Panama Canal watershed forests when other resources are held constant (Condit et al., 2013). Plant-available P varies from <0.1 to >20 mg P/kg across these forests (Condit et al., 2013). Effect size values <−0.6 and >0.6 indicate species naturally found on soils with low and high availability of P, respectively, values between −0.6 and 0.6 are referred to as "weak" associations. Effect sizes for species included in this study ranged from −1.08 to 1.18 (Table 1).

Seeds were germinated in a commercial potting soil in an open-air shade house. After *c*. 3 weeks, seedlings were transplanted into 30 cm tall, 2.65 L black tree pots (Stuewe and Sons Inc.) filled with a 50:50 soil:sand mix. Soil was collected from the Santa Rita Ridge, Panama, a site with one of the lowest soil P values in the canal watershed. Mean (± *SE*) extractable resin P for the site was 0.16 ± 0.03 mg/kg, and total soil P was 128 ± 10 mg/kg (B. Turner, unpublished data). Seedlings were grown in glasshouses in the Santa Cruz plant research facility in Gamboa, Panama. Split air-conditioning units regulated glasshouse temperatures to match outdoor temperatures (*c*. 32°C daytime, *c*. 24°C nighttime), and CO_2 concentrations were maintained at either 400 or 800 ppm. CO_2 concentration was maintained at 800 ppm by using a GMW21D carbon dioxide transmitter (Vaisala) and a CR-5000 measurement and control system (Campbell Scientific). Injection of pure CO_2 was initiated when the CO_2 concentration fell below 790 ppm and was terminated when CO_2 concentration reached 800 ppm. The CO_2 concentration was prevented from overshooting by providing CO_2 in multiple pulses of 2 s interrupted by 5 s without CO_2 injection. Seedlings were watered daily and received 150 ml of a liquid fertilization treatment weekly (as in Zalamea et

TABLE 1 Species used in the greenhouse experiment and their respective family, growth period and P effect sizes

Species	Family	Growth period (days)	P effect size
Trichospermum galeottii (Turcz.) Kosterm.	Malvaceae	62	−1.08
Cecropia insignis Liebm.	Urticaceae	55	−0.86
Ochroma pyramidale (Cav. ex Lam.) Urb.	Malvaceae	44	−0.15
Trema micrantha (L.) Blume	Cannabaceae	27	0.37
Ficus insipida Willd.	Moraceae	62	0.48
Guazuma ulmifolia Lam.	Malvaceae	41	0.69
Cecropia peltata L.	Urticaceae	53	0.99
Cecropia longipes Pittier	Urticaceae	51	1.18

Note: More negative P effect sizes indicate distributional associations with soils with lower P availability (Condit et al., 2013).

al., 2016). All seedlings received a full nutrient treatment including 4 mM KNO_3, 1.5 mM $MgSO_4$ and 4 mM $CaCl_2$, micronutrients and Fe as ethylenediaminetetraacetic acid iron (III) sodium salt. In addition, plants grown in the +P treatment received 1.33 mM NaH_2PO_4 per week, while those in the −P treatment did not. There were six replicate seedlings per species for each combination of CO_2 and P treatments. The seedlings were moved to a different location in the chamber at least twice during the experiment to reduce potential effects of bench location.

2.2 | Relative growth rate measurements

Before fertilizing the seedlings for the first time, five individuals per species were harvested and dried in an oven at 70°C for 3 days. These initial weights were used to calculate mean relative growth rate (RGR) over the experiment .

$$\mathrm{RGR} = \frac{\ln(\text{final mass}) - \ln(\text{initial mass})}{\text{Days of growth}}$$

Seedlings grew for 27–62 days depending on the species growth rate (Table 1). We aimed for plant biomass to pot volume ratios to stay, on average, <1 g/L in the +P treatment, following recommendations of Poorter, Bühler, Dusschoten, Climent, and Postma (2012). Leaf area was measured with an automated leaf area meter (LI-3000A; LI-COR). Seedlings were dried in an oven at 70°C for at least 3 days before being weighed.

2.3 | Whole-plant transpiration rates

We measured whole-plant transpiration rates gravimetrically 2–3 days before harvest. Plants were watered until soil saturation and pots sealed with plastic bags around the seedling stem base to prevent soil water evaporation. Pots were weighed directly after watering and 48 hr later to determine total daily water loss per unit leaf area (g cm^{-2} 24 hr^{-1}).

2.4 | Foliar nutrient analysis

Leaves were dried, ground and analysed for total foliar N and P. Total foliar P was determined by first ashing leaf tissue in a muffle furnace (550°C for 1 hr), and then dissolving in 1 M HCl, with P detection by molybdovanadate colorimetry on a Lachat Quikchem 8500 (Hach Ltd). Total foliar N was measured by dry combustion on a Thermo Flash EA1112 analyzer (CE Elantech).

2.5 | Photosynthetic capacity

Net photosynthesis was measured at a pre-determined saturating irradiance level of 1,200 μmol m^{-2} s^{-1} at the CO_2 concentrations of the glasshouse, that is, both at 400 and 800 ppm. Measurements were made with a LI-6400XT portable photosynthesis system (LI-COR) on one fully expanded, recently matured leaf per plant at 30.3 ± 0.3°C (mean ± *SD* of leaf temperature during measurement). Leaf-to-air vapour pressure was maintained below 2.5 kPa during all measurements. Not all treatment combinations produced leaves large enough to be enclosed in the 2 × 3 cm leaf cuvette. In total, data were obtained for 140 plants belonging to 8 species, 66 in the −P treatment and 74 in the +P treatment.

2.6 | Statistical analysis

We used linear regression analyses to estimate the relationship between the P effect size and the per cent increase in RGR, maximum photosynthetic rate, foliar nutrients and transpiration in response to P fertilization and CO_2 treatments. Regressions were performed on the per cent increase in the response variable to fertilization at 800 relative to 400 ppm. The per cent increase was calculated using the average values from each P treatment as:

$$\%\,\text{increase} = \frac{800 - 400}{400} \times 100.$$

The per cent increase in response to elevated CO_2 in the +P relative to the −P treatment was also calculated, results of which are reported in the Supporting Information (Appendix S1).

We additionally used linear mixed effect models to test whether P fertilization, CO_2 level and the CO_2 by P interaction affected the different variables: RGR, foliar nutrients, transpiration rate and maximum photosynthetic rate. Phosphorus and CO_2 treatments were set as fixed

effects and species as random. All non-normally distributed data were log transformed before analysis. Data were analysed with the package *nlme* and the *lme function* in R (version 3.5.10).

3 | RESULTS

3.1 | Overall treatment effects

The CO_2 and P treatments had similarly strong positive overall effects on seedling growth (RGR) across species (Figure 2, Table 2). However, there was no evidence that the P treatment impacted plant response to CO_2 (i.e. no significant CO_2 by P treatment interaction; Figure 2, Table 2). Similar results were found for whole-plant transpiration and foliar N concentration, with reduced rates and concentrations under elevated CO_2 and P treatments (Figure 2, Table 2). Despite reductions in foliar N, the maximum photosynthetic rate (A_{max}) was nearly doubled under elevated CO_2, but A_{max} did not respond to the P treatment nor show a CO_2 by P interaction (Figure 2, Table 2). Foliar P concentrations responded positively to the P and CO_2 treatments and showed a strong treatment interaction; a similar pattern was observed for foliar N:P, which ranged from >30 in the ambient CO_2 and low-P treatment to <15 in the high CO_2 and high-P treatments (Figure 2, Table 2). Foliar C:N increased with P addition and elevated CO_2 (Table 2).

3.2 | Species-level responses

Responses to P and CO_2 treatments varied at the species level and were often independent of the distributional association with soil P (Figure 3). We found strong support for scenarios 1 and 4 (Figure 1), indicating that species differences in allocation to P uptake and P limitation under elevated CO_2 resulted often in an absence of interactive effects between fertility and the response to CO_2. Despite large differences in growth responses among species, we did not find that the soil P association of species predicted its RGR response to elevated CO_2 either in the low-P treatment (R^2 = 0.26, p = 0.11, n = 8; Figure 3a) or in the high-P treatment (R^2 = −0.11, p = 0.59, n = 8; Figure 3a). Despite the absence of a predictable growth response, individual traits did reflect species distributions. There was a significant negative correlation between species P affinity and the per cent increase in maximum photosynthetic rate from ambient to elevated CO_2 for the +P treatment (R^2 = 0.55, p = 0.03, n = 7; Figure 3b), but not for the −P treatment (R^2 = 0.23, p = 0.19, n = 6; Figure 3b). Therefore, the photosynthetic rate of species associated with low-P soils was more strongly stimulated by elevated CO_2 in the presence of extra P compared to species associated with high-P soils. While photosynthetic rates measured at their treatment CO_2 level were always greater for the elevated CO_2 plants, when photosynthesis was compared at 400 ppm CO_2, the rates tended to be lower for plants grown

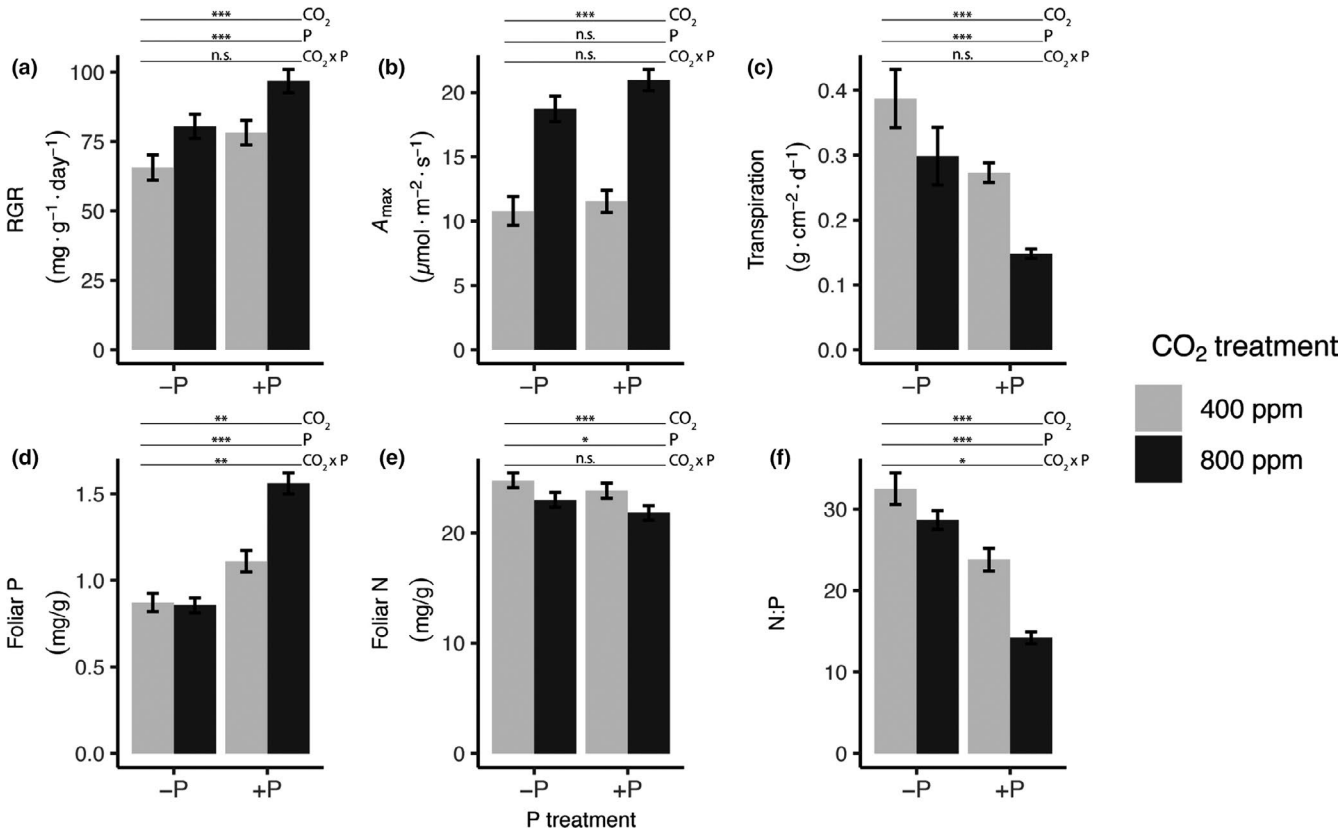

FIGURE 2 Average trait values for species across CO_2 and P treatments: (a) relative growth rate (RGR), (b) maximum photosynthetic rate, (c) transpiration, (d) total foliar P, (e) total foliar N and (f) foliar N:P ratio. Error bars represent ± 1 *SE*. For each trait, statistical significance of each treatment (i.e. CO_2, P and CO_2 by P interaction) is noted with asterisks (see Table 2 for details)

TABLE 2 Results of linear mixed-effects models for each trait

Trait	Factor		
	CO_2 treatment	P treatment	CO_2 • P treatment
Relative growth rate			
F	**47.95**	**40.15**	0.09
p	**<0.0001**	**<0.0001**	0.76
Photosynthesis			
F	**112.89**	2.82	0.93
p	**<0.0001**	0.09	0.34
Transpiration			
F	**51.12**	**21.59**	2.19
p	**<0.0001**	**<0.0001**	0.14
Foliar P			
F	**14.10**	**80.66**	**14.10**
p	**<0.001**	**<0.0001**	**<0.001**
Foliar N			
F	**22.83**	**8.12**	0.15
p	**<0.0001**	**<0.01**	0.69
N:P			
F	**31.80**	**92.51**	**4.57**
p	**<0.0001**	**<0.0001**	**0.03**
C:N			
F	**18.00**	**5.333**	0.0091
p	**<0.0001**	**0.022**	0.9240

Statistical significance of each treatment (i.e. CO_2, P, and CO_2 by P interaction) is noted in bold.

at elevated CO_2. This effect was particularly strong in the −P treatment (data not shown), indicating that photosynthetic capacity was downregulated at high CO_2 supply, especially under limiting nutrient conditions. There was no relationship between species P association and increase in transpiration rate in the −P (R^2 = −0.04, p = 0.44, n = 8; Figure 3c), nor +P (R^2 = −0.16, p = 0.87, n = 8; Figure 3c) treatments.

Foliar P followed a similar trend to photosynthesis. In the +P treatment, there was a marginally significant negative relationship between P affinity and the proportional increase in foliar P concentration between the 400 and 800 ppm chamber (R^2 = 0.40, p = 0.05, n = 8; Figure 3d). Species associated with low-P soils therefore increased foliar P more when fertilized under elevated CO_2 than species associated with high-P soils. There was no relationship in the −P treatment (R^2 = −0.04, p = 0.43, n = 8; Figure 3d). A similar pattern was observed for foliar N, with a negative relationship with P affinity in the +P treatment (R^2 = 0.56, p = 0.02, n = 8; Figure 3e), and no relationship in the −P treatment (R^2 = −0.12, p = 0.65, n = 8; Figure 3e). Finally, there was a marginally significant, negative relationship between the proportional increase in the foliar N:P ratio and P affinity in the −P treatment (R^2 = 0.29, p = 0.09, n = 8; Figure 3f), but no significant difference in the +P treatment (R^2 = 0.04, p = 0.30, n = 8; Figure 3f).

4 | DISCUSSION

Seedling growth increased in response to P addition and elevated CO_2, suggesting that growth on P-poor soils can be co-limited by P and CO_2. Likewise, photosynthesis rates were higher at elevated CO_2 and tended to be stimulated by P addition. These results are consistent with previous studies of responses of growth and photosynthesis to P addition and CO_2 fertilization in tropical trees (e.g. Cernusak, Winter, Martinez, et al., 2011). However, we did not find a significant interaction between the P and CO_2 treatments. This result indicates that P addition does not stimulate the response of plant growth and photosynthesis to CO_2 fertilization in this group of tropical pioneer species. This result adds empirical evidence to the results of the CLM4-CNP model of Yang et al. (2016) that found that a CO_2 fertilization effect in the Amazon region would be greatly overestimated if soil P availability was not considered. The model considered C, N and P cycling as well as other site-specific characteristics, but employed plant functional types (PFTs) rather than species-specific data.

The CLM4-CNP model uses two tropical PFTs, broadleaf evergreen and broadleaf deciduous, which are separated by photosynthetic parameters, stem and leaf optical properties and root distribution patterns, among others. Thus, the model assumes that all tree species fall into one of these two categories and behave similarly in terms of photosynthesis, resources use and growth. These broad categories can overly simplify forests response to elevated CO_2, or not portray a completely accurate one, as we found that even within one PFT (here, early successional, mostly broadleaf evergreen species) vary greatly in their responses to environmental changes. Below we describe the potential for P limitation to drive species-specific responses to rising atmospheric CO_2.

4.1 | How does soil P availability modulate seedling response to elevated CO_2?

Overall, elevated CO_2 decreased transpiration rates, consistent with many studies (e.g. Morison & Gifford, 1984; Carlson & Bazzaz, 1980; Winter, Aranda, et al., 2001). We also saw an effect of P treatment on transpiration, with reduced rates in the +P treatment. Cernusak, Winter, and Turner (2011) found a positive correlation between the transpiration ratio (mass of water transpired per plant carbon mass produced) and P content in tropical tree seedlings in Panama, suggesting that higher transpiration rates increase P acquisition via mass flow. Cernusak, Winter, and Turner (2011) also found that when transpiration was reduced by elevated CO_2, the leaf C:P ratio increased in *Swietenia macrophylla*, but stayed constant on *Ormosia macrocalyx*. This suggests that foliar P concentrations of some tropical tree species may decline in response to decreasing transpiration rates, whereas other species may be unaffected. Our results provide only partial support for this; in the −P treatment, foliar P did not differ between CO_2 treatments, while in the +P treatment, foliar P was further increased at elevated CO_2. These contrasting results highlight the complexity of P uptake mechanisms, with a potential

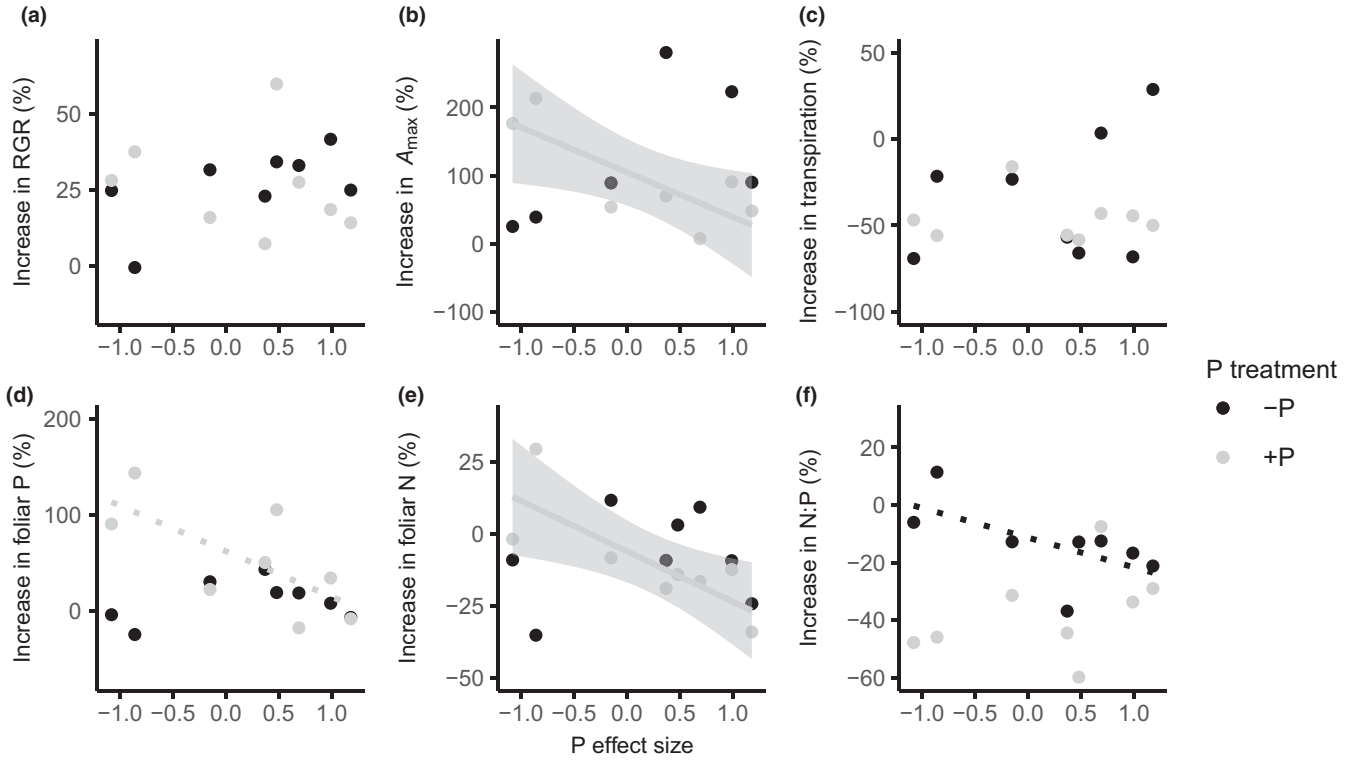

FIGURE 3 Relationships between P effect size and the per cent increase between the 400 and 800 ppm treatments for plant responses: (a) relative growth rate (RGR), (b) maximum photosynthetic rate, (c) transpiration, (d) total foliar P, (e) total foliar N and (f) foliar N:P ratio. Significant relationships are noted with a solid line and marginally significant relationships ($p < 0.1$) with a dotted line. Shaded grey bands represent 95% CI

role for mass flow in some species, but not others. Furthermore, the species-specific nature of CO_2 effects on P uptake could have major consequences for competitive interactions among species under different P environments and climate change scenarios.

Nutrient addition experiments in the field (Ostertag, 2010; Santiago et al., 2011; Wright et al., 2011) and in pot experiments (Zalamea et al., 2016) have shown that foliar P increases with P addition and, as expected, foliar P concentration increased with P addition in the current study. Foliar P also increased under elevated CO_2. Moreover, P and CO_2 treatments showed a strong interaction effect; only when P was supplied did foliar P increase under elevated CO_2. Tang, Chen, and Chen (2006) found an increase in foliar P of tropical weedy forb species with elevated CO_2, which they attributed to an increase in mycorrhizal colonization and P uptake as plants had increased nutrient demand from the stimulated growth. Carbohydrate supply to symbionts becomes less costly for plants when grown at high CO_2, leading to higher foliar P under elevated CO_2 but not under ambient CO_2. Our plants were grown on unsterilized soil collected from the field, so it is likely that our plants were colonized by mycorrhizal fungi. Nasto, Winter, Turner, and Cleveland (2019) also found increased AMF colonization and phosphatase activity under elevated CO_2, which was attributed to the trees having a greater metabolic capacity to acquire P. In our pot experiment, we did not find a root mass fraction response to elevated CO_2 (data not shown), although Liu et al. (2013) found that in a subtropical forest in China, increased root growth under elevated CO_2 increased P acquisition and foliar P. Species may overcome low soil P availability by specializing in the acquisition of different forms of P, including organic P forms (Nasto et al., 2017; Steidinger, Turner, Corrales, & Dalling, 2015), which could underlie differences in physiological responses to elevated CO_2.

Foliar N and N:P ratios were reduced under elevated CO_2 and P addition. Phosphorus addition significantly increased growth rates, and without additional N supply, the increase in growth rate may have led to N dilution in the tissue and an increase in the C:N ratio. A reduction in foliar N is commonly observed under elevated CO_2 and may be associated with a reduction of N-rich photosynthetic enzymes or increased starch content of leaves (Medlyn et al., 2002). When photosynthetic rates were measured on plants at their respective CO_2 treatment concentrations, rates were higher under elevated CO_2. However, when compared at the same CO_2 concentration, plants grown at elevated CO_2 had lower photosynthesis rates, suggesting a down-regulation of photosynthetic capacity.

Photosynthetic rates were only marginally affected by P addition in our experiment; however, we found a positive correlation between foliar P and photosynthetic rates (See Appendix S2), indicating that in addition to CO_2 limitation, photosynthesis can also be P limited, as shown previously for plants in P-limited soils (Lovelock et al., 1997; Raaimakers, Boot, Dijkstra, Pot, & Pons, 1995). This is consistent with the view that photosynthesis in tropical trees

is often co-limited by N and P (Norby et al., 2016). Lovelock et al. (1997) found that under elevated CO_2 and inoculation with AMF, the tropical tree *Beilschmiedia pendula* photosynthesized more than in ambient CO_2 and non-mycorrhizal conditions, likely due to P limitation of photosynthesis.

4.2 | Can species distributional P affinities predict species responses to elevated CO_2?

In a previous pot experiment, P affinities of species—based on their distribution within the Panama Canal area—were a strong predictor of species growth response to P addition (Zalamea et al., 2016). Thus, species with an affinity for high-P soils, indicated by a positive associational P effect size, showed a larger increase in RGR in response to P addition than those with an affinity for low-P soils. In contrast, here we found that P effect sizes could not easily predict the magnitude of species growth responses to elevated CO_2. The magnitude of growth responses to P addition increased with P effect size, both in ambient CO_2 (as in Zalamea et al., 2016) and at elevated CO_2 (see Appendix S1), but for some species the growth response was greater under elevated CO_2, while for others it was greater under ambient CO_2. Overall, the growth response to P addition at ambient CO_2 was only marginally significantly correlated with that at elevated CO_2 (Spearman's rank correlation: $\rho = 0.71$, $p = 0.057$, $n = 8$). All species responded to elevated CO_2, but the degree of growth stimulation in the two P treatments was independent of P affinity (Figure 3a). Our results strongly support scenarios 1 and 4 (Figure 1) for most of the measured traits. Thus, while there are physiological limitations to CO_2 response in the absence of P, these are generally not dependent on distributional associations to P (Figure 1—Scenario 1), or the CO_2 response is independent of P affinity when P is not limiting (Figure 1—Scenario 4).

While most trait responses to elevated CO_2 were independent of distributional P affinities, we found a significant negative correlation between P affinity and the increase in maximum photosynthetic rate from ambient to elevated CO_2 in the +P treatment. This result is driven strongly by the higher per cent increase in maximum photosynthetic rate at elevated CO_2 of the two species with the lowest P effect sizes in our experiment—*Trichospermum galeottii* and *Cecropia insignis*. These two species also had much higher foliar P at elevated than at ambient CO_2 in the +P treatment (*c*. 110% increase, compared to an average *c*. 37% for the remaining species). Curiously, at ambient CO_2 both the foliar P and photosynthetic rates of these species were much lower under +P than under −P. This suggests that photosynthesis was stimulated by foliar P regardless of the species' distributional P affinity (see Appendix S2). These photosynthesis results indicate that the effect of elevated CO_2 on carbon fixation of tropical trees will be highly species specific, and that responses may depend on P availability.

Tree species normally found in low-P environments tend to have higher P-use efficiency (PUE) than soil generalists (Gleason, Read, Ares, & Metcalfe, 2009). We found that in the ambient CO_2 and P addition treatments, species naturally distributed in high-P sites had higher concentrations of P in their leaves when compared to species naturally distributed in low-P sites (see Appendix S3), but this relationship disappeared at elevated CO_2. Furthermore, in the P addition treatment there was a marginally significant negative relationship between P affinity and the increase in foliar P concentration between ambient and elevated CO_2. In a fertilization experiment in lowland tropical China, P addition increased all four functional types of foliar P: structural P, metabolic P, nucleic acid P and residual P of tropical trees (Mo et al., 2019). The magnitude of change was species-specific, but species could reallocate P pools to meet photosynthetic demands (Mo et al., 2019), suggesting that some species may be able to overcome P limitation of certain responses in P-poor soils. These results highlight the need for further studies to understand the differences in species PUE or P uptake mechanisms that allow species to thrive in low-P environments and specifically how they may affect species responses to elevated CO_2.

Phosphorus affinities of late-successional species are as variable as those of early-successional species (Condit et al., 2013). Thus, we hypothesize that strategies to acquire and use soil available P should vary similarly among species in these two functional groups. At the early seedling stage, late-successional species are unlikely to respond strongly to P addition, regardless of CO_2 concentration, because the larger seeds of late-successional species support seedling growth much longer than the small seeds of early-successional species (Slot, Palow, & Kitajima, 2013). Foliar P concentration significantly increased with P addition (Santiago et al., 2011), but it seems unlikely that this elevated leaf P would support a strong CO_2 fertilization effect on late-successional species given the conservative growth habits of this functional group. Previous work in Panama has shown that while early-successional species respond strongly to CO_2 enrichment, late-successional species do not, even when supplied with ample mineral nutrients (Winter & Lovelock, 1999). As our study focused on small-seeded, early-successional species, firm conclusions about the community-level responses to climate change will require future studies that include late-successional species. However, we expect that species-specific effects of P addition on the physiological and growth response to elevated CO_2 found in this study for early-successional species are likely to be found on other functional groups.

Our study provides insight at the complex interactions between soil P availability and elevated CO_2 in tropical tree species. This is the first study determining responses to nutrient limitation and elevated CO_2 in relation to known P associations in the field. While we found both P and CO_2 limitation overall in the context of our pot experiment, individual species responses to elevated CO_2 and soil P were largely unrelated to their respective associations with P availability in the field. This could have implications for future forest composition, and therefore carbon storage and residency time, as species responses to CO_2 depend not only on the availability of P, but also species-specific relationships to P. At least for the eight species studied here, these relationships cannot be readily predicted from the P association of the species in the

field. These results emphasize the importance of conducting complementary in situ experiments in the tropics (Würth, Winter, & Körner, 1998), such as the planned AmazonFACE program, as well as studying species-specific responses in order to ascertain how highly productive tropical forests can sequester CO_2 under soil nutrient limitation.

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AUTHORS' CONTRIBUTIONS

J.W.D., P.-C.Z., K.W. and B.L.T. conceived and designed the study. J.B.T., P.-C.Z., M.S., J.W.D., K.W. and B.L.T. collected the data and performed the experiment. J.B.T., P.-C.Z. and M.S. analysed the data. J.B.T., P.-C.Z., J.W.D. and M.S. wrote the manuscript and all the authors commented on it.

DATA AVAILABILITY STATEMENT

Raw data are available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.777461k (Thompson et al., 2019).

ORCID

Martijn Slot https://orcid.org/0000-0002-5558-1792
Benjamin L. Turner https://orcid.org/0000-0002-6585-0722
Paul-Camilo Zalamea https://orcid.org/0000-0002-0987-4164

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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