

Convergence in phosphorus constraints to photosynthesis in forests around the world

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Tropical forests take up more carbon (C) from the atmosphere per annum by photosynthesis than any other type of vegetation. Phosphorus (P) limitations to C uptake are paramount for tropical and subtropical forests around the globe. Yet the generality of photosynthesis-P relationships underlying these limitations are in question, and hence are not represented well in terrestrial biosphere models. Here we demonstrate the dependence of photosynthesis and underlying processes on both leaf N and P concentrations. The regulation of photosynthetic capacity by P was similar across four continents. Implementing P constraints in the ORCHIDEE-CNP model, gross photosynthesis was reduced by 36% across the tropics and subtropics relative to traditional N constraints and unlimiting leaf P. Our results provide a quantitative relationship for the P dependence for photosynthesis for the front-end of global terrestrial C models that is consistent with canopy leaf measurements.

Tropical forests contain the majority of the world's higher plant species and absorb a gross of over 35 Pg carbon (C) per annum from the atmosphere, more than any other biome¹. Forests are key modulators of global climate by virtue of their large C exchange with the atmosphere^{2,3}. Amongst global forests, tropical forests comprise the most productive biome per unit land area on Earth in spite of occurring on highly weathered, nutrient-poor soils¹⁻⁴. Notwithstanding the key role played by the tropics in the global carbon cycle⁵ and hence for offsetting fossil fuel C emissions, there have been persistent uncertainties in predictions of primary productivity for these forests^{1,6,7}. The uncertainties in gross primary productivity arise from a paucity of relevant data on, and understanding of, tropical forest gross photosynthesis and C cycles and their regulation by nutrients, and particularly phosphorus (P)⁸⁻¹⁰. Leaf photosynthetic capacity is the primary

driver of C-uptake, and so it is crucial to accurately represent it in terrestrial biosphere models to enable C-cycle predictions for the present-day, and with global change^{11,12}.

Leaf nitrogen (N) has long been assumed the single, critical nutrient driving variation in photosynthetic capacity¹³ and is widely incorporated as a modulator of gross and net photosynthesis in terrestrial biosphere models^{14,15}. Most leaf N is invested in ribulose-1,5-biphosphate carboxylase/oxygenase (Rubisco; EC 4.1.1.39), the primary carboxylating enzyme in the Calvin-Benson cycle and central to present-day net photosynthesis. At about one-quarter of terrestrial canopy N, Rubisco is the single most abundant enzyme on Earth¹⁶. A further quarter of leaf N is allocated to the thylakoid membrane-bound proteins crucial for net photosynthesis¹⁷, resulting in a strong N-dependence of photosynthesis amongst plants around the world.

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The strong functional relationship between carboxylation capacity (V_{cmax} , in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$) and leaf N^{11,13} (Supplementary Fig. 1) is harnessed as a key driver in most large-scale gross photosynthesis models¹⁸. However, emerging evidence over the past decade has suggested that the strong relationship of net photosynthesis with leaf N is diminished when leaf phosphorus (P) concentrations are low^{11,19}. This important effect is not yet considered in most terrestrial biosphere models (TBMs) including those central to the terrestrial C cycle^{20,21}.

Alongside N, P has been identified as a second critical element to plant function worldwide^{22,23} but its role in photosynthetic capacity is debated. Unravelling the constraint to net photosynthesis by leaf P has been difficult^{24,25}. This difficulty is linked to the broad range of specific biological roles played by P in plants, in various compounds such as adenosine triphosphate (ATP), nucleotides and nucleic acids, sugar phosphates, and phospholipids to regulate and support photosynthesis. Theory²⁶ and biochemical analyses^{24,27} have suggested that P deficiency reduces the electron transport capacity of leaves (J , in $\mu\text{mol electrons m}^{-2} \text{ leaf s}^{-1}$; Supplementary Fig. 1) and reduces the supply of P to regenerate the key substrate for carboxylation and the Calvin-Benson cycle, ribulose-diphosphate (RuBP). As a result of the roles of N and P associated with different biochemical components controlling photosynthesis (Supplementary Fig. 1), a potential imbalance between the capacity for carboxylation versus electron transport supporting RuBP regeneration could arise in species with low P status or with high leaf N:P ratios, for example on low P soils. Alternatively, if plants maintain a similar functional balance between components of the photosynthetic apparatus, irrespective of soil nutrient concentrations, this would lead to the same ratio of maximum electron transport and RuBP regeneration (J_{max}) to carboxylation (V_{cmax}) across a range of N and P concentrations in leaves²⁸. This functional balance would explain why the Rubisco enzyme carboxylation capacity for photosynthesis is also sometimes associated with P^{11,29} even though there is no explicit role of P in carboxylation²⁶. With a paucity of data involving chronically low P sites, few studies have fully examined this functional balance hypothesis for photosynthetic components^{28,29} across different soils.

Nearly every major large-scale TBM of the C cycle incorporates some form of the Farquhar-von Caemmerer-Berry (FvCB) photosynthesis model³⁰, which implicitly assumes that N is the primary nutrient limiting photosynthesis¹²—an assumption we here term the “single nutrient-single enzyme” hypothesis (Supplementary Fig. 1). In contrast, few TBMs and only a single model (CABLE-CASA CNP) from the sixth phase of the Coupled Model Intercomparison Project (CMIP6)²¹ incorporate a direct role of P in modelled gross photosynthesis^{8,9}. Uncertainty about how to represent a general photosynthetic role for P in TBMs stems from considerable variation in reported relationships between photosynthetic biochemistry (e.g. carboxylation capacity, V_{cmax}) and leaf P (Supplementary Fig. 2), which may reflect the geographically restricted nature of previous studies, the particular geology of different continental regions³¹, and the relatively narrow range of leaf P considered³².

At the leaf scale there is growing evidence of P-limitation reducing photosynthetic capacity^{32–34}. However, broad evidence for a robust P constraint on photosynthesis and its biochemistry with chronic low P availability has been lacking for several reasons. First, regional studies have differed greatly in soil P status and soil orders owing to differences in surface geology and the extent of exposed ancient landscapes differing greatly among continents^{35,36}. Thus, they have different degrees of P influence over photosynthesis. Second, the amount of P allocated to key metabolically active compounds that regulate photosynthesis can be highly variable³⁷. Coupled with plant species variation in internal allocation of leaf P³⁷, these uncertainties have impeded inclusion of a robust and general photosynthesis-P relationship into large-scale models^{8,9}. They also suggest there could be large variation amongst different studies and continents in the relationship of photosynthetic biochemistry to leaf P.

To address the nature of the P constraint on photosynthetic biochemistry, we analysed how photosynthetic biochemistry, and specifically V_{cmax} and J_{max} , varied with leaf P at an unprecedented scale. We compiled a new dataset representing 402 species sampled from 52 sites spanning four continents across the Neotropics, Paleotropics and subtropics (Supplementary Fig. 3 and Supplementary Table 1). These are regions where the role of soil P in regulating productivity is expected to be especially important^{22,38}. The dataset includes species from over one-fifth of all known angiosperm families (Supplementary Table 2), encompassing a substantial part of global taxonomic richness and representative of the high plant diversity in the tropics and subtropics (Supplementary Fig. 4). Leaf P concentrations covered a wide range (50-fold) in contrast to previous analyses that spanned about 10-fold in the upper part of the range (Supplementary Fig. 2). We compiled raw data for net photosynthesis responses to CO_2 concentration (“ $A_{\text{net}} - C_i$ curves”), calculating light-saturated photosynthetic rates and biochemical parameters V_{cmax} and J_{max} (electron-transport enabling RuBP regeneration capacity) by inverting the FvCB model³⁹. The final dataset consisted of species-at-site mean values ($n = 446$ across sites) for light-saturated maximum net photosynthetic rate (A_{net}), V_{cmax} , J_{max} , and their mass-based quantities ($A_{\text{net, mass}}$, $V_{\text{cmax, mass}}$, $J_{\text{max, mass}}$) as well as leaf N and P concentrations (N_{mass} and P_{mass} , respectively), along with a key leaf structural trait, leaf dry mass per area (M_a).

Here we demonstrate a dependence of photosynthetic biochemistry (V_{cmax} and J_{max}) on leaf N^{12,17} but also leaf P on an unprecedented scale, across continents with different underlying soils and parent material geology and diverse plant taxa. We tested for effects of leaf P on J_{max} in accordance with theory^{24,25}, and employed the new relationships in TBM scenarios for gross primary productivity across the tropics and subtropics to establish how these new relationships affect land-atmosphere CO_2 exchange relevant to atmospheric CO_2 draw-down across the tropics. Our overall finding is that inclusion of P at the front-end of TBMs for C cycle processes has a large influence on the magnitude of gross CO_2 uptake by photosynthesis which supports the incorporation of a robust photosynthesis-P relationships into large-scale terrestrial biosphere models underpinning our assessments of the C cycle^{40,41}.

Results

Low leaf P status clearly diminished $V_{\text{cmax}}-N$ and $J_{\text{max}}-N$ relationships on a mass basis (Fig. 1a, b and Table 1). We determined this in a regression framework where we defined “low-P” status of plants based on a threshold for leaf P (P_{mass} of 0.92 mg g^{-1}). Similar relationships held at a range of leaf P_{mass} threshold values (see slopes analysed in Supplementary Fig. 5). The $V_{\text{cmax, mass}}-N_{\text{mass}}$ slope was twice as steep for “moderate-P” species in this dataset as for low-P species (Fig. 1a; Table 1): for a 5-fold increase in leaf N_{mass} , $V_{\text{cmax, mass}}$ of moderate-P species increased 3.3-fold whereas that of low-P species increased just 1.8-fold. Similarly, $J_{\text{max, mass}}-N_{\text{mass}}$ relationships were nearly 2-fold steeper for moderate-P species than for low-P species (Fig. 1b; Table 1), as were $A_{\text{net, mass}}-N_{\text{mass}}$ relationships (Table 1).

The $V_{\text{cmax}}-N$ and $J_{\text{max}}-N$ data for low P and moderate P species converged at low N_{mass} but at higher N_{mass} the fitted slopes diverged ($P < 0.01$, Table 1). At a leaf N_{mass} of 20 mg g^{-1} , near the median N_{mass} of our data, both $V_{\text{cmax, mass}}$ and $J_{\text{max, mass}}$ increased by ~40% for species from low to moderate leaf P concentrations (Fig. 1a, b). This clear inhibitory effect of low leaf P on photosynthetic-N relationships was observed when slopes were fit as either least-squares regressions or as standardised major axes (SMA) (Table 1 and Supplementary Table 3; see Methods and Supplementary text).

Relationships between photosynthetic variables and leaf P_{mass} are much less common in the literature than N-based relationships^{11,25}, but in this dataset P-based relationships were no less significant than the more common relationships with N (Fig. 1c, d). In fact, in this

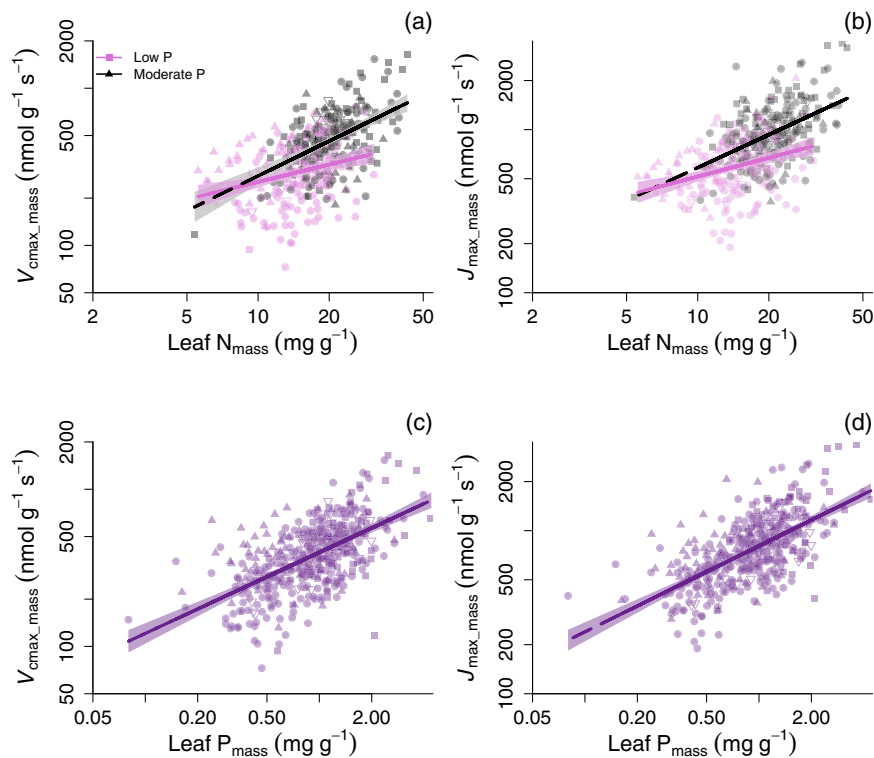


Fig. 1 | Relationships between leaf photosynthetic characteristics and leaf N and P for diverse woody species across continents. **a, b** Relationships between mass-based photosynthetic parameters and leaf N concentration (N_{mass}) for tropical and subtropical trees across four continents, for species grouped into two leaf P (P_{mass}) classes, “low P” ($P < 0.92 \text{ mg g}^{-1}$) and “moderate P” ($P \geq 0.92 \text{ mg g}^{-1}$). Low P data and lines in **a, b** are plum-coloured, with moderate P species shown as grey and black. Lines are least-squares fits and the shaded areas are the 95% CI regions. Each point represents the mean of a species-site combination, where different symbols

of the same colour denote different continents and there are $n = 445$ species-site combinations. **c, d** The relationships between mass-based photosynthetic parameters and leaf phosphorus concentration for tropical and subtropical trees across four continents, with the shaded zone denoting the 95% CI. Least-squares fits and statistics for the lines in **a–d** are shown in Table 1. Photosynthetic parameters are **a, b** leaf mass-based carboxylation capacity normalised to 25 °C ($V_{\text{cmax_mass}}$), and **c, d** leaf mass-based RuBP regeneration capacity normalised to 25 °C ($J_{\text{max_mass}}$).

Table 1 | Summary of single-factor photosynthetic-nutrient relationships for N and P

Mass-based	P status	d.f.	r^2	Slope	Intercept	F-value	P value	P value for slope diff.	
Dependent variable	Ind. variable								
A_{net}	N	Mod. P	231	0.16	0.779	2.323	66.7	<0.0001	0.0013
		Low P	212	0.19	0.369	3.242	16.3	<0.0001	
		All P	445	0.28	0.741	2.350	170.7	<0.0001	–
V_{cmax}	N	Mod. P	231	0.26	0.736	3.929	79.2	<0.0001	0.0013
		Low P	212	0.08	0.367	4.689	15.6	<0.0001	
		All P	445	0.30	0.751	3.783	194.4	<0.0001	–
J_{max}	N	Mod. P	231	0.23	0.671	4.825	67.4	<0.0001	0.0075
		Low P	212	0.10	0.382	5.366	22.0	<0.0001	
		All P	444	0.44	0.310	8.564	208.6	<0.0001	–
V_{cmax}	P	All P	445	0.34	0.515	5.983	231.4	<0.0001	–
J_{max}	P	All P	445	0.40	0.527	6.692	300.0	<0.0001	–

Slope diff. is respective to P status (low P versus moderate P concentration; see text), d.f. indicates the denominator degrees of freedom. The equivalent area-based results are shown in the standardized major axis analysis in Supplementary Table 3.

Analyses were done using ordinary least-square (OLS) regressions for different P status levels and all P levels together (‘All P’). Both the dependent and independent (‘Ind.’) variables for the least-squares regressions are natural logarithm-transformed. The difference between the low and moderate P status groups are defined in the text according to a P_{mass} threshold of 0.92 mg g^{-1} , and the differences in slopes (‘slope diff.’) were tested using separate-slopes analyses.

predominately pan-tropical dataset (Table 1), leaf P_{mass} on its own generally explained more variation in maximum photosynthesis rates and biochemistry per unit mass ($V_{\text{cmax_mass}}$ and especially $J_{\text{max_mass}}$, Fig. 1c, d) than did leaf N on its own. This demonstrates a strong modulation of photosynthetic biochemical capacity by leaf P for

diverse broadleaved plants. For either mass- and area-based J_{max} , the explanatory power (r^2) was about 9–13% higher for leaf P than for leaf N, with associated reductions in mean-square errors (Table 2) demonstrating leaf P effects on photosynthesis and the capacity for RuBP regeneration ($J_{\text{max_mass}}$; Fig. 1).

Table 2 | Summary statistics for multiple regression analyses

Dependent variable	Independent variables	d.f.	Intercept	Slopes for main effects	Slope for N × P inter-action	Overall r ²	Whole-model P value	Inter-action term P value	M _a term P value
Mass-based									
A _{mass}	N _{mass} , P _{mass}	444	3.129	0.479, 0.271	–	0.33	<0.0001	–	–
A _{mass}	N _{mass} , P _{mass} and N _{mass} × P _{mass}	443	2.998	0.513, -0.547	0.294	0.35	<0.0001	0.0003	–
A _{mass}	N _{mass} , P _{mass} , M _a and N _{mass} × P _{mass}	442	7.055	0.139, -0.259, -0.626	0.161	0.45	<0.0001	0.0330	0.0001
M _a	N _{mass} , P _{mass} and N _{mass} × P _{mass}	443	6.484	-0.598, 0.461	-0.214	0.51	<0.0001	<0.0001	–
V _{cmax, mass}	N _{mass} , P _{mass}	444	4.780	0.415, 0.347	–	0.40	<0.0001	–	–
V _{cmax, mass}	N _{mass} , P _{mass} and N _{mass} × P _{mass} *	443	4.636	0.453, -0.546	0.321	0.42	<0.0001	0.0001	–
V _{cmax, mass}	N _{mass} , P _{mass} , M _a and N _{mass} × P _{mass}	442	7.136	0.222, -0.368, -0.385	0.239	0.46	<0.0001	0.0009	0.0001
J _{max, mass}	N _{mass} , P _{mass}	444	5.667	0.354, 0.383	–	0.45	<0.0001	–	–
J _{max, mass}	N _{mass} , P _{mass} and N _{mass} × P _{mass} *	443	5.535	0.388, -0.436	0.295	0.47	<0.0001	–	–
J _{max, mass}	N _{mass} , P _{mass} , M _a and N _{mass} × P _{mass}	442	8.401	0.124, -0.232, -0.442	0.200	0.53	<0.0001	<0.0001	0.0001

d.f. indicates the denominator degrees of freedom.

Regressions showing photosynthesis and mass-based biochemical parameters (A_{mass}, V_{cmax, mass}, J_{max, mass}) and leaf mass per area (M_a) versus leaf N_{mass} and P_{mass}, including their interaction (N_{mass} × P_{mass}). Slopes for main effects are ordered according to the list of independent variables. The N_{mass} × P_{mass} interactions were positive in all cases except for M_a. All tests for interaction and additive terms were done using F-tests. All variables are natural-logarithm transformed, and the models for V_{cmax, mass} and J_{max, mass} with N_{mass} and P_{mass} are illustrated in Supplementary Fig. 8. The recommended model for TBMs is indicated by *.

We further tested whether J_{max, mass}-P_{mass} slopes fitted to individual continents differed from slopes fitted to the remainder of the dataset. Differences among continents might occur, for example, as soil orders and the predominance of ancient eroded bedrock can differ substantially among regions^{23,38}. However, continent-specific slope differences in J_{max, mass}-P_{mass} were not observed (Fig. 2, P > 0.1), nor was the J_{max, mass}-P_{mass} slope different for any continent compared to that of the remainder of the dataset (P > 0.05, using continent as a covariate; Supplementary Table 4). There were similar results for V_{cmax, mass}-P_{mass} (Supplementary Table 4). Thus the observed relationships between leaf P and photosynthetic biochemistry are robust and convergent across continents. Furthermore, climate parameters were not a significant covariate for these relationships (Supplementary Fig. 6). There were important taxonomic differences exhibited among the species sampled across continents (Supplementary Table 2), a characteristic feature of the diverse species richness in tropical forests. Hence the convergence in photosynthetic biochemistry-P_{mass} relationships across continents was particularly surprising, lending support for the robustness of these relationships and their utility in TBMs. While soil P is generally believed to not routinely limit productivity in northern temperate ecosystems^{35,42}, a limited dataset from temperate zone Northern Hemisphere analysed in the same manner as our large and diverse cross-continent dataset was combined with the relevant temperate data from TRY⁴³. Though still a very limited dataset relative to the tropical and subtropical species were analysed in Fig. 1, results in Supplementary Fig. 7 were broadly consistent with the larger dataset of broadleaved evergreen species in Fig. 1.

Considering N_{mass} and P_{mass} effects on photosynthetic traits in a multivariate regression framework (Table 2) led to conclusions consistent with the above analyses that grouped P_{mass} into low and moderate categories (Fig. 1). That is, we observed statistically significant N_{mass} × P_{mass} interactions with V_{cmax, mass} and J_{max, mass} (interactions in all cases, P < 0.001; Table 2, Supplementary Fig. 8), indicating flatter trait relationships at lower P_{mass}. Similar results of a reduced slope at low P_{mass} were found when variation in M_a was also accounted for in the model (Table 2). Together, leaf N_{mass} and P_{mass} (and their interaction) explained 43% and 48% of variation in V_{cmax, mass} and J_{max, mass}, respectively (Table 2). Moderate multicollinearity was observed with a

significant correlation between N_{mass} and P_{mass} (r² = 0.39, P < 0.0001) across the dataset. However, this does not affect predictability of V_{cmax, mass} or J_{max, mass} from N_{mass} and P_{mass}⁴⁴. On an area basis, V_{cmax}-N_{area} and J_{max}-N_{area} relationships showed significantly lower intercepts at lower leaf P status (all with P < 0.02), rather than differences in slopes (Supplementary Table 3). That is, at any given leaf N_{area}, lower P_{area} leaves tended to have lower area-based V_{cmax}, J_{max} and A_{net}.

As further evidence of leaf P effects on the J_{max} component of photosynthesis, as expected by theory^{24,27}, there was a reduction in the slope of the relationship between J_{max} and V_{cmax} that depended on leaf P status (leaf P_{mass} classes; Fig. 3). J_{max} was lower in proportion to V_{cmax} for leaves with low P_{mass} than for leaves with high P_{mass}, as would be expected by a stronger influence of leaf P_{mass} on the capacity for J_{max} than V_{cmax}. This supports the earlier evidence (Figs. 1 and 2) that there are strong effects of leaf P on J_{max}, stronger than these effects are for V_{cmax} (Table 1).

Terrestrial models of photosynthesis and GPP need to represent key biological processes. To test whether the central relationships of photosynthetic components with nutrients that we found in Fig. 1 and Table 2 (multiple regressions) could produce large enough effects on canopy photosynthesis to merit consideration in TBMs, we conducted a model experiment involving the ORCHIDEE-CNP model¹⁵ for the tropics and subtropics. We applied three-way V_{cmax, mass}-N_{mass}-P_{mass} and J_{max, mass}-N_{mass}-P_{mass} relationships (Table 2, Supplementary Fig. 9) in ORCHIDEE-CNP for latitudes <35° N and S to simulate forest canopy photosynthesis under scenarios of unlimited leaf P and limited-leaf P content (see Methods). In the equatorial zone, modelled forest GPP was reduced by 36% to just over 1800 g C m⁻² y⁻¹ in the P-limited scenario. However we found that, assuming an unlimited plant P, gross primary productivity (GPP) in equatorial latitudes was simulated to increase by almost a factor of two, approaching 3000 g C m⁻² y⁻¹ across the region^{1,45} (Fig. 4a). The total difference in modelled subtropical-and-tropical GPP comparing the unlimited P with the limited P scenario was large, at roughly 70 Pg C (Fig. 4d; between 33° N and 33° S), an over-estimate by roughly half of the expected annual total global C uptake in a year. While the upper simulated range is above observational-constrained estimates⁴³, there were similar proportional reductions in GPP with reduced P compared with unlimited P across

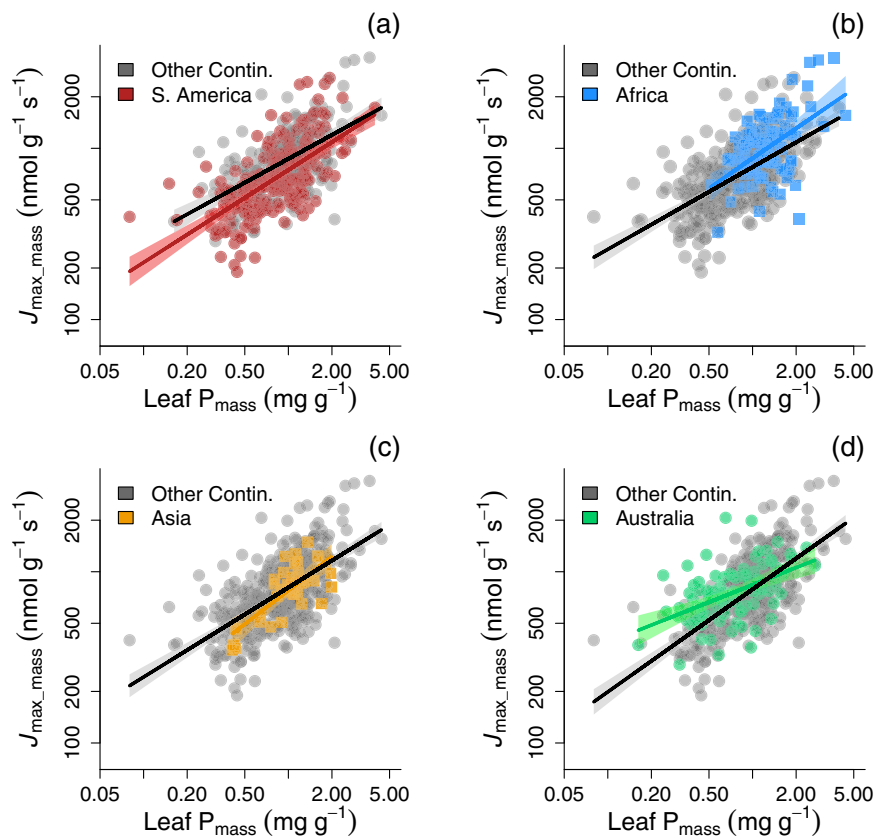


Fig. 2 | Comparison of J_{\max_mass} as a function of P_{mass} for woody species on different continents. Each continent is shown compared to the full remainder of the dataset (denoted 'Other Continents'), for **a** South America, **(b)** Africa, **(c)** Asia, **(d)** Australia). Each point denotes a different species-site mean. There was no

significant continent effect in the analysis ($P > 0.05$; see Supplementary Table 5). The 95% CI for each relationship around each line is shown in grey for 'Other Continents', and the 95% CI for each continent is shaded in the corresponding colour for each continent being compared.

the tropical domain (e.g., 36% reduction, Fig. 4c). As a result, we confirmed that a front-end control of P over canopy photosynthesis can produce significant alterations in modelled GPP estimates for this TBM.

Discussion

Considered all together, our results show strong and consistent evidence for a negative effect of low P on photosynthetic biochemistry across a large diversity of woody species, regardless of continent, the basis of expression, or the statistical approach to slope-fitting. The observed effects of both N and P and their interactions on photosynthetic biochemistry (Fig. 1 and Table 2, Supplementary Fig. 8) demonstrate a significant inhibitory effect of low leaf P on photosynthetic biochemistry that is currently captured in few TBMs⁵. These relationships are consistent with recent evidence for P limitation of tree growth in lowland tropical forests^{31,46}, the declining magnitude of P resorption across the tropics to mid-latitude regions²³ and modelled biomass C uptake and sequestration¹⁵. Moreover, we clearly show that leaf P affects photosynthetic biochemistry in a way that has not been implemented in previous models^{8,15,47,48} but is general across a wide diversity of species, and across continents, supported by extensive field observations.

We demonstrated that such P limitations can arise through reduced biochemical capacity for photosynthesis at low leaf P_{mass} in combination with moderately high leaf N_{mass} , likely in concert with low orthophosphate pools for photosynthetic biochemistry^{24,25,27}. The similarity in photosynthetic biochemistry- P_{mass} relationships across taxa and continents (Fig. 2 and Supplementary Table 4) occurs in spite of potential differences in how P is allocated to metabolic function across taxa and/or geological substrates on different continents^{31,35}.

The convergence in these relationships across continents suggests an overall similar and conservative use of P in photosynthesis across a range of soils but largely at low soil P availability. Further work is needed to disentangle changes in the botanical composition of natural vegetation in response to varying soil N and P availability from the response of individual species to contrasting N and P supply.

The proportion of leaf P involved in photosynthesis versus other functions varies among species³⁷, yet there are still too few data from field-sampled plants to draw solid generalisations about which leaf P fraction is key to regulating photosynthesis. If the fraction of P that is metabolically active varies with total P concentration in leaves, then we would have expected differences in key relationships such as J_{\max_mass} - P_{mass} across sites and continents. Instead, the striking convergence in our results from subtropical and tropical sites points to general mechanisms that may be in play for C_3 plants from other biomes where low-P soils occur. There is evidence that relationships like J_{\max_mass} - P_{mass} are generalizable to Northern Hemisphere temperate woody plants (Refs. 19, 49, and Supplementary Fig. 7) but in this regard there is a clear need for further work involving temperate coniferous and deciduous trees. In fact, in the extensive TRY database, there is a paucity of Northern Hemisphere temperate records (Supplementary Fig. 7), particularly involving species-at-site values for J_{\max} , M_a and P_{mass} measured together. We identify this as an area for further research, involving both broadleaved and needle-leaved temperate and boreal species.

The cross-continent relationships for V_{cmax_mass} and J_{\max_mass} with P_{mass} that we have presented in Fig. 1c, d establish an important benchmark in plant physiology, bearing in mind that these relationships are across plant species. Instantaneous photosynthetic P-use efficiency (the ratio of mass-based photosynthesis to leaf P

concentration) has been hypothesized to be high in plant species adapted to survive at very low soil P levels due to a variety of adaptations⁵⁰. Figure 1c, d provide a set of quantitative relationships against which elevated photosynthetic P-use efficiency can be compared to objectively test for enhanced photosynthetic P-use efficiency and enable traits that confer it to be identified.

Future analyses should clarify how components of photosynthetic biochemistry are reduced with chronic, low leaf P_{mass} in contrast to the rapid, acute P deficiency that has previously been examined²⁴. With a

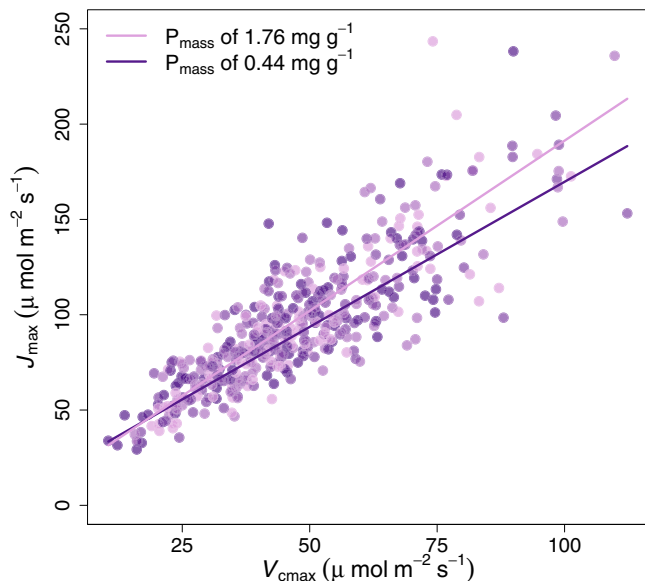


Fig. 3 | The correlation between J_{max} and V_{cmax} for leaves with different leaf P concentrations. The colour scheme indicates low leaf P_{mass} in purple shades with increasing P_{mass} corresponding to progressively lighter shades of purple to plum. Each point is a species-site mean. The lines shown are for the two end-member leaf P_{mass} classes: mean low P_{mass} of 0.44 ± 0.11 (s.d.), and mean high P_{mass} of 1.76 ± 0.55 (s.d.). The OLS regressions shown are: $J_{\text{max}} = 17.5 + 1.52 * V_{\text{cmax}}$ for low P_{mass} ($r^2 = 0.82$), and $J_{\text{max}} = 12.8 + 1.79 * V_{\text{cmax}}$ for high P_{mass} ($r^2 = 0.71$), with $P < 0.0001$ for both regressions. V_{cmax} and J_{max} are temperature-normalised to 25 °C (see methods). The slope terms of the lines are significantly different at $P = 0.0355$ using P_{mass} class as a categorical variable in interaction with the independent variable.

paucity of enzyme function work involving tropical species in realistic low-P soil conditions, there can be advances with further physiological and molecular work in tropical regions and species adapted to low-P soils⁵¹ in order to better support the mode of regulation of photosynthetic biochemistry by cellular P supplies.

The mode of action for P suggested by our analyses is likely more complex than the direct, single protein-N paradigm that has existed for Rubisco and other photosynthetic proteins¹⁷, but it is no less important. The larger proportion of variation in the biochemistry of photosynthesis described by P_{mass} versus N_{mass} in Fig. 1, and higher coefficients of determination and lower mean square error for the P-only compared to N-only models (Tables 1 and 2), and the convergence across continents (Fig. 2 and Supplementary Table 4), all indicate a strong functional role for P constraining photosynthesis. Our results demonstrate the existence of consistent, across-continent reductions in the capacity for photosynthesis with low leaf P, cutting across a wide range of higher plant families and involving all vegetated continents (Fig. 2 and Supplementary Fig. 7). This indicates a set of robust relationships that can be incorporated into TBMs for a range of plant functional types.

Functional balance of the biochemistry of photosynthesis

The $J_{\text{max}}/V_{\text{cmax}}$ ratio signifies the optimal functional balance between the two fundamental components of photosynthesis: carboxylation versus electron transport and RuBP regeneration. The $J_{\text{max}}-V_{\text{cmax}}$ connection has been extensively described and analysed^{49,52} and is capitalized as a commonly employed short-cut in TBMs¹². While it is still debated how low P affects photosynthetic biochemistry, some clues emerge from our study. The conventional hypothesis that there is little or no role of P in regulating V_{cmax} ^{11,12} is not supported by evidence here across species and soils (Fig. 1). Moreover, the idea that V_{cmax} is closely coupled to J_{max} and hence $V_{\text{cmax}}-P$ relationships are simply a consequence of its control of J_{max} and subsequent functional balance between J_{max} and V_{cmax} is partially but not fully supported by Fig. 3. Instead, acclimation of photosynthesis to low-P environments via adjustments in the $J_{\text{max}}/V_{\text{cmax}}$ ratio involves a role for P in photosynthetic protein assembly and enzyme activation via phosphorylation⁵³ which suggests an alternative set of ways that P can influence the state of Rubisco and hence V_{cmax} .

A physiological imbalance in the capacity for J_{max} versus V_{cmax} would indicate excess electron transport at light saturation. The rate of

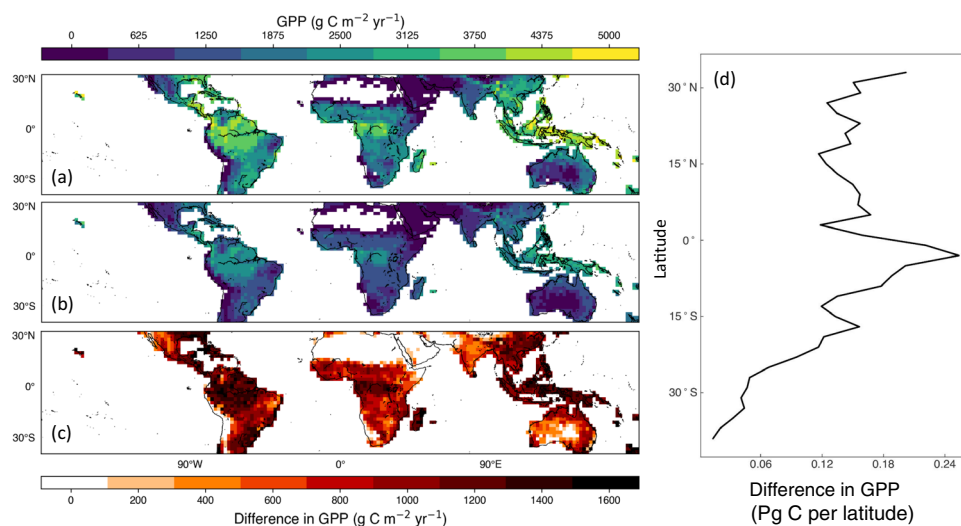


Fig. 4 | Modelled gross primary productivity (GPP) for tropical and subtropical zones with ORCHIDEE-CNP. **a** GPP from ORCHIDEE-CNP simulations assuming N constraints but a high P everywhere (no P constraint). **b** GPP as in **a**, but including P constraints according to a version of the multiple regression in Table 2. The colour

scale for **a**, **b** are at top. **c** the difference between GPP from the model with N but not P constraints as shown in **a** and the ORCHIDEE-CNP simulations with P constraints according to **b**, with colour scale at bottom. **(d)** the zonal difference in GPP shown in **c** using 2° latitudinal bands and aggregated across longitudes around the globe.

electron transport J is coupled to proton translocation and generates the trans-thylakoid pH gradient, which drives the regeneration of ATP and RuBP. Excess J would tend to risk excessive stromal acidification which itself would disrupt the electron transport chain and risk damage to the leaf tissue²⁴. The opposite situation, with excess carboxylation capacity at suboptimal J_{\max}/V_{cmax} ratio, would lead to insufficient ATP supplies to regenerate RuBP²⁶. Either phenomenon would tend to shift the capacity toward an optimal balance between the two functional components of the photosynthetic apparatus in leaves at the top of the canopy. Such shifts explain why the J_{\max}/V_{cmax} ratio is nearly constant in sunlit leaves across a wide range of situations^{28,49}. However, despite the arguments and evidence of constancy for the J_{\max}/V_{cmax} ratio⁵², the different roles of N and P in primary photosynthetic reactions (Supplementary Fig. 1) implies a small shift in J_{\max}/V_{cmax} ratio with respect to lower leaf P_{mass} that is consistent with our observations (Fig. 3). The J_{\max}/V_{cmax} shift with increasing P_{mass} in our dataset is not large (e.g., a 10% reduction with low P_{mass} ; Fig. 3), supporting a functional balance for the components of the photosynthetic apparatus²⁸. Still, the majority of TBMs that parameterise J_{\max} based on the basis of this functional balance with V_{cmax} and a highly conserved J_{\max}/V_{cmax} should consider these changes in the functional balance with low leaf P and high leaf N:P ratio and the mechanistic implications of this in models.

Model analysis and implications

Given the strong role of tropical CO_2 exchange in regulating the earth's C exchange with the atmosphere and hence climate, an influential role for leaf P concentration on photosynthesis would be expected to be manifest at large scales and impact the C cycle. The relationships in Fig. 1 and Table 2 have functional significance and should be considered in TBMs seeking to link nutrient cycles to the C cycle^{9,15}. Thus, we utilised the observed mass-based relationships for biochemistry-N and -P in a model analysis and found large proportional reductions in GPP with reduced P compared with unlimited P across the tropical and subtropical domain (Fig. 4c). Our estimate of the reductions in GPP of 36% across this key set of mid- to low-latitude biomes are large. A smaller change in GPP between unlimited leaf P and limited-leaf P scenarios could be possible for a different global model or alternative model implementation of the field results. However, our objective here was to evaluate our new formulation of photosynthetic biochemistry with a leaf P_{mass} dependence and its potential impact on large-scale C cycling, to help refine uncertainties in GPP which are large for the tropical zone⁵⁴. Future efforts should determine the effects this model parameterisation would have on net C storage in different global terrestrial models, recognising that there are a number of downstream processes after gross photosynthesis that could enhance or diminish P effects on net primary productivity at the large scale^{6,47,55} compared to GPP as analysed here.

The reduction in GPP emerging from the dependence of V_{cmax} and J_{\max} on P results in modelled tropical C uptake estimates is consistent with modelled C cycle outcomes inferred from atmospheric inversion and flux site upscaling models^{1,56} (Supplementary Fig. 9). The general and robust relationships of photosynthetic parameters with leaf P_{mass} and N_{mass} (Fig. 2) along with N-P interactions (Fig. 3) could readily be included by other terrestrial biosphere models^{8,57,58} either with a P biogeochemistry submodel⁴⁰ or with existing global datasets of P spatial variability⁵⁹. This would ensure that GPP was appropriately constrained by both leaf N and P as two major limiting macronutrients around the globe^{22,23}.

The regulation of photosynthesis by leaf P and its effect on rate-limiting biochemical parameters has demonstrable consequences for large-scale forest C uptake (Fig. 4) with important implications for understanding the C cycle not only for the tropics but for low-P sites around the world. From our findings of consistent P constraints on photosynthetic biochemistry across continents, we argue that there is

no longer any basis for ignoring the P effects on photosynthesis in TBMs even if P is not uniformly low throughout the tropics^{23,58}. Also, the P constraints implemented here for photosynthesis in the ORCHIDEE-CNP model (Fig. 4) illustrate the effects on GPP but do not address more complex ecosystem C cycle processes that can be sensitive to soil P such as biomass allocation, growth, forest structure and leaf area^{8,9}. For instance, species compositional changes along P availability gradients are an additional way in which forest productivity may be modulated by P⁴⁶. These phenomena have been proposed for modelling^{8,9} or are already implemented in TBMs⁵⁵, but the photosynthetic biochemistry proposed here is a key front-end control on the tropical and subtropical C cycle.

In TBMs that underlie our predictions of future carbon sink behaviour, projections of C uptake for the tropics and the rate of climate forcing by CO_2 ⁸ have remained unconstrained by leaf or soil P status^{8,9}, likely biasing GPP predictions for these regions. These effects are particularly important given the role of tropical and subtropical regions in regulating global CO_2 uptake and vegetation-climate interactions. Given that there are stable relationships for photosynthesis with broad range of leaf N and P across continents, global terrestrial C cycle models can now represent both nutrient constraints on net photosynthesis and its biochemical determinants to improve NPP predictions.

Methods

Leaf gas exchange

We compiled 17,913 data points for controlled photosynthetic responses to $[\text{CO}_2]$ for a set of pan-tropical sites involving published and unpublished raw data (Supplementary Table 1) that were measured using standard techniques⁶⁰ and similar instrumentation (Li-6400, Li-Cor Inc.). Mean annual precipitation at these sites varied widely, from 500 to 3000 mm y^{-1} , as did mean annual temperatures (10–30 °C, Supplementary Table 1). Data were analysed and fit for biochemical parameters in a common framework^{30,39}. The data we assembled represent the most comprehensive analysis of photosynthetic biochemistry across plant families (Supplementary Fig. 4) measured through 2019. The published data sources are Refs. 61–72 (Supplementary Table 1) with raw data for these studies as well as the unpublished data sources in Supplementary Table 1 compiled together (see Data availability statement). Climate data not available from direct measurements at the sites were estimated based on gridded climate data⁷³. Only naturally occurring trees, shrubs and lianas at mature life stages were included in the data. Gaining access by construction-style cranes, leaves were sampled at considerable heights (20 m to 70 m above the ground) at six of the sites (Lambir Hills National Park, Sarawak, Malaysia; Bubeng, China; San Lorenzo National Park, Panama; Parque Natural Metropolitano, Panama; EucFACE, NSW, Australia; and Cape Tribulation, Queensland, Australia). For the remainder of the studies ($n = 46$ sites) leaves were sampled on branches that had been collected from mid-to-upper canopy positions, placed in water and recut to maintain a viable water supply. All leaves were identified by data contributors as “sunlit” to represent photosynthetic function in the sunlit portion of the tree canopy. We required analyses of P concentrations as well as N concentrations for the dataset (Supplementary Fig. 10). Multiple individuals were measured for most of the species, and these data were averaged for a species-at-site average that was used in the analyses ($n = 471$ species-site values, $n = 446$ complete with both N_{mass} and P_{mass}). Unlike previous such analyses^{29,32}, we focused our analysis on species-level variation, given that species described the largest source of variation in leaf P⁷⁴ (Supplementary Fig. 11). This approach also avoided excessive weight given to particular species that were represented by many multiple sample leaves in the analyses and minimised the possibility of finding statistically significant correlations due to a large number of data points but with low predictive power⁶¹. A small, limited dataset from Europe and North America that

was compiled from direct measurements and from the TRY database⁴³ analysed in the same manner as our large and diverse cross-continent dataset (Supplementary Fig. 8) to compare the results with deciduous and gymnosperm species (five species of *Quercus* and *Pinus*, as major Northern Hemisphere genera).

To ensure that drought did not confound our results, measurements were collected as much as possible during the wet season or the early part of the dry season. Also, leaves that showed very low stomatal conductances ($<30 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) were removed from the analysis as photosynthetic metabolism in such cases could either be limited by low nutrients or low conductance to CO_2 diffusion and hence would not be diagnostic for low N and P concentrations. We also ensured that $A_{\text{mass}} > 20 \text{ nmol g}^{-1} \text{ s}^{-1}$ and the curve-fit CV $< 30\%$ for the initial slope as criteria for inclusion to the overall dataset, consistent with previous analyses of photosynthetic capacity^{49,60,75}. As leaf P_{mass} and other variables were approximately log-normally distributed, we transformed these variables appropriately in the analyses. In some analyses we treated leaf P as a covariate and grouped species into two leaf P classes: “moderate P” and “low P”, based on a threshold corresponding to the median leaf P concentration in the dataset (leaf P_{mass} of 0.92 mg g^{-1}) similar to what was used previously⁴⁹. In so doing, we recognize that low leaf P_{mass} may not always reflect soil availability due to species-level mechanisms that can affect P uptake⁵⁰, though leaf P_{mass} is most relevant to leaf internal physiology.

We based our analyses on mass-based photosynthetic parameters to enhance predictive capacity to use these relationships in modelling. However, the relationships examined also included area-based quantities such as V_{cmax} and J_{max} , and our findings are generally as applicable to area-based measures as mass-based ones (Supplementary Table 3). We note as in many other analyses that have been done that area-based least-squares regression fits are often significant but are weaker than the mass-based ones⁷⁶. Leaf mass per area (M_a), the conversion factor between area- and mass-bases of expression, was also included as a covariate in a subset of multiple regression analyses (Table 2). In such cases the fitted coefficients for leaf N or P effects on photosynthetic traits can be thought as being independent from the basis of expression (i.e. area vs mass, Ref. 76; Supplementary Note 1).

Data fitting and statistical analyses

The curve fitting used the *plantecophys* package³⁹ for least-squares minimisation in R. The fits were obtained using an inversion of the FvCB biochemical model of leaf photosynthesis³⁰ which is employed in the land surface portion of the World Climate Research Programme’s CMIP6 models⁷⁷ and many other land surface models²¹. Enzyme kinetic constants are used to compute V_{cmax} and J_{max} normalised to 25°C according to functions representing acclimation and adaptation of photosynthetic temperature response kinetics⁷⁸ using site temperatures summarised in Supplementary Table 1 and Ref. 73. They are reported in all figures as temperature-normalised to 25°C . We made common assumptions about the kinetic coefficients for the Rubisco enzyme and biophysical constants in the model for all species apart from these photosynthetic Arrhenius temperature response parameters in Ref. 78. We assumed an infinite mesophyll conductance term in the analysis, so rates are expressed on an apparent basis. Assuming a finite mesophyll conductance equal to the species mean stomatal conductance that was measured did not qualitatively change the results or findings.

Our statistical analyses were conducted using natural logarithm-transformed data as appropriate for nutrients per unit dry mass. Bulk leaf P concentrations were used since few studies, and less than 2% of the data here, have analysed P fractions in leaves. The main set of analyses use ordinary least-squares (OLS) regression fits to species-level data, with examination of residual and quantile (Q-Q) plots to ensure the models met assumptions of the technique. In addition, we used standardised major axis analyses as a secondary supporting

approach that avoids undue bias in slope estimates⁷⁹ for Fig. 1 (see Supplementary text). Differences in slopes in OLS regression analyses were tested using multiple regression with the appropriate categorical variable (e.g., continent, N:P ratio class, etc.) as a categorical variable along with the independent variable in an interaction model. The significance of the interaction effect was used to test for separate rather than parallel slopes⁴⁴. In Table 2, we provide appropriate functions for estimating leaf biochemistry parameters $V_{\text{cmax, mass}}$ and $J_{\text{max, mass}}$ depending on N_{mass} and P_{mass} that can be used in TBMs. A dependence of M_a on P_{mass} (Table 2) should be used to convert the estimates to an area basis.

To examine the balance between J_{max} and V_{cmax} and test if there was a dependence on leaf P_{mass} , we conducted a multiple regression involving V_{cmax} as independent variable and P_{mass} as covariate. P_{mass} was highly significant in the model ($P = 0.00129$), indicating different $J_{\text{max}}-V_{\text{cmax}}$ relationships with leaf P_{mass} . To visualise this, we further divided “low P” and “moderate P” status classes (from Fig. 1) each in half, and then tested for the difference between these classes using the two outermost extremes of P_{mass} (P_{mass} of 0.44 mg g^{-1} and $n = 111$ versus 1.76 mg g^{-1} , $n = 112$ observations). The two outer P_{mass} classes showed significantly different ($P = 0.035$) slopes for $J_{\text{max}}-V_{\text{cmax}}$ relationships using P_{mass} class as a categorical variable in interaction with the independent variable.

Model and analysis of pan-tropical P-limitations

We used the land surface model ORCHIDEE-CNP version 1.1^{40,80}. The model simulates the terrestrial biogeochemical cycles of C, N and P and their interactions as well as the water budget and the exchanges of energy, water and CO_2 and N between the atmosphere and the biosphere. ORCHIDEE-CNP version 1.1 is well evaluated at site-level, including nutrient dynamics and their effects on tropical gas exchange⁵⁵. The model is able to reproduce (1) the shift from N to P limited plant growth along a soil formation chronosequence in Hawaii⁴⁰ and (2) gas exchange measurements on P-poor tropical soils⁵⁵.

To understand the role of low P in restricting gross primary productivity based on the leaf-level responses we identified, we replaced the original N dependency of photosynthesis in the model with a new relationship based on Fig. 3. The relationships used were $V_{\text{cmax, mass}} = \exp(4.4490 + 0.3472 \cdot \ln(P_{\text{mass}}) + 0.49078 \cdot \ln(N_{\text{mass}}))$ and $J_{\text{max, mass}} = \exp(5.4944 + 0.3735 \cdot \ln(P_{\text{mass}}) + 0.4144 \cdot \ln(N_{\text{mass}}))$, which were converted to area-basis using the M_a predicted in the model. Subsequent to the modelling, data was added from two other sites (Manaus, Brazil and Bubeng, China; $n = 28$ species added), which did not appreciably or quantitatively affect the results (see newer relationships, Supplementary Fig. 7). The area-based versions of these functions were $V_{\text{cmax}} = \exp(4.308 + 0.298 \cdot \ln(P_{\text{area}}) + 0.197 \cdot \ln(N_{\text{area}}))$ and $J_{\text{max}} = \exp(5.139 + 0.325 \cdot \ln(P_{\text{area}}) + 0.112 \cdot \ln(N_{\text{area}}))$ based on fits to the raw data. The ORCHIDEE-CNP model here widened the range that leaf N:P ratio can vary from the original narrow range that was predicted in the model (N:P from 16.7–22.6 in Ref. 68) to an N:P range of 5–60, corresponding to the 25th and 75th percentiles of the N:P in the leaf photosynthesis dataset. As a result of the wider range of leaf N:P ratios, we replaced the scaling function for plant P acquisition processes (biochemical mineralisation and root uptake, Ref. 40) by a sigmoidal function $f(\text{PN}_{\text{plant}})$ and chose the coefficient such that processes sharply increases between plant labile N:P ratio of 15 to 25:

$$f(\text{PN}_{\text{plant}}) = \frac{1}{(1 + \exp(-\frac{\text{N:P}}{2}) + 10))} \quad (1)$$

The N:P ratio of 15 roughly corresponds to the ratio where plant communities have shown a switch from N to P limitation^{23,81} and we chose this ratio as the middle of the co-limitation range.

With the modified model, we performed pan-tropical and sub-tropical simulation on a $2^\circ \times 2^\circ$ spatial resolution using the simulation

protocol in Ref. 82. The protocol takes into account historic changes in land cover, CO₂ concentration, climate, and N and P deposition since 1860 (called ‘experiment SI’ in Ref. 82). Climate forcing was derived from the CRUNCEP v.7 meteorological dataset (National Centers for Environmental Prediction-National Center for Atmospheric Research (NCEP-NCAR) and Climatic Research Unit-University of East Anglia). For the simulations, first the cycles of C, N and P were brought into equilibrium (<1% in global stocks) with the boundary conditions of 1860. Second, the simulation was continued to 2012 using time series of land cover (SYNMAP), climate (CRUNCEP7), atmospheric deposition, fertilizer and CO₂ concentration (NOAA GLOBALVIEW-CO₂ dataset). For the analysis, we used the average GPP over a 21-year period (1992–2012) to represent the present-day productivity of grid cells and evaluate how the mathematical formulation for photosynthesis involving P would affect vegetation GPP.

We considered unlimited P supply to be when leaf N:P ratio was 5, and limited P when leaf N:P ratio was estimated from the model by a P biogeochemistry submodule⁴⁰. This implementation might have overestimated the P limitation effect on GPP, but was done to demarcate P-limited and non-limited photosynthesis. We diagnosed the P-unlimited GPP in the simulations by using photosynthetic parameters, J_{max} and V_{cmax} , which correspond to the computed leaf N_{mass} but assuming a maximum leaf P_{mass} calculated from the minimum N:P ratio of 5 g N (g P)⁻¹. Based on these photosynthetic parameters we recalculated GPP for the conditions (water, light, leaf area index) at each time step. The estimated GPP did not affect state variables and, thus, the feedback between GPP and LAI is not accounted for in the calculation of potential GPP. Subsequent to the modelling, data was added from two other sites, but the relationships with N and P remained similar to those used in the modelling (Fig. 3, Table 2). The relationships used by the model did not use the N × P interaction term (Table 2). Nonetheless, we found a less-pronounced effect of leaf P on GPP by about 15% with these relationships compared to the relationships based on the complete dataset shown in Table 2, so the model results we report in Fig. 4b–d are slightly more conservative than if we had implemented the relationships from the full dataset.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The photosynthesis and leaf nutrient data reported in the paper are available at <https://doi.org/10.6084/m9.figshare.20010485.v1>, and the model results are available on the European open-access repository Zenodo at <https://doi.org/10.5281/zenodo.6619615>. All other data reported in the paper are presented in the supplementary materials.

Code availability

The R code used for analyses is at https://github.com/ellswor2/photo_p_repo2.git. The source code for ORCHIDEE is at <https://doi.org/10.14768/20200407002.1>.

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Author contributions

D.S.E., K.Y.C., M.D.K. and I.J.W. designed the research, and D.S.E. compiled the raw dataset with the data contributions. D.S.E. coordinated the project with input from K.Y.C., I.J.W., M.D.K. and L.T.V., K.B., L.C., K.Y.C., T.D., M.E.D., S.G., R.G., I.A.J., B.E.M., P.M., R.J.N., L.R., L.S., T.K., T.I., J.U., L.V., A.W., M.v.W., Y.-B.Z and J.-L. Z. contributed data. M.D.K., S.Z., D.S.E., Y.S. and D.G. designed the simulation model runs for Orchidee. The model development analysis was done by D.G and Y.S. D.S.E. wrote the first draft and jointly wrote subsequent drafts of the manuscript with K.Y.C., I.J.W., M.D.K. and L.T.V. All co-authors commented on versions of the manuscript.

Competing interests

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Additional information

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