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**Global response patterns of plant functional traits to combined nitrogen and phosphorus addition are governed by additive interactions**

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**Abstract**

The availability of nutrients such as nitrogen (N) and phosphorus (P) plays an important role in shaping plant ecophysiological responses to global change. While N availability has been asserted as a key driver of plant responses to global change, the role of phosphorus – both individually and in combination with nitrogen – remains less understood due to a lack of data syntheses that precludes the development of a mechanistic framework. To address this knowledge gap, we compiled leaf and whole-plant trait data from full-factorial N and P addition experiments across the globe and conducted a meta-analysis. We used this approach to quantify the individual and interactive effects of N and P addition on leaf nutrient content, leaf photosynthetic traits, plant biomass accumulation, and biomass partitioning. Nutrient addition played no role in shaping leaf-level photosynthetic parameters. These patterns were observed despite N addition increasing leaf N content, P addition increasing leaf P content, and both nutrient additions increasing aboveground biomass and decreasing the root mass fraction. The combined effects of N and P addition on leaf and whole-plant traits were largely driven by additive interactions, indicating that these effects were the result of independent effects of each nutrient addition. Regions with greater demand for soil resources (e.g., colder and drier regions) exhibited stronger leaf N content responses to N addition as well as stronger leaf P content responses to P addition, providing some support for climate-related demand for soil resources controlling leaf nutrient responses to nutrient addition. These findings provide important information needed to understand carbon-nitrogen-phosphorus cycle dynamics and provides a foundation for better representing carbon-nitrogen-phosphorus interactions in land surface models.

**Introduction**

Biogeochemical cycles regulate terrestrial ecosystems.

[introduction, eutrophication and global change]

[N addition effects on leaf and whole-plant traits]

[P addition effects on leaf and whole-plant traits]

[Combined N and P effects on leaf and whole-plant traits, including knowledge gaps]

[study objectives]

Here, we conducted a global meta-analysis using [XX] observations from [XX] journal articles, including data compiled from an existing database of plant functional trait responses to nitrogen and phosphorus addition. Our objectives were two-fold. First, we sought to quantify the effects of N, P, and N+P addition on net photosynthesis, photosynthetic capacity, leaf nutrient content and partitioning, resource use efficiencies, plant growth, and biomass partitioning. Second, we quantified the interaction effect size of each trait to understand whether the effects of N+P addition were the product of additive, synergistic, or antagonistic individual effects of N and P addition. We used this approach to test the following hypotheses:

1. Nitrogen and phosphorus addition will increase leaf nitrogen content and leaf phosphorus content, respectively. This will lead to an increase in the leaf N:P ratio with nitrogen addition and a decrease in the leaf N:P ratio with phosphorus addition. The effects of nitrogen and phosphorus addition on leaf nitrogen and phosphorus content are expected to be amplified in regions where demand for building and maintaining photosynthetic enzymes is high (e.g., high aridity, low temperature, high light availability; (Cheaib *et al.*, 2025), or in species with high demand for building and maintaining photosynthetic enzymes (e.g., N2-fixers, AM-association species).
2. Nitrogen and phosphorus addition will not influence photosynthetic parameters unless the availability of these resources is insufficient to satisfy demand to build and maintain photosynthetic enzymes. In nitrogen-limited systems, nitrogen addition is expected to increase the maximum rate of Rubisco carboxylation. In phosphorus-limited systems, phosphorus addition is expected to increase the maximum rate of electron transport for RuBP regeneration.
3. Nitrogen and phosphorus addition will increase total biomass through stronger increases in aboveground biomass than belowground biomass, which will decrease the root-to-shoot ratio and root mass fraction.
4. The combined effects of nitrogen and phosphorus addition on leaf and whole-plant traits will be the sum of the corresponding individual effects of nitrogen and phosphorus addition. That is, plant responses to nitrogen and phosphorus addition will be the product of additive responses.

**Materials and Methods**

*Data compilation*

Initial data for the meta-analysis were collected using citations listed in the Manipulation Experiments Synthesis Initiative (MESI) database (Van Sundert *et al.*, 2023). We selected manipulation experiments that added N and P in a full-factorial design to ensure that any comparisons made between N, P, and N+P addition responses were from the same subset of experiments. All data for manuscripts included in the MESI database that fit these criteria were downloaded or extracted using a plot digitizer to ensure that all relevant traits were included in the meta-analysis and undergo a round of quality control to avoid any data entry issues that may arise when using large ecological datasets (Augustine *et al.*, 2024). To supplement studies included in the MESI database, studies that reported data from Nutrient Network experiments were also included in the meta-analysis, including only measurements collected from control, N, P, and N+P addition plots. Each site in each paper that reported data from Nutrient Network experiments was treated as an independent experiment, following that the Nutrient Network is a globally distributed experiment where independent sites share the same nutrient addition and experimental design scheme (Borer *et al.*, 2014). Specifically, we added leaf nutrient data from Firn et al. (2019), biomass partitioning data from Cleland et al. (2019), and photosynthetic data from Hersch-Green et al. (2024).

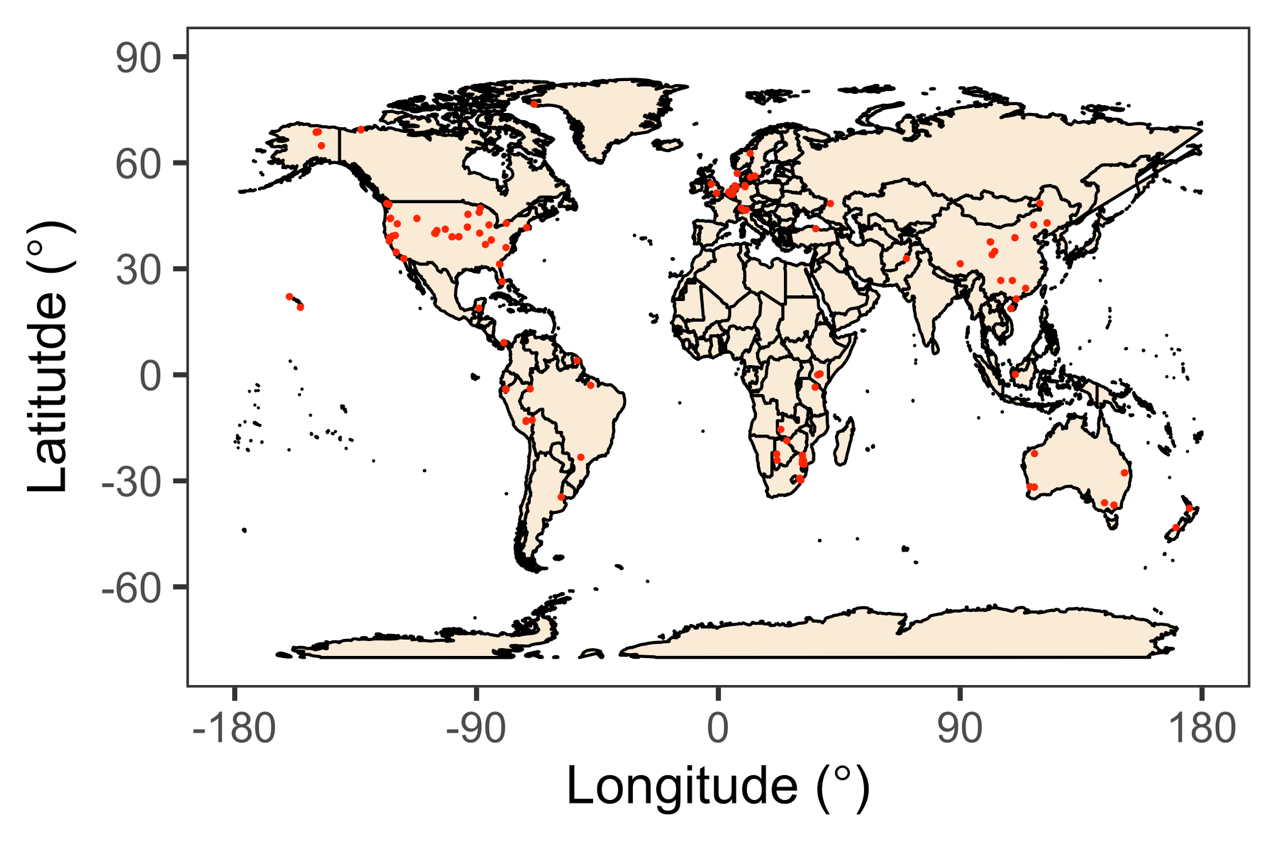
To supplement MESI and Nutrient Network datasets, we added additional manipulation experiments using journal articles published on or before March 2025. We selected manipulation experiments where N and P were added in a full-factorial design. From this, we selected experiments that measured traits related to leaf photosynthesis (e.g., net photosynthesis maximum rates of Rubisco carboxylation and electron transport for RuBP regeneration), leaf nutrient content (e.g., mass- or area-based leaf nitrogen content, mass- or area-based leaf phosphorus content), biomass (e.g., above-ground or belowground biomass), biomass partitioning (e.g., root:shoot ratio), or nutrient partitioning of the biomass (e.g., aboveground N standing stock, aboveground P standing stock). Finally, we selected experiments that included explicit explanations of treatment replication schemes to accurately calculate summary statistics. We first searched for studies that followed these guidelines using citations included in the MESI and Nutrient Network papers. To supplement these studies, we also created a search query in Web of Science using similar search terms as in (Liang *et al.*, 2020). Specifically, our query mined for the following topics: (nitrogen AND phosphorus) AND (fertiliz\* OR addition) AND (effect\* OR respon\* OR affect\* OR impact\* OR increas\* OR decreas\* OR alter\* OR deposition OR enrich\*) AND (leaf nitrogen\* OR leaf phosphorus\* OR \*use efficiency OR biomass OR mass fraction OR root:shoot OR LMA OR SLA OR chlorophyll OR photosynthesis OR Vcmax OR Jmax) NOT (animal\* OR medic\* OR chemist\*).

*Data extraction*

One mean value ± standard deviation per trait per species per nutrient fertilization treatment per experimental site was considered one observation for experiments that reported results at the species level. Observations for different species from the same study were considered independent, allowing us to determine the effects of species identity traits (e.g., mycorrhizal type, photosynthetic pathway, growth form) in modifying plant responses to nutrient treatments. For experiments that reported results at the treatment level, one mean value ± standard deviation per trait per nutrient fertilization treatment per experimental site was considered one observation.

Observations were integrated into a compiled dataset through multiple pathways. First, summary statistics (mean, standard deviation, replication scheme) were calculated directly from published datasets from studies that adopted open data practices. Where possible, summary statistics were extracted from tables included in the main text or supplemental information if studies did not explicitly publish their data. If studies did not include their data or provide summary statistics in tables, we digitized plots using information about treatment and sample replication information. Plots were digitized in R (version 4.4.2) using the ‘metadigitise’ package (Pick *et al.*, 2019). Studies that did not include clear descriptions about the replication scheme were not included in the dataset. Overall, this data extraction approach rendered 4680 observations (1560 observations each for N, P, and N+P treatments) from 85 studies. Of these studies, 78 were field manipulation experiments, 6 were greenhouse manipulation experiments, and 1 was a growth chamber experiment. Of the field manipulation experiments, 166 independent sites were represented, spanning a broad global gradient and diverse array of biome types (Table S1; Fig. 1; Fig. S1). The dataset also includes data comprising 170 species from 54 families, representing diverse growth forms, growth durations, nutrient acquisition strategy, and photosynthetic pathway.

**Figure 1**



**Figure 1**

*Moderator variables*

All field experiments reported site latitude and longitude coordinates. Using these coordinates, we extracted site mean monthly temperature, precipitation, and solar radiation spanning 1970-2000 using the Climatic Research Unit Time Series v4.09 (CRU TS v4.09) gridded data product (Harris *et al.*, 2020) downscaled to a 30 arc-second spatial resolution with WorldClim 2.1 (Fick & Hijmans, 2017). We also extracted site aridity using a complementary gridded data product (Global-AI\_PET\_v3) using the same time period (1970-2000) and spatial resolution (30 arc-seconds) (Zomer *et al.*, 2022). This product uses WorldClim 2.1 to calculate monthly aridity as a function of mean monthly precipitation per unit mean monthly potential evapotranspiration, estimating potential evapotranspiration using the Penman-Monteith approach.

Mean monthly temperature (°C), mean monthly precipitation (mm), mean daily solar radiation (kJ m-2 day-1), and mean monthly aridity (unitless) were extracted from the grid cell containing each site using the “extract” function in the “raster” R package (Hijmans, 2010). Solar radiation values (from kJ m-2 day-1) were converted to photosynthetically active radiation (μmol m-2 s-1) assuming a conversion factor of 2.1 μmol m-2 s-1per unit W m-2. Site mean growing season temperature (*T*g; °C), growing season precipitation (*P*g), growing season PAR (*PAR*g; μmol m-2 s-1), and growing season aridity (*AI*g; unitless) were estimated using the months where mean temperature was above 0°C. All growing season climate data are reported in Table X.

Species identity traits were included for all measurements that were collected at the species level. Specifically, we included information about species family, growth form (tree/shrub, graminoid, forb), growth duration (annual, perennial), photosynthetic pathway (C3, C4), N2-fixation ability (N2-fixer or non-fixer), and mycorrhizal type (AM, EcM, dual AM-EcM, facultative AM, ErM, and non-mycorrhizal). N2-fixation ability was determined based on whether species were in the *Fabaceae* family. Mycorrhizal type was assigned from the FungalRoot database using the genus of each species (Soudzilovskaia *et al.*, 2020).

*Determination and analysis of individual and interaction effect sizes*

We followed an established framework for assessing individual and interactive effects of multiple treatments in meta-analysis (Yue *et al.*, 2017). First, we used the natural logarithm of the response ratio (ln RR) to determine the individual effects of N, P, and N+P addition on leaf and whole-plant traits. For each observation *i* (i.e., trait per species per site per experiment), we calculated the natural logarithm of the response ratio (ln RR) as:

(1)

Where is the mean value of a treatment (i.e., N, P, or N+P addition) and is the mean value of the control treatment for each observation. We determined the weighted log-response ratio () across observations as:

(2)

Where ln RRi is the log-response ratio of observation *i* given in (1), *w*i is the weight of each log-response ratio, and *k* is the total number of observations. *w*i was calculated as the inverse of the variance (*v*i) of observation *i* (that is, *w*i = 1 / *v*i). *v*i was calculated as:

(3)

Where *s*t and *s*c are the standard deviations of the treatment and control groups, respectively, and *n*t and *n*c are the sample sizes of the treatment and control groups.

Next, we used Hedge’s *d* to determine the interactive effect of N and P addition on leaf and whole-plant traits (Yue *et al.*, 2017; Ding *et al.*, 2025). For each observation *i*, the interactive effect size of N and P addition (dNPi) was calculated as:

(4)

Where ,,, and refer to the mean of the N, P, N+P, and control treatments, respectively, for each observation *i*. *s*int\_i refers to the pooled standard deviation across treatments, calculated as:

(5)

Where *N*ci, *N*ni, *N*pi, and *N*npi refer to the sample sizes of control, N, P, and N+P treatments, respectively. *S*ci, *S*ni, *S*pi, and *S*npi refer to the sample sizes of control, N, P, and N+P treatments, respectively, for each observation. In (6), *J*int\_i refers to a correction term for small sample size bias, calculated as:

(6)

We determined the weighted interaction effect size () of each trait across experiments as:

(7)

Where *d*NPi is the interaction effect size of observation *i* given in (6), *w*dnpi is the associated weight of each interaction effect size, and *k* represents the total number of observations. *w*dnpi was calculated as the inverse of the variance (*vd*NPi) of observation *i* (that is, *w*dnpi = 1 / *vd*NPi). *vd*NPi was calculated as:

(8)

*Data analysis*

We constructed a series of mixed-effects meta-regression models to understand the individual and interactive effects of N and P addition on leaf and whole-plant traits. Three separate models were created for each trait to assess the individual effects of N, P, and N+P addition using log-response ratios and their associated variances. We created a fourth model for each trait to assess the interactive effect of N and P addition using *d*NPi values and their associated variances and weights. We also assessed the role of climate or species identity moderated the response of each trait to N, P, or N+P addition by including *T*g, *AI*g, *PAR*g, photosynthetic pathway, N2-fixation ability, and mycorrhizal strategy as moderator variables. In all cases, we built mixed-effects meta-regression models using the ‘rma.mv’ function in the ‘metafor’ R package (Viechtbauer, 2010), manually specifying the weights of each observation as explained above, fitting each model using restricted maximum likelihood estimation, and including experiment as a random intercept term. We also used the ‘orchaRd’ R package to assess and visualize moderator effects (Nakagawa *et al.*, 2023).

Interactions between N and P addition on leaf and whole-plant traits were classified into three categories: additive, synergistic, and antagonistic. Following Yue et al. (2017), null interaction effects (i.e. the 95% confidence intervals overlapped with zero) were classified as additive effects, where the combined effect of N and P addition had similar effects as the sum of the individual effects of N and P addition. An interaction was classified as synergistic (i.e. the combined effect of N and P addition was stronger than predicted through individual effects) if positive individual effects of N and P addition correspond with a significant positive interaction effect, if negative individual effects of N and P addition correspond with a significant negative interaction effect, or if mixed sign individual effects (e.g., one positive and one negative effect) correspond with a significant negative interaction effect. An interaction was classified as antagonistic (that is, the combined effect of N and P addition was weaker than predicted through individual effects) if positive individual effects of N and P addition correspond with a significant negative interaction effect, if negative individual effects of N and P addition correspond with a significant positive interaction effect, or if mixed sign individual effects correspond with a significant positive interaction effect.

**Results**

*Leaf chemistry*

N addition significantly decreased *M*area and *P*mass, but increased *N*mass, *N*area, and leaf N:P, and had no effect on *P*area (Table SX; Fig. 2a). P addition had no effect on *M*area, *N*mass, *N*area, but increased *P*mass and *P*area and decreased leaf N:P (Table SX; Fig. 2a). N+P addition reduced *M*area and leaf N:P, and increased *N*mass, *N*area, *P*mass, and *P*area (Table SX; Fig. 2a). Interaction effect sizes indicated that the responses of *M*area, *N*mass, *N*area, *P*mass, and *P*area to N+P addition were largely additive, while the response of leaf N:P was synergistic (Table SX; Fig. 2b).

*T*g decreased the effect of N addition on *N*mass (Table SX), *N*area (Table SX), and leaf N:P (Table SX), but did not modify the effects of N addition on *M*area, *P*mass, or *P*area (Table SX). *AI*g had a marginally significant negative effect on the response of *N*mass and leaf N:P to N addition, but did not modify any of the other leaf chemistry trait response to N addition (Table SX). *PAR*g did not modify any leaf chemistry trait response to N addition.

*T*g decreased the effect of P addition on *P*mass (Table SX) had a marginally significant negative effect on the response of *P*area to P addition (Table SX), and increased the effect of P addition on leaf N:P (Table SX), but did not modify any nitrogen-related chemistry trait (Table SX). *AI*g similarly

, but did not modify any other leaf chemistry trait response to P addition

The effects of N addition on *N*mass and *N*area were strongest in colder, drier climates, as indicated by a negative effect of increasing *T*g and *AI*gon the responses of *N*mass and *N*area to N addition. Similar patterns were observed with phosphorus, where the effects of P addition on *P*mass and *P*area were strongest in colder and drier climates due to negative effects of increasing *T*g and *AI*gon the responses of *P*mass and *P*area to P addition. These patterns scaled to modify leaf trait responses to N+P addition, where N+P addition effects on *N*mass and *P*mass were strongest under

There was no evidence to suggest that *PAR*g modified leaf chemistry responses to N or P addition.

Similarly, there was a negative effect of increasing *T*g on the response of *P*mass and a marginally significant negative effect of increasing *T*g on the response of *P*area to P addition. *AI*g decreased the response of *N*mass to N addition

and on the response of *P*mass to P addition. We also observed a negative effect of increasing *AI*g on the response of *N*mass to N addition and marginally significant negative effect

Growing season temperature had a negative effect on the response of *N*mass and *N*areato N addition and the response of *P*mass to P addition, leading to significant positive effects of these responses under low

and *P*mass

Growing season temperature played no role in shaping *M*area responses

*Leaf photosynthetic traits*

N addition had no effect on any photosynthetic parameter (*A*sat, *V*cmax, *J*max, *PNUE*, *PPUE*), although there was a marginally significant positive effect on *J*max:*V*cmax (Table SX, Fig. 3a). P addition increased *J*max but had no effect on any other photosynthetic parameter (Table SX, Fig. 3a). While N and P addition individually had no effect on *A*sat, their combined addition significantly increased *A*sat (Table SX, Fig. 3a). Additionally, N+P addition increased *J*max and *J*max:*V*cmax and had no effect on *V*cmax, *PNUE*, or *PPUE* (Table SX, Fig. 3a). All leaf photosynthetic trait responses to N+P addition were the product of additive interactions (Table SX, Fig. 3b).

*Whole-plant traits*

N addition did not affect total biomass or belowground biomass, but strong increases in aboveground biomass led to reductions in the root mass fraction and root:shoot ratio (Table X; Fig. 4a). Both P and N+P addition increased total biomass through increased aboveground biomass and no change in belowground biomass, yielding a marginally significant reduction in the root mass fraction and reduction in the root:shoot ratio (Table X; Fig. 4a). All whole-plant trait responses to N+P addition were the product of additive interactions, except aboveground biomass, which exhibited a synergistic response. This interaction indicated a stronger positive effect of N+P addition on aboveground biomass than expected from the sum of individual N and P addition effects (Table SX; Fig. 4b).

*Climate moderator effects*

Climate played no role in modifying *M*area responses to N addition. Growing season aridity had a positive effect on the response of *M*area to P addition and N+P addition

Growing season temperature and light availability did not modify *M*area responses to N or P addition, but increasing growing season temperature had a marginal positive effect on the response of *M*area to N+P addition ()

the effects of N or P addition on *M*area

There was no effect of *T*g or

Climate variables did not modify the effects of N addition on *M*area

Climatic variables (growing season temperature, growing season aridity index, growing season light availability) did not modify the effects of N addition on *M*area, . However, N addition

were unimportant for clarifying the role of N, P, or N+P addition on *M*area

Climatic variables indicated that the leaf nutrient responses to N and P addition were modulated by factors that influenced demand for building and maintaining photosynthetic enzymes.

**Discussion**

Here, we conducted a global meta-analysis to determine the effects of N, P, and the combined effect of N and P on a series of plant functional traits ranging from leaf morphological and chemical traits to whole-plant biomass. We used this approach to understand general effects of N and P addition on plant functional traits and to determine whether these responses were the product of additive, synergistic, or antagonistic responses. In general, our results indicate that nitrogen and phosphorus addition played a stronger role in modifying leaf morphological and chemical traits and whole-plant traits than photosynthetic traits, consistent with patterns expected from eco-evolutionary optimality theory (Stocker *et al.*, 2025). Additionally, our results indicate that plant responses to N and P addition in combination were largely the response of additive interactions between N and P addition, supporting previous work noting that interactive effects of global change factors are often the product of additive interactions (Yue *et al.*, 2017; Ding *et al.*, 2025). In other words, plant responses to N and P addition in combination were no different than the sum of the individual effects of N and P addition. This was true for all traits with the exception of leaf N:P and aboveground biomass, which showed synergistic responses to N and P addition. Below, we explain and contextualize these patterns and use the responses observed here to suggest areas of future research to refine our understanding of interactions between nitrogen and phosphorus cycling.

*Plant responses to combined N and P addition are driven by additive interactions*

The majority of plant responses to N and P addition were driven by additive interactions. This was true regardless of whether plant functional traits were at the leaf or whole-plant level, with the exception of leaf N:P and aboveground biomass

*Leaf nutrient and biomass responses to N and P additions are stronger than photosynthetic responses*

In general, leaf nutrient and biomass responses to N and P additions were stronger in magnitude than photosynthetic responses. N addition had no role in shaping photosynthetic traits, while P addition weakly increased *J*max and had no effect on any other photosynthetic trait. Previous work has demonstrated that investment in photosynthetic enzymes is largely determined as a function of demand for soil resources, where demand to build and maintain photosynthetic enzymes determines nutrient allocation to photosynthetic enzymes (Smith *et al.*, 2019, 2024; Harrison *et al.*, 2021; Stocker *et al.*, 2025; Perkowski *et al.*, 2025).

*Climatic demand determines plant responses to nutrient addition*

The effects of N addition on *N*mass and *N*area were strongest in colder, drier climates, as indicated by a negative effect of increasing *T*g and *AI*gon the responses of *N*mass and *N*area to N addition. Similar patterns were observed with phosphorus, where the effects of P addition on *P*mass and *P*area were strongest in colder and drier climates due to negative effects of increasing *T*g and *AI*gon the responses of *P*mass and *P*area to P addition. These patterns scaled to modify leaf trait responses to N+P addition, where N+P addition effects on *N*mass and *P*mass were strongest under

*Future research needs and directions*

Unfortunately, we could not investigate the role of climate in modulating photosynthetic responses to nitrogen and phosphorus addition. This limitation was due to the limited number of full-factorial nitrogen and phosphorus experiments that are conducted in the field, representing a clear future area of needed research and key knowledge gap that remains in our understanding of how photosynthetic processes respond to nutrient additions. Previous work has shown that climatic factors which influence demand play a predictable and key role in determining leaf nitrogen allocation responses to nitrogen and phosphorus addition (Cheaib *et al.*, 2025). Our work supports these findings by showing that leaf nutrient allocation responses to nitrogen and phosphorus addition are at least partly dependent on climate and associated demands for soil resources. However, similar field analyses that scale these patterns to photosynthetic traits remain lacking. Quantifying these responses is particularly important, as recent work has highlighted that the fraction of leaf nutrients (nitrogen in this case) allocated to photosynthetic tissues decrease in response to increasing nitrogen availability and are dependent on climate-related demand for soil resources (Waring *et al.*, 2023; Cheaib *et al.*, 2025; Perkowski *et al.*, 2025). Without field experiments that quantify leaf photosynthetic responses to nutrient treatments, we are not able to comment on whether these responses scale with leaf nutrient allocation responses in ways that are predicted through eco-evolutionary optimality.

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