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Co-Evaluation of Plant Leaf Nutrient Concentrations and Resorption in Response to Fertilization under Different Nutrient-Limited Conditions

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Abstract: Plant leaf nutrient concentrations and resorption are sensitive to fertilization, yet their co-responses under different nutrient-limited conditions have not been well studied. We conducted a meta-analysis from a global dataset of 43 reports, including 130 observations of studies with plant leaf nitrogen (N) or phosphorus (P) concentrations and nitrogen resorption efficiency (NRE) or phosphorus resorption efficiency (PRE), in response to fertilization under different nutrient-limited conditions divided by the thresholds of leaf N:P ratio values of 10 and 20. The results showed that N fertilization generally increased leaf N concentration and decreased NRE, with greater magnitudes under N-limited conditions. P fertilization also generally increased leaf P concentration and decreased PRE, with greater magnitudes under P-limited conditions. N fertilization decreased leaf P concentration and increased PRE only under the N-limited condition. Under the P-limited or N and P co-limited conditions, however, N fertilization increased leaf P concentration and did not change PRE. Moreover, P fertilization did not change leaf N concentration under all nutrient-limited conditions but significantly increased NRE under the N-limited or N and P co-limited conditions. These findings suggest that plants cope with fertilization-induced N limitation vs. P limitation at the leaf level with different nutrient-use strategies.

Keywords: N addition; P addition; N and P co-addition; nutrient limitation; nutrient resorption efficiency

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1. Introduction

Leaf nutrient concentration and resorption play an important role in determining plant nutrient-use strategies [1]. High leaf nutrient concentration and low leaf nutrient resorption generally reflect a "resource spending" nutrient use strategy for plants to quickly grow and develop [2]. However, low leaf nutrient concentration and high leaf nutrient resorption usually reflect a "conservative consumption" nutrient use strategy for plant survival and reproduction [3]. Leaf nutrient concentration and stoichiometry also reflect plant nutrient status and the strength of nutrient limitation in plants [4,5]. Moreover, leaf nutrient resorption is a fundamental process through which perennial plants withdraw nutrients from leaves before abscission, which is important for plants to improve nutrient use efficiency and reduce the dependence on external nutrient supply [6]. Nutrient resorption also strongly influences ecosystem nutrient cycling by affecting litter quality and thus litter decomposition rates [7,8]. Therefore, a better study of combined leaf nutrient concentration and nutrient resorption efficiency (NuRE, percentage of nutrient recovered from senescing leaves) is vital for the accuracy of terrestrial biogeochemical models in predicting plant productivity [8].

Nutrient limitation to plant growth is widespread in terrestrial ecosystems, and nitrogen (N) and phosphorus (P) are the most common limiting elements, both individually and in combination [9]. While many studies have concentrated on understanding the nutritional controls of leaf nutrient concentrations and resorption, most focused on leaf N and P concentrations, nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE) [10–12]. Overall, the leaf nutrient concentrations enhanced while NuREs declined with the respective nutrient fertilization on a global scale [13]. Fertilization with N alone or P alone usually breaks the balance between N and P in the soil, causing the shift of relative nutrient limitation. However, the responses of leaf P concentration and PRE to N fertilization or the responses of leaf N concentration and NRE to P fertilization were highly variable [13], showing negative [2], neutral [3,14,15] and positive changes [5,16]. These contrasting responses have previously tried to be attributed to plant growth types, ecosystem types, climate factors, soil nutrient status and fertilization measures [16]. Plants growing under different nutrient limitations usually adopt different nutrient use strategies, with lower leaf nutrient concentration and higher NuRE in infertile than in fertile conditions. Plant nutrient regimes (such as N-limited, N and P co-limited and P-limited conditions) across the world may also significantly influence the response pattern of leaf nutrient concentration and resorption to fertilization, yet this hypothesis has not been well studied.

Here, we explored the combined responses of plant leaf nutrient (N and P) concentrations and NuREs (NRE and PRE) to fertilization by collecting published data from global nutrient (N, P or both) fertilization experiments conducted in field environments, including 130 observations of 43 studies (Figure 1). The thresholds of leaf N:P ratios (for example, 10:1 versus 20:1) have been widely used to indicate N or P limitation indirectly, and N and P co-limitation when 10 < N:P < 20 [9]. This will provide an opportunity for us to evaluate how different nutrient-limited conditions regulate the responses of leaf nutrient concentration and NuRE to fertilization on a global scale. We expected that the responses of leaf nutrient concentration and NuRE to fertilization varied under different nutrient-limited conditions divided by the thresholds of leaf N:P ratios. Specifically, we hypothesized that: (1) N fertilization enhanced leaf N concentration and reduced NRE greater than under N-limited conditions, while P fertilization enhanced leaf P concentration and reduced PRE greater than under P-limited conditions; (2) N fertilization reduced leaf P concentration and enhanced PRE greater than under P-limited conditions, while P fertilization reduced leaf N concentration and enhanced NRE greater than under N-limited conditions; (3) N and P co-fertilization would enhance both leaf nutrient concentrations and reduce NuRE, with greater magnitudes than for leaf N concentration and NRE under N-limited conditions as well as for leaf P concentration and PRE under P-limited condition.

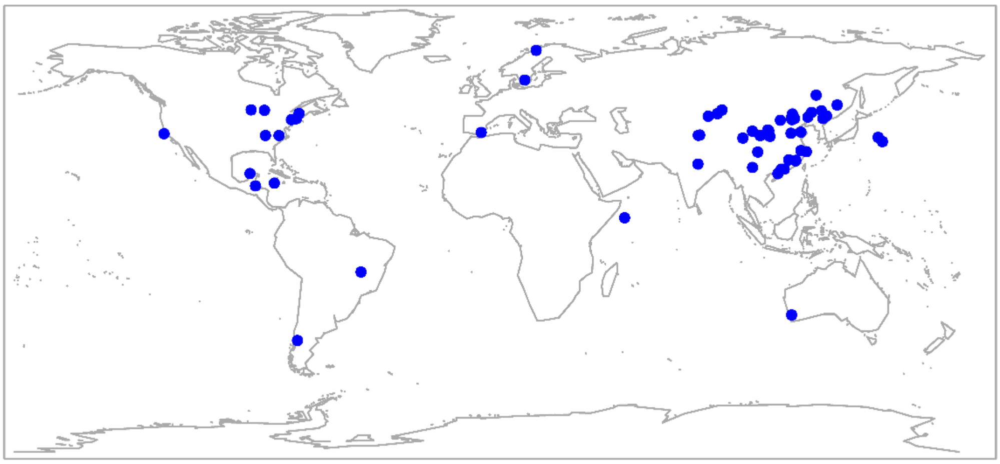

Figure 1. Global distribution of sites included in this study. The blue points represent each data sampling site around the world.

2. Materials and Methods

We searched for published papers reporting the impacts of fertilization on the leaf NRE and PRE, as well as N and P concentrations in green and senesced leaves, using Web of Science and Google Scholar. The searches included combinations of the terms 'nitrogen fertilization', 'nitrogen addition', 'nitrogen deposition', 'nitrogen enrichment', 'phosphorus fertilization', 'phosphorus addition', 'phosphorus deposition', 'phosphorus enrichment', and 'nutrient resorption efficiency', 'nitrogen resorption efficiency', 'phosphorus resorption efficiency', 'nitrogen or phosphorus concentrations in green and senesced leaves'. All the original data were extracted from tables and figures in the published papers using GETDATA (http://getdata-graph-digitizer.com/ (accessed on 15 March 2021)).

All published results were systematically reviewed before September 2021. We included studies with N or P fertilization and the combination of N and P fertilization. Only the data including both leaf nutrient concentrations and NuREs from field experiments were included. If the target variables from the same field observation experiment were published in different journal articles, we only used the average values for the analysis. Our data covered the terrestrial ecosystem types of forests, grasslands, wetlands and deserts. We also collected plant growth type, the fertilization source and rates, location (latitude (°) and longitude (°)), climatic factors (i.e., mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm)) and climate zone (see Supplementary Materials). The threshold of leaf N:P ratios (for example, 10:1 versus 20:1) has been widely used to indicate N or P limitation indirectly. Hence, we further divided the leaf N:P ratio values of 10–20 as the N and P co-limited condition, N:P < 10 as the N-limited condition, and N:P > 20 as the P-limited condition, respectively. The final data set was drawn from 43 unique studies [3,17–58] representing 130 observations (Figure 1).

Considering the leaf mass loss during leaf senesces, we corrected the senesced-leaf nutrient concentrations via the mass loss correction factor (MLCF) to compensate for the underestimation of NuRE. In this study, NuRE was recalculated with the following Equations:

$$Nu'_{senesced} = Nu_{senesced} \times \text{MLCF}$$

$$\text{NuRE} = \frac{Nu_{green} - Nu'_{senesced}}{Nu_{green}} \times 100\%$$

where Nu_{green} and $Nu'_{senesced}$ are nutrient concentrations in green and senesced leaves recalculated with MLCF. MLCF here is a global average value, 0.784 for deciduous plants, 0.78 for evergreen angiosperms, 0.745 for conifers, 0.713 for graminoids and 0.64 for forbs [8].

To examine the effects of fertilization on leaf nutrient concentration and NuRE, we calculated response ratios of each observation by:

$$\text{RR} = \ln\left(X_e / X_c\right) = \ln(X_e) - \ln(X_c) \quad (1)$$

where RR is the ratio of the mean value of the chosen variable (leaf nutrient concentrations or NuREs) in the treatment group (X_e) to that in the control group (X_c), an index of the effect of the experimental treatment on the target variable.

We used sample size and standard deviations to weigh the RR (w) [59,60], i.e.,

$$w = \frac{1}{v} \quad (2)$$

where,

$$v = \frac{S_e^2}{n_e X_e^2} + \frac{S_c^2}{n_c X_C^2} \quad (3)$$

where S_e and S_c are the standard deviations and n_e and n_c are the sample sizes for the experimental treatment and the control groups, respectively.

In this meta-analysis, we calculated a weighted response ratio (RR++) from individuals by giving greater weight to studies. The weighted mean log response ratio (RR++) is calculated by:

$$\mathrm{RR}++ = \frac{\sum_{i=1}^{m}(RR_i \times w_i)}{\sum_{i=1}^{m}(w_i)} \quad (4)$$

where i = 1, 2, 3, ... , m; with the standard error as:

$$\mathrm{s}(\mathrm{RR}++) = \sqrt{\frac{1}{\sum_{i=1}^{m} w_i}} \quad (5)$$

The 95% confidence interval for the log response ratio is

$$95\%\ \mathrm{CI} = \mathrm{RR}{+}{+} \pm 1.96 \times \mathrm{s}(\mathrm{RR}{+}{+}) \quad (6)$$

The meta-analysis was conducted using "metacont" and "forest" functions in the R package "meta" (https://cran.r-project.org/web/packages/meta/index.html (accessed on 20 February 2022)). Because of the non-Gaussian distribution of the effect sizes, we used nonparametric approaches to test the hypothesis that the mean effect size is not equal to zero (that is, $\log_e(1/1)$). We bootstrapped 95% confidence intervals by sampling from the distribution of response ratios 10,000 times with replacements and taking the 2.5th and 97.5th quantiles of the bootstrapped distribution. The fertilization effect was considered to be significant if the 95% confidence interval (CI) of RR++ did not overlap with zero [61]. To quantify the importance of different predictors in determining the response of leaf nutrient concentrations and NuRE to fertilization, we also used the machine learning technique 'random forests'. We generated 10,000 regression 'trees' each recursively portioning the observation into groups, using the "gbm" function in the R package "gbm" (https://cran.r-project.org/web/packages/gbm/index.html (accessed on 20 April 2022)). After the analyses, among the potential influencing factors, including categorical factors (ecosystem type, plant growth type, fertilization types, climate zone and different nutrient-limited conditions) and continuous factors (experimental duration, fertilization application rate, MAT and MAP), we found that the most important influencing factor was the plant nutrient-limited condition (see Figures S3 and S4). Therefore, in this study, we focused on exploring how leaf N or P concentrations and NRE or PRE responded to fertilization under different nutrient-limited conditions. The mean RR++s were then compared under different nutrient-limited conditions using an approach analogous to one-way weighted ANOVA.

All statistical analyses were performed using the R package 4.1.3 software. Packages of ggplot2, meta, maps, mapdata, gbm and svglite were used.

3. Results

3.1. Effects of N Fertilization on Leaf Nutrient Concentrations and Resorption

N fertilization significantly increased leaf N concentration in general, with a greater increase under N-limited than P-limited and N and P co-limited conditions (Figure 2A). N fertilization increased leaf P concentration under P limitation and N and P co-limitation but decreased P concentration under N limitation (Figure 2B). N fertilization significantly decreased NRE under N-limited and N and P co-limitation but not under P limitation (Figure 2C). N fertilization did not have a significant effect on PRE under P limitation and N and P co-limitation but significantly increased PRE under N limitation (Figure 2D).

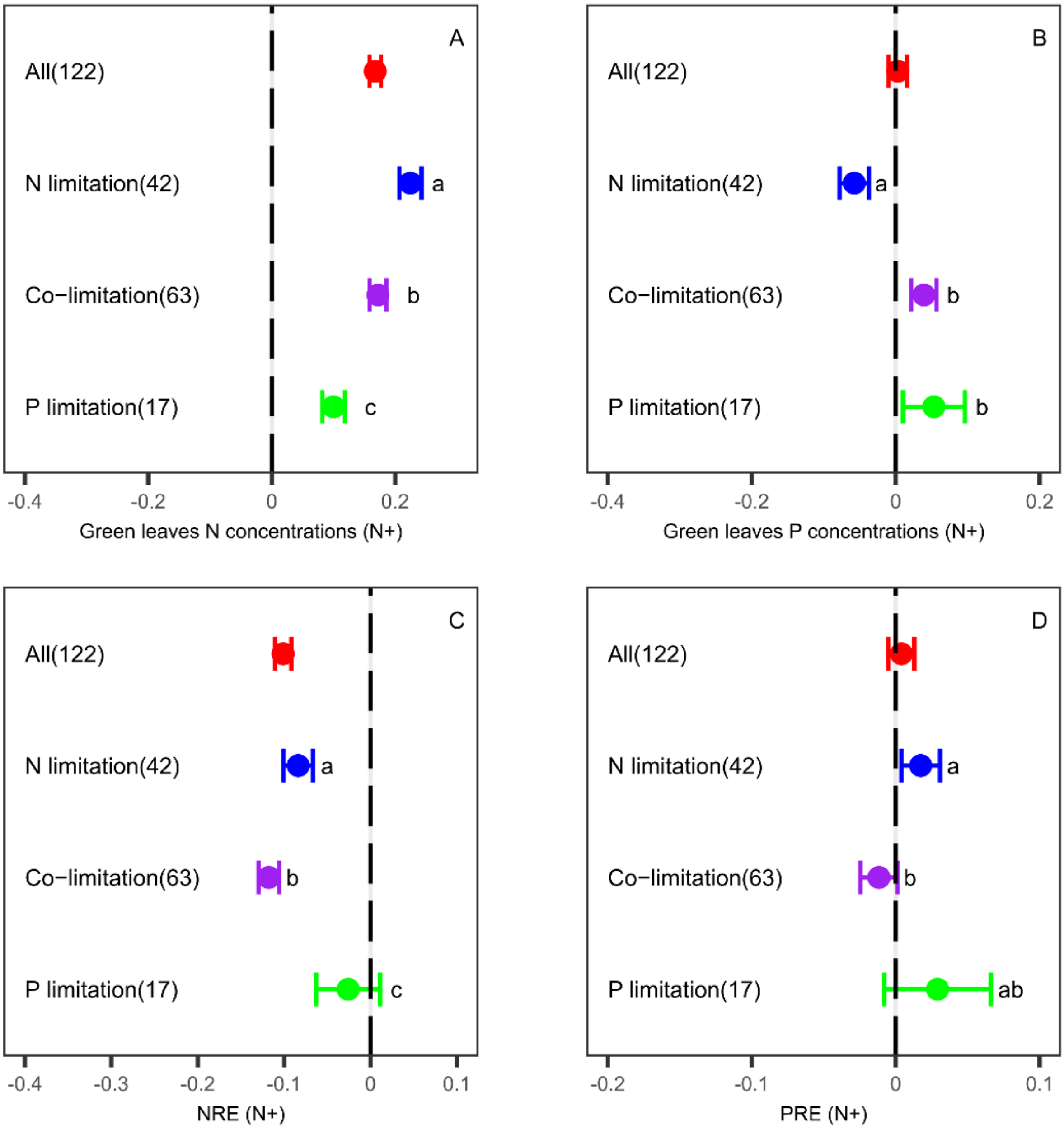

Figure 2. Responses of leaf nitrogen (**A**) and phosphorus (**B**) concentrations, nitrogen resorption efficiency (NRE) (**C**) and phosphorus resorption efficiency (PRE) (**D**) to N fertilization (N+). Error bars are the 95% confidence intervals of the mean. Different letters indicate the significant differences among different nutrient limitations under N fertilization. The red (bule, purple and green) points represent leaf N (P/NRE/PRE) in general, under N limitation, co-limitation and P limitation, respectively.

3.2. *Effects of P Fertilization on Leaf Nutrient Concentrations and Resorption*

P fertilization did not change leaf N concentration but increased leaf P concentration with a greater increase under P-limited than N-limited and co-limited conditions (Figure 3A,B). P fertilization significantly increased NRE in general, under N-limited and N and P co-limited conditions (Figure 3C). P fertilization decreased PRE significantly under all conditions (Figure 3D).

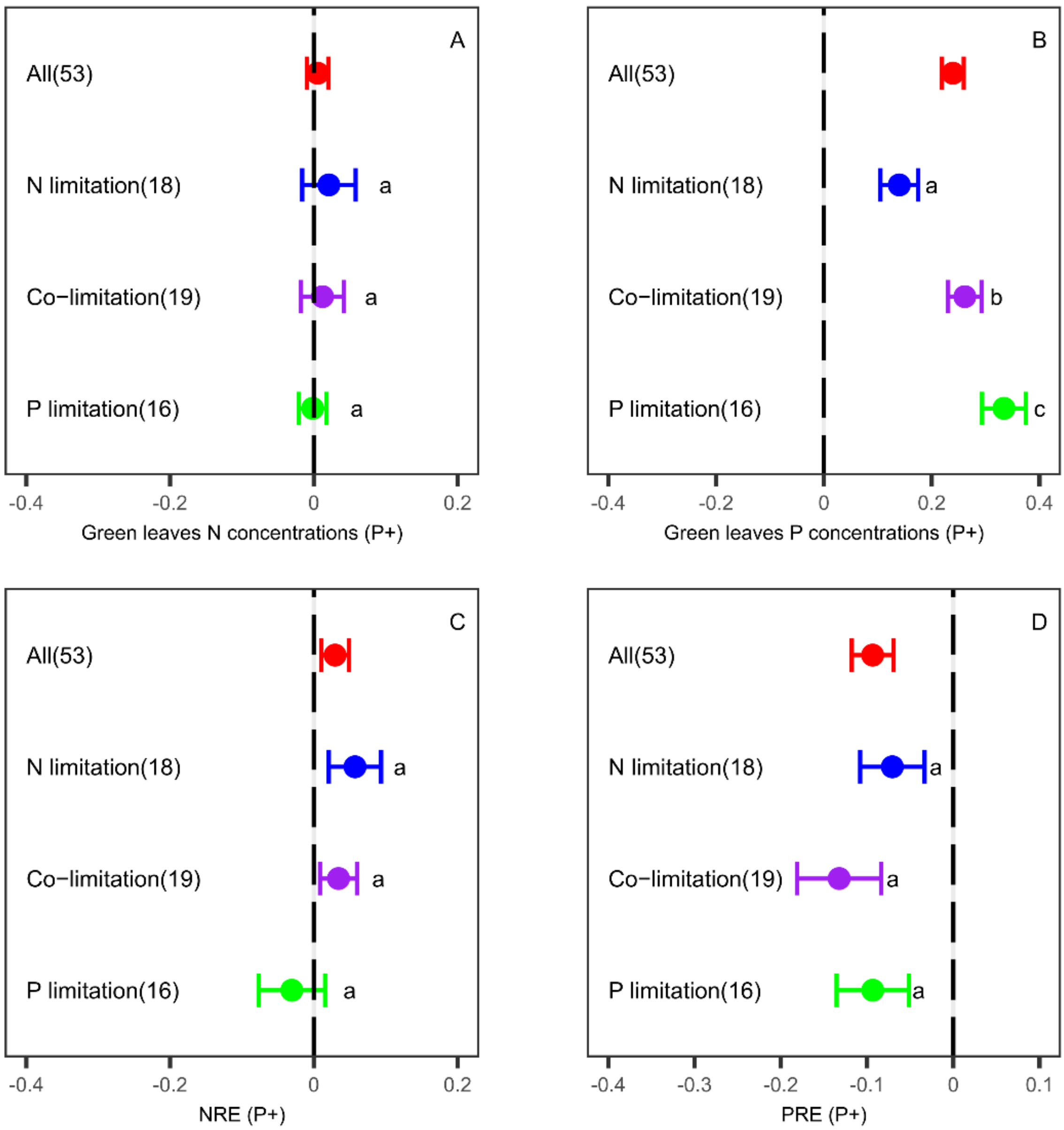

Figure 3. Responses of leaf nitrogen (**A**) and phosphorus (**B**) concentrations, nitrogen resorption efficiency (NRE) (**C**) and phosphorus resorption efficiency (PRE) (**D**) to P fertilization (P+). Error bars are the 95% confidence intervals of the mean. Different letters indicate the significant differences among different nutrient limitations under P fertilization. The red (bule, purple and green) points represent leaf N (P/NRE/PRE) in general, under N limitation, co-limitation and P limitation, respectively.

3.3. Effects of N and P Co-Fertilization on Leaf Nutrient Concentrations and Resorption

N and P co-fertilization increased leaf N and P concentrations, with greater increases under their respective nutrient-limited conditions (Figure 4A,B). For example, leaf N concentration increased more under N-limited and N and P co-limited conditions than under P limitation. Leaf P concentration increased more under P-limited conditions than under N-limited and N and P co-limited conditions. In general, N and P co-fertilization significantly decreased NRE and PRE (Figure 4C,D). While NRE under P limitation and PRE under N limitation did not show significant responses to N and P co-fertilization, NRE and PRE both decreased significantly in general under other nutrient-limited conditions (Figure 4C,D).

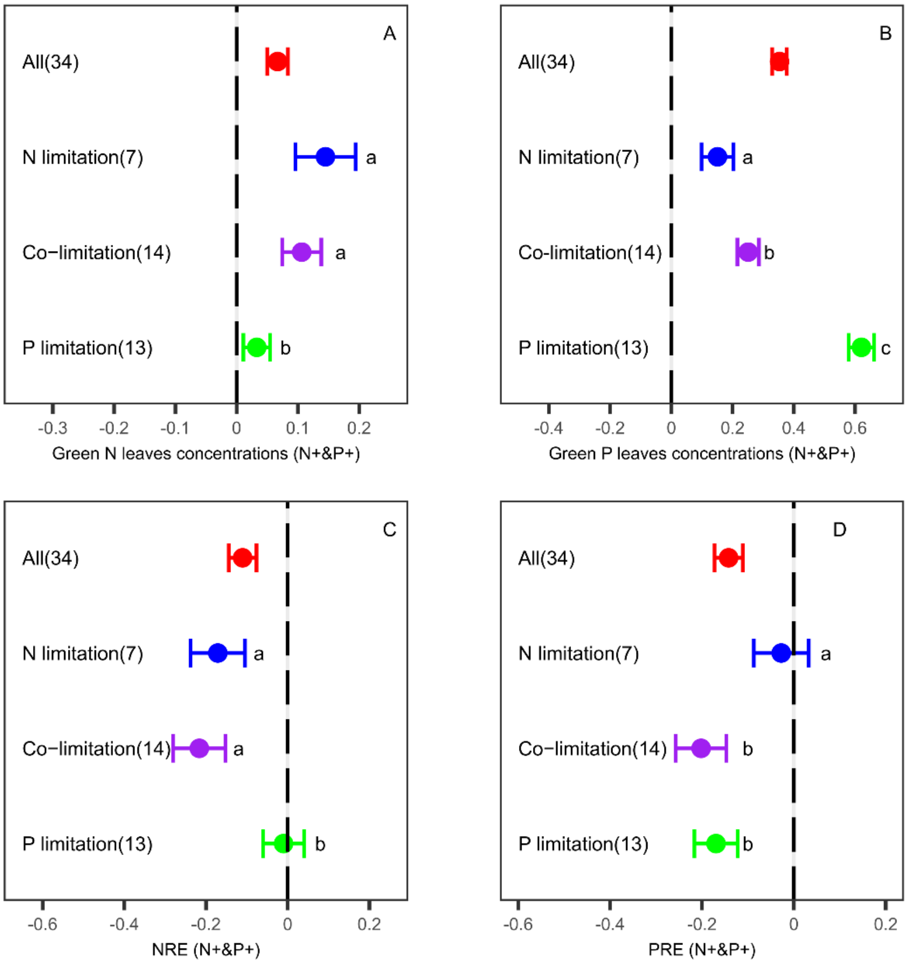

Figure 4. Responses of leaf nitrogen (**A**) and phosphorus (**B**) concentrations, nitrogen resorption efficiency (NRE) (**C**) and phosphorus resorption efficiency (PRE) (**D**) to the combination of N and P fertilization (N+ & P+). Error bars are the 95% confidence intervals of the mean. Different letters indicate the significant differences among different nutrient limitations under N and P co-fertilization. The red (bule, purple and green) points represent leaf N (P/NRE/PRE) in general, under N limitation, co-limitation and P limitation, respectively.

4. Discussion

Similar to the previous meta-analysis study [62], our results showed that, overall, N and P fertilization significantly enhanced their respective leaf nutrient concentrations but significantly reduced NRE and PRE, respectively. Co-fertilization with N and P significantly enhanced both leaf N and P concentrations and significantly reduced both NRE and PRE. These findings confirm that, when increasing nutrient N or P supplies, plants tend to absorb more respective N or P in green leaves and less from senescing leaves.

With the machine learning technique, in this study, we also showed that plant nutrient-limited conditions divided by the thresholds of leaf N:P ratios was the most important predictor in determining the response of leaf nutrient concentrations and NuREs to fertilization. For example, N fertilization generally increased leaf N concentration and decreased NRE, with greater magnitudes under the N-limited condition. P fertilization also generally increased leaf P concentration and decreased PRE, with greater magnitudes under the P-limited condition. This is not surprising and is consistent with our first hypothesis. Plants growing in infertile soils are usually limited by nutrient availability; in order to survive and reproduce, they have to adopt a “conservative consumption” nutrient use strategy with low leaf nutrient concentrations and high NuRE [3]. Fertilization to such infertile soils could significantly improve nutrient availability, thus greatly enhancing leaf nutrient concentrations while reducing NuREs. In contrast, plants growing in fertile soils are not limited by nutrient availability and usually adopt a "resource spending" nutrient use strategy with high leaf nutrient concentrations and low NuREs for fast growth and development [2]. Fertilization of the fertile soils would not significantly promote plant nutrient absorption and growth and thus had relatively less effects on leaf nutrient concentrations and NuREs.

Inputs with N alone or P alone usually induce an imbalance between N and P in the soil, leading to a relatively greater limitation of P and N, respectively [63]. However, plants could regulate leaf nutrient absorption and/or resorption to maintain a balance between N and P in their organs and tissues [64]. In our study, leaf N concentration did not change under all nutrient-limited conditions with P fertilization, but NRE enhanced significantly under the N-limited or N and P co-limited conditions. This suggests that plants might mainly adopt a "conservative consumption" nutrient use strategy with high NRE to alleviate N shortage (N-limited and N and P co-limited conditions) under P fertilization. Intriguingly, we found that N fertilization reduced leaf P concentration and increased PRE only under the N-limited condition. Under the P-limited or N and P co-limited conditions, N fertilization enhanced leaf P concentration and did not change PRE. This suggests that plants alleviate P shortage under N fertilization primarily through improving P absorption from the soil. However, we noted that the responses of PRE to N fertilization between the N-limited condition and the P-limited condition did not significantly differ, hence needing more studies to verify the second hypothesis in the future. The difference in plants that cope with fertilization-induced N vs. P limitation is probably attributed to a greater capacity of the plants to resorb P (upper limit ~90%) than N (upper limit ~80%), as reported by previous studies [1,3,65]. For example, added N could usually stimulate substantial phosphatase activity and enhance soil P availability [66], as the phosphatase enzymes are rich in N. Moreover, plants can develop various strategies to enhance P acquisition and maintain leaf P concentration under the P-limited condition through modifying root morphology, increasing root exudation or interactions with soil microorganisms [67]. However, soil N mineralization is generally thought to be regulated by microbial activity depending largely on temperature, moisture and substrate [68]. Under the N-limited condition, N fertilization has a stronger potential to promote plant growth. The N-stimulated phosphatase activity or increase in soil availability may not meet plant P demand under the N-limited condition, thus enhancing PRE.

5. Conclusions

In general, the leaf nutrient concentrations enhanced while NuREs reduced with the respective nutrient fertilization. With N and P co-fertilization, both leaf N and P concentrations were enhanced under all nutrient-limited conditions, and NRE and PRE were reduced except under P-limited and N-limited conditions, respectively. Furthermore, N fertilization enhanced leaf N concentration and reduced NRE most under the N-limited condition (N:P < 10). Accordingly, P fertilization enhanced leaf P concentration and reduced PRE most under the P-limited condition (N:P > 20). In addition, P fertilization did not change leaf N concentration under all nutrient-limited conditions but significantly enhanced NRE under the N-limited or N and P co-limited conditions. Nitrogen fertilization reduced leaf P concentration and enhanced PRE only under the N-limited condition. Under the P limitation or N and P co-limitation, N fertilization enhanced leaf P concentration and did not change PRE. These findings suggest that plants cope with fertilization-induced N limitation vs. P limitation differently, with different leaf-level nutrient-use strategies, whereas such differential responses in plant nutrient concentrations and NuREs were insufficiently considered in either modeling or experimental frameworks. Therefore, our results foster the understanding of the response patterns and mechanism controls of leaf nutrient concentrations and resorption to fertilization, which may enable us to better predict how nutrient change connects with terrestrial biogeochemical cycles.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14050385/s1, Figure S1: Frequency distribution of the change in nitrogen resorption efficiency (NRE) under natural conditions (a)–(c); and the corresponding change in NRE under N addition (d), P addition (e) and N and P co-addition (f) on a global scale. The curves were fitted by a Gaussian function. Figure S2: Frequency distribution of the change in phosphorus resorption efficiency (PRE) under natural conditions (a)–(c); and the corresponding change in PRE under N addition (d), P addition (e) and N and P co-addition (f) on a global scale. The curves were fitted by a Gaussian function. Figure S3: The relative influence (%) of the effects of nutri. limit. (nutrient limitation, N-limitation, when green leaf N:P < 10, N and P co-limitation, when 10 < N:P < 20 and P-limitation when, N:P > 20), mean annual temperature (MAT), mean annual precipitation (MAP), fer. rate (fertilizer rates), fer. type (fertilizer types), latitude, longitude, species, ecosystem types and climate zones on the RRs (green leaf N and P concentration, NRE and PRE) under N fertilization (N+). Figure S4: The relative influence (%) of the effects of nutri. limit. (nutrient limitation, N-limitation, when green leaf N:P < 10, N and P co-limitation, when 10 < N:P < 20 and P-limitation, when N:P > 20), mean annual temperature (MAT), mean annual precipitation (MAP), fer. rate (fertilizer rate), fer. type (fertilizer types), latitude, longitude, species, ecosystem types and climate types on mean RR (green leaf N and P concentration, NRE and PRE) under P fertilization (P+).

Author Contributions: Conceptualization, J.L. and Q.D.; data collection, M.Z.; data curation and analysis, M.Z. and L.Z.; writing—original draft preparation, M.Z.; writing—review and editing, M.Z., L.Z., X.Y., J.L. and Q.D.; supervision, J.L. and Q.D.; project administration, J.L. and Q.D.; funding acquisition, X.Y. All authors have read and agreed to the published version of the manuscript.

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