

Down-regulation of tissue N:P ratios in terrestrial plants by elevated CO₂

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Abstract. Increasing atmospheric CO₂ concentrations generally alter element stoichiometry in plants. However, a comprehensive evaluation of the elevated CO₂ impact on plant nitrogen:phosphorus (N:P) ratios and the underlying mechanism has not been conducted. We synthesized the results from 112 previously published studies using meta-analysis to evaluate the effects of elevated CO₂ on the N:P ratio of terrestrial plants and to explore the underlying mechanism based on plant growth and soil P dynamics. Our results show that terrestrial plants grown under elevated CO₂ had lower N:P ratios in both above- and belowground biomass across different ecosystem types. The response ratio for plant N:P was negatively correlated with the response ratio for plant growth in croplands and grasslands, and showed a stronger relationship for P than for N. In addition, the CO₂-induced down-regulation of plant N:P was accompanied by 19.3% and 4.2% increases in soil phosphatase activity and labile P, respectively, and a 10.1% decrease in total soil P. Our results show that down-regulation of plant N:P under elevated CO₂ corresponds with accelerated soil P cycling. These findings should be useful for better understanding of terrestrial plant stoichiometry in response to elevated CO₂ and of the underlying mechanisms affecting nutrient dynamics under climate change.

Key words: climate change; element stoichiometry; elevated CO₂; growth rate hypothesis; meta-analysis; nutrient dynamics; progressive nitrogen limitation; terrestrial ecosystems.

INTRODUCTION

Stimulation of plant growth by rising atmospheric CO₂ concentration (i.e., the CO₂ fertilization effect) is well documented and has been incorporated into terrestrial biogeochemical models of global land carbon (C) dynamics (Norby et al. 2005, IPCC 2013). However, the magnitude of the CO₂ fertilization effect is still uncertain, largely due to uncertainty about the impact of nutrient limitation and stoichiometric nutrient coupling on plant growth (Zhang et al. 2011, 2014, Goll et al. 2012). Integrating nutrient dynamics into terrestrial C cycle models, in particular the limitations on plant growth imposed by N and P availability, has suggested that models without these limitations tend to overestimate the land C sink (Hungate et al. 2003, Wang and Houlton 2009, IPCC 2013, Zhang et al. 2014). Both experimental and modeling studies have shown that

elevated CO₂ stimulates plant C and N uptake, but a disproportionate increase in biomass C relative to N results in higher tissue C:N ratios (Luo et al. 2006). This probably leads to progressive N limitation, PNL (Luo et al. 2004, Reich et al. 2006, Norby et al. 2010). Plant uptake of P and the stoichiometry of tissue N:P ratios under elevated CO₂ levels have received considerably less attention, making the impact of P limitation more uncertain (Elser et al. 2007, Vitousek et al. 2010).

Because of limited P supplies, P sequestered in long-lived plant biomass pools can limit new plant growth (Vitousek et al. 2010). Therefore, over the long term, P limitation of plant growth could become more severe due to the stimulation of P uptake under elevated CO₂ (Goll et al. 2012, Peñuelas et al. 2013, Zhang et al. 2014). Moreover, recent progress in implementing mechanistic N and P schemes in terrestrial ecosystem models underscores the importance of P dynamic feedbacks (Zhang et al. 2011, 2014, Goll et al. 2012). However, despite these advances, a major uncertainty associated with these model predictions is the assumption that N and P concentrations or pools in terrestrial plants grown under elevated CO₂ vary in a similar proportion,

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maintaining a homeostatic N:P ratio in plant biomass (Ågren 2008, Zhang et al. 2011, 2014, Goll et al. 2012). This assumption that plants will maintain a homeostatic N:P ratio independent of environmental conditions is unlikely to be true, as it has been shown that this ratio is sensitive to environmental change (Loladze and Elser 2011, Ågren and Weih 2012). Thus, understanding how elevated CO₂ impacts plant N:P ratios is critical to making accurate predictions for C fixation in terrestrial ecosystems under future climate change.

The theory of stoichiometry predicts that plants grown in high CO₂ should tend to exhibit lower concentrations of all elements except those that make up carbohydrates (C, H, and O); furthermore, it predicts that elevated CO₂ should affect some minerals more than others (Loladze 2002). This means that elevated CO₂ should change plant stoichiometry. Indeed, a recent meta-analysis of 27 elements in foliar and edible tissues of 130 plant species and cultivars found that elevated CO₂ decreased N concentrations by ~15%, cf. ~8–9% decline in the concentrations of P and other minerals. It also found that elevated CO₂ lowered plant N:P and N:S by ~7%, and lowered the ratio of N to the rest of the plant ionome (Loladze 2014; see also Sardans et al. 2012, Yuan and Chen 2015). However, a comprehensive evaluation of elevated CO₂ impacts on plant N:P ratios and the underlying mechanism for those impacts has not been done.

Plant uptake of N and P may shift due to imbalances in N and P availability in soil under elevated CO₂ (Taub and Wang 2008) or because of differential nutrient investments for various biochemical responses to altered CO₂ availability (Sternner and Elser 2002). It is generally accepted that elevated CO₂ decreases soil N availability (de Graaff et al. 2006, Cheng et al. 2012), limits plant uptake of N from soil, and increases plant C:N ratios (Luo et al. 2004). Foliar concentrations of N generally decline more than other elements in plants exposed to elevated CO₂ (Loladze 2014), as (1) high CO₂ decreases the concentration of Rubisco, a major N pool in photosynthetic tissues (Bowes 1991, Taub and Wang 2008); and (2) high CO₂ reduces nitrate assimilation (Bloom et al. 2010). However, our understanding of plant physiological responses in P uptake to altered CO₂ is still limited. The growth rate hypothesis, one of the central paradigms of ecological stoichiometry, predicts a low plant N:P ratio under enhanced growth rates (Sternner and Elser 2002, Elser et al. 2010) because fast-growing organisms need relatively more P-rich RNA to support rapid rates of protein synthesis. If this is true, terrestrial plants grown under elevated CO₂ may have a lower N:P ratio due to faster growth, and thus take up more P from the soil, assuming that it is available (Güsewell 2004). Although the growth rate hypothesis has strong experimental support in freshwater ecosystems (Hessen et al. 2013), it has not been widely tested in terrestrial ecosystems (Peñuelas and Sardans 2009, Reich et al. 2010). In particular, how elevated CO₂

impacts soil P dynamics, and eventually alters the N:P ratio in plants is still not clear (Dijkstra et al. 2012, Sardans et al. 2012).

In this study, we first conducted a meta-analysis to evaluate the shift of tissue N:P ratios in terrestrial plants grown under elevated CO₂. We then tested whether plant N:P ratios decrease with increased rates of plant growth, as predicted by the growth rate hypothesis. Because the role of N limitation in plant stoichiometry is relatively well known, we focused on the relationships between plant stoichiometry and P dynamics. We further evaluated soil P dynamics under elevated CO₂. Finally, we tested whether shifts in soil P dynamics contribute to the plant N:P response under elevated CO₂.

MATERIALS AND METHODS

We searched for published studies reporting the impact of elevated CO₂ on plant N:P ratio using Google Scholar, Google, and ISI Web of Science, with no restriction on publication year. We also screened previous reviews and meta-analyses on plant element stoichiometry (Gifford et al. 2000, Sardans et al. 2012, Loladze 2014). Studies were selected on the basis of the following criteria: (1) experiments had at least one pair of relevant data (ambient and elevated CO₂ treatments); (2) initial environmental condition, plant species composition, and soil properties were the same and experiments were performed at the same temporal and spatial scale in the control and treatment plots; (3) data for both plant N and P concentrations/pools or N:P ratio were reported; and (4) only experiments conducted in terrestrial ecosystems were included.

In total, we collected 2024 records from 112 published articles, each including both plant N and P concentrations or pools, N:P ratio, and plant growth (see Appendix A and Supplement 1). Most of the data were either obtained from tables or extracted from figures using the GetData Graph Digitizer (version 2.24, 1990 release, S. Federow, Moscow, Russia). Some of the tissue N:P ratios were calculated using N and P concentrations or N and P pools, and some plant N or P pools were calculated using plant biomass and N or P concentrations. The compiled database includes the source of the data, field site, ecosystem type, experimental approach, experimental CO₂ concentration, plant species, the plant tissues measured, and N treatment in each record. The experimental approach was divided into growth chamber (GC), open-top chamber (OTC), and free-air CO₂ enrichment (FACE). Studies with plants grown in pots in greenhouses and growth chambers were lumped together into the GC category. Ecosystem types included croplands, grasslands, shrublands, and forests. Plant tissues included aboveground (e.g., leaf, stem, and grain), belowground (root and tuber), and whole-plant biomass. For N treatment, we only considered two treatment levels: low and high. If there were more than two experimental levels of N

treatment, only the lowest (low, often the ambient N) and the highest (high) treatments were included in the database. Experimental manipulations of other factors (e.g., temperature, precipitation/moisture, O₃, and species composition) were not explicitly analyzed, but these data were included in the meta-analysis.

To explore potential mechanisms of altered plant N:P ratio and its impacts on P dynamics, we further collected 1168 observations of soil P dynamics (including phosphatase activity, labile P, and total P) from 57 published articles (see Appendix B and Supplement 2) that report results from experiments with both ambient and elevated CO₂ treatments.

We quantified the effect of elevated CO₂ on plant N and P concentrations and pools, plant N:P ratio, plant growth, soil phosphatase, labile P, and total P by calculating the natural log of the response ratio (RR), a metric commonly used in meta-analyses (Hedges and Olkin 1985, Luo et al. 2006, Wang 2007):

$$RR = \ln(X_t/X_c) = \ln(X_t) - \ln(X_c)$$

where RR is the ratio of the mean value of the chosen variable in the treatment group (X_t) to that in the control group (X_c), an index of the effect of the experimental treatment on the target variable. A weighted RR was computed from individual RR by giving greater weight to studies whose estimates have greater precision, i.e., lower variance (Hedges and Olkin 1985, Luo et al. 2006). The treatment effect of elevated CO₂ was considered to be significant if the 95% confidence interval (CI) of RR did not overlap with zero (Hedges and Olkin 1985, Luo et al. 2006). The significance among groups was detected by comparing the overlap of 95% CI between adjacent groups. If the 95% CI of one group did not overlap with another, we assumed significant difference between these two groups. Furthermore, we investigated the relationships between the response ratio of plant growth and that of N, P, or N:P ratio, respectively, in order to understand what drives the observed change in the response ratios. We also summarized the effect of elevated CO₂ on plant growth (biomass) from the selected studies.

To evaluate the potential influence of publication bias and data independence within each study, we performed sampling analysis on the sensitivity of RR of N:P ratio under elevated CO₂ (Philibert et al. 2012, García-Palacios et al. 2013, Loladze 2014). To check for data independence, we sampled one observation from each study and estimated the RR of the N:P ratio. We iterated this sampling 1000 times and calculated the sample RR of N:P ratio for each sample. The mean and standard deviation of RR of the N:P ratio were then calculated and compared to the RR of the N:P ratio with all data. To assess the impact of publication bias, we conducted two tests. One involved randomly sampling a certain number of observations (from 20 to 1000) in the database and estimating the RR of the N:P ratio (Loladze 2014). The other involved removing one

study from the database each time and estimating the RR of N:P (Philibert et al. 2012).

All data analyses were carried out using SAS software version 9.3, 2010 release (SAS Institute, Cary, North Carolina, USA). Sampling was programmed in QBasic. The codes for conducting the meta-analysis and for sampling are available upon request.

RESULTS

Impacts of elevated CO₂ on plant growth, N and P concentrations and pools, and N:P ratio

Elevated CO₂ significantly enhanced plant growth (biomass) in all plant tissues, ecosystem types, and experimental approaches assessed in this study (Fig. 1a–d), consistent with previous meta-analyses (de Graaff et al. 2006, Luo et al. 2006). On average, elevated CO₂ enhanced plant growth by 12.7% (Fig. 1a).

Overall, elevated CO₂ reduced the concentrations of plant N and P by 12.7% and 4.0%, respectively (Fig. 1a), with the exception that there was no significant change of plant P concentration under elevated CO₂ for studies where FACE was employed or where there were high-N additions (Fig. 1b, e). In contrast to N and P concentration in plant tissues, elevated CO₂ significantly enhanced the pools of plant N and P in all plant tissues, ecosystem types, and experimental approaches (Fig. 1b–e). Overall increases in total plant N and P were 7.9% and 17.5%, respectively (Fig. 1a). The increases of plant N and P pools exposed to elevated CO₂ were generally larger when grown under high-N conditions (Fig. 1e).

Elevated CO₂ significantly reduced the N:P ratio in plant biomass by 8.7% overall, with 9.2% and 6.0% decreases in aboveground and belowground biomass, respectively (Fig. 1c). Average biomass N:P ratios in croplands, grasslands, shrublands, and forests decreased by 11.4%, 8.4%, 5.9%, and 6.9%, respectively, under elevated CO₂ compared to ambient CO₂ (Fig. 1d). The experimental approaches to elevated CO₂ concentration did not alter the direction of the effect (Fig. 1b). Nitrogen treatment did not significantly alter the down-regulated magnitude of N:P ratios in plants exposed to elevated CO₂, even the CO₂-induced plant N:P ratios showed a decreasing trend in high-N vs. low-N treatments (Fig. 1e).

The RRs of plant N:P ratio from the bootstrap samples ranged from –11.7% to –5.0%, and the mean bootstrap RR was very close to the RR using all data (–8.4% vs. –8.3%, respectively). These results suggest that publication bias in the data set was insignificant (Fig. 2). The range of variation was significantly reduced when sample size was larger than 500. The plot was funnel-shaped and mostly symmetric around the mean RR of the N:P ratios (Fig. 2a). Removing one study from the database had very limited influence on the RR (Fig. 2b). Only a few studies had relatively large impacts on the RR of N:P ratio.

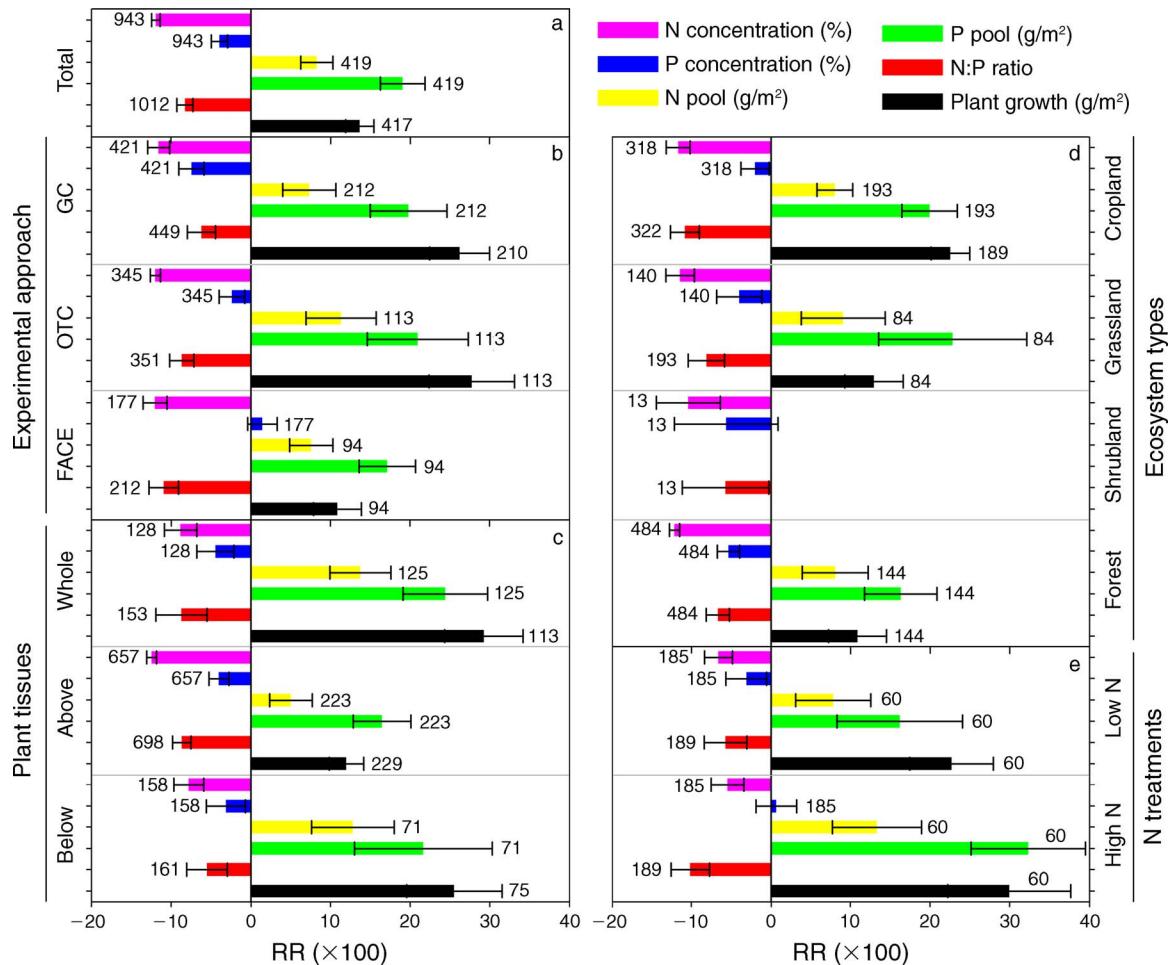


FIG. 1. Response ratios, RR (scale numbers have been multiplied by 100), of N and P concentrations, N and P pools, N:P ratio, and plant growth biomass to elevated CO₂ (a) in total and in (b) various experimental approaches (GC, growth chamber; OTC, open-top chamber; FACE, free-air CO₂ enrichment), (c) plant tissues (aboveground, belowground, and whole-plant), (d) ecosystem types, and (e) N treatments. Error bars indicate 95% confidence intervals. The sample size for each variable is shown next to the error bar.

Relationships of response ratios of plant N and P concentrations or pools, N:P ratio, and plant growth

The response ratios of plant N and P pools (RR_{Np} and RR_{Pp}) were positively correlated with that of plant growth (RR_{PG}) in all ecosystem types (Fig. 3a–f), whereas the response ratios of plant N:P (RR_{N:P}) were negatively correlated with RR_{PG} in croplands and grasslands (Fig. 3g, h). There was no significant relationship between RR_{N:P} and RR_{PG} in forest ecosystems (Fig. 3i). The RR_{N:P} was negatively correlated with the response ratios of plant P pools or concentrations (RR_{Pp} and RR_{Pc}) across all studies (Fig. 4b, d) and in all ecosystem types (Appendix C d–f and D e–h). The RR_{N:P} was also positively correlated with the response ratios of plant N concentration (RR_{Nc}) across all studies, but the r² value was only 0.17 (Fig. 4c). There was no significant relationship between RR_{N:P} and RR_{Np} overall (Fig. 4a).

Impacts of elevated CO₂ on soil P dynamics

On average, elevated CO₂ significantly stimulated soil phosphatase activity by 19.3% (Fig. 5). Both soil alkaline and acid phosphatase activity responded similarly to elevated CO₂ treatment (P > 0.05). Elevated CO₂ also slightly enhanced soil labile P by 4.2%, but significantly reduced the total P pool by 10.1% in soil across all studies (Fig. 5).

DISCUSSION

Our results demonstrate that, overall, both plant N and P concentrations decreased significantly under elevated relative to ambient CO₂, whereas plant N and P pools significantly increased in all plant tissues (i.e., aboveground, belowground, and whole-plant biomass) and ecosystem types (croplands, grasslands, shrublands, and forests) (Fig. 1a, c, d). One exception is that in the FACE studies, plant P concentrations showed no

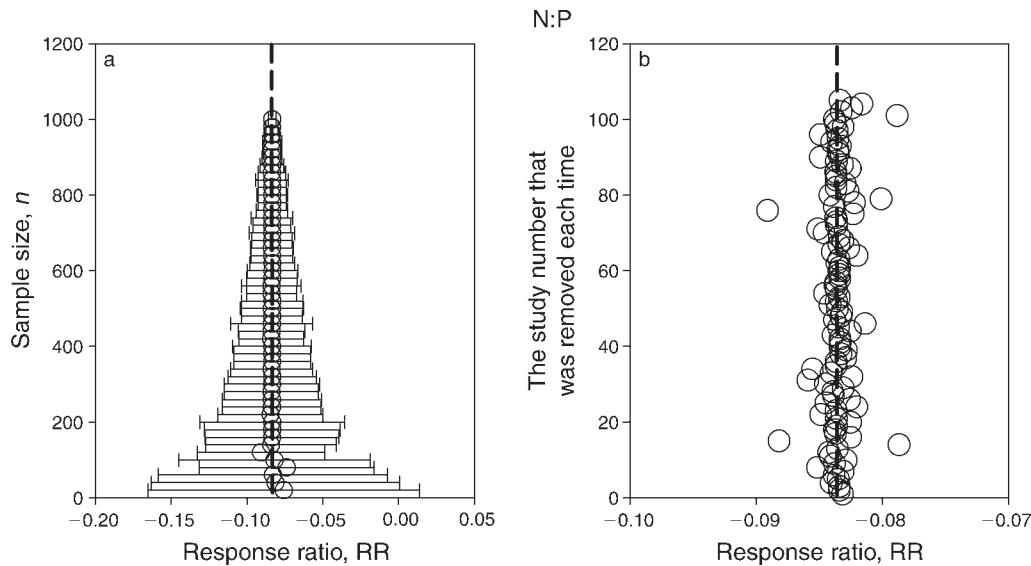


FIG. 2. Testing for publication bias and data independence within each study on response ratio (RR) of plant N:P ratio under elevated CO_2 . (a) A funnel plot of the RR of N:P ratio plotted against the sample size. (b) RR of N:P ratio by removing one study from database each time. The error bars in the plot (a) indicate the ranges of RR from the lowest to the highest values. The black dashed line in both panels represents the mean RR of N:P ratio under elevated CO_2 (-8.3%).

significant change in elevated compared to ambient CO_2 (Fig. 1b), probably due to the fact that the FACE data included P fertilization studies. The disproportionate change in plant N and P under elevated CO_2 , with a stronger decrease in N concentration than in P concentration and a stronger increase in P pools than in N pools, led to significantly lower N:P ratios across all plant tissues and ecosystem types (Fig. 1). On average, the N:P ratio in plant biomass decreased by 8.3% under elevated CO_2 (Fig. 1a). These results are consistent with a recent meta-analysis that reported lower plant N:P ratios under elevated CO_2 (Loladze 2014, Yuan and Chen 2015).

We confirmed that enhanced plant growth under elevated CO_2 coincided with a disproportionate increase in N and P pools and a significant decrease in plant N:P (Fig. 1). Moreover, the shift in $\text{RR}_{\text{N:P}}$ was negatively correlated with RR_{PG} (Fig. 3g–i), in agreement with predictions of the growth rate hypothesis that faster growing plant species should have lower N:P ratios because they need relatively more P-rich RNA to support rapid rates of N-rich protein synthesis (Sterner and Elser 2002, Elser et al. 2010). Both $\text{RR}_{\text{N:P}}$ and RR_{PP} in plant tissue were positively correlated with RR_{PG} (Fig. 3a–f), indicating that elevated CO_2 stimulates both N and P uptake in order to meet the demands of faster plant growth (Vitousek et al. 2010). In contrast, the reduced N concentration in plants under elevated CO_2 might reflect enhanced N use efficiency for photosynthesis (Peterson et al. 1999). In turn, this lower protein concentration should require fewer P-rich ribosomes to produce and maintain, consistent with lower P concentrations in plants grown under elevated CO_2 (Fig. 1).

Although only a few studies have attempted to relate plant N:P to growth and biomass (Ågren 2004, Matzek and Vitousek 2009), several studies have demonstrated that foliage N:P is related to plant leaf traits such as specific leaf area, leaf photosynthetic capacity, or leaf metabolome (Ågren 2004, Cernusak et al. 2010, Reich et al. 2010, Rivas-Ubach et al. 2012). It is worth noting that the growth rate hypothesis may not be directly applied to all terrestrial situations (Peñuelas and Sardans 2009), especially in situations in which P is not limiting (Hessen et al. 2013). Indeed, a very weak relationship between RR_{PG} and $\text{RR}_{\text{N:P}}$ in forests was found (Fig. 3i), similar to observations of Ågren (2004) and Matzek and Vitousek (2009). This may be because trees have larger plant bodies and longer life cycles than grasses and crop plants. Although on an annual basis, much of the N and P taken up by trees would go into leaves, trees invest nontrivial amounts of N and P in inert mechanical structures (wood and skeleton), storage, etc., in allocations that often exceed the amounts invested in growth and metabolically active tissues (Ågren 2004, Matzek and Vitousek 2009). Although the relationship between RR_{PG} and $\text{RR}_{\text{N:P}}$ in forests was weak, elevated CO_2 still decreased N:P in forests (Fig. 1). Therefore, further studies including protein:RNA ratios are required to provide a direct test of the growth rate hypothesis in terrestrial plants (Matzek and Vitousek 2009).

Shifts in soil nutrient availability under elevated CO_2 may also contribute to the decline of plant N:P ratios. It is well known that N limitation under elevated CO_2 usually increases C:N ratios and may decrease plant N:P ratios. For example, a sharper decline in N than P

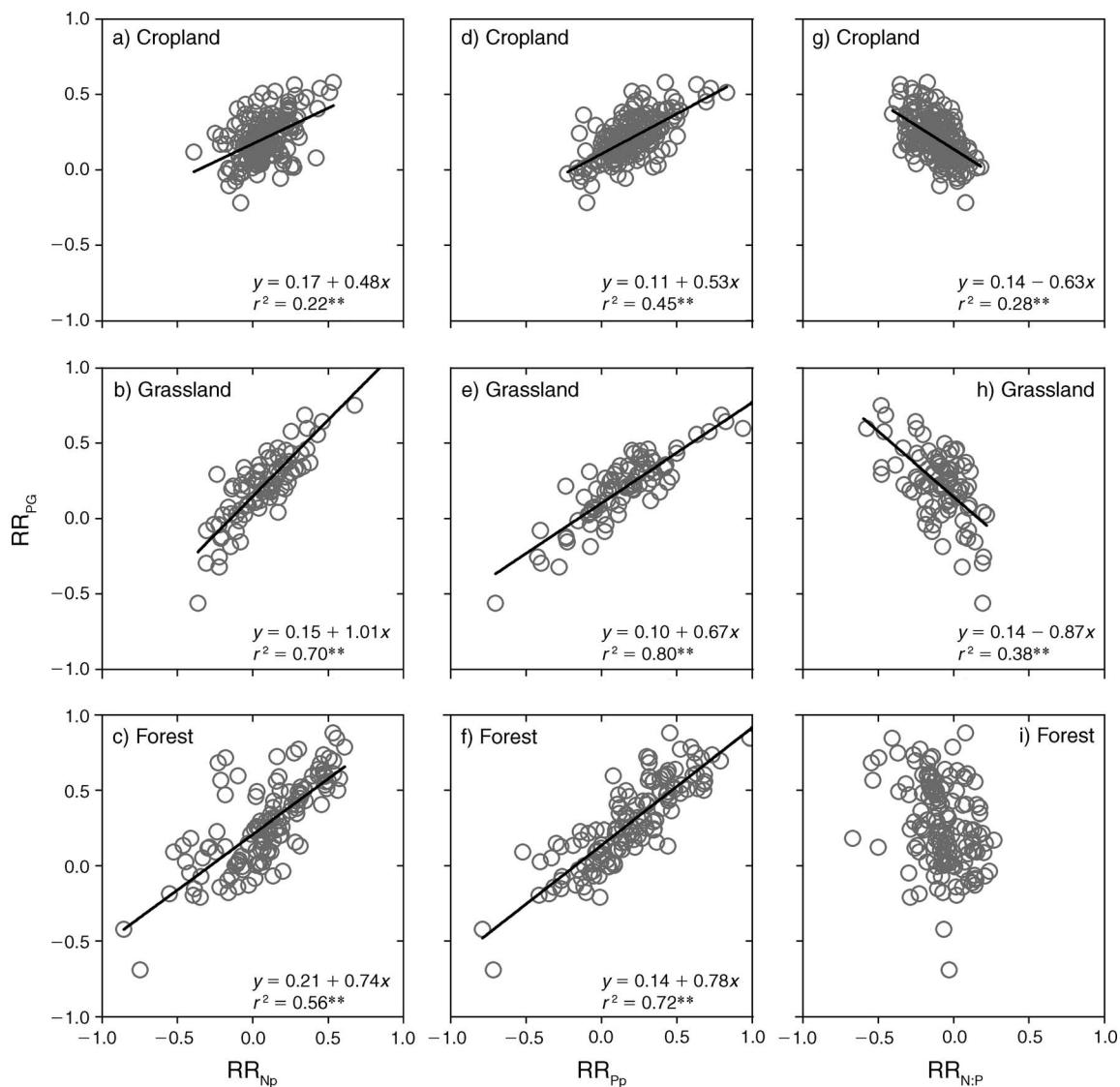


FIG. 3. The relationships between the response ratio of plant growth (RR_{PG}) and that of N pool, P pool, or N:P ratio ($RR_{N:P}$, RR_{Pp} , or RR_{Np}) under elevated CO_2 in various ecosystem types (cropland, grassland, and forest); ** indicates significant at the $\alpha = 0.01$ level.

concentrations has been observed in both Loladze (2014)'s and our study. However, it is not clear whether altered P dynamics under elevated CO_2 would also influence plant N:P ratio. The finding of a stronger relationship between plant N:P ratio and P under elevated CO_2 than between plant N:P ratio and N (Fig. 4) suggests that plant N:P ratio shifts in response to elevated CO_2 were primarily determined by the changes in the pool of P rather than N.

In addition to N limitation, down-regulation of plant N:P under elevated CO_2 is potentially regulated by P dynamics. Further analyses of soil phosphatase activity and labile P confirmed the importance of altered P dynamics under high CO_2 concentrations. Both soil phosphatase activity and labile P were enhanced under

elevated CO_2 (Fig. 5). It is likely that the increase of soil P availability allows plants to take up more P, contributing to a weak decline in P concentration and a lower N:P ratio in plant biomass under elevated CO_2 . Therefore, the CO_2 -induced down-regulation in plant N:P may reflect more P accumulation in long-lived pools (e.g., plant biomass), and over the long term could result in soil P depletion (Zhang et al. 2011, 2014, Goll et al. 2012). Indeed, our meta-analysis on soil P pools showed that elevated CO_2 significantly decreased total P by 10.1% in soils (Fig. 5), which would be likely to limit plant growth and ecosystem C fixation in the future depending on the total P stock at the site. Such shifting of P from soil to plant biomass could have a greater impact in harvested systems, as biomass is removed through harvest.

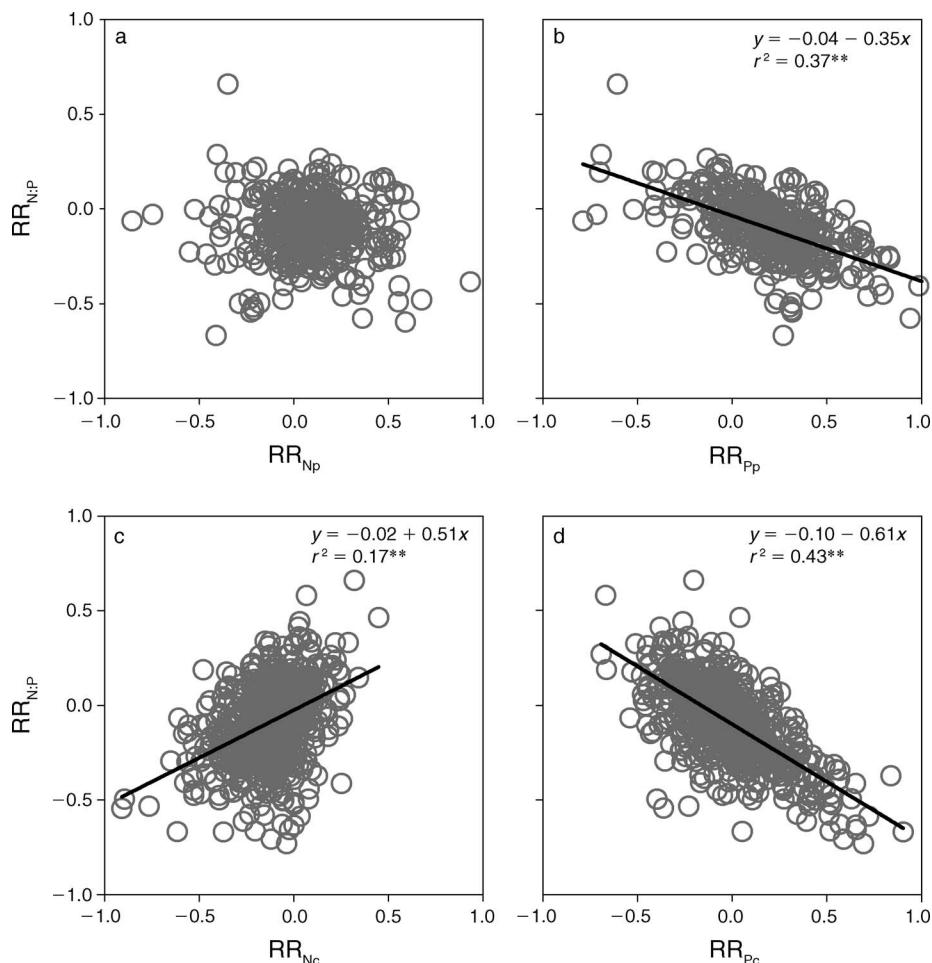


FIG. 4. The relationships of response ratio of N:P ratio ($RR_{N:P}$) with that of N pool or P pool (RR_{Np} or RR_{Pp}), and N concentration or P concentration (RR_{Nc} or RR_{Pc}), respectively, under elevated CO_2 levels; ** indicates significant at the $\alpha = 0.01$ level.

We further compared the responses of plant growth and N:P ratios to elevated CO_2 under low- and high-N treatments. Theoretically, if N limitation under elevated CO_2 is the major factor driving the down-regulation of plant N:P, an increase in N inputs should cancel N limitation and enhance the CO_2 fertilization effects on plant growth and N uptake (Luo et al. 2004, 2006), ultimately weakening the down-regulation in plant N:P ratio. However, we found that the P pool was enhanced more than the N pool; as a result, the CO_2 -induced changes in plant N:P did not significantly vary under N treatments and plant N:P was even slightly lower under high- than low-N treatments (Fig. 1d). These findings are also in agreement with the growth rate hypothesis, and highlighted the role of P in regulating plant N:P ratio change under elevated CO_2 .

The results reported here could be explained by altered soil P dynamics under different N treatments. Phosphatase production requires a significant investment of N (Treseder and Vitousek 2001). Nitrogen addition has been shown to enhance phosphatase

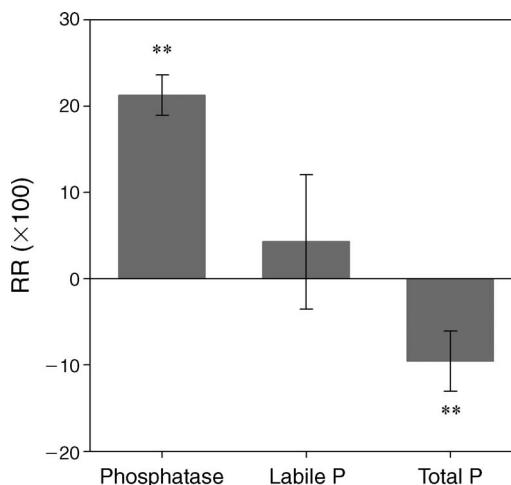


FIG. 5. Response ratios, RR (scale numbers have been multiplied by 100), of soil phosphatase, labile P, and total P to elevated CO_2 . Error bars indicate 95% confidence intervals; ** indicates significant at $\alpha = 0.01$ level.

activity across a wide variety of terrestrial ecosystems (Marklein and Houlton 2012). The increase in phosphatase activity presumably increases P availability in the soil and supports faster plant growth under elevated CO₂ and soil N levels. Thus, even in regions with high N deposition and/or low-P soils, elevated CO₂ might allow plants to mitigate P limitation and to down-regulate N:P ratio by more strongly influencing P dynamics than N (Wang et al. 2010, Zhang et al. 2014). Indeed, a significant decrease of plant N:P ratio and increase in plant growth under elevated CO₂ and/or high soil N availability has been reported (Liu et al. 2013). Further studies involving low-P ecosystems are needed to accurately evaluate the role of P limitation on plant growth under climate change.

Overall, our results indicate that elevated CO₂ down-regulates the N:P ratio in all plant tissues and across all ecosystems, regardless of soil N availability. These results may have significant implications for biogeochemical modeling, because fixed N:P ratios are often used in terrestrial ecosystem models to represent the relative demands of N and P for plant growth (Wang et al. 2010). If this CO₂-induced down-regulation of plant N:P ratio indeed exists, plant uptake of P from soil might be underestimated in such models. Moreover, we found that in addition to N limitation, down-regulation of plant N:P under elevated CO₂ was potentially regulated by soil P dynamics. Consistent with this, we observed higher soil phosphatase activity and labile P under elevated CO₂, and ultimately a 10.1% decrease in total soil P. To our knowledge, this is the first study to show that down-regulation of plant N:P under elevated CO₂ corresponds with accelerated soil P cycling. Insights from ecological stoichiometry under climate change may be critical in building next-generation terrestrial biogeochemical models that take into account the complex interactions between plant growth and the dynamics of multiple nutrients so that they can more accurately predict ecosystem responses to future climate change (Hessen et al. 2013).

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–D and Supplements 1 and 2 are available online: <http://dx.doi.org/10.1890/15-0217.1.sm>