

Decoupling of nitrogen and phosphorus in terrestrial plants associated with global changes

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Living organisms maintain a balance of chemical elements for optimal growth and reproduction, which plays an important role in global biogeochemical cycles^{1–5}. Human domination of Earth's ecosystems has led to drastic global changes^{6–8}, but it is unclear how these affect the stoichiometric coupling of nutrients in terrestrial plants, the most important food source on Earth. Here we use meta-analyses of 1,418 published studies to show that the ratio of terrestrial plant nitrogen (N) to phosphorus (P) decreases with elevated concentrations of CO₂, increasing rainfall, and P fertilization, but increases with warming, drought, and N fertilization. Our analyses also reveal that multiple global change treatments generally result in overall additive effects of single-factor treatments and that the responses of plant nutrients and their stoichiometry are similar in direction, but often greater in controlled than in natural environments. Our results suggest a decoupling of the P biogeochemical cycle from N in terrestrial plants under global changes^{6–8}, which in turn may diminish the provision of ecosystem services^{1,5,9}.

From cellular metabolism to ecosystem structure and nutrient cycling, C, N and P are biologically coupled through their effects on the biochemical reactions that control primary production, respiration and decomposition in terrestrial ecosystems^{1–5,8,10–12}. In the biosphere, living organisms, the major part of biogeochemical cycles, require elements in strict proportions to catalyse metabolic reactions and synthesize essential compounds with specific ratios of C:N:P (refs 1,2). The biological control—that is, the conserved elemental stoichiometry of organisms—couples biogeochemical cycles to one another³. However, owing to different degrees of control by biological and geochemical processes, biogeochemical C, N and P cycles could be unbalanced or decoupled under rapid global changes^{2,8,13}. For example, an increase in aridity with climate changes can reduce soil C and N, but increase soil P in global drylands¹³, indicating that the coupling between biogeochemical cycles is fragile in drylands in the face of rapid climate change. The decoupling of the biogeochemical cycles of C, N and P may also lead to nutrient decoupling in plants that form the base of food chains^{5,8} and consequently can negatively influence the trophic structures and the services of terrestrial ecosystems¹⁴.

Global changes have drastically affected the biogeochemical cycles of carbon and nutrient elements of Earth's ecosystems^{6,15}. The simultaneous changes in global-scale biogeochemical cycles (for example, elevated CO₂ concentration [CO₂], atmospheric N deposition, and N and P fertilization) and in climates (increasing temperature and altered rainfall) are anticipated to have stoichiometric consequences worldwide (Fig. 1). For example, elevated [CO₂] can increase plant C fixation, but stimulated

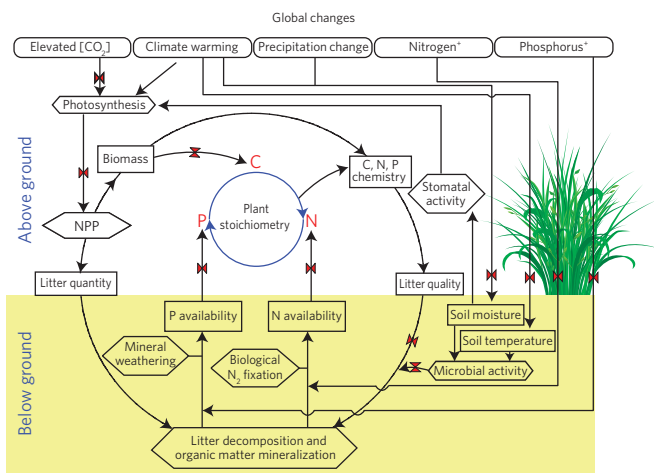


Figure 1 | A conceptual diagram of the influence of global changes on processes controlling the stoichiometry of plant C, N and P. Rectangles are nutrient pools, hexagons indicate biogeochemical processes and valves (red symbols) are controls on plant C, N and P. Plant illustration © Elena Belyakova/Thinkstock.

plant photosynthesis, growth and overall production may lead to decreases of plant nutrient concentrations—that is, the ‘dilution effect’^{16,17}. Warming tends to increase soil microbial activity, but may induce warming-associated droughts, both of which affect plant photosynthesis and plant stoichiometry. The same is true for changes in precipitation that affect plant stoichiometry via soil water availability.

It is likely that N and P inputs, through fossil fuel combustions, cropland fertilization, and human-driven-N fixation, can greatly enhance substrate nutrient availability for plants to uptake and grow (Fig. 1). However, not only the absolute amount, but also the relative ratios between essential elements (stoichiometric coupling), influence long-term organismal performance and plant community dynamics^{1,10}. A lack of understanding of the factors influencing stoichiometry limits their incorporation into ecological and biogeochemical models. Albeit previous work has predicted the possible constraints of coupled biogeochemical cycles on organismal responses to global changes², we still do not know how and to what degree terrestrial plant C, N and P respond to these changes, particularly in a changing world.

Numerous global change experiments have individually examined typically one or two nutrients in plants to one or two global change drivers. Several recent conceptual syntheses or

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meta-analyses have examined the impacts of global changes on plant nutrients and stoichiometry, mainly on C and N contents and C:N response to elevated $[\text{CO}_2]$ (refs 2,16–19). Despite this recent focus, understanding the effects of global changes on plant N:P remains highly elusive¹⁹. Furthermore, it is unclear whether the responses of plant N and P stoichiometry to multiple global change drivers are additive and whether the responses are more pronounced in controlled than in natural environments. Here, we report responses of terrestrial plant N and P ratios to elevated $[\text{CO}_2]$, warming, altered precipitation, atmospheric N deposition, and N and P fertilization by compiling published data from global change experiments conducted in natural environments, including 24,770 observations from 1,418 publications (Supplementary Fig. 1). To compare experimental results from natural and controlled environments, we also include 7,797 observations from 367 publications conducted in controlled environments such as greenhouses and growth chambers (Supplementary Data 1 and Supplementary References).

Our analysis revealed that plant N:P in natural environments responded strongly to global change treatments (Fig. 2a), as a result of different responses of carbon, nitrogen and phosphorus concentrations (hereafter [C], [N] and [P], respectively) to these treatments (Supplementary Fig. 2). Elevated $[\text{CO}_2]$ tended to decrease plant N:P, but warming increased it. Increased rainfall reduced N:P, whereas reduced rainfall increased N:P. Nitrogen fertilization increased N:P, whereas P fertilization decreased N:P (Fig. 2a). Under controlled environments such as greenhouses and growth chambers, the response ratios of plant nutrients and their stoichiometric ratios, including N:P, demonstrated similar overall trends to those observed in natural environments, but the responses to treatments were generally greater in controlled than in natural environments (Fig. 2a and Supplementary Fig. 2).

When the responses to multiple global change treatments were compared with those to single-factor treatments, the responses of N:P to multiple treatments were generally additive, as indicated by nonsignificant interactive effects of multiple treatments (Fig. 2b). Additive effects were also common in concentrations of C, N and P, and in stoichiometric ratios of C:N and C:P in plants (Supplementary Figs 3 and 4). For example, plant [N] in the combined treatment of elevated $[\text{CO}_2]$ and warming decreased at a similar rate as it did with only elevated $[\text{CO}_2]$, as warming alone did not affect plant [N] (Supplementary Figs 3 and 4). Plant [N] increased with N fertilization combined with any other treatments, showing a dominant role of N fertilization on plant [N]. Similarly, plant [P] increased when P fertilization was applied in combination with other treatments. Plant C:N increased with elevated $[\text{CO}_2]$ combined with warming, but decreased with N fertilization combined with elevated $[\text{CO}_2]$, warming, increasing rainfall, or P fertilization. Plant C:P decreased with combined N and P fertilization. Plant N:P increased with N fertilization combined with elevated $[\text{CO}_2]$ or rainfall, but decreased with combined N and P fertilization.

There was one exception to additive effects of N:P in natural environments: combined increased rainfall and N fertilization resulted in greater positive effects on N:P than the sum of the negative effect of increased rainfall and the positive effect of N fertilization (Figs 2a,b). The positive effect of the combined increased rainfall and N fertilization is nevertheless similar to those of N fertilization alone (Figs 2a and Supplementary Fig. 3), indicating a dominant influence of N fertilization on plant N:P even with increased rainfall. By performing a ‘paired meta-analysis’—that is, taking into account only those experiments that tested all single and combined treatments—we found that plant N:P responses were related to the effects of both single-factor treatments (Fig. 3a). Plant N:P responses to combined elevated $[\text{CO}_2]$ and warming, combined elevated $[\text{CO}_2]$ and N fertilization, and combined increased rainfall and N fertilization were attributed to both single-factor effects, especially the latter. Plant N:P responses of combined N and

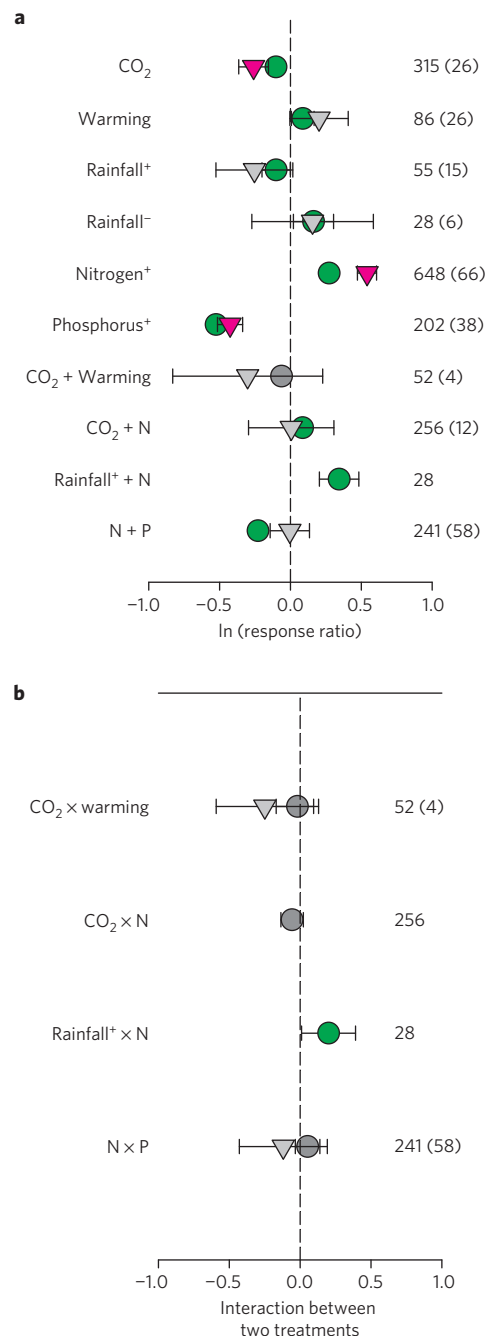


Figure 2 | Responses of plant N:P to global change treatments. a, Natural log response ratios of single and combined treatments. **b**, Parameter estimates for two-way interaction terms between global change treatments. Only studies reporting single and combined factors experiments simultaneously are included in determining parameter estimates for two-way interaction terms. Circles are for results in natural environments, with grey and green representing insignificant ($P > 0.05$) and significant ($P \leq 0.05$) difference between the log response ratio and zero, respectively. Triangles are for results in controlled environments, with grey and pink representing insignificant ($P > 0.05$) and significant ($P \leq 0.05$) difference between the log response ratio and zero, respectively. Error bars are the 95% confidence intervals for the mean. CO_2 , Warming, Rainfall⁺, Rainfall⁻, Nitrogen⁺ and Phosphorus⁺ represent elevated $[\text{CO}_2]$, increasing temperature, increasing rainfall, decreasing rainfall, nitrogen fertilization and phosphorus fertilization, respectively. The numbers out- and inside parentheses represent the numbers of observations for experiments in natural and controlled environments, respectively.

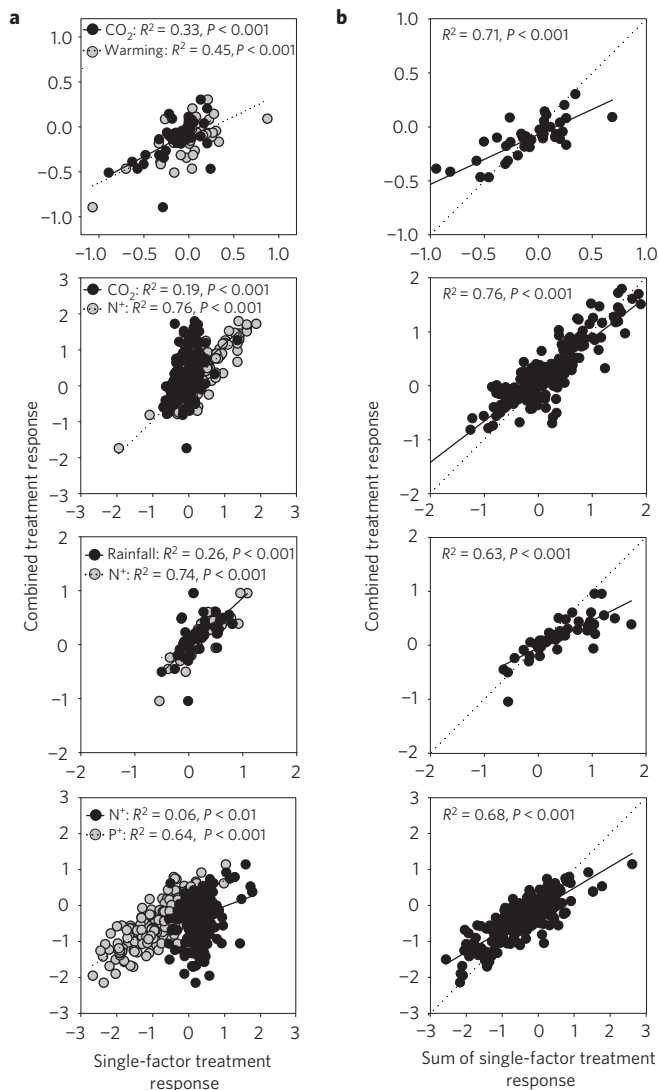


Figure 3 | Paired meta-analysis of multi-factor studies. **a**, Relations of combined treatment response against single-factor treatment response. **b**, Relations of combined treatment response against the sum of single-factor treatment response. Data are reported as log (treatment/control). *P*-values and R^2 values for linear regressions are shown in each panel for the first and second single factors.

P fertilization were dominated by the effect of P fertilization. When plant N:P responses to combined treatments are compared to the summed responses of the single-factor treatments, additive interactions between individual treatments were evident, as individual observations were situated across the 1:1 line (Fig. 3b), supporting the result of an additive effect shown in Fig. 2b. However, synergistic interactions tended to occur with low effect sizes and antagonistic interactions occurred with high effect sizes.

Because treatments differed in quantities, we tested the sensitivities of plant nutrients and their ratios to quantities of global change drivers (Fig. 4). Plant N:P decreased with quantities of added or reduced rainfall, increased with the amount of N fertilization, and decreased with the amount of P fertilization. Plant N:P was not sensitive to the amount of elevated [CO₂] or warming, possibly a result of the limited ranges of elevated [CO₂] or warming applied in available experiments. Plant [C], [N], [P], C:N and C:P were also sensitive to the amounts of global changes (Supplementary Fig. 5).

Here we quantified the effects of multiple climate change drivers on plant nutrients and stoichiometry by a suite of meta-analyses

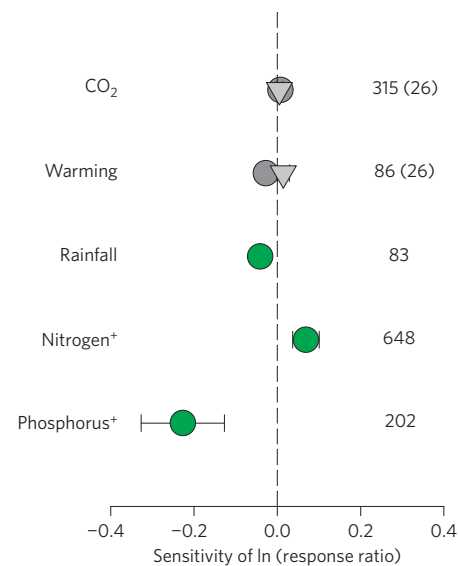


Figure 4 | Sensitivities of plant N:P response ratios to quantities of global change treatments. The uses of symbols, colours, error bars and abbreviations are same as in Fig. 2. Because application rates of water, nitrogen and phosphorus fertilization can not be standardized to the same units in controlled environments, only the responses to elevated [CO₂] and warming treatments in controlled environments are presented.

of published data. Our analyses support several predictions and the idea that global changes have induced decoupling of C, N and P in plants and possibly resulted in a decoupling of their biogeochemical cycles in Earth's life system^{2,8,13}. First, global change drivers affect plant nutrients and stoichiometry, unbalancing C, N and P biogeochemistry in plant biomass. Elevated [CO₂] decreased N:P as a result of decreases in plant [N] (refs 1,16,18,19), but had no effect on plant [P], probably due to compensation by the 'dilution effect' and rapid growth-induced P demand¹. As atmospheric [CO₂] continues to rise globally, N and P decoupling is expected to occur in all terrestrial ecosystems.

Our analysis showed that both warming and drought increase N:P. The increase of N:P by warming can be attributed to increases in net N mineralization and nitrification¹² and to reduction in soil P availability²⁰ with warming. The decoupled nutrient uptake under warming might be particularly serious in environments where P is more limited, such as in lowland tropics^{11,21}. The positive impact of drought and negative impact of increased rainfall in plant N:P observed in manipulation experiments contrast the decrease in soil N:P with increasing aridity in drylands¹³, suggesting different mechanisms driving plant and soil stoichiometry¹¹. The negative relationship between plant N:P and water availability is possibly a result of faster plant growth under higher water availability requiring more P relative to N (refs 1,22). Our analysis indicates that altered global water availability with climate change²³ can result in shifts in plant [N] and [P], decoupling N:P in plants^{5,24}. In a warmer and drier world, plant productivity may rely more on P than N availability^{7,23}.

Our results show that plant N increases are higher than plant P increases with N fertilization, resulting in higher plant N:P, and consequently P limitation on productivity of terrestrial ecosystems. By contrast, P fertilization can induce a shift from P to N limitation for plant production. The patterns of plant N:P under N fertilization are similar to the large-scale observations in lakes²⁵, indicating that the increased N-deposition-induced shift from N to P limitation occurs regardless of ecosystem type. The contrasting N:P patterns with experimental N and P manipulations show that global

changes in substrate nutrient availability^{6,15}, in addition to elevated [CO₂], warming and altered rainfall, are important mechanisms in determining stoichiometric relationships. We note that N:P increases in most natural environments due to disproportionate N and P inputs: N input comes at a greater scale than P input as N increases globally from fossil fuel combustions and fertilization to fields as well as biological processes such as N fixation, whereas P comes from only cropland fertilization^{5,8}.

The second prediction from our analyses is that the responses of plant stoichiometry to combined treatments are usually close to the sum of single-factor effects. The generally additive effects indicate that elevated [CO₂], increased precipitation, and P fertilization, at least in part, could offset the effects of warming, drought and N fertilization on stoichiometric coupling of N and P. The total net effect of global changes on plant nutrients and their coupling depends on the relative magnitudes of global changes. We note that our conclusion of additive responses of multiple global changes is based on a limited number of manipulation experiments that simultaneously tested multiple factors. Furthermore, our paired meta-analysis reveals that individual experiments situated across the 1:1 line, but plant N:P ratio responses to combined treatments are synergistic at low responses and antagonistic at high responses.

Third, our analysis shows that the responses of plant nutrients and their stoichiometry are similar in direction, but often greater in controlled than in natural environments. These results confirm that the patterns observed in controlled environments are useful in predicting responses in natural environments, but their magnitudes may be poorly predicted²⁶. The difference may be attributed to the resilience of natural environments. Alternatively, experiments in controlled environments are more often designed to work on smaller, younger plants, and with shorter durations, all of which can affect the magnitudes of plant responses^{27,28}.

Manipulative global change experiments synthesized here provide valuable mechanistic insights into plant stoichiometry. It is, however, difficult to make a direct inference for the overall changes in plant stoichiometry of natural terrestrial ecosystems that experience increasing [CO₂], warming, altered precipitation, and N deposition simultaneously for several few reasons. First, manipulative global change experiments are typically carried out with large-step increases in treatments and observed for short durations whereas global change drivers increase gradually over a long period of time in a natural setting. Second, despite apparent additive effects of combined global change drivers found here for most sets, substantially fewer studies have examined multiple global change drivers that operate simultaneously in a natural setting. Third, our analyses reflect an overall response of terrestrial plants. When the N:P response to rainfall treatment was examined, we find that the N:P response to rainfall addition increased with background aridity, but the N:P response to drought did not change with background aridity (Supplementary Fig. 6). Fourth, the response of plant nutrients and their ratios to global change drivers is dependent on the magnitude of the global changes (Fig. 4), tends to decrease with experimental duration^{27,28}, and probably differs with biome (Supplementary Table 1), plant tissue²⁹, plant functional types (Supplementary Figs 7–13), species and life stage. However, despite the large data set collected in this study, the number of observations becomes too small to allow meaningful tests for potential different responses associated with plant tissue, species, life stage and growing environments.

Our analyses show that global changes alter the stoichiometry of N and P in terrestrial plants. The N:P responses to global changes may indicate that P limitation could be more widespread than generally acknowledged in a changing world in which ecologists have focused primarily on N. These changes likely affect competitive interactions among autotroph species and on

stoichiometric processing of autotroph production by consumers^{1,9}, which consequently can lead to food quality limitations and a reduction of 'gross growth efficiency' for herbivores. In response to global changes, terrestrial plant N:P changes in different directions and to varying extents, altering global N and P cycles, plant and microbial diversity and activity, and ultimately on primary productivity from local to global scales⁵. Although the spatial extents differ among elevated [CO₂], warming, altered rainfall, and N and P supply, the stoichiometric changes would not be solved without drastic changes made by our society to mitigate global changes, in particular to reduce CO₂ emission and to moderate the use of fertilizers.

Methods

We searched databases of ISI Web of Science, PubMed, Google Scholar and JSTOR (Supplementary References). Our data covered a wide range of all terrestrial ecosystem types including Arctic tundra, forests, and grasslands (Supplementary Fig. 1). All original data were extracted from the text, tables, figures and appendices in the publications. When data were presented graphically, numerical data were obtained by Image-Pro Plus 7.0 (Media Cybernetics). Measurements from different ecosystem types, species, plant tissue types and treatment levels within a single study were considered independent observations. If multiple observations from different sampling dates at the same site were reported, we used the first observation in the analysis (Supplementary Data 1).

To examine the effects of global change treatments on plant stoichiometric C, N and P, we calculated response ratios from each individual study as described in ref. 30. Natural log response ratio (ln RR) was calculated as $\ln(X_e/X_c) = \ln X_e - \ln X_c$, where X_e and X_c are the response values of each individual observation in the treatment and in the control, respectively. The corresponding sampling variance for each ln RR was calculated as $\ln[(1/n_e) \times (S_e/X_e)^2 + (1/n_c) \times (S_c/X_c)^2]$ in R with the package 'metafor' 1.9-2, where n_e , n_c , S_e , S_c , X_e and X_c are sample sizes, standard deviations and mean response values in the treatment and in the control, respectively. The natural log response ratios to individual and combined treatments were determined by specifying studies as random factor using the *rma* model in metafor. The effects of global change treatments on plant stoichiometric C, N and P were considered significant if the 95% confidence intervals (CI) of ln RR did not overlap zero. To compare whether the responses of plant nutrients and their stoichiometric ratios differ between studies conducted in natural environments and controlled environments, such as greenhouse and growth chamber experiments, we compared estimated ln RR by their CIs.

To examine whether treatment effects are additive on plant nutrients and their stoichiometric ratios, we tested whether the interactions between multiple treatments are significant by using *rma.uni* models in metafor with treatments as categorical predictors. A significant interaction between treatments indicates that the treatment effects are not additive. Because of limited data for three or more combined treatments, we considered only two-way interactions. In addition, we performed paired meta-analyses³¹, a more conservative comparison in which interactive effects of all observations from multiple-factor studies were examined by comparing the sum of effect sizes of single factors with the effect size of combined factors. Individual experiments of synergistic, antagonistic and additive responses should be situated above, below and across the 1:1 line, respectively³¹.

Because global change treatments vary strongly in quantities applied within and among studies, we examined the sensitivities of plant nutrients and their stoichiometric ratios to the quantities applied for all global change treatments by using REML estimation in the *rma.uni* model for metafor with the applied rates of global change treatments as continuous variables. In this analysis, we considered only the responses of plant nutrients and their stoichiometric ratios to individual global change treatments owing to limited data availability for multiple treatments as well as additivity of multiple treatments. To examine whether N:P responded to water addition, or drought experiments differ with background water availability, we derived an aridity index, given by the ratio of precipitation to potential evapotranspiration, by using data interpolations provided by WorldClim (<http://WorldClim.org>) and by CGIAR-CSI (<http://www.cgiar-csi.org/data/global-aridity-and-pet-database>). We then tested whether the log N:P response ratio changed with the aridity index. All statistical analyses were performed in R 3.0.2.

Received 22 April 2014; accepted 16 January 2015;
published online 9 March 2015

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Acknowledgements

This work was financially supported by the Natural Science and Engineering Council of Canada (Discovery Grant 283336), an Early Researcher Award and an Ontario Post-Doctoral Fellowship from the Ontario Ministry of Research and Innovation, National Natural Sciences Foundation of China (31370455) and 100 Talents Program of The Chinese Academy of Sciences. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Author contributions

Z.Y.Y. and H.Y.H.C. designed the project. Z.Y.Y. compiled the data set. Z.Y.Y. and H.Y.H.C. performed the analysis and wrote the manuscript.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to H.Y.H.C.

Competing financial interests

The authors declare no competing financial interests.