Variations in foliar carbon:nitrogen and nitrogen:phosphorus ratios under global change: a meta-analysis of experimental field studies

Shan Xu1,2*, Jordi Sardans2,3, Jinlong Zhang4 & Josep Peñuelas2,3

Foliar stoichiometry plays an important role in ecosystem elemental cycling. Shifts in foliar ratios of carbon to nitrogen (C:N) and nitrogen to phosphorus (N:P) in response to global change can therefore have a large impact upon ecosystem function. We conducted a meta-analysis with 2,236 paired observations from 123 published studies to investigate the responses of foliar C:N and N:P ratios to experimental global change treatments, i.e. warming, increased precipitation, drought, N addition and elevated carbon dioxide concentration (eCO2), in field conditions. Foliar C:N and N:P ratios were neither affected by warming nor by increased precipitation. Foliar C:N ratio increased with drought and eCO2, and decreased with N addition. Foliar N:P ratios declined with eCO2, and increased under drought and N addition. Our results suggested the responses of the C:N ratio to global change were mainly related to shifts in foliar [N], whereas changes in the N:P ratio were related to the responses of both [N] and [P]. Moreover, the response magnitude of foliar N:P ratio decreased with treatment duration under increased precipitation, N addition and eCO2. Our findings are important for our understanding of plant nutrient dynamic and modeling of nutrient biogeochemistry under global change.

Concentration-based ratios of carbon to nitrogen (C:N) and nitrogen to phosphorus (N:P) are key indicators of foliar chemistry and stoichiometry, which play important roles in ecosystem energy and nutrient dynamics1–3. Foliar C:N ratio is closely related to litter C:N ratio and reflect leaf litter quality, which will affect the proportion of litter-derived C accumulated in soils4; Whereas foliar N:P ratio is an important indicator of ecosystem nitrogen (N) or phosphorus (P) limitation5,6. Multiple global changes, including warming, altered precipitation (increased precipitation or drought), atmospheric nitrogen (N) deposition, and elevated carbon dioxide (CO2) concentrations (eCO2), interact to have substantial impacts upon terrestrial ecosystems and alter biogeochemical cycling7–9. Although some previous meta-analyses have investigated the responses of N:P ratios to global changes at the whole-plant level10, the responses at the foliar level have received less attention. In addition, the responses of foliar [C] and foliar C:N ratio to global change have received less attention11–13, and there is very little information about changes in foliar stoichiometry in response to warming and increased precipitation14–16. Therefore, it is urgent to investigate the responses of foliar C:N and N:P ratios to global change, including warming, changes in precipitation, N deposition and eCO2.

Foliar C accumulation is mainly derived from the balance between foliar photosynthesis and respiration17–19, which is less investigated. In contrast to foliar [C], shifts in foliar [N] and [P] in response to global change have been more extensively studied9. Differences in the elemental cycles of N and P are important in their responses to global change. Ecosystem N cycling is underpinned by several mechanisms of biological control (N fixation,
nitrification, denitrification, nitrate-photosynthetic reduction\textsuperscript{20–22}, and is also influenced by atmospheric N-deposition\textsuperscript{23}. However, ecosystem P cycling depends on fewer biological mechanisms, but has a greater dependence on the initial P content of the bedrock and the processes of soil development\textsuperscript{9,14}, and deposition of P largely limited to areas with intense agriculture\textsuperscript{24}. As a result, global change has the potential to alter ecosystem N-cycling by affecting various biological mechanisms. But climate change also can strongly affect P-cycling by modifying physicochemical variables that in turn can displace the equilibrium among the great array of P-chemical forms of P in soils\textsuperscript{25}. Moreover, given the difference in solubilization between chemical forms of N and P in soil, global changes in temperature and precipitation can also alter N and P availability and uptake. Despite the potential importance of foliar stoichiometry as an indicator of change, the responses of foliar-level C:N and N:P ratios to global change drivers are still unclear\textsuperscript{14,15}.

Previous meta-analyses have demonstrated global change impacts on C:N and N:P ratios at the whole-plant level\textsuperscript{10,16}, by combining the results of experimental field manipulations, natural environmental gradients, and controlled greenhouse or pot experiments. Although these studies have provided important insights into plant responses to change, it is important to evaluate the results from field experiments separately, as these can differ markedly from observations along natural gradients and greenhouse or pot experiments\textsuperscript{26,27}. To gain a better understanding of the overall responses of foliar-level C:N and N:P ratios to global change, we conducted a meta-analysis with 2,236 observations from 123 reports based on field manipulative experiments, including warming (343 observations), shifts in precipitation (158 observations for increased precipitation and 655 observations for drought), N addition (750 observations) and eCO\textsubscript{2} (330 observations). Our study aimed to address the following questions: (1) How do foliar-level C:N and N:P stoichiometry respond to global change? (2) The shifts in which element concentrations ([C], [N] and [P]) have the greatest influence on foliar C:N and N:P ratios under global change? (3) Is the magnitude of shifts in foliar C:N and N:P ratios correlated with the intensity and duration of a given global change?

Results

**Responses of foliar C:N and N:P stoichiometry to global change.** Our traditional meta-analysis demonstrates how changes in the concentrations of C, N and P have a variable influence on foliar stoichiometry under different global changes. Shifts in foliar C:N ratios largely tracked changes in foliar [N]. Foliar [C] increased slightly under N addition (n = 78, Fig. 1d), but was not affected by any other global change factors (n = 60 for warming, n = 8 for increased precipitation, n = 122 for drought, n = 49 for eCO\textsubscript{2}, Fig. 1a–c,e), whereas foliar [N] decreased under warming (n = 114), increased precipitation (n = 61), eCO\textsubscript{2} (n = 133) and increased markedly under N addition (n = 194) (Fig. 1). Accordingly, foliar C:N ratio decreased under N addition (n = 78), but increased under eCO\textsubscript{2} (n = 49) (Fig. 1). Although foliar [N] decreased under increased precipitation (n = 61), there was no change in foliar C:N ratios (n = 8) (Fig. 1b). Conversely, foliar C:N ratios increased slightly under
drought (n = 90), even though neither foliar [C] nor [N] were significantly affected by drought (n = 122 and n = 238, respectively) (Fig. 1c).

However, the response ratio (LnRR) of foliar C:N ratios was positively correlated with the LnRR of foliar [C] only under increased precipitation (Fig. 3b), but negatively correlated with the LnRR of [N] under warming (Fig. 3f), increased precipitation (Fig. 3g), drought (Fig. 3h), N addition (Fig. 3i) and eCO2 (Fig. 3j).

For the response of foliar [P], it increased under warming (n = 45), increased precipitation (n = 22), and N addition (n = 163), but decreased under drought (n = 160) (Fig. 1). Interestingly, foliar N:P ratios were influenced by shifts in the concentrations of both nutrients, with no change under warming (n = 35) and increased precipitation (n = 22), an increase under drought (n = 45) and N addition (n = 163), but decreased under drought (n = 160) (Fig. 1).

Thus, the LnRR of foliar N:P ratios was positively correlated with the LnRR of [N] and negatively correlated with the LnRR of [P] under warming (Fig. 4a,f), N addition (Fig. 4d,i) and eCO2 (Fig. 4e,j), but also negatively correlated with foliar [P] under increased precipitation (Fig. 4g) and drought (Fig. 4h).

Foliar nitrogen resorption efficiency (NRE) did not change under warming (n = 24) and eCO2 (n = 20), but decreased under both increased precipitation (n = 23) and N addition (n = 36) (Fig. 1). For phosphorus resorption efficiency (PRE), it did not change under warming (n = 5), but decreased under increased precipitation (n = 14), N addition (n = 38) and eCO2 (n = 7) (Fig. 1).

### Phylogenetic signal test and phylogenetic meta-analysis.

Phylogenetic signal test have been done for the response ratios of each variable. The results showed the phylogenetic signal is significant for foliar N:P ratio under warming (K = 0.219, P = 0.028), foliar [N] under increased precipitation (K = 0.332, P = 0.023), foliar N:P ratio under N addition (K = 0.149, P = 0.039), and foliar C:N ratio under eCO2 (K = 0.642, P = 0.006) (Table 1). The phylogenetic signal is marginally significant for foliar [C] under warming (K = 0.121, P = 0.086), foliar [N] (K = 0.129, P = 0.067) and [P] (K = 0.132, P = 0.066) under N addition, foliar [N] under eCO2 (K = 0.167, P = 0.080) (Table 1).

The results from phylogenetic meta-analysis showed that foliar N:P ratio was not altered by warming (Fig. 2), which was consistent with the result from traditional meta-analysis (Fig. 1a). However, the unchanged foliar

| Treatment       | Variable     | K     | P     |
|-----------------|--------------|-------|-------|
| Warming         | Foliar [C]   | 0.121 | 0.086 |
| Warming         | Foliar [N]   | 0.027 | 0.477 |
| Warming         | Foliar [P]   | 0.083 | 0.314 |
| Warming         | Foliar CN    | 0.025 | 0.420 |
| Warming         | Foliar NP    | 0.219 | 0.027 |
| Warming         | NRE          | 0.116 | 0.794 |
| Warming         | PRE          | 0.388 | 0.894 |
| Increased precipitation | Foliar [C] | 1.108 | 0.103 |
| Increased precipitation | Foliar [N]  | 0.332 | 0.022 |
| Increased precipitation | Foliar [P] | 0.491 | 0.113 |
| Increased precipitation | Foliar CN | 0.879 | 0.609 |
| Increased precipitation | Foliar NP  | 0.187 | 0.946 |
| Increased precipitation | NRE        | 0.998 | 0.907 |
| Increased precipitation | PRE       | 0.694 | 0.521 |
| N addition      | Foliar [C]   | 0.325 | 0.448 |
| N addition      | Foliar [N]   | 0.129 | 0.071 |
| N addition      | Foliar [P]   | 0.132 | 0.066 |
| N addition      | Foliar CN    | 0.167 | 0.536 |
| N addition      | Foliar NP    | 0.149 | 0.038 |
| NRE             | Foliar [C]   | 0.117 | 0.593 |
| NRE             | Foliar [N]   | 0.218 | 0.913 |
| NRE             | Foliar [P]   | 0.323 | 0.595 |
| NRE             | Foliar CN    | 0.167 | 0.080 |
| NRE             | Foliar NP    | 0.241 | 0.689 |
| NRE             | NRE          | 0.642 | 0.006 |
| NRE             | PRE          | 0.512 | 0.142 |
| NRE             | PRE          | 0.162 | 0.256 |
| NRE             | PRE          | 0.606 | 0.360 |

Table 1. The results for the test of phylogenetic signal. The phylogenetic signal was significant when K < 1.00 and P < 0.05. N nitrogen, eCO2: elevated carbon dioxide concentration, [C]: carbon concentration, [N]: nitrogen concentration, [P]: phosphorus concentration, foliar CN: foliar carbon to nitrogen ratio, foliar NP: foliar nitrogen to phosphorus ratio, NRE: nitrogen resorption efficiency, PRE: phosphorus resorption efficiency.
N:P ratio under N addition and foliar C:N ratio under eCO2 were inconsistent with the results from traditional meta-analysis (Figs. 1d,e, 2).

**Correlations of the response magnitudes of foliar C:N and N:P ratios with latitude, MAP and MAT.** Linear regressions were used to analyze the correlations among the variations (log of response ratio: LnRR) of foliar stoichiometry with latitude, MAP, MAT under warming, increased precipitation, N addition and eCO2. We found relationships between the response magnitude of foliar C:N and N:P ratios with latitude, MAP, MAT were weaker under warming and eCO2, but stronger under increased precipitation and N addition (Table 2). Under increased precipitation, the LnRR of foliar C:N ratio was negatively related to latitude (R² = 0.34, P = 0.036) and MAT (R² = 0.34, P = 0.036), but positively related to MAP (R² = 0.34, P = 0.036) (Table 2). For foliar N:P ratio, it was positively related to latitude (R² = 0.19, P < 0.0001) and MAP (R² = 0.686, P < 0.0001), but negatively related to MAT (R² = 0.458, P = 0.000) under increased precipitation (Table 2).

**Correlations of the response magnitudes of foliar C:N and N:P with treatment levels and durations.** We further investigated how the level of different global change treatments affected the magnitude of the response in foliar C:N and N:P ratios (Fig. 5). The LnRR of N:P ratios were not related to treatment level for any of the studied global change drivers (Fig. 5e–h) and treatment level had no influence on the LnRR of foliar C:N to increasing temperature (Fig. 5a) or precipitation (Fig. 5b). However, the LnRR of foliar C:N ratios decreased with increasing rate of N addition (R² = 0.17, P = 0.0002, Fig. 5c), and there was a bimodal relationship between the LnRR of foliar C:N and eCO2, whereby the increase in foliar C:N ratios was greatest at intermediate [CO₂] treatment levels (R² = 0.30, P = 0.004, Fig. 5d).

We also assessed how the treatment duration affected the magnitude of the response in foliar C:N and N:P ratios (Fig. 6). We found the LnRR of foliar N:P ratio decreased with treatment duration under increased precipitation (R² = 0.25, P = 0.01), N addition (R² = 0.20, P < 0.0001) and eCO2 (R² = 0.12, P = 0.04) (Fig. 6f–h).
Table 2. Linear correlations between the variations (log of response ratio: lnRR) of foliar C:N ratio and N:P ratio with latitude, MAP, MAT under warming, increased precipitation, N addition and eCO₂. The correlations were significant when \( P < 0.05 \). MAP: mean annual precipitation (mm), MAT: mean annual temperature (°C), \([\text{CO}_2]\): carbon dioxide concentration, N: nitrogen, C:N: foliar carbon to nitrogen ratio, N:P: foliar nitrogen to phosphorus ratio.

| Treatment       | Independent variables | Dependent variables | a       | b       | \( x0 \) | \( y0 \) | \( r^2 \) | P          |
|-----------------|-----------------------|---------------------|---------|---------|---------|---------|---------|------------|
| Warming         | Latitude              | C:N                 | –       | –       | –       | –       | –       | –          |
|                 |                       | N:P                 | –       | –       | –       | –       | –       | –          |
|                 | MAP                   | C:N                 | –       | –       | –       | –       | –       | –          |
|                 |                       | N:P                 | –       | –       | –       | –       | –       | –          |
|                 | MAT                   | C:N                 | –       | –       | –       | –       | –       | –          |
|                 |                       | N:P                 | –       | –       | –       | –       | –       | –          |
| Increased precipitation | Latitude              | C:N                 | –0.214  | 9.465  | –       | –       | 0.340   | 0.036      |
|                 |                       | N:P                 | 0.085   | –3.634 | –       | –       | 0.190   | 0.029      |
|                 | MAP                   | C:N                 | 0.001   | –0.159 | –       | –       | 0.340   | 0.036      |
|                 |                       | N:P                 | 0.726   | 78.638 | 267.856 | –0.351 | 0.686   | <0.0001    |
|                 | MAT                   | C:N                 | –0.02   | 0.199  | –       | –       | 0.340   | 0.036      |
|                 |                       | N:P                 | –0.042  | 0.309  | –       | –       | 0.458   | 0.000      |
| N addition      | Latitude              | C:N                 | 0.014   | –0.725 | –       | –       | 0.173   | <0.0001    |
|                 |                       | N:P                 | –       | –       | –       | –       | –       | –          |
|                 | MAP                   | C:N                 | –0.001  | 0.107  | –       | –       | 0.115   | 0.002      |
|                 |                       | N:P                 | –       | –       | –       | –       | –       | –          |
|                 | MAT                   | C:N                 | –       | –       | –       | –       | –       | –          |
|                 |                       | N:P                 | –       | –       | –       | –       | –       | –          |
| eCO₂            | Latitude              | C:N                 | –       | –       | –       | –       | –       | –          |
|                 |                       | N:P                 | –       | –       | –       | –       | –       | –          |
|                 | MAP                   | C:N                 | –       | –       | –       | –       | –       | –          |
|                 |                       | N:P                 | –       | –       | –       | –       | –       | –          |
|                 | MAT                   | C:N                 | –       | –       | –       | –       | –       | –          |
|                 |                       | N:P                 | –       | –       | –       | –       | –       | –          |

Figure 3. Correlations between the natural log response ratio (lnRR) of the foliar C:N ratio and [C] under (a) warming, (b) increased precipitation, (c) drought, (d) N addition and (e) eCO₂ and the relationship between the lnRR of the foliar C:N ratio and [N] under (f) warming, (g) increased precipitation, (h) drought, (i) N addition and (j) eCO₂. See Fig. 2 for definitions of the abbreviations. Red and blue dots represent negative and positive responses of the C:N ratio, respectively. The figure was performed using Sigmaplot version 11.0 (Systat Software, Inc.).
Discussion

In this study, we investigated how foliar C:N and N:P ratios respond to global change, including warming, increased precipitation, drought, N addition and eCO₂ by a global meta-analysis. We demonstrate that the response of foliar C:N ratio to global change was largely explained by shifts in foliar [N], whereas the response of foliar N:P ratio was influenced by shifts in both [N] and [P]. When doing linear regressions, we found the response magnitudes of foliar C:N and N:P ratios were largely affected by latitude, MAP and...
MAT under increased precipitation treatment. When doing multiple regressions, we found the effects of “latitude + MAP + MAT + branch length + treatment duration + treatment level” on the LnRRs of foliar C:N and N:P ratios were significant under N addition treatment. In contrast to previous meta-analyses, our study only included the results of field manipulative experiments, which are subject to much greater environmental variability than pot and greenhouse studies. Further, distinct responses of foliar nutrients to global change, compared to responses at the whole-plant level, can reflect important shifts in nutrient allocation among plant parts.

Responses of foliar C:N ratio were mainly related to shifts in foliar [N] under global change. Our results showed changes in foliar C:N ratios were mainly explained by shifts in foliar [N] (Figs. 1, 3), whereas foliar [C] was generally unaffected by global change treatments (Fig. 1). This is perhaps not surprising because increased CO₂ uptake by plants via photosynthesis is largely constrained by foliar [N] and foliar [C] reflects the balance of foliar-level photosynthesis and respiration. Nonetheless, we detected a small increase in foliar [C] in response to N addition (Fig. 1d), which could indicate greater investment in structural C or chemical defenses against herbivory with increasing foliar [N]. Indeed, the large increase in foliar [N] under N addition resulted in lower foliar C:N ratios despite increased foliar [C] (Fig. 1d), which would make leaves more palatable to herbivores. Lower C:N ratios under N addition were also mediated by increased foliar [N] (Figs. 1d, 3d, i), consistent with studies along fertility gradients, and previous meta-analyses in which a negative correlation between the C:N ratio and [N] in foliar tissues were observed.

Responses of foliar N:P ratio were related to altered [N] and [P] under global change. Although foliar [N] and [P] showed distinct and variable responses to global change (Fig. 1), shifts in the N:P ratio were consistently positively correlated with the response of foliar [N] and negatively related to the response of foliar [P] under all global change factors (Fig. 4, Table S3). Hence, shifts in the foliar N:P ratio in response to global change are determined by contrasting changes in both nutrients, even though the individual responses of [N] and [P] were not always statistically significant. Foliar N:P ratios were not altered by warming or increased precipitation.
The response of foliar N:P ratios to drought was negatively correlated with the response of foliar [P] (Fig. 4h). An increase in soil P mineralization as a result of N-investment in phosphatase production38,39. It is noteworthy that the changes in [P] we observed in field manipulation studies were inconsistent with the results from previous global meta-analyses, which found that N fertilization did not affect foliar [P] and decreased root [P]15. Taken together with our results, this suggests that plants respond to N enrichment by increasing P allocation to leaves and decreasing the allocation of P to roots. The increased foliar N:P ratio under N addition nevertheless implies that P limitation will become more severe in areas with continuing substantial atmospheric N deposition.

Both foliar [N] and [P] increased under N addition, but the magnitude of the increase was significantly higher for [N] than [P] (Fig. 1d). Accordingly, the increase in the N:P ratio under N addition was largely attributed to increased foliar [N] (Fig. 1d), consistent with a previous meta-analysis at the whole-plant level33, even though N addition decreased NRE (Fig. 1d). The observed increase in foliar [P] under N addition was probably related with changes in PRE, because PRE was decreased by N addition (Fig. 1d), and was marginally correlated with changes in foliar [P] (Fig. S10b, R² = 0.25, P = 0.07). It is conceivable that increased [P] with N-addition is due to an increase in soil P mineralization as a result of N-investment in phosphatase production38,39. It is noteworthy that the changes in [P] we observed in field manipulation studies were inconsistent with the results from previous global meta-analyses, which found that N fertilization did not affect foliar [P] and decreased root [P]15. Taken together with our results, this suggests that plants respond to N enrichment by increasing P allocation to leaves and decreasing the allocation of P to roots. The increased foliar N:P ratio under N addition nevertheless implies that P limitation will become more severe in areas with continuing substantial atmospheric N deposition.

How do global change treatment intensities and duration affect the response of foliar C:N or N:P ratios? Characterizing how the magnitude of global change will affect foliar C:N and N:P ratios is important for predicting future biogeochemical cycling under different global change scenarios. Unexpectedly, both the C:N and N:P ratios were resistant to global warming in our study, even though warming levels were as high as 5 °C (Fig. 5a,c), and although there were trends towards declining foliar N:P ratios with the level of N addition and eCO₂, these were not significant. By contrast, the response magnitude of foliar C:N ratio declined with N addition rate, especially at loads above c. 10 g N m⁻² y⁻¹ (Fig. 5c). The results from multiple regressions also showed N addition rate significantly affected the response of foliar C:N ratio to N addition (Table S3). Interestingly, the increase in foliar C:N ratios with CO₂ enrichment was highest at intermediate eCO₂ levels (Fig. 5d), which indicates plant physiological constraints to responses in foliar stoichiometry above c. 350 µmol mol⁻¹ CO₂. For increased precipitation, although the response magnitude of foliar C:N and N:P ratios were not affected by the level of increased precipitation (Fig. 5h), the LnRRs of foliar C:N ratio and foliar N:P ratio were positively related to MAP (Table 2). These results suggested the responses of foliar stoichiometry to increased precipitation were specific among sites with different levels of MAP, which results in the overall non-significant response of foliar stoichiometry to increased precipitation (Fig. 1b).

Our results suggested that treatment duration did not affect the response magnitudes of foliar C:N ratio to global change (Fig. 6a–d). But the LnRR of foliar N:P ratio decreased with treatment duration under increased precipitation, N addition and eCO₂ (Fig. 6f–h). This was probably attributed to the correlation between foliar [P] and treatment duration under increased precipitation, N addition and eCO₂ (Fig. S13j–l). This also confirmed ecosystem P cycling is more conserved compared to ecosystem N cycling33,34, thus can be significantly affected by treatment duration under global change. These results are important for us to predict spatiotemporal variations in foliar stoichiometry under future global change.

Final remarks and conclusions

Our results suggested the effects of the studied global change drivers on foliar C:N ratios were due mainly to changes in [N], but the shifts in N:P ratio were more complex. Warming enhanced foliar [P] and decreased foliar [N] with a resulting statistically not-significant trend to decreased foliar N:P ratio. Further studies are needed to separate the effects of warming in wetter and drier sites when more data will be available, since warming can have opposite effects in wetter and drier sites given its impact enhancing aridity in drier sites. Increased precipitation and drought had greater effects on foliar [P] than on foliar [N], and increased precipitation enhanced foliar [P]...
whereas drought reduced foliar [P]. These results indicate that availability of soil water has a great impact on plant uptake capacity of P than N given that soil P is often immobile compared to soil N. N addition increased foliar N:P due to the larger increases in [N] than in [P], and eCO2 reduced foliar N:P due to the decrease in [N] but not in [P].

In contrast to previous meta-analyses, by limiting our study to in situ experiments, we demonstrate that shifts in foliar N:P ratios in response to global changes can be attributed to changes in the foliar concentrations of both N and P. In addition, their responses to global change were independent of their phylogenetic signal. We propose that greenhouse or laboratory studies may limit the influence of the distinct motilities of N and P in the soil and therefore plant nutrient uptake in response to global changes in small-scale experiments may not reflect the true responses of plants under field conditions. Our findings are important for our understanding of plant nutrient dynamic and modeling of nutrient biogeochemistry under global change.

**Material and methods**

**Data selection.** A comprehensive search of relevant peer-reviewed articles and dissertations published from 1997 to 2017 was conducted using the databases of the Web of Science, ProQuest and China National Knowledge Infrastructure (CNKI). We also cross-checked the references of selected articles to identify other potential book chapters and peer-reviewed reports using combinations of the following keywords: carbon, concentration, C:N, leaf, CO₂, leaf, needle, nitrogen, N:P, phosphorus, plant, ratio, stoichiometric, stoichiometry, warming, increased precipitation, drought and N deposition/addition. We extracted data for foliar [C], [N], [P] and N- and P-resorption efficiencies of different plant species. These plant species covered multiple life forms including crop species, grasses, mosses, shrubs and trees. When data from multiple years were given for the same study, we only selected data from the last year to avoid temporal pseudo-replication⁴⁶. We also recorded foliar C:N and N:P ratios or calculated them using the ratios of foliar [C], [N] and [P] (i.e. foliar C:N = foliar [C]/[N] and foliar N:P = foliar [N]/[P]) when only foliar [C], [N] and [P] were given and there was no data for C:N and N:P in the literature. Numerical values were extracted from graphically presented data by digitizing the figures using Engauge Digitizer (Free Software Foundation, Inc., Boston, USA). The experimental sites included in our study are shown in Fig. S1, which was generated in R version 3.4.2 (R Core Team, 2017, https://www.R-project.org/) using ggplot2⁴³ and the R packages ggsm⁴⁴ and legendMap⁴⁵.

**Meta-analysis.** The data were analyzed as described by Hedges et al.⁴⁶. The effect sizes for warming, altered precipitation, N addition and eCO₂ for each observation were represented by log response ratios (RR): lnRR = ln(Xt/Xc), where Xc is the control mean, and Xt is the treatment mean. The publication bias was estimated by the Gaussian function (Figs. S2–S6 in the Supporting Information, which was generated by R version 3.3.3 (R Core Team, 2017, https://www.R-project.org/), and the frequency distributions of all the RR values of the target variables followed a normal distribution, indicating an absence of publication bias in our study. The average RR for each global change was calculated using the mixed model of the meta-analytical program METAWIN (Sinauer Associates, Inc. Sunderland, USA) and the variances of the mean effect sizes were calculated using resampling techniques⁴⁷. If the lower bound of the 95% confidence interval (CI) of a given RR was > 1, then the response was significantly positive at P < 0.05. If the upper bound of the 95% CI of RR was < 1, then the response was significantly negative at P < 0.05. A subgroup analysis was conducted for each parameter to identify differences in effect sizes among different life forms. Total heterogeneity (Qₜ) was partitioned into within-group (Qₓ) and between-group (Qₜ) heterogeneities, whereby a significant Qₓ indicates a different RR among groups⁴⁸ and group means were considered significantly different if their 95% CIs did not overlap. A full description of the meta-analysis is provided in SI Appendix B. Figure 1 was performed using Sigmaplot version 11.0 (Systat Software, Inc.).

**The phylogenetic information of plant species and phylogenetic meta-analysis.** We created the phylogenetic tree by "phy tools" package (phylogenetic tools for comparative biology—and other things)⁴⁶ in R version 3.3.3 (R Core Team, 2017, https://www.R-project.org/) based on the Scientific names of the species given in the literature and got the branch length (million years) of each species, which represents the phylogenetic information, i.e. evolutionary history, of each species. The branch length of the plant species can be found in the SI Appendix B.

We used the function "phylosignal" in R to test whether there is phylogenetic signal for the response ratio of each variable in R version 3.3.3 (R Core Team, 2017, https://www.R-project.org/). When a phylogenetic signal exists in the corresponding response ratio, then we did the meta analysis including phylogeny, i.e. phylogenetic meta-analyses. The detailed methods for phylogenetic meta-analyses referred to the methods in the papers Adams⁴⁹ and Yan et al.⁵⁰. We did phylogenetic meta-analyses in R version 3.3.3 (R Core Team, 2017, https://www.R-project.org/). The R code was detailed in SI Appendix C.

**Regression analyses.** Linear and nonlinear correlations were used to analyze the relationships among the variation (log of response ratio: lnRR) of each variable and latitude, mean annual precipitation (MAP), mean annual temperature (MAT) under warming, increased precipitation, N addition and eCO₂. To test whether the phylogenetic information for specific species affect the response of foliar stoichiometry to global change, we analyzed the correlations between foliar stoichiometry with the branch length (million years) away from the phylogenetic tree of each species. To identify whether changes in foliar stoichiometry were best explained by changes in foliar [C], [N] or [P], we also analyzed the relationships between RR of the C:N ratio and foliar [C] or [N], as well as between RR of the N:P ratio and foliar [N] or [P] using Pearson’s correlations. The treatment levels for increased temperature (°C), altered precipitation (mm), rate of N addition (g m⁻² years⁻¹) and eCO₂...
(µmol mol⁻¹) were available in 63% CO₂ enrichment treatment, 88% N addition treatment, 80% warming treatment, 89% increased precipitation treatment. Therefore, we used linear regression to assess the influence of treatment levels on the RR of foliar C:N or N:P ratios. We also used linear regression to assess the influence of treatment duration (year) on the RR of foliar C:N and N:P ratios. All linear analyses were performed using R version 3.3.3 (R Core Team, 2017, https://www.R-project.org/). Figures S8–S13 was performed using Sigmaplot version 11.0 (Systat Software, Inc.).

Multiple regressions were used to analyze the effects of "latitude + MAP + MAT + branch length + treatment duration + treatment level" on the LnRR of foliar C:N and N:P ratios when all the information are given simultaneously. The multiple regression analyses were performed using the R code 'lm' in R version 3.3.3 (R Core Team, 2017, https://www.R-project.org/). The results are detailed in Table S3.

Data availability
The data set of the peer-reviewed publications will be accessible after acceptance.

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Author contributions
S.X. designed this study. S.X. collected the data for warming, increased precipitation, N addition and eCO2, analyzed the data and wrote the paper. J.S. and J.P. provided the data for drought and wrote the paper. J.Z. did the phylogenetic signal test and phylogenetic meta-analysis.

Competing interests
The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to S.X.

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