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Effects of elevated CO_2 on plant C-N-P stoichiometry in terrestrial ecosystems: A meta-analysis

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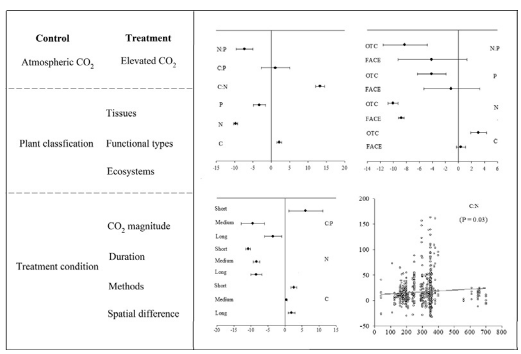
HIGHLIGHTS

- Elevated CO_2 enhanced plant C, C:N but decreased plant N, P and N:P.
- Plant leaf and herbaceous plant type showed more sensitivity to rising CO_2.
- Plant C and N and C:P ratio showed an obvious "CO_2 acclimation".
- Compared to FACE, OTC showed larger changes of C, N, P, and N:P.

GRAPHICAL ABSTRACT



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ABSTRACT

A substantial number of experiments have so far been carried out to study the response of the C-N-P stoichiometry of terrestrial plants to the rising CO_2 level of the earth. However, there is a need of systematic evaluation for assessing the impact of the elevated CO_2 on plant C-N-P stoichiometry. In the present investigation, a comprehensive meta-analysis involving 386 published reports and including 4481 observations has been carried out. The goal of the research was to determine the response of plants to their C-N-P stoichiometry due to elevated levels of global atmospheric CO_2. The results showed that rising CO_2 altered the concentration of C (+2.19%, $P < 0.05$), N (−9.73%, $P < 0.001$) and P (−3.23%, $P < 0.001$) and C:N (+13.29%, $P < 0.001$) and N:P ratios (−7.32%, $P < 0.0001$). Overall, a slightly increasing trend in the C:P ratio ($P > 0.05$) in the plant was observed. However, plant leaf, shoot and herbaceous type of plants showed more sensitivity to rising CO_2. CO_2 magnitude exhibited a positive effect ($P < 0.05$) on C:N ratio. Additionally, "CO_2 acclimation" hypothesis as proposed by the authors of the current paper was also tested in the study. Results obtained, especially, show changes of C and N concentrations and C:P ratio to an obvious down-regulation for long-term CO_2 fumigation. At spatial scales, a reduction of plant N concentration was found to be higher in the southern hemisphere. The CO_2 enrichment methods affected the plant C-N-P stoichiometry. Compared to FACE (free-air CO_2 enrichment), OTC (open top chamber) showed larger changes of C, N, P, and N:P. The results of the present study should, therefore, become helpful to offer a better understanding towards the response of the terrestrial plant C-N-P stoichiometry to an elevated global atmospheric CO_2 in the future.

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1. Introduction

Atmospheric CO_2 concentration has been increasing, especially since the advent of the era of industrialization. The Intergovernmental Panel on Climate Change (IPCC) has published five assessment reports, of which the 5th one showed that the atmospheric CO_2 concentration increased from 280 ppm during the pre-industrial era to 390 ppm until 2013 (Stocker et al., 2013). Increasing CO_2 concentration profoundly affects the terrestrial ecosystems as well as the biogeochemical cycle (Salazar-Parra et al., 2015). The key elements (C, N and P) in plant, play significant role on the sustainability in agriculture (Butterly et al., 2015) by maintaining grain quality (Pleijel and Uddling, 2012), and plant-herbivore interactions (Couture et al., 2012; Sardans et al., 2017). Assessment and simulation of the plant growth (Norby et al., 2005) under rising CO_2 level have been incorporated into models of land C biogeochemical cycle (Stocker et al., 2013). The adjustment of the plant to changes in climate has also been incorporated in the ecosystem models (Achat et al., 2016). Theory of ecological stoichiometry had been developed from aquatic ecosystems, but from the last decade it is being used in the analyses of terrestrial ecosystems (Austin and Vitousek, 2012). Elemental stoichiometry is related to the nutrient cycle right from the molecules to the biosphere (Sterner and Elser, 2002). Recently, an increasing attention has been paid to the effect of global change on the ecological stoichiometry, not only in soil but also in microbes and higher plants (Zechmeister-Boltenstern et al., 2015). However, the effect of increasing atmospheric CO_2 concentration on the plant C-N-P stoichiometry still remains incomplete. For example, there was a lacking detailed analysis of duration and spatial difference. This not only influenced the accuracy of the model and evaluation of nutrient cycling in the future global climate change, but also offer a detailed tracking of the nutrient ratios in plants. The results of tracking thus assist in predicting the plant productivity and C fixation (Elser et al., 2007). Elevated CO_2 may affect the plant elements and growth rate. The latter is closely related to the C-N-P stoichiometry (Elser et al., 2010; Sterner and Elser, 2002). Elevated CO_2 may also change the quality of the plant concerned and thus cascade the human nutrition. Loladze (2014) showed the relationship between the minerals of plants and human nutrition in response to rising CO_2 at large spatial scales.

Numerous artificial simulation experiments were designed in order to study how the key elements of plant respond to the increasing atmospheric CO_2 level. In general, on a short-term basis, the elevated CO_2 affects plant C-N-P stoichiometry by altering soil, microbial biomass and nutrient cycling (Fig. 1). It is possible that rising CO_2 may lead to higher stomatal closure (Samarakoon and Gifford, 1995), thereby causing a decrease in the rate of transpiration and increasing the soil moisture (Del Pozo et al., 2007) and also water or N-use efficiency (Jin et al., 2015). Many plants probably enhance the rate of photosynthesis (Comins and McMurtrie, 1993) and the net primary production (NPP), and alters litter quantity under rising CO_2 (Sardans and Penuelas, 2012; Zheng et al., 2010). Especially, shifting the C concentration of the litter and C:N ratio (Zheng et al., 2010) may stimulate microbial (biomass, activity, community) decomposition and biogenic weathering (Andresen et al., 2010). Rising CO_2 enhances the microbial C efficiency and lowers soil N availability (Carrillo et al., 2014). Increasing organic matter decomposition and rock weathering may also enhance the P availability (Hoosbeek, 2016), which affects the plant nutrient allocation or C-N-P stoichiometry (Sardans and Penuelas, 2012; Yuan and Chen, 2015; Zechmeister-Boltenstern et al., 2015). In the long run, the primary production may get decreased due to the limitation of N and P or both (Finzi et al., 2006; Sokolov et al., 2008), which leads to the "CO_2 acclimation" (Zhang et al., 2011). In a first attempt of CO_2 fertilization to young bean plant, it was found that not only N, but also P concentration in leaf declined by about 25% (Porter and Grodzinski, 1984). Since then, a number of studies were published to find out the response of elevated CO_2 on terrestrial plant C-N-P stoichiometry. These studies include

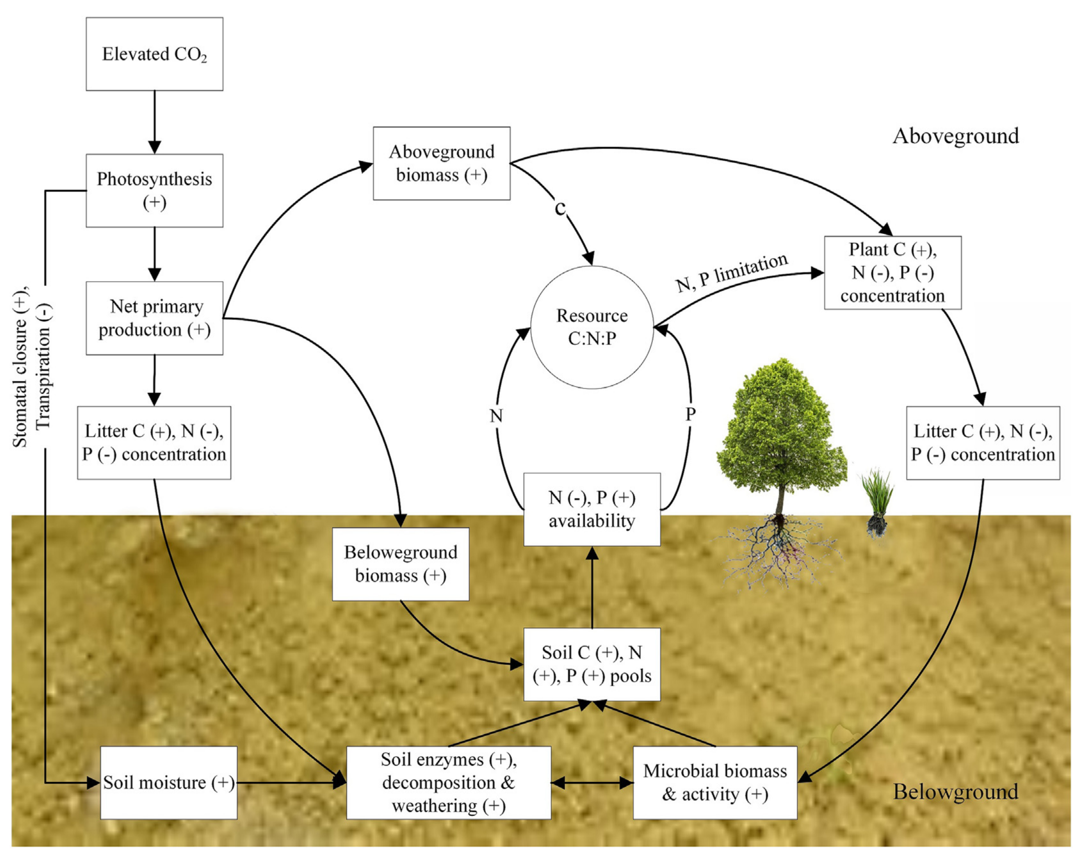

Fig. 1. Effect of elevated CO_2 on processes controlling plant C-N-P stoichiometry at a short-term scale. Increased (+) and decreased (−) effects were showed in parentheses.

Table 1
Summary of previous published meta-analysis of the effect of elevated CO_2 on plant C-N-P stoichiometry.

	Plant C-N-P stoichiometry	Reference
Overall	*C*: Increased (+6%)	Loladze, 2014
	N: Decreased (−12.7%)	Deng et al., 2015
	Decreased (−12%)	Huang et al., 2015
	Decreased (−8%)	Dumont et al., 2015
	P: Decreased (−4%)	Deng et al., 2015
	No-significant change	Dumont et al., 2015
	Decreased (−4%)	Huang et al., 2015
	C:N ratio: Increased (+25%)	Loladze, 2014
	C:P ratio: Increased (+16%)	Loladze, 2014
	N:P ratio: Decreased (−7%)	Loladze, 2014
	Decreased (−11%)	Huang et al., 2015
Tissue	*N*: Aboveground (−14%) *vs* belowground (−9%)	Cotrufo et al., 1998
	Decreased (about −12.5%) in leaf	Curtis, 1996
	Aboveground decreased higher *vs* belowground	Deng et al., 2015
	Decreased (−9%) less in leaf *vs* aboveground (−23%)	Wang et al., 2013
	Decreased in root and leaf	Sardans et al., 2017
	P: Aboveground decreased higher *vs* belowground	Deng et al., 2015
	Insignificantly changed in leaf and root	Sardans et al., 2017
	C:N ratio: Increased higher in shoot (+13.8%) *vs* root (+6.6%)	Yang et al., 2011
	N:P ratio: Aboveground (−9.2%) decreased higher *vs* belowground (−6.0%)	Deng et al., 2015
	Decreased in root significantly but no leaf	Sardans et al., 2017
Functional type	*C*: Only herb and N-fixing plants significantly increased	Yuan and Chen, 2015
	N: C3 (−16%) *vs* C4 and N-fixing (−7%), woody (−19%) *vs* non-woody (−17%)	Cotrufo et al., 1998
	Decreased higher in C3 (−21%) leaf *vs* C4 (−6%)	Wand et al., 1999
	N-fixing decreased less *vs* others	Yuan and Chen, 2015
	P: Only grass and conifer decreased significantly	Yuan and Chen, 2015
	C:N ratio: C3 Increased (+20.6%) *vs* C4 (−1.9%)	Dumont et al., 2015
	N:P ratio: C3 decreased larger *vs* C4	Yuan and Chen, 2015
	Only woody decreased, but slightly for herb and moss	Yue et al., 2017
Ecosystem type	*N*: Decreased by 6%, 8%, and 12% in grassland, cropland, and forest, respectively	Feng et al., 2015
	C:P ratio: Only grassland ecosystem and herb increased significantly	Yue et al., 2017
Method	*N*: Non-FACE studies (about −16%) declined higher *vs* FACE (about −12%)	Loladze, 2014
	Controlled environment declined higher *vs* natural environment	Yuan and Chen, 2015
	P: Non-FACE studies (about −10%) declined higher *vs* FACE (about −5.8%)	Loladze, 2014
	No change in FACE, decreased in OTC	Deng et al., 2015
	C:N ratio: Controlled environment increased higher *vs* natural environment	Yuan and Chen, 2015
	OTC increased larger *vs* FACE	Yue et al., 2017
	N:P ratio: FACE decreased larger *vs* OTC	Deng et al., 2015
	Controlled environment declined higher *vs* natural environment	Yuan and Chen, 2015

grasslands, croplands, forests and so on. Functional patterns of different plant tissues were also considered in those researches. Although a variety of results are available, but many of those seems to be controversial and uncertain. Hence, it is necessary to carry out a comprehensive analysis in summarizing the effect of rising CO_2 on terrestrial plant C-N-P stoichiometry. A meta-analysis is a statistical approach to the results of multiple independent experiments addressing the same topic.

Meta-analysis carried out earlier, focused mainly on plant N concentration, especially on N content of leaf related to photosynthesis under rising CO_2 (Cotrufo et al., 1998; Curtis, 1996; Wand et al., 1999; Wang et al., 2013). In recently carried out meta-analyses, C:N, C:P, and N:P ratios have also been focused (Table 1). However, a diverse change in plant C-N-P stoichiometry was observed in previous meta-analyses. In those, N:P ratio decreased by 7%, 8.7%, and 11% as showed by Deng, Huang and Loladze, respectively (Deng et al., 2015; Huang et al., 2015; Loladze, 2014). Effects of CO_2 fumigation on plant C-N-P stoichiometry remained elusive, for example, P decreased by 4% in the research of Deng but it was not significant in Dumont (Deng et al., 2015; Dumont et al., 2015). Furthermore, plant C-N-P stoichiometry was very different for tissues. For instance, N:P ratio declined in root but not in the leaf (Sardans et al., 2017) and C:N ratio increased higher in shoot than root (Yang et al., 2011). Plant C-N-P stoichiometry of different functional (*i.e.*, C4 or C3, woody or non-woody) and ecosystem (*i.e.*, grassland, forest, cropland) types also showed different responses to elevated CO_2 (Feng et al., 2015; Yuan and Chen, 2015). In addition, methods of CO_2 enrichment affected plant C-N-P stoichiometry, for example, results from Yuan and Chen showed that N and N:P ratio declined steeply in the controlled environment than natural (Yuan and Chen, 2015). According to the published literature on meta-analysis, few of the previous studies were devoted to assessing treatment duration and spatial differences (Table 1). To our knowledge, the present study is the first of its kind to test "CO_2 acclimation" hypothesis by using plant C-N-P stoichiometry.

We hypothesize that, (i) the impact of rising CO_2 on plant elemental composition differ between plant tissues, ecosystems, functional types and methods owing to their different functions, their local environments and vegetation types, (ii) the response of plant C-N-P stoichiometry to elevated CO_2 differ between durations owing to the growth stage, element cycle feature and "CO_2 acclimation". To test these hypotheses, we conducted a global meta-analysis of published papers on the response of plant C-N-P stoichiometry under elevated CO_2 level.

2. Materials and methods

2.1. Experimental sites

All the data for the present meta-analysis, came from 386 independent individual studies (Fig. 2). Experimental duration of elevated CO_2, ranged from few days to seventeen years. The exposure time (in years) was the duration from the start of the experiment to the time when the plants were finally collected. In the experiment, seven ecosystems with elevated CO_2 experiment were considered. Those were grasslands (alpine grassland and temperature grassland), deserts, croplands, tundras, wetlands, forests (subtropical, temperature and tropical), and shrublands. All the methods of CO_2 enrichment, namely, OTC (open top chamber), FACE (free-air CO_2 enrichment), GC (closed growth chamber, including environment chamber, green house and growth chamber), and NS (natural spring) were considered. Each study plant

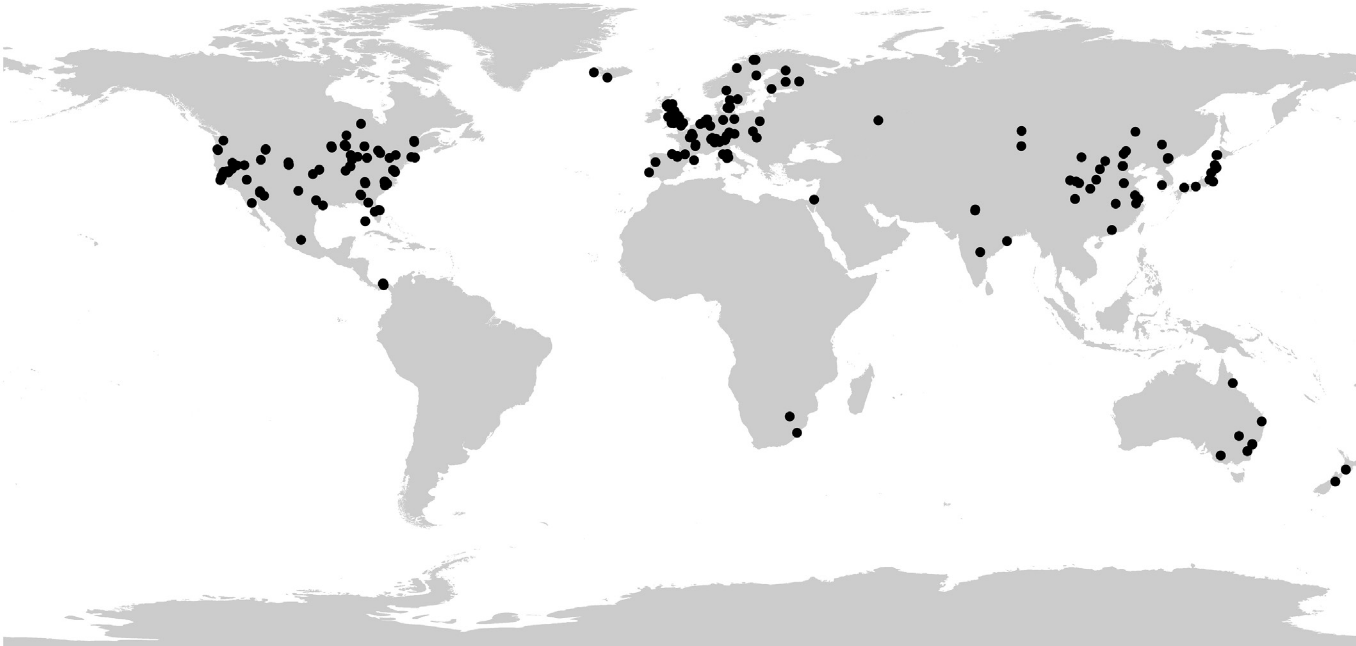

Fig. 2. Global distribution of studies included in the meta-analysis.

was classified as either woody or herbaceous (excluding mosses), and the organ of the plants was classified as leaf, root, stem, branch, shoot, seed, whole plant, above ground, and/or litter.

2.2. Data collection

We collected all of the published studies before December 2017. We used the 'Web of Science' to search for primary studies. The searching keywords used in the database were either rising CO_2, elevated CO_2, CO_2 enrichment, CO_2 fertilization and/or increased CO_2 and plant and C, or N, or P, or C:N, or C:P, or N:P, or C:N:P and stoichiometry. Finally, 386 published papers in between the publishing years 1984 and 2017 were collected (Appendix S1). A total of 4482 records included in our database (Table S1). If the reported data was shown in tables, we calculated the mean and SD, and if the reported data was shown in figures, we extracted the data by *Getdata 2.24*, USA (http://getdata-graph-digitizer.com/). The final data-base had 437, 2337 and 704 records for plant C, N and P concentrations (mg/g, dry mass), respectively. There were also 775, 65 and 163 records for the C:N, C:P and N:P ratios, respectively (Table S1).

For each study, the data was available with appropriate GPS (geographical positioning system, *i.e.*, latitudes and longitudes) of the location. The other descriptive variables collected from the studied papers were the treatments (ambient CO_2/control and elevated CO_2 method), ecosystem types, plant functional types, plant tissues and the duration of the treatments. The magnitude of the rising CO_2 (ppm), sample size (n), mean value and SD (standard deviation) of the controls and the experimental plant along with their C, N and P concentrations and their ratios, like C:N, C:P and N:P were collected. If the error was shown by SE (standard error), SD was calculated by using the following formula: SD $= \mathrm{SE} \times \sqrt{n}$.

2.3. Meta-analysis

Meta-analysis was performed to analyze the responses of plant C, N and P concentrations and C:N, C:P and N:P ratios to the elevated CO_2 level. The analysis required the difference of the result of each study in the form of a measure of the magnitude of the effect in all experiments, or "effect size". It was needed to explain a common scale among the studies. There are many choices of effect size, here, we selected the "response ratio (lnRR)" index to calculate the response of plant C-N-P stoichiometry to the elevated CO_2 (Hedges et al., 1999).

In each case study, the effect size was calculated as the response ratio (lnRR):

$$\ln \mathrm{RR} = \ln\left(\frac{X_e}{X_a}\right)$$

where, X_a and X_e are the averages of a specific variable in the ambient CO_2 groups and elevated CO_2 groups, respectively.

The weighted mean response ratio ($\ln\underline{\mathrm{RR}}$) was calculated to determine the overall effect of the elevated CO_2 on plant C-N-P stoichiometry to elevated CO_2. The calculation formula used was:

$$\ln \mathrm{RR}_{\_} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n} w_{ij}\ln\mathrm{RR}}{\sum_{i=1}^{m}\sum_{j=1}^{n} w_{ij}}$$

where, m is the number of groups, n is the number of in the ith group, and w is the weight of each response ratio.

The percentage of change of plant C-N-P stoichiometry under elevated CO_2 was calculated using the following equation:

$$\left(e^{\ln \mathrm{RR}_{\_}} - 1\right) \times 100\%$$

where, $\ln\underline{\mathrm{RR}}$ is the weighted mean response ratio.

When we conducted subgroup analysis of the tissue, ecosystem, functional type, treatment duration and treatment method, we examined *P*-value associated with $Q_{between}$, which describes the heterogeneity of effect size ($\ln\underline{\mathrm{RR}}$) related to differences between categories to make categorical comparisons. $Q_{between}$ statistic was calculated by using a chi-squared test. A significant $Q_{between}$ indicates that the effect sizes ($\ln\underline{\mathrm{RR}}$) are not equal across categories plant C-N-P stoichiometry.

All meta-analysis was conducted using the "*meta*" package (*4.9-0*) in *R.3.4.3* (https://www.r-project.org/), a general package for meta-analysis. We chose the random effects to estimate the meta-analysis outcome data, and inverse variance weighting was used for pooling. If the 95% CI (confidence interval) for the response ratio ($\ln\underline{\mathrm{RR}}$)

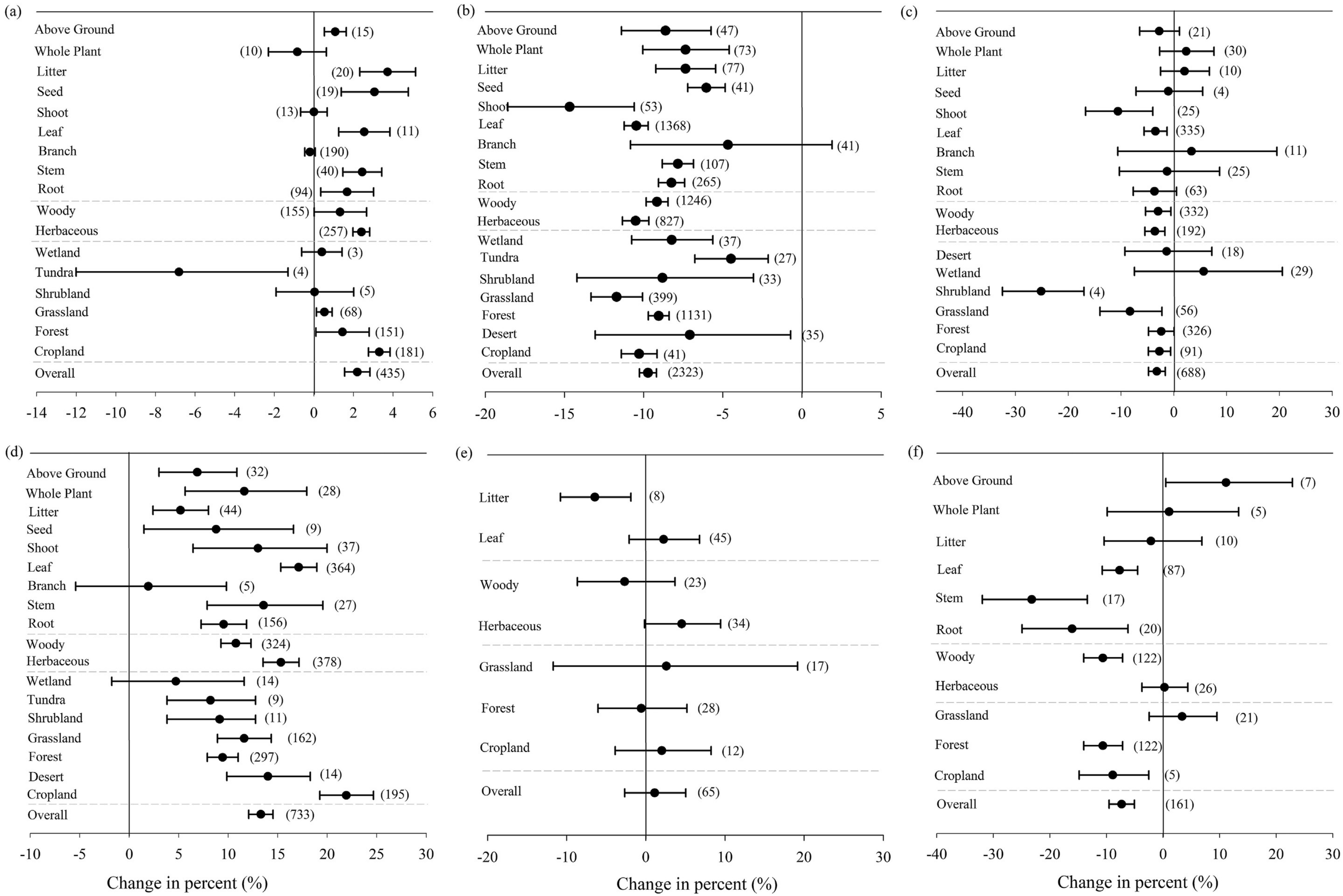

Fig. 3. Effects of elevated CO_2 on plant C (a), N (b), P (c) concentrations, C:N ratio (d), C:P ratio (e) and N:P (f) ratio. Values are change in percent (%) and 95% confidence intervals (CI). Sample size number is showed in parentheses; results are not presented when the sample size was less than three.

overlapped with zero, the response at elevated CO_2 was not significantly different from that at ambient CO_2. Otherwise, the treatment was statistically different. The CO_2 elevated effects on plant C-N-P stoichiometry was either positive or negative. We included individual study where plant C-N-P stoichiometry was all computed from the same plant to avoid bias. We also plotted funnel plot to assess possible publication bias. The funnel plot of plant C-N-P stoichiometry was symmetrical, which indicated that there was an absence of publication bias. Furthermore, we conducted simple linear regression analysis between each change in the percent of plant C-N-P stoichiometry and elevated CO_2 magnitude.

3. Results

3.1. Elevated CO_2 alters the plant C-N-P stoichiometry

Overall, the elevated CO_2 showed significant effects on plant C (+2.19%, $P < 0.05$), N (-9.73%, $P < 0.001$) and P concentrations (-3.23%, $P < 0.001$) at a global scale (Fig. 3), N declines more than P. Plant C ($Q_{between} = 16.72$, $P = 0.0051$), N ($Q_{between} = 35.10$, $P < 0.0001$) and P concentrations ($Q_{between} = 35.10$, $P < 0.0001$) showed significant changes in different ecosystems. C concentration increased by 1.44% significantly in forest but decreased by 6.82% in tundra. The N concentration of all the plants of the studied ecosystems declined under CO_2 enrichment. A higher reduction of N was observed in the cropland and grassland ecosystems compared to tundras. The P concentration increased in wetlands. For the different plant functional types, C, N and P concentrations changed to a greater extent in the herbaceous than woody plants. However, the concentration of C, N and P did not show any significant changes in the branches of the studied plants. The N and P concentrations in the leaf and shoot decreased to a greater extent than other parts of the plants.

Elevated CO_2 treatment significantly altered the plant C:N (+13.29%, $P < 0.0001$) and N:P ratios (-7.32%, $P < 0.001$) but not on C:P ratio at a global scale (Fig. 3). The C:N ratio of plants increased significantly in all ecosystems except wetland under the rising concentration of CO_2. The N:P ratios of plants in croplands and forests decreased significantly. But this was not observed in the case of grassland ecosystems. The C:N ratio of herbaceous plant increased (15.32%) to a greater extent than woody plants (10.77%). But an opposite trend was observed for the N:P ratio. C:N ratios of all plant tissues increased significantly except in the case of branch. The C:N ratio of leaf showed higher values than other plant tissues. The N:P ratios of the stem, root and leaf of the experimental plants decreased significantly.

3.2. The magnitude of elevated CO_2 affecting the plant C-N-P stoichiometry

Many researchers designed a variety of CO_2 concentrations, ranging from 40 to 1500 ppm. The C concentration increased under the rising CO_2 (200–400 ppm) but declined when CO_2 magnitude was >600 ppm (Fig. 4a). From Fig. 4d, it can be seen that changes in the C:N ratio increased significantly with an increase in the concentration of CO_2 level.

3.3. Effect of experimental conditions on plant C-N-P stoichiometry

We subdivided the durations of elevated CO_2 treatment for plant into long (5–17 years), medium (2–4 years) and short term (0–1 year) (Fig. 5a). The change of plant C and N concentrations and C:P ratio under elevated CO_2 showed a "CO_2 acclimation" (Cruz et al., 2013). That is, the change of plant C and N and C:P ratio in short-term is greater than medium-term. It showed a downward trend when exposed on a long-term basis. However, for plant P, C:N and N:P ratios, no "CO_2 acclimation" was found. Especially, change of plant P concentration showed no-significant effects when exposed short-term and medium-term bases to a CO_2-enriched atmosphere.

The different CO_2 enrichment methods showed significant effects over the change of plant C, N and P concentrations and C:P ratio (all $P < 0.05$). The effect, was, however, insignificant on C:N and N:P ratios. Plant C, N, P concentrations and N:P ratio showed a greater change in the OTC method than FACE method (Fig. 5b). All the four CO_2 enrichment methods decreased plant N concentration, however, change of plant P concentration was significantly reduced under OTC and GC but not in case of FACE. FACE significantly reduced the plant C:P ratio while OTC and GC increased the C:P ratio of plants, although their 95% CI crossed zero.

4. Discussion

Our results verified previous studies in a sense that elevated CO_2 enrich C concentration (2.19%) in the plant (Baslam et al., 2012; Han et al., 2011; Ji et al., 2011; McKenzie et al., 2016; Peltonen et al., 2010). Meta-analysis (Curtis and Wang, 1998) study showed that total biomass increased significantly under enriched CO_2 concentration, which means that capability of C sequestration in plants superimposed not only due to the enhancement of biomass but also due to the increase in the C concentration under elevated CO_2. This increased C concentration of plants indicates the potential for elevated CO_2 to the C uptake efficiency of the ecosystem in the future. Duration of treatment, significantly affected the plant C concentration. From Fig. 5a, it can be seen that long term (5–17 years) treatment with elevated CO_2 increased the C concentration significantly but short term (0–1 year) treatment gave insignificant results. It is necessary to study whether the plant can adapt to a higher CO_2 level in the future climate change scenario and also can keep on rising C sequestration among them. The N pools of plants and the soil moisture increases under elevated CO_2 that may prevent the complete down-regulation of long-term CO_2 stimulation of C sequestration (Luo et al., 2006). However, elevated CO_2 exhibited significant negative effect ($P < 0.0001$) on the plant N and P concentrations that may overvalued terrestrial C sink (Wang and Houlton, 2009; Zhang et al., 2014). In soil parent material (Augusto et al., 2017), the linkage between actual N and P pools of soils and the chemical properties under global climate change may limit C fixation because of nutrient availability. Elevated CO_2 decreased significantly the plant N and P concentration by 9.73% ($P < 0.001$, Fig. 3b) and 3.23% ($P < 0.001$, Fig. 3c), respectively. This was related to the "dilution effect" by the enhancement of C fixation (Sardans and Penuelas, 2013; Taub and Wang, 2008). N declines more than P (Fig. 3b). For N concentration, rising CO_2 not only cause "dilution effect", but also reduced Rubisco and suppressed nitrate uptake or assimilation (Loladze, 2014; Taub and Wang, 2008). The was consistent with previous studies (Deng et al., 2015; Sardans et al., 2017) but not in the magnitude as expected. This, may be due to the incorporation of inconsistent plant organs, as plant tissues showed a response to the N and P concentrations. Furthermore, the whole plant was not included in the study by Deng. While Sardans considered only roots and leaves (Deng et al., 2015; Sardans et al., 2017).

Overall, the elevated CO_2 significantly influenced the plant C:N ratio (+13.29%, $P < 0.001$) and N:P ratio (−7.32%, $P < 0.0001$), which is consistent with an earlier study (Yue et al., 2017). However, the observed insignificant effect on plant C:P ratio can be due to a lesser sample size used in the database. Increasing sample size can decrease the likelihood of false negatives (Loladze, 2014; Yue et al., 2017). So more research works on C:P ratio need to be considered. The increase of C:N and C:P ratios were related to the reduction of N and P (Fig. 3), but rising CO_2 and C enhancement, increased the soil C:P and C:N ratios (Sardans and Penuelas, 2012). Changes occurred in the plant N:P ratio reflect that under elevated CO_2, the decrease in the P concentration was less than that of the N concentration (Fig. 3). These observations were consistent with the previous studies (Deng et al., 2015; Loladze, 2014) which showed that phosphorous pool was higher than N pool in plants under elevated CO_2. Plant N:P ratio was associated with the differences in root allocation, biomass turnover, nutrient uptake and reproductive

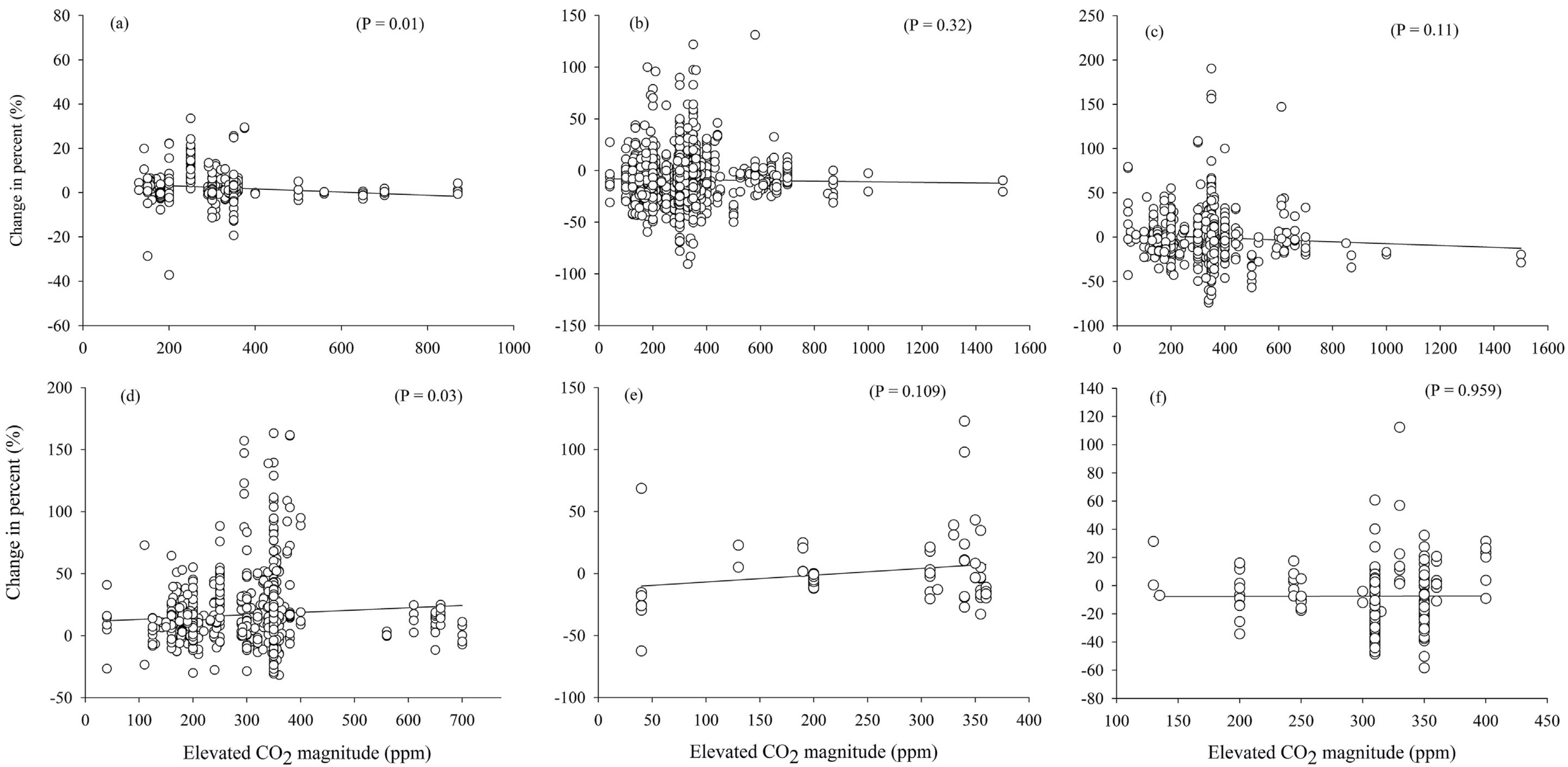

Fig. 4. Effects of elevated CO_2 magnitude (+ambient CO_2 concentration) on plant C (a), N (b), P (c) concentrations, C:N ratio (d), C:P ratio (e) and N:P (f) ratio.

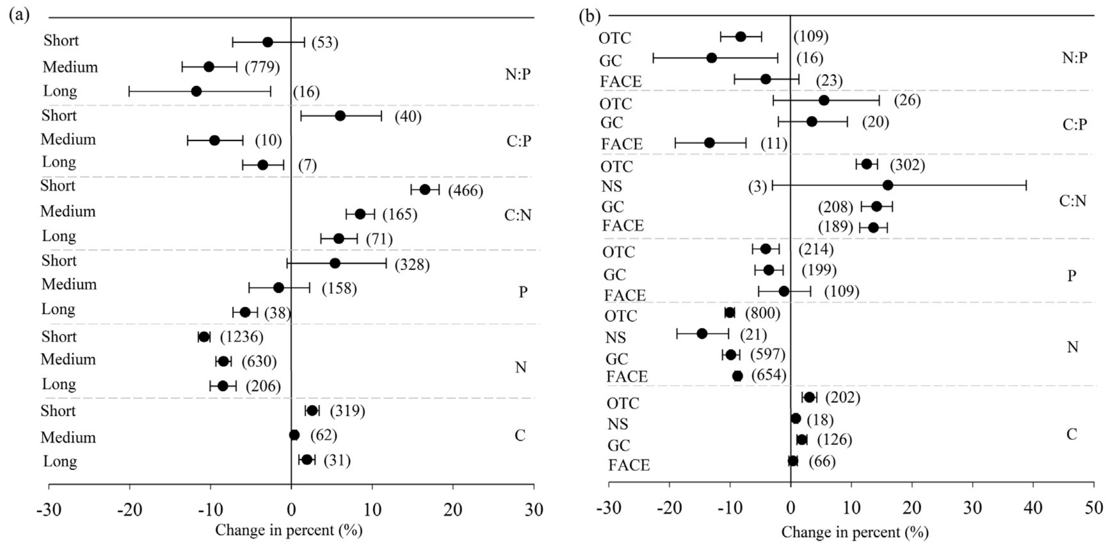

Fig. 5. Effect of elevated CO_2 treatment durations (a) and methods (b) on the plant C-N-P stoichiometry. Values are change in percent (%) and 95% confidence intervals (CI). Treatment durations were subdivided into short (0–1 year), medium (2–4 years) and long term (5–17 years). Elevated CO_2 methods were FACE (free-air CO_2 enrichment), NS (natural spring), GC (closed growth chamber), and OTC (open top chamber). Sample size number is showed in parentheses, results are not presented when the sample size was less than three.

output (Gusewell, 2004). Greater C:N ratio may be attributed to the dilution of N and P concentrations by a 46% increased accumulation of non-structural carbohydrates (TNC, mainly starch and sugars) (Loladze, 2014). Greater C-based secondary metabolic products could also lower the N concentration (Gifford et al., 2000). Elevated CO_2 decreased the N:P ratio (Fig. 3f) and increased the growth rates (Jongen et al., 1996; Zhao et al., 2011). This finding is consistent with the growth rate hypothesis which states that, the lower the N:P ratio, the higher the growth rates since plant organs need P-rich RNA to sustain rapid protein synthesis (Sterner and Elser, 2002).

4.1. Effect of elevated CO_2 on plant tissues C-N-P stoichiometry

The changes of plant C-N-P stoichiometry in response to elevated CO_2 were of different magnitudes when plants were subdivided into tissues (Fig. 3). This is in line with our first hypothesis (i) as proposed before. In terms of plant tissues, there are different metabolic pathways that get altered under rising CO_2. For example, in plants increase in biomass occurs with the rising CO_2 level by enhancing the efficiency of leaf N (Farquhar et al., 1980; Farquhar et al., 1989). In addition, faster turnover of Rubisco enzyme is guided (enrichment of N but not P) to fix C, which might lead to different concentration of N and P in leaf than other tissues. Different tissues exhibit a different sensitivity under elevated CO_2. Fig. 3 showed that N and P concentrations decreased more in leaf and shoot than other tissues. But branch showed insignificant changes, suggesting that the branch served only as a support structure for plant and has less sensitivity. C:N ratio increase was observed in leaves and flowers but not in wood fractions of *Calluna* under elevated CO_2 (Larsen et al., 2011). From Fig. 3 it can be seen that C-N-P stoichiometry in the branch of plant showed insignificant effect under elevated CO_2, which supported this hypothesis. On the contrary, plant roots are an organ that absorbs nutrients from the ground, which showed a different effect when compared with other tissues (Fig. 3). However, plant C-N-P stoichiometry of root and leaf showed mostly similar effects in term of direction under elevated CO_2, but difference in magnitude. The results are consistent with a previous study (Sardans et al., 2017). Elevated CO_2 significantly reduced the N content in plant tissues (Curtis, 1996; Curtis and Wang, 1998), which is consistent with our study. Nonetheless, the N content of plant tissue significantly decreased under elevated CO_2 in a meta-analysis study (Cotrufo et al., 1998), that highlighted the negative effects on the physiological process of plants and N uptake under elevated CO_2 (Yue et al., 2017). A significant change of plant C-N-P stoichiometry in different organs is contributed to the nutrients allocation, for instance, when proportionally less N was used by aboveground green organs, and more N was allocated to the root (Van Oosten and Besford, 1994). Similarly, P exhibited a higher allocation in the leaf than wood in plants of forest types (Sardans and Penuelas, 2013). The occurrence of nutrient related redistribution also affects plant C-N-P stoichiometry from root to shoot. Increase of C:nutrient cannot be detected in shoot (Newbery et al., 1995), if there would be no nutrient distribution, on the contrary, an increase of C:nutrient was not detected in root but significantly in leaf (Saxe et al., 1998). Fig. 6a showed that elevated CO_2 exerted effects in a similar direction on plant C-N-P stoichiometry between above-ground and below-ground, but there are differences in the magnitude of the changes. For example, elevated CO_2 had little influence on the partitioning of C above-ground and below-ground (Hungate et al., 2013). Homeostatic ability of tissues led to different sensitivities. For example, N:P ratio was less responsive (Garrish et al., 2010) in leaf than in stem or root under rising CO_2, which was consistent to our results (Fig. 3f). Although leaf showed a more active metabolism than root and stem, leaf reflected a short term nutrient supply or physiology, whereas, stem and root reflected a longer life in future environment change (Liu et al., 2013).

4.2. Effect of elevated CO_2 on plant C-N-P stoichiometry in different ecosystems

The changes of plant C-N-P stoichiometry in response to elevated CO_2 were of different magnitude and direction when plants were subdivided into different functional ecosystems, which is in line with our first (i) hypothesis. Results showed that elevated CO_2 had different effects showing the dependency of form on different vegetation and function types. Moreover, ecosystem functions varied across different ecosystem types under elevated CO_2 (Huang et al., 2015; Yue et al., 2016). For instance, plant N and P concentrations, C:N and N:P ratios showed significantly different responses between woody and herbaceous plants (Fig. 3). The findings thus indicate that woody and herbaceous plants had different sensitivity under elevated CO_2. N concentration in cropland plants decreased faster while C:N ratio increased to a greater extent than others (Fig. 3). This suggests that cropland plants showed more sensitivity than plants belonging to other ecosystems. Thus, there is a need to pay more attention to the cropland ecosystems, since rice and wheat from this type of ecosystems are grown and supplied mainly for human food consumption. Local

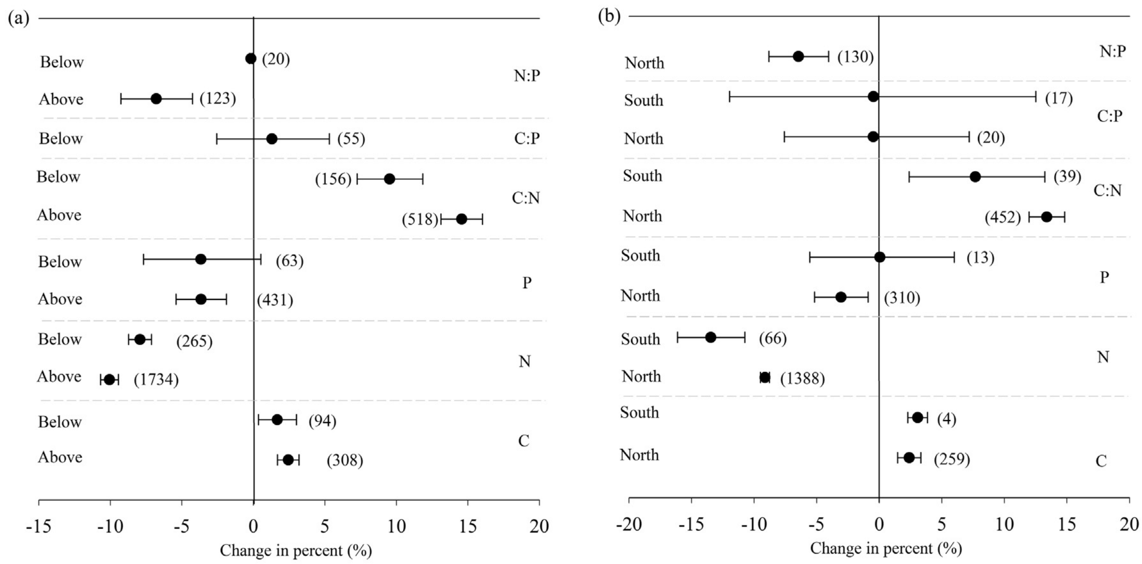

Fig. 6. Response of plant tissues (a) and spatial (b) C-N-P stoichiometry under elevated CO_2. Values are change in percent (%) and 95% confidence intervals (CI). Plant tissues were subdivided into above (above-ground) and below (below-ground). Plants were subdivided into north (northern hemisphere), south (southern hemisphere). Sample size number is showed in parentheses, results are not presented when sample size are less than three.

environments modulated the nutrient limitation, such as P enrichment occurred in wetland ecosystems (Osborne et al., 2014), especially in intensively fertilized agricultural lands and near urban areas (Yan et al., 2016). Freshwater ecosystems and its macrophytes had higher N and P concentrations and higher N:P ratio in sparsely human-impacted environments than the heavily ones. Our results showed that elevated CO_2 only increased P concentration in wetland but decreased in other ecosystems (Fig. 3). Moreover, compared with human-impacted ecosystems, natural terrestrial ecosystems had a higher possibility to undergo N and P limitation under global climate change (LeBauer and Treseder, 2008; Penuelas et al., 2013; Sardans et al., 2012; Yan et al., 2016). Additionally, natural ecosystems have much widespread N enrichment than P (Penuelas et al., 2013; Wang et al., 2015). N deposition (25–30 Tg per year) (Galloway et al., 2004) and elevated CO_2 (Deng et al., 2015) increased soil N pools, which may relieve N limitation but not in case of P in terrestrial ecosystems (Tissue and Lewis, 2010), especially in densely populated areas. Moreover, vegetation C drove P demand in tropical ecosystems because of high C:P ratio in woody biomass (Penuelas et al., 2013). Elevated CO_2 may alter plant C-N-P stoichiometry in different ecosystems by altering soil moisture. Soil moisture increases by a reduction of plant stomatal conductance under elevated CO_2. Dijkstra found strong evidence that the opposing effects of CO_2 enrichment N:P ratio in plants and microbes were driven by variations in soil moisture in semiarid grasslands (Dijkstra et al., 2012). An increase in soil moisture enhanced the diffusivity of P, thereby increasing the assimilation by plants and microbes (Lambers et al., 2006). Rising CO_2 mitigates the drought stress (Robredo et al., 2007), especially for arid and semi-arid ecosystems, Niboyet found that rising CO_2 increased the soil moisture and DOC by 21, and 78%, respectively (Niboyet et al., 2017). The plant C:N ratio revealed the interactive effects of rising CO_2 and drought in grassland. Compared to warmer ecosystems, leaf N concentration was high in plants of the temperate ecosystems (Inauen et al., 2012). Our results showed that tundra plants had a higher N concentration than other ecosystems (Fig. 3b). A concomitant change of soil temperature should be considered under rising CO_2. Carrillo found that elevated CO_2 reduced the temperature on an average by 0.25 °C during two years treatments (Carrillo et al., 2011). For the temperate ecosystems, there were no changes of soil C:N and inorganic N pools, suggesting that elevated CO_2 stimulated plants growth but had no potential to change the ecosystem balance between C and N in soil (Dawes et al., 2013). There was also no decreased effect of leaf N concentration in *Vaccinium* and *Larix* for 9 years after a CO_2 enrichment experiment.

Plant C-N-P stoichiometry varied significantly with species, under rising CO_2, suggesting the different ability to compete and the different demand for N and P and among different plant species (Gusewell and Koerselman, 2002). The difference of plant C-N-P stoichiometry under elevated CO_2 can also be due to other classifications such as in cases of C_3 and C_4 plants (Loladze, 2014), N-fixing (leguminous) or non-N-fixing (non-leguminous) plants (Jablonski et al., 2002). For example, C:N and C:P increased in C3 but not in C4 plants under rising CO_2 (Sardans et al., 2012). N and C:N ratio of pea (leguminous and N-fixing) changed insignificantly under rising CO_2 but changes significantly in wheat, which is a non-leguminous (Butterly et al., 2015).

4.3. Effect of experimental duration and spatial difference on plant C-N-P stoichiometry

The changes of plant C-N-P stoichiometry in response to different elevated CO_2 duration were of different magnitude and direction, which is in line with our second (ii) hypothesis. Additionally, we also tested "CO_2 acclimation" hypothesis, change of C and N concentrations and C:P ratio, which showed an obvious down-regulation for long term CO_2 fumigation. Spatial and temporal scales influenced plant C-N-P stoichiometry under elevated CO_2 (Gifford et al., 2000). Sampling time or treatment duration significantly affected plant C-N-P stoichiometry under elevated CO_2, indicating ecosystem nutrient cycle feedback and local environment (Gifford et al., 2000; Huang et al., 2012). On a short term scale, plant C-N-P stoichiometry varied as a result of the growth stage of the plant, the N concentration in the leaf of *Larrea tridentata* decreased significantly during April-June but not in July-August in a FACE experiment (Aranjuelo et al., 2011). N concentration in the above-ground plant parts decreased significantly at the onset of blooming stage but showed no effect at the onset of pod and seeding stage and/or harvest stage under elevated CO_2 level (Hao et al., 2016). Moreover, the plant may release N from old leaf to enhance N availability (Zhu et al., 2009). During short treatment, the N and C:N ratio in cotton altered significantly after 45 days but were insignificant after 75 days or 105 days under elevated CO_2 (Zhang et al., 2017). On the seasonal scales, the plant C-N-P stoichiometry showed varied with elevated CO_2, for instance, C:N ratio of *Bromus mollis* leaf was higher for 60 days under elevated CO_2 but remained steady at 130 days (Larigauderie et al., 1988). The P concentration of rice grain decreased in the first growing season but increased in the second growing season (Lieffering et al., 2004). Nutrient (N and P) dilution through the accumulation of non-structural carbohydrates may vary on medium term scales in elevated CO_2. It has been observed that N and P dilution only in first year treatment in *A. acuminatissima* or *S. hancei* but not in two or longer year (Huang et al., 2012). The N concentration of *Alnus glutinosa* decreased significantly in the first year but insignificantly in the second and third year in a FACE treatment (Smith et al., 2013). Variety of plant C-N-P stoichiometry under rising CO_2 for medium term may be due to climatic parameters (rainfall, temperature). For example, N:P ratios were less in wet years than dry years under rising CO_2 (Liu et al., 2013). The plant *Ambrosia* had higher N and P resorption efficiency in dry years than wet years (Housman et al., 2012).

Elevated CO_2 had sustained effects on the plant biomass increase (Norby et al., 2010), but the photosynthesis or growth rate in plants slow down at a long term treatment (Bloom et al., 2010). In it, the plant growth increased 34% at first 3 years, but only 6% was seen in the next 4 years in a FACE treatment study (Oren et al., 2001), N and P declined with long treatment indicating "dilution effects"(Fig. 5a). According to the growth rate hypothesis (Sterner and Elser, 2002), longer term treatment had higher N:P ratio than short or medium term (Fig. 5a), which slowed down the growth rate at longer duration treatment. Other factors may have also been involved for longer treatment. This followed especially for soil N, P pools and C:N, C:P and N:P ratios that increased significantly (Yu et al., 2018). Although, these feedback effects should be investigated further. Plant C-N-P stoichiometry changed with long duration treatment due to a tendency of maintaining the nutrient balance under changes in the environment. For example, a leaf of *P. taeda* was relatively stable over 10 years under elevated CO_2 level (Ellsworth et al., 2012). Our results suggested that plants N concentration decreased in short term treatment more, when compared with the medium and long term, which reflects the environmental adaptability of the plants (Fig. 4a). P limitation approaches first followed by N limitation at the global scale (Penuelas et al., 2013). This occurs because of the slow rate of P release from weathering. Compared with the short and medium term, long term treatment can promote P release from rock weathering. Our results showed that plant P concentration increased with treatment duration of CO_2 enrichment (Fig. 5a). Furthermore, long term treatment relieved P limitation in terrestrial ecosystems, and the C:P and N:P ratios of plant showed the obvious difference with treatment duration (Fig. 5a) than can be associated with a change of P concentration. The P and N concentrations of plant tissues decrease with elevated CO_2 level if the nutrient availability is growth restrictive (Gifford et al., 2000). P and N limitation jointly reduce the future C storage in natural ecosystems (Penuelas et al., 2013). In general, P limitation occurs in tropical forests and N limitation occurs in the temperate areas (Zhang et al., 2011), but there is still disagreement at large on the spatial pattern of future nutrient limitation (Zaehle and Dalmonech, 2011).

We only selected OTC and FACE experiments for spatial scales analysis, Fig. 6b showed that elevated CO_2 showed similar direction influence on plant C, N and C:N ratio. Nonetheless, change of N concentration in southern hemisphere was higher than northern hemisphere, which may due to a warmer native climate that has a tendency of increasing NPP (Drake et al., 1997). Stimulation of CO_2 uptake was observed in the warmer ecosystems (Drake et al., 1996) but not in the colder arctic tundras (Oechel et al., 1994). Although, the change of C:P ratio was insignificant, there was a same direction for C:P ratio between northern hemisphere and southern hemisphere. For southern hemisphere, however, had a large area of the tropical ecosystem because of high C:P ratio of woody biomass (Penuelas et al., 2013).

4.4. Effect of experimental methods on plant C-N-P stoichiometry

The changes of plant C-N-P stoichiometry in response to different elevated CO_2 methods were of different magnitude even and of different direction, which is in line with our first (i) hypothesis, which indicates that the influence of elevated CO_2 on plant C-N-P stoichiometry depend on methods of CO_2 enrichment. For example, although elevated CO_2 from OTC, NS, GC and FACE studies all significantly decreased plant N concentration, their magnitude varied significantly ($Q_{between} = 8.47$, $P = 0.0373$, Fig. 5b). However, CO_2 enrichment methods showed similar effects on plant C:N ratio, although NS showed insignificant effect on the plant C:N ratio which can be attributed to the small sample sizes. This result is in consistent with previous study (Sardans et al., 2012). A significant decline of P concentration in OTC and GC, but insignificant, in case of FACE were observed in both Deng's and our study (Fig. 5b). This had happened probably because of the FACE data included N or P fertilization or both. Low N condition decreased plant P concentration but not significantly at highly elevated CO_2 level (Deng et al., 2015). P fertilization effected significant increase in leaf N concentration under elevated CO_2 (Tissue and Lewis, 2010). Under glasshouse plant C:N increased but under OTC it decreased (Yue et al., 2017). The facts remain unclear whether closed or opened top of rising CO_2 chamber would have an effect on plant C-N-P stoichiometry. Different methods exhibited significantly different effects on soil moisture and temperature. For example, a FACE experiment enhanced soil moisture by 2.1% (Carrillo et al., 2011), however a mesocosm study increased the same by 21% (Niboyet et al., 2017). Our results indicated that OTC method leads a higher change in C, N, P, and N:P than *in situ* FACE method. The OTC method was performed widely during 1980s and 1990s, but the method has a disadvantage of changing the plant's surrounding microclimate and of a small growing space (Pleijel and Hogy, 2015). However, FACE was usually conducted in the larger scale *in situ* experiments without the limiting growing space, precipitation or changing microclimate (Ainsworth et al., 2008). Therefore, the response of plant stimulation to elevated CO_2 was lower in FACE (Ainsworth et al., 2008; Long et al., 2006). Furthermore, in the present study, the CO_2 level was compared between FACE and OTC methods and it was found that the higher average was obtained in the latter (+312 ppm) than the former (+222 ppm). This result is in agreement with previous study (Loladze, 2014). Artificial facilities of CO_2 enrichment yielded mixed statistically significant results in response of mineral change. For example, observations made by Loladze indicated that both FACE and non-FACE studies decreased plants N, P concentrations significantly (Loladze, 2014). However, the results obtained *via* CO_2 enrichment method, considered most accurate in the field experiment, still remains unclear. So, there are needs to carry out individual study to choose one of the rising CO_2 methods, rather than two or more different methods. Thus, there exists a lack of comparison study of different elevated CO_2 methods.

5. Conclusion

Our study revealed that elevated CO_2 increased C concentration and C:N ratio but decreased the concentration of N, P and N:P ratio significantly. Among the different plant tissues, leaf and shoot exhibited more sensitivity for elevated CO_2 than branch. Change of C, N and P concentrations and C:N ratio were higher in herbaceous plants. N concentration of plants in all ecosystems declined under CO_2 enrichment. P concentration decreased significantly in grasslands and shrublands but insignificantly in wetlands. At spatial scales, a greater reduction in the concentration of N was observed in the southern hemisphere compared to the northern ones. C:N ratio increased significantly with elevated CO_2 magnitude. The change of plant C and N concentrations and C:P ratio under elevated CO_2 showed a "CO_2 acclimation". In the present investigation, the results obtained in the FACE, when compared with OTC, a higher change of C, N, P, and N:P were observed *in situ*.

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