Changes in nutrient concentrations of leaves and roots in response to Global Change factors.

JORDI SARDANS[,2], ORIOL GRAU[1,2], HAN Y. H. CHEN[3], IVAN A. JANSSENS[4], PHILIPPE CIAIS[5], SHILONG PIAO[6], JOSEP PEÑUELAS[1,2]

[1] CSIC, Global Ecology Unit CREAF-CEAB-UAB, Cerdanyola del Vallès, 08193 Catalonia, Spain.
[2] CREAF, Cerdanyola del Valles, 08193 Catalonia, Spain.
[3]Faculty of Natural Resources Management, Lakehead University, 955 Oliver Road, Thunder Bay, Ontario, P7G 1A6, Canada.
[4]Research Group of Plant and Vegetation Ecology (PLECO), Department of Biology, University of Antwerp, B-2610 Wilrijk, Belgium.
[5] Laboratoire des Sciences du Climat et de l'Environnement, IPSL, 91191 Gif-sur-Yvette, France.
[6]Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China.

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Abstract

Global Change impacts on biogeochemical cycles have been widely studied, but our understanding of whether the responses of plant elemental composition to Global Change drivers differ between above- and belowground plant organs remains incomplete. We conducted a meta-analysis of 201 reports including 1,687 observations of studies that have analyzed simultaneously N and P concentrations changes in leaves and roots in the same plants in response to drought, elevated [CO_2], and N and P fertilization around the world, and contrasted the results within those obtained with a general database (838 reports and 14,772 observations) that analyzed the changes in N and P concentrations in leaves and/or roots of plants submitted to the commented global change drivers. At global level, elevated [CO_2] decreased N concentrations in leaves and roots and decreased N:P ratio in roots but no in leaves, but was not related with P concentration changes. However, the response differed among vegetation types. In temperate forests elevated [CO_2] was related with lower N concentrations in leaves but not in roots, whereas in crops the contrary patterns were observed. Elevated [CO_2] decreased N concentrations in leaves and roots in tundra plants, whereas not clear relationships were observed in temperate grasslands. However, when elevated [CO_2] and N fertilization coincided, leaves had lower N concentrations whereas root had higher N concentrations suggesting that more nutrients will be allocated to roots to improve uptake of the soil resources not directly provided by the global change drivers. N fertilization and drought increased foliar and root N concentrations while the effects on P concentrations were less clear. The changes in N and P allocation to leaves and root, especially those occurring in opposite direction between them have the capacity to differentially affect above- and below-ground ecosystem functions, such as litter mineralization and above- and belowground food webs.

Keywords. CO_2; ecological stoichiometry; drought, N deposition; nitrogen; N:P; phosphorus.

Introduction

Global Change is characterized by simultaneous shifts in multiple factors that affect ecosystem functioning, such as elevated [CO_2], N deposition, warming and drought, species invasion, and many others (Elser *et al*., 2010; Sardans *et al*., 2012; Peñuelas *et al*., 2013). Several of these Global Change drivers are known to affect nutrient cycling and availability. Several interactions among drivers of Global Change, such as elevated CO_2 concentrations, N and P fertilization, drought or species invasion, with ecosystemic nutrient availability and cycles have been reported (Sardans & Peñuelas, 2012). A recent meta-analysis by Yuan and Chen (2015) reported different shifts in whole-plant N and P concentrations and in C:P, C:N and N:P ratios in response to elevated [CO_2], N and P fertilization, drought and warming, consistent with previous studies (Sardans *et al*., 2008; Duval *et al*., 2012). Another recent meta-analysis (Deng *et al*., 2015) reported decreases in plant N and P concentrations and N:P ratios under elevated [CO_2]. Foliar nutrient concentrations correlate with overall shifts in plant and ecosystemic functioning (Kerkhoff *et al*., 2005; Kerkhoff & Enquist, 2006), so the results of these meta-analyses have motivated modelers to include N, and more recently P controls on photosynthesis and plant growth for projecting the future evolution of carbon sinks (Peñuelas *et al*., 2013; Van der Velde *et al*., 2014).

Changes in nutrient use and allocation in response to changes in environmental conditions are likely to vary among plant organs as a consequence of their particular functions. Recent studies by Gargallo-Garriga *et al*. (2014, 2015) have observed different metabolic and nutrient responses in photosynthetic tissues and roots in different grasses submitted to distinct levels of drought and warming. Root metabolism under drought shifted toward the up-regulation of primary metabolism linked with growth and energy production, whereas photosynthetic tissues in the same plants shifted toward the up-regulation of secondary metabolism associated with anti-stress and conservative functions and toward the down-regulation of primary metabolism (growth and energy production). These asymmetrical effects on metabolic function between photosynthetic organs and roots of the same plants were also correlated with asymmetrical allocations of N and P to photosynthetic organs and roots, with more nutrients to roots to allow that up-regulation and less to leaves related to the observed down-regulation (Gargallo-Garriga *et al*., 2014, 2015).. Interactions between different drivers such as CO_2 and nutrient fertilization introduce further complexity, because their effects can be synergistic or antagonistic, and not simply additive (Churkina *et al*., 2009; Leuzinger *et al*., 2011; Dieleman *et al*., 2012; Reich & Hobbie, 2012; Thomas *et al*., 2013). Meyerholt & Zaehle (2015) reported that a model of forest production consistently produced the best results when changes in the C:N ratio were decoupled among different plant organs Thus, the possible different relationships of global change drivers with distinct plant organs warrant investigation. Despite previous studies have demonstrated general effects of global change drivers such as elevated [CO_2], drought, warming, N and P fertilization and species invasion on plant N and P concentrations and N:P ratios (Yuan and Chen, 2015; Deng et al., 2015; Sardans et al., 2017), these studies have not distinguished among plant organs and have mainly focused on aboveground data, so a clear understanding of whether the effects of global change drivers are different in distinct plant organs, issues that can only be determined by using studies that provided simultaneous data for the different plant organs of the same plants submitted to different environmental conditions.

All these empirical data illustrate the need to account separately for nutrient adjustments in different plant organs to better understand carbon and nutrient cycles. Several experiments have observed different responses to elevated CO_2 of both N (Li *et* *al*., 2013; Liu *et al*., 2013a) and P (Duval *et al*., 2012; Li *et al*., 2013; Liu *et al*., 2013b) concentrations in different plant organs. *In situ* climate manipulation experiments have also revealed asymmetrical relationships of warming and/or drought, with contrasting changes in N (Sardans *et al*., 2008a; Akmal *et al*., 2010) and P (Sardans *et al*., 2008b) concentrations among different plant organs. These asymmetrical relationships between leaves and roots have been observed not only for N and P but also for other elements (Gargallo-Garriga *et al*., 2014, 2015). The response of the elemental compositions of leaves and roots to environmental changes, hereafter elevated [CO_2], N and P fertilization and drought, however, has not yet been analyzed globally and for different vegetation types. Such global analysis of plant leaves and roots is crucial to project global change impacts on the functional composition of plant communities, plant-microbe-soil interactions and possible mismatches between aboveground versus belowground processes.

We hypothesized that the impacts of Global-Change drivers on plant elemental composition differ between leaves and roots due to their different functions. We hypothesize that more nutrients will be allocated to roots to improve uptake of the resources not provided by the global change drivers. For example, more nutrients should be allocated to roots under drought, to enhance root primary metabolism and growth for uptake of soil water. To test this hypothesis, we conducted a global meta-analysis of published data on the response of nutrient concentrations in foliar and root tissues of different vegetation types elevated [CO_2], N and P fertilization and drought and their interactions.

Material and Methods

Data collection

We searched the ISI Web of Science using combinations of the following keywords: availability, carbon, concentration, content, C:N, C:P, deposition, foliar, CO_2, leaf, needle, nitrogen, N:K, N:P, phosphorus, plant, potassium, P:K, ratio, root, soil, solution, stoichiometric and stoichiometry. We obtained 838 reports with 14, 772 observations from around the world (see Figures 1-3, S1, S3-S5 ; Table S1, Supplementary Material).

Data analyses

We examined the effects of Global-Change drivers on the differences of foliar and root elemental compositions and stoichiometries between control and treated plants by calculating the response ratios from each study, as described by Hedges *et al*. (Hedges et al., 1999). The natural-log response ratio (ln*RR*) was calculated as ln (X_i/X_n) = lnX_i – lnX_n, where X_i and X_n are the values of each observation in the treated and control plants, respectively. The sampling variance for each ln*RR* was calculated as $\ln[(1/n_\mathrm{i}) \times (S_\mathrm{i}/X_\mathrm{i})^2 + (1/n_\mathrm{n}) \times (S_\mathrm{n}/X_\mathrm{n})^2]$ using the R package metafor 1.9–2 (Viechtbauer, 2012), where n_i and n_n, S_i and S_n and X_i and X_n are the treated and control sample sizes, standard deviations and mean response values, respectively. The natural-log response ratios were determined by specifying studies as random factors using the *rma* model in metafor. The difference in the N and P concentrations and N:P ratios between the leaves and roots of treated and control plants were considered significant if the 95% confidence interval of ln*RR* did not overlap zero. All statistical analyses were performed in RStudio 3.1.2 (R Core team, 2015). We analyzed only the variables with more than 30 observations available at the Global scale. We thereafter examined the sensitivities of plant nutrient concentrations and their stoichiometries to the Global-change drivers using REML estimation in the rma.unl model for metafor. We defined sensitivity as the change of the variable (N and P concentrations, in mg g^{-1}, and N:P ratios in roots and leaves) as a function of the unit of the Global-Change driver, i.e. ppm CO_2 for elevated [CO_2], kg ha^{-1} for N and P fertilization and l m^{-2} of rainfall for drought. To avoid the possible bias we have focused on the meta-analyses of the studies that simultaneously analyzed leaves and roots of the same plants. We have also analyzed data from the studies that analyzed leaves and roots of the same plants or different plants to only confirm the results (results provided in supplementary material). The number of reports and observations used for the statistical analysis of each foliar and root variable studied are shown in Figures 1-3. The equivalent meta-analysis on global data set with all reports with information on leaf and/or roots was also shown (Figures S1-S6, Supplementary Material). We also analyzed the natural-log response ratio of different biomes when possible (more than 15 different observations).

Results

General stoichiometric responses of leaves and roots

Studies providing data for leaves and roots of the same plants showed that elevated [CO_2] is associated with decreases in both foliar and root N concentrations (Figure 1; Table 1). The natural-log response ratios (from here onward simplified as response ratios) of N concentrations was thus negative in leaves and roots associated to elevated [CO_2], whereas no effect was observed for foliar and root P concentrations (Figure 1) With drought, both leaf and root N concentrations increased, root P increased marginally ($P<0.1$), whereas leaf P did not change (Figure 1). N fertilization increased N concentrations in both leaves and roots and decreased in P concentrations in roots (Figure 1). These changes translated into increases in the leaf and root N:P ratio under drought (Figure 1).

The combination of elevated [CO_2] and N fertilization was related with an increase of root N and P concentrations and also a decrease in leaf N concentrations (Figure 1). Fertilization with both N and P increased both foliar and root N and P concentrations (Figure 1). Table 1 summarizes these results from studies where leaves and roots were simultaneously measured.

Studies providing all available data, including also root-only or foliage-only responses from different experiments, reported similar results (Figure S1). There were similar responses of N and P concentrations to elevated [CO_2] (Figures S1). Leaves had lower N:P ratio under elevated [CO_2], whereas no effects were observed in roots (Figure S1). Drought was associated with higher N concentrations in leaves and roots, but with a more pronounced increase in roots than in leaves. Drought was related with higher root P concentrations and lower foliar P concentrations (Figure S1). The increases in the response ratio of root P concentrations were more accentuated for severe droughts (Figure S2). N fertilization was associated with higher leaf and even higher root N concentrations (Figure S1). Higher leaf P concentrations and higher root N:P ratio were also associated to N fertilization (Figure S1). Similarly, P fertilization was related with increases in N and P concentrations in leaves and roots (Figure S1). The combination of elevated CO_2 and N fertilization was related with an increase of root N concentration (Figure S1).

The response ratios of N and P concentrations in leaves and roots in studies providing data for leaves and roots of the same plants thus show a negative sensitivity of leaf and root N concentration to elevated [CO_2]and positive N sensitivities of N concentrations in leaves and roots to N fertilization whereas no differences were observed in the corresponding sensitivities of natural log response ratios of P (Figure 2).

Differential stoichiometry responses among vegetation types

Elevated [CO_2] differentially altered nutrient concentrations in different vegetation types. Decreases in leaf N concentrations but not in root N concentrations were observed in grasslands, whereas the opposite pattern was observed in croplands exposed to elevated [CO_2] (Figure 3). Decreases in foliar N concentrations and, on the contrary, increases in root N concentrations were observed in temperate forests (Figure 3). As also observed when analyzing all vegetation types together, leaf and root N concentrations increased in temperate forests under N fertilization (Figure 3). However, we had not sufficient data to analyze boreal and tropical ecosystems separately.

Studies providing data for leaves and/or roots but not of the same plants also reported that elevated [CO_2] and drought were associated with different changes depending on vegetation type. Under elevated [CO_2], decreases in the leaf N concentrations were observed in the three vegetation types studied (temperate forests, temperate grasslands and crops) (Figure S3), whereas decreases in root N concentrations were observed only in temperate forests (Figure S3).

Drought was associated with increases in foliar N concentrations in temperate grasslands and decreases of foliar P concentration in temperate forest, and with increases in root N and P concentrations in crops (Figure S3). All studied vegetation types showed increases in foliar and root N concentrations associated with N fertilization (except root N concentrations in tropical forests) (Figure S3). N fertilization was also associated to an increase in response ratio of P leaves concentrations in temperate grasslands (Figure S3).

A sensitivity analysis of these heterogeneous data confirmed the positive relationships between drought and N and P concentrations in roots and the negative relationships between drought with N and P concentrations in leaves (Fig. S4). As a result, the N:P ratios in roots presented positive responses to elevated [CO_2], whereas the N:P ratio in leaves presented negative responses (Fig S4).

Discussion

The changes in N and P concentrations and N:P ratios in response to the drivers studied were mostly similar in leaves and roots, but in some cases and vegetation types were of different magnitudes and even of different directions. Our results confirmed previous studies (Deng *et al*., 2015; Peñuelas & Matamala, 1990) that reported a dilution effect under elevated [CO_2], with lower leaf and root N concentrations. Moreover, elevated [CO_2] was associated with changes in N but not in P concentrations. The decreases in leaf and root N concentrations were not accompanied by significant decreases in P leaf and root concentrations in response to elevated [CO_2] observing a decrease in roots N:P ratio. Deng *et al*. (2015) also showed that CO_2 enhancement had no effect on P concentrations in plant tissues, when analyzing data coming only from FACE experiments. These results suggest that increased plant biomass under elevated [CO_2] can be achieved with a more efficient use of N (consistent with a faster turnover of N-rich Rubisco enzymes to fix more carbon), but not of P, resulting in lower tissue N:P ratios. These lower N:P ratios, especially when both nutrients are not limiting, are thus associated with the higher growth rates observed under elevated [CO_2], consistent with the growth rate hypothesis (Sterner & Elser, 2002). Faster growth would be associated with lower N:P ratios due to the need for more P-rich RNA to sustain rapid protein synthesis (Sterner & Elser, 2002).

Moreover, elevated [CO_2] in temperate forests decreased foliar N concentration but not root N concentration. In contrast, in temperate grasslands, tundra and crops N concentration changes under elevated [CO_2] were not different between leaves and roots. This shows that the impacts of global change drivers are different depending on vegetation types and biomes. In this case, the results suggested that the root nutrient concentrations in trees are more responsive than those of grasslands or crops. More N is thus allocated to roots of trees under elevated [CO_2] suggesting a tree investment in the uptake of more soil resources.

Higher N inputs were associated with a general increase in N concentrations and N:P ratios in leaves and roots. Higher N inputs may thus increase the uptake of N but can decrease P concentration in roots but not in leaves. Leaf N concentration increased in all studied vegetation types by N fertilization, whereas leaf P concentrations increased in response to N fertilization depending on the vegetation types. Higher foliar N and P concentrations may be associated with larger C-assimilation and growth-rate capacities (Sterner & Elser 2002; Bandau *et al*., 2015). Increases in N availability at short to medium terms (months to a few years, depending on input rate) enhance the capacity of plants to take up other nutrients such as P (Coblentz *et al*., 2004; Zhang *et al*., 2004; Silva *et al*., 2015). Long-term N inputs, however, may eventually decrease growth by causing soil-plant nutrient imbalances (Jonard *et al*., 2015; Kou *et al*., 2015), which can in turn decrease foliar P concentrations (Wang *et al*., 2015). However, when increasing atmospheric [CO_2] coincides with N fertilization higher allocation of N and P to roots is observed suggesting that the lack of P drives the allocation of N mainly to roots to increase the uptake capacity of soil resources. Thus, at the root level, there was a compensatory effect on the response ratio of N and P concentrations when increasing atmospheric [CO_2] were combined with higher N availability. The N-dilution effect frequently observed under increasing atmospheric [CO_2] is thus logically counteracted by the higher nutrient availability in those combined experiments. However, leaves responded differently than roots. Despite the increased N availability, concentrations of N increased only in roots and still declined in the leaves (Fig. 1).

The observed differences between N concentrations in leaves and in roots under N fertilization and increasing atmospheric [CO_2] should be embedded into models of N and P cycles for projecting future scenarios of increasing atmospheric [CO_2], climate change and N deposition and they are likely to affect above- and belowground food webs differently.

P enrichment is less widespread than N enrichment in natural terrestrial ecosystems (Peñuelas *et al*., 2013; Wang *et al*., 2015), but P enrichment does nonetheless occur in specific ecosystems, such as wetlands (Osborne *et al*., 2014), especially near intensively fertilized agricultural lands or near urban areas (Chen *et al*., 2014; Yan *et al*., 2016). P fertilization experiments showed increased foliar and root P concentrations, but also higher foliar and root N concentrations. These results are consistent with the fact that most studies have observed increased N-uptake capacity due to increases in P availability (Scheiner *et al*., 2002; Graciano *et al*., 2006), despite some studies that did not observe this pattern (Graciano *et al*., 2006). P fertilization can improve N uptake in different ways. Firstly, P fertilization can increase soil N availability (Reed et al., 2007), by increasing the activity of free living N_2-fixing soil microbes (Reed *et al*., 2007; Alguacil *et al*., 2010) and epiphytic lichens (Abbasi *et al*., 2008) and increasing plant nodulation in N_2-fixing plants (Alguacil *et al*., 2010; Djumaeva *et al*., 2013; Benner & Vitousek, 2007). The increase in P availability, though, can also increase plant N content by enhancing N-uptake capacity from increases in the density (Sheng *et al*., 2012) and length (Sheng *et al*., 2012; Fageria *et al*., 2014) of fine roots or by improving the efficiency of N resorption (Wienend & Stock, 1995; Ruiz & Romero, 2000). The increases in N concentrations associated with P fertilization can have great consequences in nutrient limited ecosystems where plants have a low investment in reproduction that is strongly related to plant nutrient concentrations (Fujita *et al*., 2010).

Under drought P concentrations increased in roots but not in leaves. This result is consistent with previous experiments showing that plants under drought reallocate more resources from growth and energy metabolism, including the allocation of N and P and other nutrients towards roots for increasing water uptake (Gargallo-Garriga *et al*., 2014, 2015). Changes in P concentrations were thus observed in roots but not in leaves when plants suffered from drought. Increases in root N concentration and decreases in foliar N concentration occurred when increasing atmospheric [CO_2] coincided with N fertilization All these different responses in roots than in leaves will likely have different ecological consequences on above- and belowground processes. For example, they could imply a different impact on root-based relative to leaf-based food webs. Changes in plant-host stoichiometry affect the stoichiometry (Kay *et al*., 2003; Abbas *et al*., 2004) and growth and survival (Audusseau *et al*., 2015) of herbivorous insects. Different changes in foliar and root N and P concentrations can also affect the respective resorption processes differently and thus above- versus belowground food webs (Sterner & Elser, 2002). Similarly, other important ecosystemic processes such as the decomposition of organic matter, food fluxes and generally all nutrient and C cycles can also be affected by changes in N and P concentrations and N:P ratios (Schade *et al*., 2003; Grover, 2003; Cleveland, 2006; Jonas & Joern, 2008; Sardans *et al*., 2012b). Some studies of terrestrial ecosystems show that higher N availability increases body N:P ratios and reduces the species diversity of communities, whereas increases in P availability have opposite effects on food resources, with lower N:P ratios increasing the transfer of energy to higher food levels, further favoring larger food webs (Sardans *et al*., 2012b). All these shifts in the elemental composition of plant organs can thus have important flow-on effects on food webs and ecosystemic structure that could be asymmetrical between above- and belowground ecosystemic compartments in some cases and some ecosystem types by the influence that plant above- and below-ground elemental composition exert on the own food web but also with the food web of the other respective plant compartment (Peñuelas & Matamala 1990, Sterner & Elser, 2002). Johnson *et al*. (2013) observed that the relationships between belowground herbivores and root plant nutrient contents also affect aboveground herbivores and ultimately populations of parasites and predators of aboveground herbivores. A global data synthesis showed that the C:N:P ratios of leaves and roots and the respective above- and below-ground food webs are interconnected (Mulder *et al.*, 2013).

We conclude that increasing atmospheric [CO_2], N and P fertilization and drought typically affect the concentrations of N and P in leaves and roots similarly, but in some cases they affect them differently or even oppositely, such as when increasing atmospheric [CO_2] is combined with N fertilization. The overall analyses of the changes in N and P concentrations in leaves and roots in response to the studied global change drivers and their combinations suggested that an equilibrium of the concentration effect (in the case of drought or N and P fertilization) and the dilution effect (in the case of elevated [CO_2]) with the increasing N and P allocation to roots to enhance the uptake of other soil resources when N and/or P availability increased. Then the results suggest that when several different resources are provided at once enhancing the potential for plant production capacity, more sources are allocated to roots to improve the uptake of complementary resources to those enhanced by environmental changes. This occurs for N and P under drought, for N under N fertilization, for P under P fertilization, for N and P under N and P fertilization and for N when N and CO_2 increase. This is not observed under elevated CO_2. The dilution effect together with the necessity to maintain N in photosynthetic tissues to take profit of higher CO_2 could explain it. The results also suggest that above- and belowground processes could sometimes be affected differently and even oppositely by the drivers of Global Change. Such differential shifts in above- versus below-ground elemental composition can change ecosystem function, for example by affecting the corresponding food webs differently. Furthermore, several models of carbon cycles in terrestrial ecosystems have been developed to determine the mechanisms behind the shoot/root allocation of carbon (Wilson, 1988; Cannell & Dewar, 1994). The results suggest the need to also incorporate flexible allocations of N and P concentrations to different plant organs in the distinct biomes into models projecting effects under different scenarios of climate and fertility.

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Additional information

Supplementary information for only on-line publication is added

Competing interests

The authors declare no competing financial interests.

Table 1. Summary of the results of the meta-analyses for the concentrations of N and P and the corresponding ratios in response to the Global-Change drivers.

Global-Change driver	[N]		[P]	
	Leaves	Roots	Leaves	Roots
Elevated [CO_2]	↓	↓	=	=
N fertilization	↑	↑	=	↓
P fertilization	NA	NA	↑	↑
Drought	↑	↑	=	↑
[CO_2] + N fertilization	↓b	↑a	=	↑
N + P fertilization	↑	↑	↑	↑

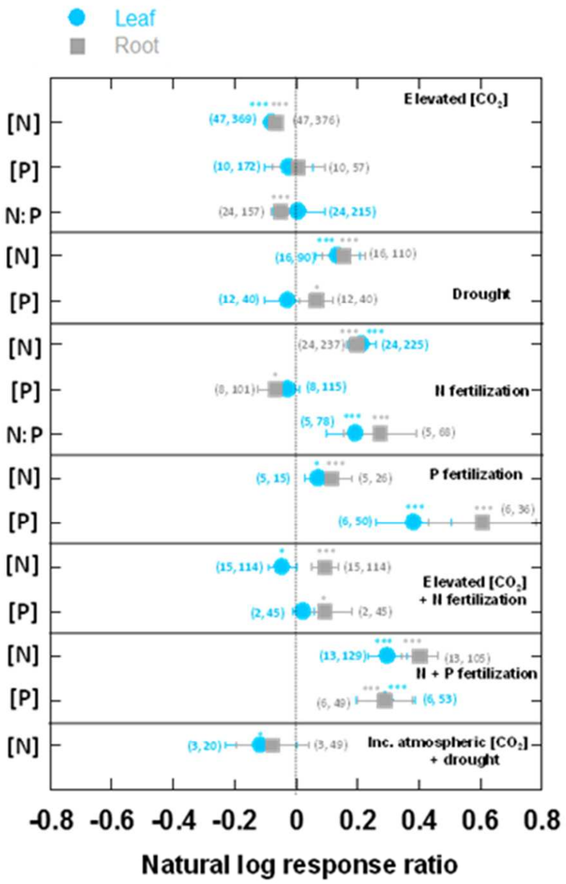
↑, significant (*P* < 0.05) increases in meta-analysis; ↓, significant decreases (*P* < 0.05) in meta-analysis; **=,** no change in meta-analysis; NA, not available. Different letters indicate significant differences (*P*< 0.05) in response ratios between leaves and roots. Different letters indicate significant differences (*P* < 0.05) in response ratios between photosynthetic tissues and roots only when overall data was analyzed including studies with data of leaf and/or roots.

Figure Captions

Figure 1. Natural log response ratios of N and P concentrations and N:P ratios in leaves (blue) and roots (grey) due to elevated [CO_2], drought, N fertilization, P fertilization, elevated [CO_2] + N enrichment, N + P enrichment and elevated [CO_2] + drought. The meta-analyses were conducted only with studies that provided data of leaves and roots measured simultaneously in the same plants. Error bars indicate the mean response ratio with 95% confidence intervals. The numbers between brackets indicate the number of reports and observations, respectively, used in the meta-analysis of each variable. (***), (**), and (*) indicate significant differences at ($P<0.001$), ($P<0.01$) and ($P<0.05$) respectively, between treated plants compared with the control plants. Positive response ratios mean that the corresponding global change drivers increased the value of the variable with respect to the control conditions.

Figure 2. Sensitivity of the natural log response ratios of N and P concentrations (by ppm of elevated [CO_2]) in leaves and roots to elevated [CO_2] and sensitivity of the natural log response ratios of N and P concentrations (by kg ha^{-1} of N enhancement) in leaves and roots to N fertilization obtained in studies that provided data of leaves and roots of the same plants. Error bars indicate the 95% confidence intervals for the mean response ratio. The numbers between brackets indicate the number of reports and observations, respectively, used in the meta-analysis of each variable. (***), (**), and (*) indicate significant differences, at ($P<0.001$), ($P<0.01$) and ($P<0.05$) respectively, between treated plants compared with the control plants. Positive response ratios mean that the corresponding global change drivers increased the value of the variable with respect to the control conditions.

Figure 3. Natural log response ratios due to elevated [CO_2] and to N fertilization on N concentrations in leaves and roots in different vegetation types obtained in studies that provided data of leaves and roots of the same plants. Error bars indicate the 95% confidence intervals for the mean response ratio. The numbers between brackets indicate the number of reports and observations, respectively, used in the meta-analysis of each variable. (***), (**), and (*) indicate significant differences, at ($P<0.001$), ($P<0.01$) and ($P<0.05$) respectively, between treated plants compared with the control plants. Positive response ratios mean that the corresponding global change drivers increased the value of the variable with respect to the control conditions.



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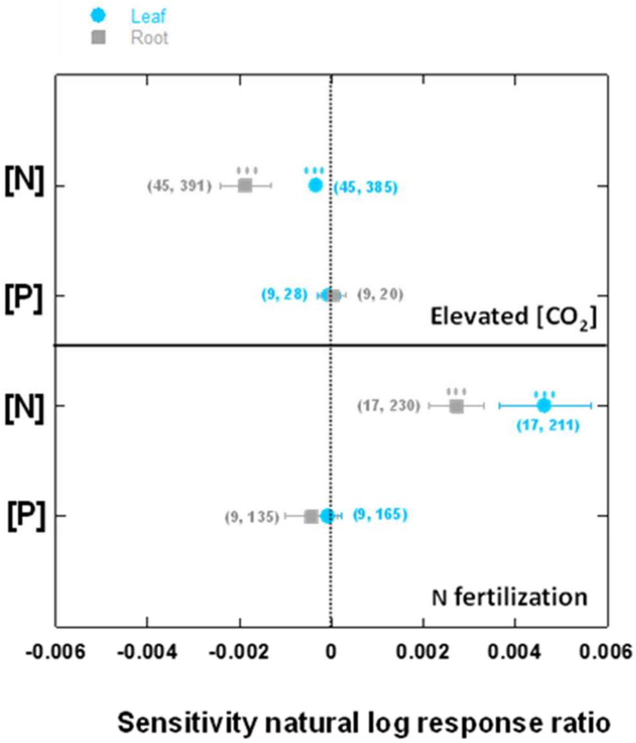

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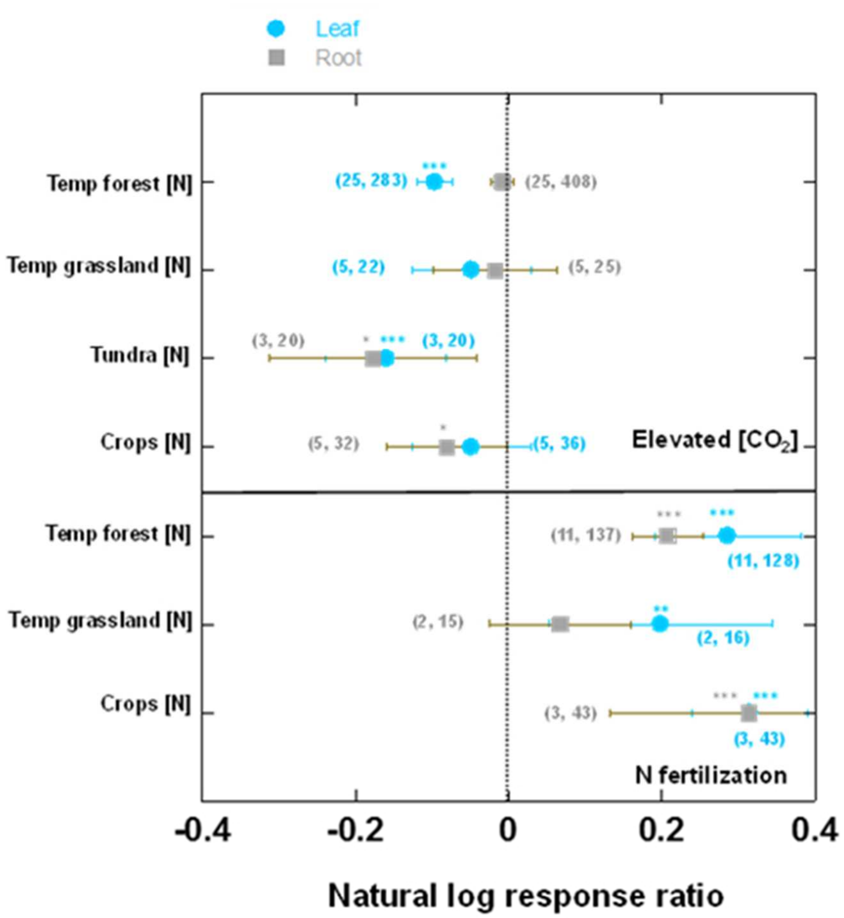

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