Changes in nutrient concentrations of leaves and roots in response to global change factors

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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 [CO2], 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 [CO2] decreased N concentrations in leaves and roots and decreased N:P ratio in roots but no in leaves, but was not related to P concentration changes. However, the response differed among vegetation types. In temperate forests, elevated [CO2] was related with lower N concentrations in leaves but not in roots, whereas in crops, the contrary patterns were observed. Elevated [CO2] decreased N concentrations in leaves and roots in tundra plants, whereas not clear relationships were observed in temperate grasslands. However, when elevated [CO2] 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 belowground ecosystem functions, such as litter mineralization and above- and belowground food webs.

Keywords
CO2, drought, ecological stoichiometry, N deposition, N:P, nitrogen, phosphorus

1 INTRODUCTION

Global change is characterized by simultaneous shifts in multiple factors that affect ecosystem functioning, such as elevated [CO2], N deposition, warming and drought, species invasion, and many others (Elser, Fagan, Kerkhoff, Swenson, & Enquist, 2010; Sardans, Rivas-Ubach, & Periuelas, 2012; Periuelas 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 CO2 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 (Duval, Blankinship Dijkstra, & Hungate, 2012; Sardans, Peñuelas, & Ogaya, 2008; Sardans, Peñuelas, Prieto, & Estiarte, 2008). 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 & Enquist, 2006; Kerkhoff, Enquist, Elser, & Fagan, 2005), 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 upregulation of primary metabolism linked with growth and energy production, whereas photosynthetic tissues in the same plants shifted toward the upregulation of secondary metabolism associated with anti-stress and conservative functions and toward the downregulation 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 upregulation and less to leaves related to the observed downregulation (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; Dieleman et al., 2012; Leuzinger et al., 2011; Reich & Hobbie, 2012; Thomas, Bonan, & Goodele, 2013). Meyerholt and Zaehe (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 (Deng et al., 2015; Sardans et al., 2017; Yuan & Chen, 2015), 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, Huang et al., 2013) and P (Duval et al., 2012; Li et al., 2013; Liu, Zhang, et al., 2013) 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 (Akmal, Schelberg, & Khattak, 2010; Sardans, Peñuelas, & Ogaya, 2008) and P (Sardans, Peñuelas, Prieto, et al., 2008) 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 vs. 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.

2 | MATERIALS AND METHODS

2.1 | 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; Table S1).

2.2 | 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, Gurevitch, & Curtis, (1999). The natural-log response ratio (lnRR) was calculated as ln (X/$X_0$) = ln$X_1$ - ln$X_0$, where $X_1$ and $X_0$ are the values of each observation in the treated and control plants, respectively. The sampling variance
for each lnRR was calculated as \( \ln\left[\frac{1}{n_i} \times \left( \frac{S_i}{X_i}\right)^2 \right] \) using the R package \texttt{metafor} 1.9-2 (Viechtbauer, 2012), where \( n_i \) and \( n_{i0} \), \( S_i \) and \( S_{i0} \), and \( X_i \) and \( X_{i0} \) 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 \texttt{rma} model in \texttt{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 lnRR did not overlap zero.

All statistical analyses were performed in \texttt{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 \texttt{rma.unl} model for \texttt{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, that is, 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

**FIGURE 1** Natural log response ratios of N and P concentrations and N:P ratios in leaves (blue) and roots (gray) 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 (*) indicates significant differences at (\( p < .001 \)) and (\( p < .05 \)), 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 [Colour figure can be viewed at wileyonlinelibrary.com]

**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. (***) indicates significant differences, at (\( p < .001 \)) 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 [Colour figure can be viewed at wileyonlinelibrary.com]
data set with all reports with information on leaf and/or roots was also shown (Figs S1–S3). We also analyzed the natural-log response ratio of different biomes when possible (more than 15 different observations).

3 | RESULTS

3.1 | General stoichiometric responses of leaves and roots

Studies providing data for leaves and roots of the same plants showed that elevated [CO₂] 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 were thus negative in leaves and roots associated to elevated [CO₂], 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 < .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 [CO₂] 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 (Fig. S1). There were similar responses of N and P concentrations to elevated [CO₂] (Fig. S1). Leaves had lower N:P ratio under elevated [CO₂], whereas no effects were observed in roots (Fig. 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 (Fig. S1). The increases in the response ratio of root P concentrations were more accentuated for severe droughts (Fig. S2). N fertilization was associated with higher leaf and even higher root N concentrations (Fig. S1). Higher leaf P concentrations and higher root N:P ratio were also associated to N fertilization (Fig. S1). Similarly, P fertilization was related with increases in N and P concentrations in leaves and roots (Fig. S1). The combination of elevated CO₂ and N fertilization was related with an increase of root N concentration (Fig. 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 [CO₂] 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).

### 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

<table>
<thead>
<tr>
<th>Global change driver</th>
<th>Leaves</th>
<th>Roots</th>
<th>Leaves</th>
<th>Roots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevated [CO₂]</td>
<td>↓</td>
<td>↓</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>N fertilization</td>
<td>↑</td>
<td>↑</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>P fertilization</td>
<td>NA</td>
<td>NA</td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td>Drought</td>
<td>↑</td>
<td>↑</td>
<td>–</td>
<td>↑</td>
</tr>
<tr>
<td>[CO₂] + N fertilization</td>
<td>↓</td>
<td>↑</td>
<td>–</td>
<td>↑</td>
</tr>
<tr>
<td>N + P fertilization</td>
<td>↑</td>
<td>↑</td>
<td>↑</td>
<td>↑</td>
</tr>
</tbody>
</table>

↓, 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. [Colour table can be viewed at wileyonlinelibrary.com]
3.2 | Differential stoichiometry responses among vegetation types

Elevated [CO₂] 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 [CO₂] (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 [CO₂] and drought were associated with different changes depending on vegetation type. Under elevated [CO₂], decreases in the leaf N concentrations were observed in the three vegetation types studied (temperate forests, temperate grasslands, and crops) (Fig. S3), whereas decreases in root N concentrations were observed only in temperate forests (Fig. 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 (Fig. S3). All studied vegetation types showed increases in foliar and root N concentrations associated with N fertilization (except root N concentrations in tropical forests) (Fig. S3). N fertilization was also associated to an increase in response ratio of P leaves concentrations in temperate grasslands (Fig. 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. As a result, the N:P ratios in roots presented positive responses to elevated [CO₂], whereas the N:P ratio in leaves presented negative responses.

4 | 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 [CO₂], with lower leaf and root N concentrations. Moreover, elevated [CO₂] 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 [CO₂] observing a decrease in roots N:P ratio. Deng et al. (2015) also showed that CO₂ 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 [CO₂] 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 [CO₂], 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 [CO₂] 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 [CO₂] 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 [CO₂] 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 (Bandau, Decker, Gundale, & Albrechtsen, 2015; Sterner & Elser, 2002). 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 (Coble et al., 2004; Silva, Gomez-Guerrero, Doane, & Howarth, 2015; Zhang, Kang, Zhang, Zhang, & Li, 2004). Long-term N inputs, however, may eventually decrease growth by causing soil-plant nutrient imbalances (Jonard et al., 2015; Kou, Guo, Yang, Gao, & Li, 2015), which can in turn decrease foliar P concentrations (Wang et al., 2015). However, when increasing atmospheric [CO₂] 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 [CO₂] were combined with higher N availability. The N-dilution effect frequently observed under increasing atmospheric [CO₂] 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 (Figure 1).

The observed differences between N concentrations in leaves and in roots under N fertilization and increasing atmospheric [CO₂] should be embedded into models of N and P cycles for projecting future scenarios of increasing atmospheric [CO₂], climate change,
and N deposition and they are likely to affect above- and below-
ground 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, Yavitt, & Hu, 2014; Yan
et al., 2016). P fertilization experiments showed increased foliar and
root P concentrations, but also higher foliar and root N concentra-
tions. These results are consistent with the fact that most studies
have observed increased N-uptake capacity due to increases in P
availability (Graciano, Goya, Frangi, & Guiamet, 2006; Scheiner,
Gutierrez-Boem, & Lavado, 2002), 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 activ-
ity of free living N2-fixing soil microbes (Alguacil, Lozano, Campoy,
& Roldan, 2010; Reed et al., 2007) and epiphytic lichens (Abbasi,
Majeed, Sadiq, & Khan, 2008) and increasing plant nodulation in
N2-fixing plants (Alguacil et al., 2010; Benner & Vitousek, 2007; Dju-
maeva, Lamers, Khazmzina, & Vlek, 2013). The increase in P availabil-
ity, however, can also increase plant N content by enhancing N-
uptake capacity from increases in the density (Sheng, Lalande,
Hamel, Ziadi, & Shi, 2012) and length (Fageria, Moreira, Moraes,
& Moraes, 2014; Sheng et al., 2012) of fine roots or by improving the
efficiency of N resorption (Ruiz & Romero, 2000; Wienend & Stock,
1995). The increases in N concentrations associated with P fertiliza-
tion 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., 2014).

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 toward 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 [CO2] coinci-
cided 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 differ-
et impact on root-based relative to leaf-based food webs. Changes in
plant–host stoichiometry affect the stoichiometry (Coblenz et al.,
2004; Kay et al., 2003) and growth and survival (Audusseau, Kolb, &
Janz, 2015) of herbivorous insects. Different changes in foliar and
root N and P concentrations can also affect the respective respor-
tion processes differently and thus above- vs. 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 (Cleveland, Reed,
& Townsend, 2006; Grover, 2003; Jonas & Joern, 2008; Sardans
et al., 2012; Schade, Kyle, Hobbie, Fagan, & Elser, 2003). Some stud-
ies 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.,
2012). All these shifts in the elemental composition of plant organs
can thus have important flow-on effects on food webs and ecosys-
temic 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,
Mitchell, McNicol, Thompson, and Karley (2013) observed that the
relationships between belowground herbivores and root plant nutri-
ent contents also affect aboveground herbivores and ultimately pop-
ulations 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 belowground food webs are
interconnected (Mulder et al., 2013).

We conclude that increasing atmospheric [CO2], N and P fertil-
ization and drought typically affect the concentrations of N and P in
leaves and roots similarly, but in some cases, they affect them differ-
etly or even oppositely, such as when increasing atmospheric [CO2]
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
[CO2]) 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 envi-
nronmental 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 CO2 increase. This is not
observed under elevated CO2. The dilution effect together with the
necessity to maintain N in photosynthetic tissues to take profit of
higher CO2 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- vs. belowground 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 (Cannell &
Dewar, 1994; Wilson, 1988). The results suggest the need to also
incorporate flexible allocations of N and P concentrations to differ-
etent plant organs in the distinct biomes into models projecting effects
under different scenarios of climate and fertility.
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COMPETING INTERESTS

The authors declare no competing financial interests.

REFERENCES


SUPPORTING INFORMATION

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