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

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► **To cite this version:**

Jordi Sardans, Oriol Grau, Han Chen, Ivan Janssens, Philippe Ciais, et al.. Changes in nutrient concentrations of leaves and roots in response to global change factors. *Global Change Biology*, 2017, 23 (9), pp.3849-3856. 10.1111/gcb.13721 . hal-02903769

**HAL Id: hal-02903769**

**<https://hal.science/hal-02903769v1>**

Submitted on 7 Jun 2023

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

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20 Running head: Foliar and root nutrients under global change

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This is the accepted version of the following article: Sardans, J. et al. "Changes in nutrient concentrations of leaves and roots in response to global change factors" in *Global change biology*, vol. 23, issue 9 (Sep. 2017), p. 3849-3856, which has been published in final form at DOI 10.1111/gcb.13721. **This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.**

32 **Abstract**

33 Global Change impacts on biogeochemical cycles have been widely studied, but our  
34 understanding of whether the responses of plant elemental composition to Global Change  
35 drivers differ between above- and belowground plant organs remains incomplete. We  
36 conducted a meta-analysis of 201 reports including 1,687 observations of studies that  
37 have analyzed simultaneously N and P concentrations changes in leaves and roots in the  
38 same plants in response to drought, elevated [CO<sub>2</sub>], and N and P fertilization around the  
39 world, and contrasted the results within those obtained with a general database (838  
40 reports and 14,772 observations) that analyzed the changes in N and P concentrations in  
41 leaves and/or roots of plants submitted to the commented global change drivers. At global  
42 level, elevated [CO<sub>2</sub>] decreased N concentrations in leaves and roots and decreased N:P  
43 ratio in roots but no in leaves, but was not related with P concentration changes. However,  
44 the response differed among vegetation types. In temperate forests elevated [CO<sub>2</sub>] was  
45 related with lower N concentrations in leaves but not in roots, whereas in crops the  
46 contrary patterns were observed. Elevated [CO<sub>2</sub>] decreased N concentrations in leaves  
47 and roots in tundra plants, whereas not clear relationships were observed in temperate  
48 grasslands. However, when elevated [CO<sub>2</sub>] and N fertilization coincided, leaves had lower  
49 N concentrations whereas root had higher N concentrations suggesting that more nutrients  
50 will be allocated to roots to improve uptake of the soil resources not directly provided by  
51 the global change drivers. N fertilization and drought increased foliar and root N  
52 concentrations while the effects on P concentrations were less clear. The changes in N  
53 and P allocation to leaves and root, especially those occurring in opposite direction  
54 between them have the capacity to differentially affect above- and below-ground  
55 ecosystem functions, such as litter mineralization and above- and belowground food webs.

56 **Keywords.** CO<sub>2</sub>; ecological stoichiometry; drought, N deposition; nitrogen; N:P;  
57 phosphorus.

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62 **Introduction**

63 Global Change is characterized by simultaneous shifts in multiple factors that affect  
64 ecosystem functioning, such as elevated [CO<sub>2</sub>], N deposition, warming and drought,  
65 species invasion, and many others (Elser *et al.*, 2010; Sardans *et al.*, 2012; Peñuelas *et*  
66 *al.*, 2013). Several of these Global Change drivers are known to affect nutrient cycling and  
67 availability. Several interactions among drivers of Global Change, such as elevated CO<sub>2</sub>  
68 concentrations, N and P fertilization, drought or species invasion, with ecosystemic  
69 nutrient availability and cycles have been reported (Sardans & Peñuelas, 2012). A recent  
70 meta-analysis by Yuan and Chen (2015) reported different shifts in whole-plant N and P  
71 concentrations and in C:P, C:N and N:P ratios in response to elevated [CO<sub>2</sub>], N and P  
72 fertilization, drought and warming, consistent with previous studies (Sardans *et al.*, 2008;  
73 Duval *et al.*, 2012). Another recent meta-analysis (Deng *et al.*, 2015) reported decreases  
74 in plant N and P concentrations and N:P ratios under elevated [CO<sub>2</sub>]. Foliar nutrient  
75 concentrations correlate with overall shifts in plant and ecosystemic functioning (Kerkhoff  
76 *et al.*, 2005; Kerkhoff & Enquist, 2006), so the results of these meta-analyses have  
77 motivated modelers to include N, and more recently P controls on photosynthesis and  
78 plant growth for projecting the future evolution of carbon sinks (Peñuelas *et al.*, 2013; Van  
79 der Velde *et al.*, 2014).

80 Changes in nutrient use and allocation in response to changes in environmental  
81 conditions are likely to vary among plant organs as a consequence of their particular  
82 functions. Recent studies by Gargallo-Garriga *et al.* (2014, 2015) have observed different  
83 metabolic and nutrient responses in photosynthetic tissues and roots in different grasses  
84 submitted to distinct levels of drought and warming. Root metabolism under drought  
85 shifted toward the up-regulation of primary metabolism linked with growth and energy

86 production, whereas photosynthetic tissues in the same plants shifted toward the up-  
87 regulation of secondary metabolism associated with anti-stress and conservative functions  
88 and toward the down-regulation of primary metabolism (growth and energy production).  
89 These asymmetrical effects on metabolic function between photosynthetic organs and  
90 roots of the same plants were also correlated with asymmetrical allocations of N and P to  
91 photosynthetic organs and roots, with more nutrients to roots to allow that up-regulation  
92 and less to leaves related to the observed down-regulation (Gargallo-Garriga *et al.*, 2014,  
93 2015).. Interactions between different drivers such as CO<sub>2</sub> and nutrient fertilization  
94 introduce further complexity, because their effects can be synergistic or antagonistic, and  
95 not simply additive (Churkina *et al.*, 2009; Leuzinger *et al.*, 2011; Dieleman *et al.*, 2012;  
96 Reich & Hobbie, 2012; Thomas *et al.*, 2013). Meyerholt & Zaehle (2015) reported that a  
97 model of forest production consistently produced the best results when changes in the C:N  
98 ratio were decoupled among different plant organs. Thus, the possible different  
99 relationships of global change drivers with distinct plant organs warrant investigation.  
100 Despite previous studies have demonstrated general effects of global change drivers such  
101 as elevated [CO<sub>2</sub>], drought, warming, N and P fertilization and species invasion on plant N  
102 and P concentrations and N:P ratios (Yuan and Chen, 2015; Deng *et al.*, 2015; Sardans *et*  
103 *al.*, 2017), these studies have not distinguished among plant organs and have mainly  
104 focused on aboveground data, so a clear understanding of whether the effects of global  
105 change drivers are different in distinct plant organs, issues that can only be determined by  
106 using studies that provided simultaneous data for the different plant organs of the same  
107 plants submitted to different environmental conditions.

108 All these empirical data illustrate the need to account separately for nutrient  
109 adjustments in different plant organs to better understand carbon and nutrient cycles.  
110 Several experiments have observed different responses to elevated CO<sub>2</sub> of both N (Li *et*

111 *al.*, 2013; Liu *et al.*, 2013a) and P (Duval *et al.*, 2012; Li *et al.*, 2013; Liu *et al.*, 2013b)  
112 concentrations in different plant organs. *In situ* climate manipulation experiments have also  
113 revealed asymmetrical relationships of warming and/or drought, with contrasting changes  
114 in N (Sardans *et al.*, 2008a; Akmal *et al.*, 2010) and P (Sardans *et al.*, 2008b)  
115 concentrations among different plant organs. These asymmetrical relationships between  
116 leaves and roots have been observed not only for N and P but also for other elements  
117 (Gargallo-Garriga *et al.*, 2014, 2015). The response of the elemental compositions of  
118 leaves and roots to environmental changes, hereafter elevated [CO<sub>2</sub>], N and P fertilization  
119 and drought, however, has not yet been analyzed globally and for different vegetation  
120 types. Such global analysis of plant leaves and roots is crucial to project global change  
121 impacts on the functional composition of plant communities, plant-microbe-soil interactions  
122 and possible mismatches between aboveground versus belowground processes.

123 We hypothesized that the impacts of Global-Change drivers on plant elemental  
124 composition differ between leaves and roots due to their different functions. We  
125 hypothesize that more nutrients will be allocated to roots to improve uptake of the  
126 resources not provided by the global change drivers. For example, more nutrients should  
127 be allocated to roots under drought, to enhance root primary metabolism and growth for  
128 uptake of soil water. To test this hypothesis, we conducted a global meta-analysis of  
129 published data on the response of nutrient concentrations in foliar and root tissues of  
130 different vegetation types elevated [CO<sub>2</sub>], N and P fertilization and drought and their  
131 interactions.

## 132 **Material and Methods**

### 133 *Data collection*

134 We searched the ISI Web of Science using combinations of the following keywords:  
135 availability, carbon, concentration, content, C:N, C:P, deposition, foliar, CO<sub>2</sub>, leaf, needle,

136 nitrogen, N:K, N:P, phosphorus, plant, potassium, P:K, ratio, root, soil, solution,  
137 stoichiometric and stoichiometry. We obtained 838 reports with 14,772 observations from  
138 around the world (see Figures 1-3, S1, S3-S5 ; Table S1, Supplementary Material).

139

#### 140 *Data analyses*

141 We examined the effects of Global-Change drivers on the differences of foliar and root  
142 elemental compositions and stoichiometries between control and treated plants by  
143 calculating the response ratios from each study, as described by Hedges *et al.* (Hedges et  
144 al., 1999). The natural-log response ratio ( $\ln RR$ ) was calculated as  $\ln (X_i/X_n) = \ln X_i - \ln X_n$ ,  
145 where  $X_i$  and  $X_n$  are the values of each observation in the treated and control plants,  
146 respectively. The sampling variance for each  $\ln RR$  was calculated as  $\ln[(1/n_i) \times (S_i/X_i)^2 +$   
147  $(1/n_n) \times (S_n/X_n)^2]$  using the R package metafor 1.9–2 (Viechtbauer, 2012), where  $n_i$  and  $n_n$ ,  
148  $S_i$  and  $S_n$  and  $X_i$  and  $X_n$  are the treated and control sample sizes, standard deviations and  
149 mean response values, respectively. The natural-log response ratios were determined by  
150 specifying studies as random factors using the *rma* model in metafor. The difference in the  
151 N and P concentrations and N:P ratios between the leaves and roots of treated and control  
152 plants were considered significant if the 95% confidence interval of  $\ln RR$  did not overlap  
153 zero. All statistical analyses were performed in RStudio 3.1.2 (R Core team, 2015). We  
154 analyzed only the variables with more than 30 observations available at the Global scale.  
155 We thereafter examined the sensitivities of plant nutrient concentrations and their  
156 stoichiometries to the Global-change drivers using REML estimation in the *rma.uni* model  
157 for metafor. We defined sensitivity as the change of the variable (N and P concentrations,  
158 in  $\text{mg g}^{-1}$ , and N:P ratios in roots and leaves) as a function of the unit of the Global-Change  
159 driver, i.e. ppm  $\text{CO}_2$  for elevated  $[\text{CO}_2]$ ,  $\text{kg ha}^{-1}$  for N and P fertilization and  $\text{l m}^{-2}$  of rainfall  
160 for drought. To avoid the possible bias we have focused on the meta-analyses of the  
161 studies that simultaneously analyzed leaves and roots of the same plants. We have also

162 analyzed data from the studies that analyzed leaves and roots of the same plants or  
163 different plants to only confirm the results (results provided in supplementary material).  
164 The number of reports and observations used for the statistical analysis of each foliar and  
165 root variable studied are shown in Figures 1-3. The equivalent meta-analysis on global  
166 data set with all reports with information on leaf and/or roots was also shown (Figures S1-  
167 S6, Supplementary Material). We also analyzed the natural-log response ratio of different  
168 biomes when possible (more than 15 different observations).

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191 **Results**192 *General stoichiometric responses of leaves and roots*193 Studies providing data for leaves and roots of the same plants showed that elevated [CO<sub>2</sub>]

194 is associated with decreases in both foliar and root N concentrations (Figure 1; Table 1).

195 The natural-log response ratios (from here onward simplified as response ratios) of N

196 concentrations was thus negative in leaves and roots associated to elevated [CO<sub>2</sub>],

197 whereas no effect was observed for foliar and root P concentrations (Figure 1) With

198 drought, both leaf and root N concentrations increased, root P increased marginally

199 ( $P < 0.1$ ), whereas leaf P did not change (Figure 1). N fertilization increased N

200 concentrations in both leaves and roots and decreased in P concentrations in roots (Figure

201 1). These changes translated into increases in the leaf and root N:P ratio under drought

202 (Figure 1).

203 The combination of elevated [CO<sub>2</sub>] and N fertilization was related with an increase

204 of root N and P concentrations and also a decrease in leaf N concentrations (Figure 1).

205 Fertilization with both N and P increased both foliar and root N and P concentrations

206 (Figure 1). Table 1 summarizes these results from studies where leaves and roots were

207 simultaneously measured.

208 Studies providing all available data, including also root-only or foliage-only

209 responses from different experiments, reported similar results (Figure S1). There were

210 similar responses of N and P concentrations to elevated [CO<sub>2</sub>] (Figures S1). Leaves had211 lower N:P ratio under elevated [CO<sub>2</sub>], whereas no effects were observed in roots (Figure

212 S1). Drought was associated with higher N concentrations in leaves and roots, but with a

213 more pronounced increase in roots than in leaves. Drought was related with higher root P  
214 concentrations and lower foliar P concentrations (Figure S1). The increases in the  
215 response ratio of root P concentrations were more accentuated for severe droughts  
216 (Figure S2). N fertilization was associated with higher leaf and even higher root N  
217 concentrations (Figure S1). Higher leaf P concentrations and higher root N:P ratio were  
218 also associated to N fertilization (Figure S1). Similarly, P fertilization was related with  
219 increases in N and P concentrations in leaves and roots (Figure S1). The combination of  
220 elevated CO<sub>2</sub> and N fertilization was related with an increase of root N concentration  
221 (Figure S1).

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

#### 227 *Differential stoichiometry responses among vegetation types*

228 Elevated [CO<sub>2</sub>] differentially altered nutrient concentrations in different vegetation types.  
229 Decreases in leaf N concentrations but not in root N concentrations were observed in  
230 grasslands, whereas the opposite pattern was observed in croplands exposed to elevated  
231 [CO<sub>2</sub>] (Figure 3). Decreases in foliar N concentrations and, on the contrary, increases in  
232 root N concentrations were observed in temperate forests (Figure 3). As also observed  
233 when analyzing all vegetation types together, leaf and root N concentrations increased in  
234 temperate forests under N fertilization (Figure 3). However, we had not sufficient data to  
235 analyze boreal and tropical ecosystems separately.

236 Studies providing data for leaves and/or roots but not of the same plants also  
237 reported that elevated  $[\text{CO}_2]$  and drought were associated with different changes  
238 depending on vegetation type. Under elevated  $[\text{CO}_2]$ , decreases in the leaf N  
239 concentrations were observed in the three vegetation types studied (temperate forests,  
240 temperate grasslands and crops) (Figure S3), whereas decreases in root N concentrations  
241 were observed only in temperate forests (Figure S3).

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

248 A sensitivity analysis of these heterogeneous data confirmed the positive  
249 relationships between drought and N and P concentrations in roots and the negative  
250 relationships between drought with N and P concentrations in leaves (Fig. S4). As a result,  
251 the N:P ratios in roots presented positive responses to elevated  $[\text{CO}_2]$ , whereas the N:P  
252 ratio in leaves presented negative responses (Fig S4).

253

254

255 **Discussion**

256 The changes in N and P concentrations and N:P ratios in response to the drivers studied  
257 were mostly similar in leaves and roots, but in some cases and vegetation types were of  
258 different magnitudes and even of different directions. Our results confirmed previous  
259 studies (Deng *et al.*, 2015; Peñuelas & Matamala, 1990) that reported a dilution effect  
260 under elevated [CO<sub>2</sub>], with lower leaf and root N concentrations. Moreover, elevated [CO<sub>2</sub>]  
261 was associated with changes in N but not in P concentrations. The decreases in leaf and  
262 root N concentrations were not accompanied by significant decreases in P leaf and root  
263 concentrations in response to elevated [CO<sub>2</sub>] observing a decrease in roots N:P ratio.  
264 Deng *et al.* (2015) also showed that CO<sub>2</sub> enhancement had no effect on P concentrations  
265 in plant tissues, when analyzing data coming only from FACE experiments. These results  
266 suggest that increased plant biomass under elevated [CO<sub>2</sub>] can be achieved with a more  
267 efficient use of N (consistent with a faster turnover of N-rich Rubisco enzymes to fix more  
268 carbon), but not of P, resulting in lower tissue N:P ratios. These lower N:P ratios,  
269 especially when both nutrients are not limiting, are thus associated with the higher growth  
270 rates observed under elevated [CO<sub>2</sub>], consistent with the growth rate hypothesis (Sterner &  
271 Elser, 2002). Faster growth would be associated with lower N:P ratios due to the need for  
272 more P-rich RNA to sustain rapid protein synthesis (Sterner & Elser, 2002).

273 Moreover, elevated [CO<sub>2</sub>] in temperate forests decreased foliar N concentration but  
274 not root N concentration. In contrast, in temperate grasslands, tundra and crops N  
275 concentration changes under elevated [CO<sub>2</sub>] were not different between leaves and roots.  
276 This shows that the impacts of global change drivers are different depending on vegetation  
277 types and biomes. In this case, the results suggested that the root nutrient concentrations  
278 in trees are more responsive than those of grasslands or crops. More N is thus allocated to

279 roots of trees under elevated [CO<sub>2</sub>] suggesting a tree investment in the uptake of more soil  
280 resources.

281 Higher N inputs were associated with a general increase in N concentrations and  
282 N:P ratios in leaves and roots. Higher N inputs may thus increase the uptake of N but can  
283 decrease P concentration in roots but not in leaves. Leaf N concentration increased in all  
284 studied vegetation types by N fertilization, whereas leaf P concentrations increased in  
285 response to N fertilization depending on the vegetation types. Higher foliar N and P  
286 concentrations may be associated with larger C-assimilation and growth-rate capacities  
287 (Sterner & Elser 2002; Bandau *et al.*, 2015). Increases in N availability at short to medium  
288 terms (months to a few years, depending on input rate) enhance the capacity of plants to  
289 take up other nutrients such as P (Coblentz *et al.*, 2004; Zhang *et al.*, 2004; Silva *et al.*,  
290 2015). Long-term N inputs, however, may eventually decrease growth by causing soil-  
291 plant nutrient imbalances (Jonard *et al.*, 2015; Kou *et al.*, 2015), which can in turn  
292 decrease foliar P concentrations (Wang *et al.*, 2015). However, when increasing  
293 atmospheric [CO<sub>2</sub>] coincides with N fertilization higher allocation of N and P to roots is  
294 observed suggesting that the lack of P drives the allocation of N mainly to roots to increase  
295 the uptake capacity of soil resources. Thus, at the root level, there was a compensatory  
296 effect on the response ratio of N and P concentrations when increasing atmospheric [CO<sub>2</sub>]  
297 were combined with higher N availability. The N-dilution effect frequently observed under  
298 increasing atmospheric [CO<sub>2</sub>] is thus logically counteracted by the higher nutrient  
299 availability in those combined experiments. However, leaves responded differently than  
300 roots. Despite the increased N availability, concentrations of N increased only in roots and  
301 still declined in the leaves (Fig. 1).

302 The observed differences between N concentrations in leaves and in roots under N  
303 fertilization and increasing atmospheric [CO<sub>2</sub>] should be embedded into models of N and P

304 cycles for projecting future scenarios of increasing atmospheric [CO<sub>2</sub>], climate change and  
305 N deposition and they are likely to affect above- and belowground food webs differently.

306 P enrichment is less widespread than N enrichment in natural terrestrial  
307 ecosystems (Peñuelas *et al.*, 2013; Wang *et al.*, 2015), but P enrichment does  
308 nonetheless occur in specific ecosystems, such as wetlands (Osborne *et al.*, 2014),  
309 especially near intensively fertilized agricultural lands or near urban areas (Chen *et al.*,  
310 2014; Yan *et al.*, 2016). P fertilization experiments showed increased foliar and root P  
311 concentrations, but also higher foliar and root N concentrations. These results are  
312 consistent with the fact that most studies have observed increased N-uptake capacity due  
313 to increases in P availability (Scheiner *et al.*, 2002; Graciano *et al.*, 2006), despite some  
314 studies that did not observe this pattern (Graciano *et al.*, 2006). P fertilization can improve  
315 N uptake in different ways. Firstly, P fertilization can increase soil N availability (Reed *et al.*,  
316 2007), by increasing the activity of free living N<sub>2</sub>-fixing soil microbes (Reed *et al.*, 2007;  
317 Alguacil *et al.*, 2010) and epiphytic lichens (Abbasi *et al.*, 2008) and increasing plant  
318 nodulation in N<sub>2</sub>-fixing plants (Alguacil *et al.*, 2010; Djumaeva *et al.*, 2013; Benner &  
319 Vitousek, 2007). The increase in P availability, though, can also increase plant N content  
320 by enhancing N-uptake capacity from increases in the density (Sheng *et al.*, 2012) and  
321 length (Sheng *et al.*, 2012; Fageria *et al.*, 2014) of fine roots or by improving the efficiency  
322 of N resorption (Wienend & Stock, 1995; Ruiz & Romero, 2000). The increases in N  
323 concentrations associated with P fertilization can have great consequences in nutrient  
324 limited ecosystems where plants have a low investment in reproduction that is strongly  
325 related to plant nutrient concentrations (Fujita *et al.*, 2010).

326 Under drought P concentrations increased in roots but not in leaves. This result is  
327 consistent with previous experiments showing that plants under drought reallocate more  
328 resources from growth and energy metabolism, including the allocation of N and P and

329 other nutrients towards roots for increasing water uptake (Gargallo-Garriga *et al.*, 2014,  
330 2015). Changes in P concentrations were thus observed in roots but not in leaves when  
331 plants suffered from drought. Increases in root N concentration and decreases in foliar N  
332 concentration occurred when increasing atmospheric [CO<sub>2</sub>] coincided with N fertilization  
333 All these different responses in roots than in leaves will likely have different ecological  
334 consequences on above- and belowground processes. For example, they could imply a  
335 different impact on root-based relative to leaf-based food webs. Changes in plant-host  
336 stoichiometry affect the stoichiometry (Kay *et al.*, 2003; Abbas *et al.*, 2004) and growth and  
337 survival (Audusseau *et al.*, 2015) of herbivorous insects. Different changes in foliar and  
338 root N and P concentrations can also affect the respective resorption processes differently  
339 and thus above- versus belowground food webs (Sterner & Elser, 2002). Similarly, other  
340 important ecosystemic processes such as the decomposition of organic matter, food fluxes  
341 and generally all nutrient and C cycles can also be affected by changes in N and P  
342 concentrations and N:P ratios (Schade *et al.*, 2003; Grover, 2003; Cleveland, 2006; Jonas  
343 & Joern, 2008; Sardans *et al.*, 2012b). Some studies of terrestrial ecosystems show that  
344 higher N availability increases body N:P ratios and reduces the species diversity of  
345 communities, whereas increases in P availability have opposite effects on food resources,  
346 with lower N:P ratios increasing the transfer of energy to higher food levels, further  
347 favoring larger food webs (Sardans *et al.*, 2012b). All these shifts in the elemental  
348 composition of plant organs can thus have important flow-on effects on food webs and  
349 ecosystemic structure that could be asymmetrical between above- and belowground  
350 ecosystemic compartments in some cases and some ecosystem types by the influence  
351 that plant above- and below-ground elemental composition exert on the own food web but  
352 also with the food web of the other respective plant compartment (Peñuelas & Matamala  
353 1990, Sterner & Elser, 2002). Johnson *et al.* (2013) observed that the relationships  
354 between belowground herbivores and root plant nutrient contents also affect aboveground

355 herbivores and ultimately populations of parasites and predators of aboveground  
356 herbivores. A global data synthesis showed that the C:N:P ratios of leaves and roots and  
357 the respective above- and below-ground food webs are interconnected (Mulder *et al.*,  
358 2013).

359         We conclude that increasing atmospheric [CO<sub>2</sub>], N and P fertilization and drought  
360 typically affect the concentrations of N and P in leaves and roots similarly, but in some  
361 cases they affect them differently or even oppositely, such as when increasing  
362 atmospheric [CO<sub>2</sub>] is combined with N fertilization. The overall analyses of the changes in  
363 N and P concentrations in leaves and roots in response to the studied global change  
364 drivers and their combinations suggested that an equilibrium of the concentration effect (in  
365 the case of drought or N and P fertilization) and the dilution effect (in the case of elevated  
366 [CO<sub>2</sub>]) with the increasing N and P allocation to roots to enhance the uptake of other soil  
367 resources when N and/or P availability increased. Then the results suggest that when  
368 several different resources are provided at once enhancing the potential for plant  
369 production capacity, more sources are allocated to roots to improve the uptake of  
370 complementary resources to those enhanced by environmental changes. This occurs for N  
371 and P under drought, for N under N fertilization, for P under P fertilization, for N and P  
372 under N and P fertilization and for N when N and CO<sub>2</sub> increase. This is not observed under  
373 elevated CO<sub>2</sub>. The dilution effect together with the necessity to maintain N in  
374 photosynthetic tissues to take profit of higher CO<sub>2</sub> could explain it. The results also  
375 suggest that above- and belowground processes could sometimes be affected differently  
376 and even oppositely by the drivers of Global Change. Such differential shifts in above-  
377 versus below-ground elemental composition can change ecosystem function, for example  
378 by affecting the corresponding food webs differently. Furthermore, several models of  
379 carbon cycles in terrestrial ecosystems have been developed to determine the



380 mechanisms behind the shoot/root allocation of carbon (Wilson, 1988; Cannell & Dewar,  
381 1994). The results suggest the need to also incorporate flexible allocations of N and P  
382 concentrations to different plant organs in the distinct biomes into models projecting effects  
383 under different scenarios of climate and fertility.

384

### 385 **Acknowledgements**

386 The authors would like to acknowledge the financial support from the European Research Council  
387 Synergy grant ERC-SyG-2013-610028 IMBALANCE-P, the Spanish Government grant CGL2013-  
388 48074-P and the Catalan Government grant SGR 2014-274.

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566 **Additional information**

567 Supplementary information for only on-line publication is added

568

569 **Competing interests**

570 The authors declare no competing financial interests.

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

Global-Change driver	[N]		[P]	
	Leaves	Roots	Leaves	Roots
Elevated [CO <sub>2</sub> ]	↓	↓	=	=
N fertilization	↑	↑	=	↓
P fertilization	NA	NA	↑	↑
Drought	↑	↑	=	↑
[CO <sub>2</sub> ] + N fertilization	↓ <sup>b</sup>	↑ <sup>a</sup>	=	↑
N + P fertilization	↑	↑	↑	↑

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

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591 Figure Captions

592 Figure 1. Natural log response ratios of N and P concentrations and N:P ratios in leaves  
593 (blue) and roots (grey) due to elevated [CO<sub>2</sub>], drought, N fertilization, P fertilization,  
594 elevated [CO<sub>2</sub>] + N enrichment, N + P enrichment and elevated [CO<sub>2</sub>] + drought. The  
595 meta-analyses were conducted only with studies that provided data of leaves and roots  
596 measured simultaneously in the same plants. Error bars indicate the mean response ratio  
597 with 95% confidence intervals. The numbers between brackets indicate the number of  
598 reports and observations, respectively, used in the meta-analysis of each variable. (\*\*\*),  
599 (\*\*), and (\*) indicate significant differences at ( $P < 0.001$ ), ( $P < 0.01$ ) and ( $P < 0.05$ )  
600 respectively, between treated plants compared with the control plants. Positive response  
601 ratios mean that the corresponding global change drivers increased the value of the  
602 variable with respect to the control conditions.

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

614 Figure 3. Natural log response ratios due to elevated [CO<sub>2</sub>] and to N fertilization on N  
615 concentrations in leaves and roots in different vegetation types obtained in studies that  
616 provided data of leaves and roots of the same plants. Error bars indicate the 95%  
617 confidence intervals for the mean response ratio. The numbers between brackets indicate  
618 the number of reports and observations, respectively, used in the meta-analysis of each  
619 variable. (\*\*\*), (\*\*), and (\*) indicate significant differences, at ( $P < 0.001$ ), ( $P < 0.01$ ) and  
620 ( $P < 0.05$ ) respectively, between treated plants compared with the control plants. Positive  
621 response ratios mean that the corresponding global change drivers increased the value of  
622 the variable with respect to the control conditions.

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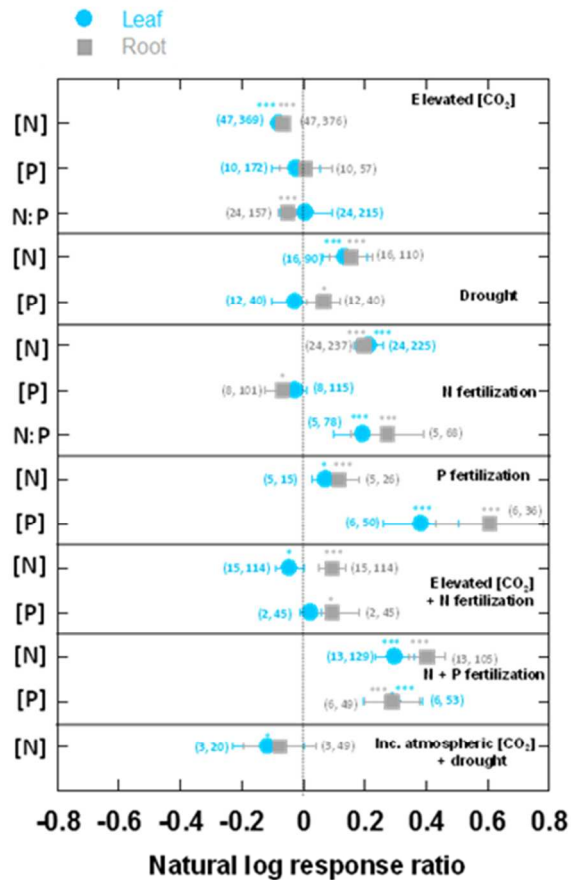


Figure 1. Natural log response ratios of N and P concentrations and N:P ratios in leaves (blue) and roots (grey) due to elevated [CO<sub>2</sub>], drought, N fertilization, P fertilization, elevated [CO<sub>2</sub>] + N enrichment, N + P enrichment and elevated [CO<sub>2</sub>] + drought. The meta-analyses 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.



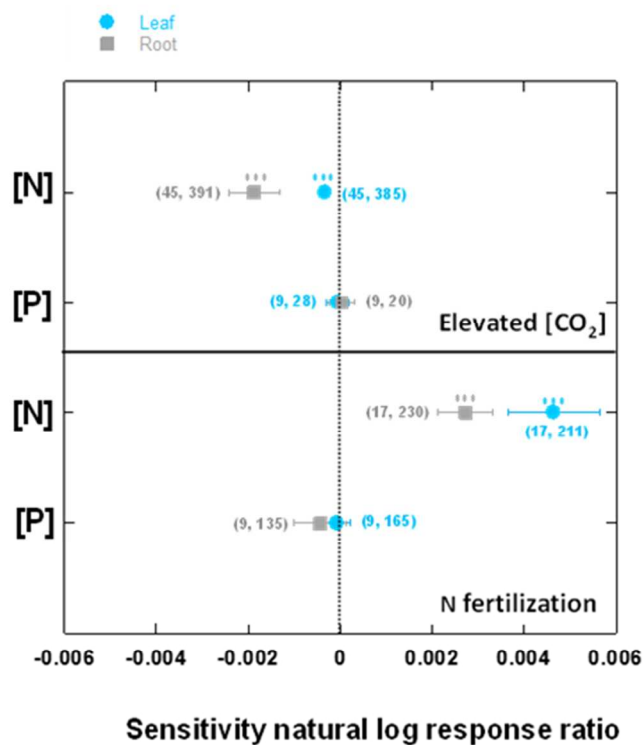


Figure 2. Sensitivity of the natural log response ratios of N and P concentrations (by ppm of elevated [CO<sub>2</sub>]) in leaves and roots to elevated [CO<sub>2</sub>] and sensitivity of the natural log response ratios of N and P concentrations (by kg ha<sup>-1</sup> of N enhancement) in leaves and 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.

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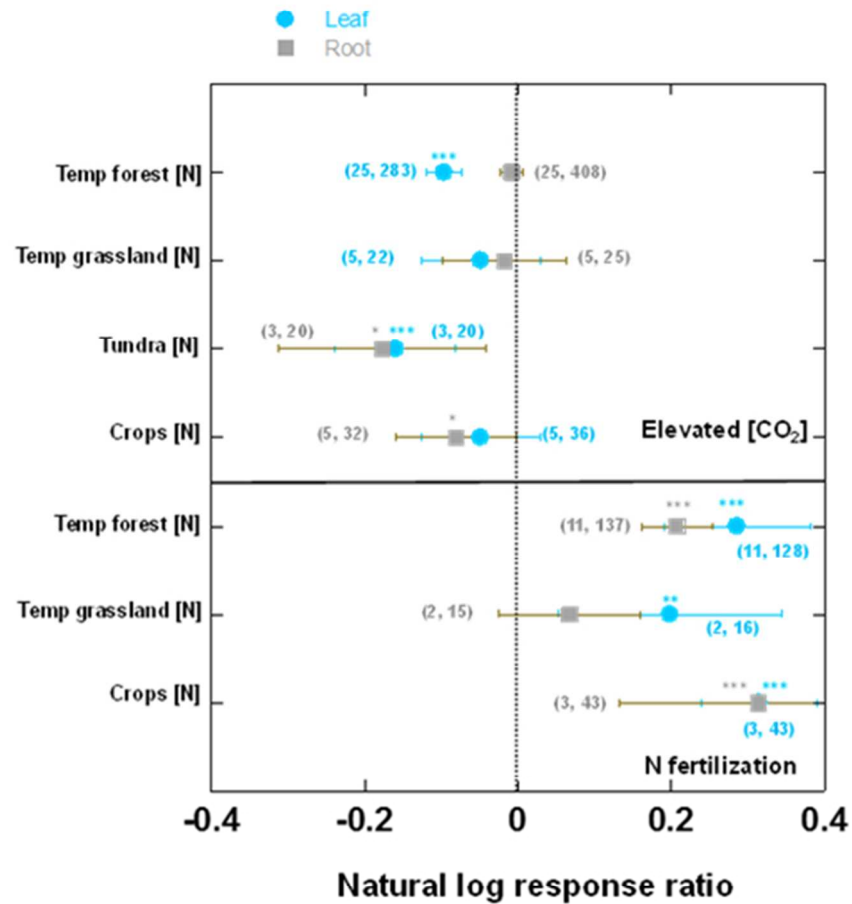


Figure 3. Natural log response ratios due to elevated [CO<sub>2</sub>] and to N fertilization on N concentrations in leaves and roots in different vegetation types obtained in studies that provided data of leaves and roots of the same plants. Error bars indicate the 95% confidence intervals for the mean 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.