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4 **Foliar C, N, and P stoichiometry characterize successful plant ecological strategies in the Sonoran Desert.**

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## Foliar C, N, P stoichiometry in drylands

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### **Abstract**

Ecological processes are centered to water availability in drylands, however less known nutrient stoichiometry can help explain much of their structure and ecological interactions. Here we look to the foliar stoichiometry of carbon (C), nitrogen (N) and phosphorus (P) of 38 dominant plant species from the Sonoran Desert, grouped in four different functional types to describe ecological characteristics and processes. We found that foliar N, C:N, C:P and N:P stoichiometric ratios, but not P, were higher than those known to most other ecosystems and indicate P but not N limitations in leaves. Biological N fixers (BNF) had even higher leaf N concentrations, but bio-elemental concentrations and stoichiometry ratios were not different to other non-N fixing legume species which underscores the need to understand the physiological mechanisms for high N, and to how costly BNF can succeed in P-limiting drylands environments. Stoichiometry ratios, and to lesser extent elemental concentrations, were able to characterize BNF and colonizing strategies in the Sonoran Desert, as well as explain leaf attribute differences, ecological processes and biogeochemical niches in this dryland ecosystem, even when no direct reference is made to other water—limitation strategies.

**KEYWORDS.** Foliar stoichiometry; Nutrient-use efficiency; Drylands plants; Sonoran Desert; Biological nitrogen fixers; Invasive species.

48

49 **Introduction**

50

51 Drylands are widespread and cover more than 40 % of Earth's terrestrial surface (Dregne and Chou 1992; Evenari et  
52 al. 1985; Právãlie 2016). Much studies of drylands studies have water pulses as drivers of major ecological functions  
53 (Huxman et al. 2004; Noy-Meir 1973; Ogle and Reynolds 2004), but the water-centered approach neglects many  
54 important processes and interactions in which nutrients play a more important role (Austin et al. 2004). Drylands  
55 contribute about a third of the net productivity of terrestrial ecosystems (Asner et al. 2004; Field et al. 1995), play an  
56 important role in the sequestration and storage of carbon (C) globally (Jackson 2000; Lal 2004; Ma et al. 2014) and  
57 have a noticeable impact on the seasonality of the global C cycle (Poulter et al. 2014), and nutrients are key drivers  
58 in all these ecosystem functioning processes. As such, a major concern now is that changes in nutrient cycles linked  
59 to current global trends of increasing dryness will have unknown consequences to productivity in arid ecosystems  
60 (Delgado-Baquerizo et al. 2017; Yuan and Chen 2015).

61 We have limited information on how nutrients may feed back to other plant physiological and ecological  
62 processes in drylands ecosystems. Different studies and climate change scenarios have established that soil nutrient  
63 cycles will uncouple with increasing drought, increasing nitrogen (N) depletion and phosphorus (P) availability  
64 (Delgado-Baquerizo et al. 2017; Delgado-Baquerizo et al. 2013; Yuan and Chen 2015). In plants under experimental  
65 drought however, both N and P concentrations decreased (Dijkstra et al. 2016; He and Dijkstra 2014). These  
66 potential conflicting results may require better knowledge on how N and P concentrations and their stoichiometry  
67 ratios, which may have important effects for nutrient cycling in drylands ecosystems. Understanding the  
68 stoichiometric relationships of C, N and P among different species and functional groups should help to understand  
69 many of today's physiological and ecological unknowns of species interactions in drylands ecosystems, that the  
70 water-centered approach has not resolved (Austin 2011).

71 Nitrogen is a key element that limits productivity in arid ecosystems (Skujins 1981), but it has been largely  
72 ignored (Austin 2011). Drylands are known to be limited by low soil N (Nieder and Benbi 2008; West and Skujins  
73 1978) and P concentrations (Kajtha et al. 1987; Schlesinger 1997), when water is available. However, despite the  
74 known low N soil concentrations, the leaves of drylands species are known to have higher N concentrations (Skujins  
75 1981; West 1981; West and Klemmedson 1978; West and Skujins 1978), although some controversy still remains  
76 (Killingbeck and Whitford 1996; Reich and Oleksyn 2004). Global surveys contain limited data specific to drylands  
77 species and document high foliar N concentrations (Killingbeck and Whitford 1996; Tao et al. 2016), which calls for  
78 more survey studies to characterize drylands plant species elemental nutrient concentrations and stoichiometry  
79 ratios.

80 A water—centered approach may have missed to explain how species and functional groups interact in drylands  
81 ecosystems. Diverse strategies have been documented in different species and growth forms for N uptake (Belnap et  
82 al. 2001; Berdugo et al. 2014; Virginia et al. 1992), reabsorption (Killingbeck 1993, 1996), mineralization (Reyes-  
83 Reyes et al. 2003), use and loss (Schlesinger and Pilmanis 1998; Schlesinger et al. 2000), as well as P soil and plant  
84 heterogeneous distribution (Schlesinger and Pilmanis 1998), and how those nutrients drive the above- and below-  
85 ground interactions in drylands ecosystems (McCulley et al. 2004). A key to understand drylands ecosystems

## Foliar C, N, P stoichiometry in drylands

86 nutrient cycling processes and species interactions is to know the species leaf concentration and stoichiometry ratios.  
87 Here, we determined total C, N and P concentrations and stoichiometric ratios in the leaves of 38 dominant  
88 species in the southwestern region of the Sonoran Desert in central Sonora. We grouped plant species in different  
89 functional groups, for growth form, leaf habit, N-fixing ability and colonizing capability. We used these functional  
90 groups to test how foliar stoichiometry traits can help to explain successful ecological strategies in drylands  
91 environments.

92

### 93 **Methodology**

94 The study area was in northwestern Mexico (28-30°N, 110-112°W) in the Sonoran Desert region of central Sonora,  
95 Mexico (Figure 1). We chose thirty one sites within the boundaries of five major proposed conservation areas. The  
96 climate in the region is hot and dry, with mean annual temperatures from 20 to 24 °C and annual rainfall between  
97 135 and 555 mm, mostly during the summer monsoon (80-90%) from July to September, with fall or winter  
98 precipitation during some years (Brito-Castillo et al. 2010). Temperatures usually remain above freezing during the  
99 winter, although some frosts have been reported in recent years that have led to some tree mortality. The soils at the  
100 sites were mostly Lithosols, Eutric Regosols and Xerosols (INIFAP-CONABIO 2001), consistently with more than  
101 80% sand, although the soils differ at some microsites.

102

### 103 *Vegetation sampling and functional groups*

104 The plant communities in the region are dominated by trees and shrubs with variable herbaceous coverage during  
105 the growing season in different years. The sampled dominant plant associations were Mezquital (*Prosopis velutina*  
106 and *Olneya tesota*), microphyllous desert shrublands (*Larrea tridentata*, *Ambrosia dumosa* and *A. cordifolia*) and  
107 subtropical shrublands (*Lysiloma divaricata* and *Acacia cymbispina*) (Brown 1982; INEGI 2000; Shreve and  
108 Wiggins 1964).

109 We sampled the dominant species from 31 sites with native vegetation and no major signs of disturbance.  
110 We selected species for nutrient and stoichiometric comparisons from the two or three most dominant height strata  
111 using the *relevé* method. Dominance/abundance was determined for each site from categories of species  
112 coverage/abundance (Mueller-Dumbois and Ellenberg 1974) obtained along three 150-200 m transects at each site.  
113 The species representing up to 80% of the cover for the community on each transect were identified and assigned to  
114 the various functional groups.

115 At each site, the most dominant species were almost always different. We compared all different species  
116 and then assigned them to different functional groups. We compared functional groups for growth form (trees,  
117 shrubs, subshrubs, herbs and grasses, and succulent cacti), foliar phenology (deciduous, evergreen and succulent  
118 cacti), colonizing capability (invasive, pioneers and other native species) and biological N fixation (Fabaceae and  
119 Mimosaceae, as BNF species) for statistical differences in elemental and stoichiometric ratios. All sites were native,  
120 but most had some degree of cattle grazing. The spontaneous presence of the exotic buffelgrass (*Cenchrus ciliaris*)  
121 was found at some of the sites (<1-5%) and was included in the analyses. Vegetation sampling, local knowledge  
122 (COTECOCA 2002), a regional floristic database (SEINET) and previous field experience were used to determine

## Leaf C, N, P stoichiometry in drylands functional groups

123 the colonizing capability of the species. Such strategy is one of the most important traits in desert species after local  
124 disturbances.

125 Fully exposed mature leaves were collected from each of the dominant species, only during the peak of the  
126 growing season in two different years. Once collected, leaves were immediately transferred to plastic bags  
127 containing a wet paper towel, stored in an ice chest, transported to the laboratory and stored at  $-4\text{ }^{\circ}\text{C}$  until leaf area  
128 was measured. The areas of fresh leaves were measured with a scanner using ImageJ (Schneider et al. 2012), dried  
129 in a ventilated oven at  $60\text{ }^{\circ}\text{C}$  for 48 h and stored in a desiccator to equilibrate and then weighed. The leaf mass area  
130 (LMA), the projected area per unit dry weight, was then obtained.

### 131 132 *Laboratory analysis*

133 The same dried leaf samples were ground to a 40-mesh size. Total foliar C and N concentrations were measured  
134 with an Elemental Analyzer (Perkin-Elmer CHNS/O 2400, Waltham, USA) after sample combustion in an oxygen  
135 atmosphere at  $925\text{ }^{\circ}\text{C}$ . Total Kjeldahl P was also obtained from these ground samples after acid digestion with  
136 copper sulfate as a catalyst and an ammonium molybdate colorimetric reaction, using an automated rapid-flow  
137 analyzer (SEAL, Norderstedt, Germany). For each species, mean nutrient concentrations were obtained from  
138 determinations in leaves from three individuals. C, N and P concentrations and stoichiometric ratios are expressed as  
139 mass units ( $\text{mg g}^{-1}$ ) and fractions for comparison with most recent studies.

### 140 141 *Statistical analysis*

142 All nutrient concentration and stoichiometric data were  $\log_{10}$ -transformed for ANOVAs and correlation analyses as  
143 suggested by Sterner and Elser (2002). Since most of our data exhibited non-normal distribution within species, bio-  
144 elemental concentrations and their ratios were  $\log_{10}$  transformed to meet normality assumptions. Nutrient and  
145 stoichiometry ratio differences between species, growth form, leaf habit and BNF capacity were determined using  
146 ANOVAs of the  $\log_{10}(X)$  transformed data and HSD-Tukey's a posteriori tests for differences. The data were  
147 retransformed after the analyses. ANOVAs statistical analyses were performed using JMP 9 (SAS Institute Inc.,  
148 Cary, NC, USA). We also performed discriminant functional analyses (DFAs) to determine whether the  
149 concentrations of C, N and P and their ratios could discriminate among the functional groups for detecting possible  
150 differences in the use of these three bio-elements, depending on the ecological and growth strategies of the species.  
151 DFA assumes that the used variables are normally distributed (McLachlan et al. 2004).  $\log_{10}(X)$  transformation of  
152 all variables was needed to normalize them. DFA is a supervised statistical algorithm that will derive an optimal  
153 separation between groups established a priori by maximizing between-group variance while minimizing within-  
154 group variance (Raamsdonk et al. 2001). The DFAs were performed using Statistica 8.0 (StatSoft, Inc., Tulsa,  
155 USA).

### 156 157 **Results**

158 Mean cover among sites was obtained independently for the tree, shrub and herb strata. Mean percent coverage was  
159  $<20\%$  for any of the strata we sampled. Our *relevés* indicated that on average, more land was covered by shrubs than

## Foliar C, N, P stoichiometry in drylands

160 trees, and BNF species, although the number of BNF species was lower (Table 1).

161

### 162 *Stoichiometry differences among species*

163 Foliar C concentrations varied from 359.7 to 486.8 mg C g<sup>-1</sup> for all species, with lowest C in the photosynthetic  
164 stems of cholla cacti. Those same species were five to eight-fold different in foliar N (9.03 to 40.45 mg N g<sup>-1</sup>) and P  
165 concentrations (0.60 to 5.06 mg P g<sup>-1</sup>), and were consequently highly variable (427.5 ± 68.5 mg C g<sup>-1</sup>, 23.0 ± 9.0 mg  
166 N g<sup>-1</sup> and 1.6 ± 0.9 mg P g<sup>-1</sup>). A significant but low correlation and slope was found between species foliar N and P  
167 (Figure 2). N and P in the photosynthetic tissues (succulent stems) of cholla cactus species (*Cylindropuntia*  
168 *versicolor*) were the lowest, and the highest in the subshrub *A. cordifolia* (40.4 ± 5.6 mg N g<sup>-1</sup>, 2.8 ± 0.5 mg P g<sup>-1</sup>;  
169 Supplemental Table S1). A weak negative correlation for leaf C:N ratio and P was found ( $r^2=0.164$ , Figure 3).

170

### 171 *Differences among growth forms and leaf habits*

172 Elemental concentrations were significantly different among growth forms (Table 2). Foliar N concentration were  
173 higher in shrubs, trees and subshrubs (25.9 ± 0.78 mg N g<sup>-1</sup>) than herbs and grasses (15.0 ± 1.07 mg N g<sup>-1</sup>) and cacti  
174 (11.01 ± 0.87 mg N g<sup>-1</sup>). In contrast, mean foliar P mass concentrations were significantly higher in subshrub, herbs  
175 and grasses (2.1 ± 0.16 mg P g<sup>-1</sup>) than trees, shrubs and cacti ( $F=5.6$ ,  $p<0.0003$ ). C:P ratios were significantly higher  
176 in trees (355.01 ± 19.1).

177 Species with deciduous leaves were more common (30 species) and abundant than evergreens (6) and  
178 succulents (2). C, N and P concentrations were always lowest in the photosynthetic tissues of succulent cholla cacti,  
179 while in deciduous species C was lower ( $F=91.9$ ,  $p<0.0001$ ) and P higher ( $F=3.9$ ,  $p<0.022$ ) compared to evergreens,  
180 but no differences in N concentrations were found (Table 2). In evergreens, C:P ratio was higher (380.7 ± 30.2), but  
181 for deciduous and evergreens C:N was lower ( $F=47.4$ ,  $p<0.0001$ ) and N:P higher than in the photosynthetic tissues  
182 of Cholla cacti.

183

### 184 *Stoichiometry of BNF and pioneers*

185 We tested for stoichiometry differences in biological nitrogen fixers (BNF), legumes and other Sonoran Desert  
186 species. N leaf concentration in BNF species was much higher than overall species and functional group means, but  
187 was not correlated to P, although a significant negative correlation was found between C:N and P ( $F=10.7$ ,  $p\leq 0.002$ ,  
188  $r^2=0.189$ ). C:N ratio was significantly lower and N:P higher in BNF species ( $F=10.1$ ,  $p<0.0018$ ; Table 2).

189 Grouped by their capability to colonize post-disturbance habitats, invasive species had the lowest foliar C  
190 and N but highest P concentrations than non-invasive species (Table 2). Invasive species had higher C:N ratios  
191 (35.38 ± 2.74;  $F=59.00$ ,  $p<0.0001$ ), despite their low foliar C and N concentrations, and the lowest N:P ratios (8.0 ±  
192 1.61;  $F=17.93$ ;  $p<0.0001$ ). Because the large variability in C:P ratios, there were no significant differences between  
193 colonizing capability.

194 BNF and colonizing capabilities were clearly differentiated along the stoichiometric-ratio axes. The  
195 discriminant functional analyses (DFA) showed significant squared Mahalanobis distances among functional groups  
196 with respect to their foliar C, N and P concentrations and stoichiometry ratios when both colonizing potential

## Leaf C, N, P stoichiometry in drylands functional groups

197 (pioneers, invasives, natives) and N-fixation capability ecological groups (non-N-fixing pioneers, N-fixing pioneers,  
198 non-N-fixing invasives, non-N-fixing natives and N-fixing natives) were considered (Figure 4). The DFA found that  
199 invasive species had the highest C:N ratios but lowest N concentrations and N:P ratios (Figure 4). Bio-elemental  
200 composition and C:N and C:P ratios differed in pioneers, with higher C:N ratios and C and N concentrations, but  
201 lower C:P ratios in BNF pioneers.

202

203

### 204 **Discussion**

205 Bio-elemental C, N and P concentrations and their stoichiometric ratios were highly variable and skewed. Elemental  
206 and nutrient investment in leaves are adaptive traits in plants to ensure the C gains over their life span (Harper  
207 1989). Such adaptive strategies allow plants to adjust bio-elemental stoichiometric ratios to optimize the investment  
208 of nutrients and energy to the photosynthetic, light capture, survival and defense functions in the leaves (Westoby  
209 and Wright 2006; Wright et al. 2004). Here we analyzed the foliar C, N and P concentrations and stoichiometric  
210 ratios from 38 plant species of the Sonoran Desert, and their ecological significance when grouped in four different  
211 plant functional types.

212 Species had a large variability in C, N and P concentrations (Supplemental Table S1). We found ten- to  
213 twenty-fold differences in elemental concentrations but only about three- to five-fold in the stoichiometric ratios in  
214 all sampled individuals. Other studies have reported species variability in elemental concentrations, three- to ten-  
215 fold differences in N and P concentrations in wetland species (Koerselman and Meuleman 1996), and up to 20-fold  
216 (N) and 30-fold (P) in global analyses (Elser et al. 2010). Intra-specific differences in all those studies were highly  
217 skewed and were larger than inter-specific differences at different sites (Koerselman and Meuleman 1996; Reich and  
218 Oleksyn 2004), even when changes in species composition were considered (Yang et al. 2016). The large intra-  
219 specific variation we found in the elemental composition of Sonoran Desert species may indicate high homeostatic  
220 plasticity, considered to be advantageous in unpredictable and drylands environments (Elser et al. 2010; Sistla and  
221 Schimel 2012; Sterner and Elser 2002).

222 Our data identified patterns of high N foliar concentration and significant differences among species and  
223 functional groups, although high leaf N in drylands has been a matter of controversy. We found an overall mean N  
224 concentration ( $23.66 \pm 0.52 \text{ mg N g}^{-1}$ ) that is higher to the mean of  $20.1 \pm 8.7 \text{ mg N g}^{-1}$  in global databases (Elser et  
225 al. 2010; Reich and Oleksyn 2004; Wright et al. 2004), similar to those from grasslands ( $24 \text{ mg N g}^{-1}$ ), and drylands  
226 like the Taklamakan ( $24.7 \pm 1.8 \text{ mg N g}^{-1}$ ) and higher than the Aixa Desert ( $10.65 \pm 1.4 \text{ mg N g}^{-1}$ ) in China (Tao et  
227 al. 2016). There are reports of high N in leaves of desert species (Skujins 1981; West 1981; West and Klemmedson  
228 1978; West and Skujins 1978), while others have contended such findings (Killingbeck and Whitford 1996; Lamont  
229 et al. 2002). Some studies suggest that foliar N should be low because limiting N and volumetric soil moisture  
230 concentrations in arid soils which may constraint nutrient uptake and transport within the plant.

231 In contrast to N, species had low P concentrations. We found that foliar P was lower ( $1.62 \pm 0.06 \text{ mg P g}^{-1}$ )  
232 than mean concentrations ( $1.77$  to  $1.90 \text{ mg P g}^{-1}$ ) in extensive global data sets (Elser et al. 2007; He et al. 2008;  
233 Reich and Oleksyn 2004; Tao et al. 2016; Wu et al. 2012). In our data, although N and P were co-limited (Figure 2),



## Foliar C, N, P stoichiometry in drylands

234 we found a weak N - P correlation compared to other studies (Elser et al. 2010; Reich et al. 2010), and a lower slope,  
235 but the specific mechanisms by which this may happen, deserve to be determined. We encourage complimentary  
236 surveys, physiological studies and stoichiometric approaches to gain better understanding of the N and P  
237 relationships in leaves of drylands species, in particular those in the Sonoran Desert, although some initial results  
238 suggest that nitrogen fixing species contribute to such weak correlation.

239

### 240 *High N and P limitation in leaves of BNFs and legumes*

241 The abundance and dominance of legumes (Mimosaceae, Fabaceae, Caesalpinaceae), some of which are known  
242 BNFixers (Felker and Clark 1980; Felker and Clark 1981; Shreve and Wiggins 1964; Van Devender et al. 2010;  
243 Virginia and Jarrell 1983), is an important characteristic of the plant communities of the South - Southeastern  
244 regions of the Sonoran Desert, as it merges with the tropical deciduous forest biogeographic ecotone (Brown 1982;  
245 Castellanos et al. 2010; Rzedowski 1993; Shreve and Wiggins 1964). We found that about 15% of the dominant  
246 species we sampled were legumes and contributed with about a third of the mean coverage at the sites, although  
247 their species richness was lower than non-fixing species (Table 1).

248 As found for species in general, BNF species had leaf N (mass and area) concentrations that were  
249 significantly higher to the species mean (Table 2). High leaf N in BNF species are known from tropical, dry-forests,  
250 drylands and in global databases (Adams et al. 2016; Hedin et al. 2009; Vergutz et al. 2012; Wolf et al. 2017). The  
251 benefits of higher N in leaves is related to high photosynthetic capacity in most C<sub>3</sub> species (Evans 1989; Field et al.  
252 1983), although more recent evidence suggest that N<sub>area</sub> may not be related to photosynthetic performance in BNF  
253 species (Adams et al. 2016; Funk et al. 2013). As in other C<sub>3</sub> species (Adams et al. 2016; Cernusak et al. 2013; Field  
254 et al. 1983), high N<sub>area</sub> has been related in the past with high intrinsic water use efficiency ( $A_{\text{sat}}/g_s$ ) in BNF species  
255 (Adams et al. 2016; Field et al. 1983), the increase in N-based defensive compounds (Coley et al. 1985), and  
256 physiological flexibility under limiting and heterogeneous N soil availability (Wolf et al. 2017), but see (McKey  
257 1994), and reduced transpiration that may limit nutrient uptake (Cramer et al. 2009).

258 But high N in leaves is not only the outcome of nitrogen fixation, as we found no elemental and  
259 stoichiometric differences between legumes and BNF species (Table 3). Some studies suggest that all legumes, and  
260 not only BNF, have hard-wired intrinsic physiological and phylogenetic mechanisms that allow for high N in leaves  
261 (Fyllas et al. 2009), as we found in Sonoran Desert legumes, although other studies have found differently (Wolf et  
262 al. 2017).

263 High N in leaves may reduce the use efficiency of nitrogen in BNF (Menge et al. 2008) as P limits nitrogen  
264 fixation. Stoichiometry ratios may be used as proxys for elemental C, N or P use efficiencies. In the Sonoran Desert,  
265 high N:P ratios in BNF suggests that P and not N may be the most limiting resource (Table 2). Because fixing  
266 nitrogen is energy expensive and requires large amounts of P which is limiting under arid conditions (Delgado-  
267 Baquerizo et al. 2017; Dijkstra et al. 2016), the N:P ratio is an important stoichiometric variable that indicates N  
268 (N:P <14) or P (N:P >16) limitation (Aerts and Chapin 2000; Koerselman and Meuleman 1996). We found that  
269 almost 92% of the species in our study had P-limited leaves (mean N:P = 16.8 ± 0.73; Table S1), much stronger than  
270 in other regional and global data sets (Niklas and Cobb 2005; Reich and Oleksyn 2004; Yang et al. 2016).

## Leaf C, N, P stoichiometry in drylands functional groups

271 High N and N:P ratios because low P in leaves indicate that Sonoran Desert species and functional types  
272 are much more limited by P than N. BNF species may not be viable in arid areas with limited soil P, due to the high  
273 energy costs and P concentrations required to build and maintain bacterial nodules, N fixation and foliar  
274 concentrations (Phillips 1980; Vance and Heichel 1991), and their presence may be paradoxical in drylands as in  
275 other subtropical regions (Hedin et al. 2009). How N fixation can succeed under limited P and drought conditions is  
276 not completely understood yet, it may include processes to lower metabolic costs by synthesis of ureides that allow  
277 N export from nodules (Valentine et al. 2017), increase allocation of P from roots to shoots, and enhancing root  
278 phosphatase activity to increase P availability in the soil (Houlton et al. 2008; Png et al. 2017; Tapia-Torres et al.  
279 2015). All three strategies to enhance P availability and competitive ability of BNF may be important, but more  
280 experimental studies may help understand which of those mechanism allow the success of BNF in the Sonoran  
281 Desert and other dryland environments.

282

### 283 *C:N stoichiometry ratio and colonizing capability*

284 Higher C:N ratios in leaves may be correlated with the physiological and ecological strategies required for  
285 maximizing C gain (Harper 1989; Wright et al. 2004) and light-use (Sterner and Elser 2002) for any given N in the  
286 leaf, which may be expressed as stoichiometry ratio or efficiency. The light:nutrient hypothesis states that C:N ratios  
287 are higher in bright environments, because gains in photosynthetic C increase for any given N concentration (Sterner  
288 and Elser 2002; Sterner et al. 1997).

289 Even though we did not measure photosynthetic performance, we found that foliar C:N ratios, but not N  
290 concentrations, were significantly higher in pioneer-colonizers (native invasive species *sensu* Alpert et al. 2000) and  
291 invasives (Figure 4). We found that high C:N ratios were found in two contrasting growth strategies, e.g. the pioneer  
292 - photosynthetic CAM cholla cacti ( $37.8 \pm 2.62$ ) and the invasive exotic C<sub>4</sub> buffelgrass ( $35.4 \pm 2.74$ ), both with  
293 some of the lowest N concentrations in photosynthetic tissues ( $11.0 \pm 0.9$  and  $14.6 \pm 1.03$  mg N g<sup>-1</sup> respectively,  
294 Table 2). The high C:N stoichiometry ratio in these two contrasting strategies may indicate a closer relationship with  
295 a high light:nutrient efficiency hypothesis for drylands plant species (Sterner et al. 1997), even though their reported  
296 photosynthetic and growth rates may be at opposite extremes, higher for the invasive buffelgrass (Castellanos et al.  
297 2010; Larcher 1995), and lowest in cholla cacti (Nobel and Bobich 2002; Nobel et al. 1991; Patten and Dinger 1969;  
298 Tschirley et al. 1964). It is to note that the buffelgrass and cholla cactus have contrasting photosynthetic pathways,  
299 C<sub>4</sub> and CAM, and because they both share a more effective concentrating CO<sub>2</sub> mechanism in photosynthesis than in  
300 C<sub>3</sub> species (the phosphoenolpyruvate (PEP) carboxylase) (Osmond et al. 1982; Patten and Dinger 1969), their  
301 investments in other carboxylase enzymes (and N) may be much lower (Funk et al. 2013; Sage et al. 1987).

302 C:N but not C:P stoichiometry ratios were differentiated among successful pioneers and invaders (Figure  
303 4). Species in those groups, pioneers and invaders, have different photosynthetic pathways, e.g. C<sub>3</sub> (*Encelia*  
304 *farinosa*), CAM (*Cylindropuntia fulgida*) and C<sub>4</sub> (*Cenchrus ciliaris*), all with previously reported high water use  
305 efficiency mechanisms (Castellanos et al. 2010). As CAM species seem to grow slowly, while the C<sub>3</sub> and C<sub>4</sub> species  
306 grow faster, growth rates does not seem to be a common characteristic of these group of successful pioneers and  
307 invader species, however it is interesting that their N:P ratios were low, a stoichiometry ratio characteristic linked to

## Foliar C, N, P stoichiometry in drylands

308 fast grown species, as found for the invasive buffelgrass.

309 High photosynthetic rates and photosynthetic nitrogen use efficiency (PNUE), a ratio of photosynthetic C  
310 gains per unit of N invested in leaves, has been documented for invasive species (McDowell 2002; Peñuelas et al.  
311 2010), and has been related to invasive success in nutrient-limited environments (Funk 2013; Funk and Vitousek  
312 2007). High C:N stoichiometry ratios may not result in higher PNUE, particularly in arid environments, because  
313 other processes such as photorespiration, photoinhibition, growth and maintenance respiration and defense  
314 mechanisms may account for some of the foliar N (Demmig-Adams and Adams 2006; Lea and Morot-Gaudry 2001;  
315 Leegood et al. 1995; Osnas et al. 2013), but this needs to be documented further. Similar to our findings, other  
316 studies have found increase in C:N foliar stoichiometry with drought (He and Dijkstra 2014; Sardans et al. 2008;  
317 Sardans et al. 2012), even though their physiological links are inconclusive and require further understanding of the  
318 physiological and ecological mechanisms that relate stoichiometry ratios and colonizing ability in hot arid  
319 ecosystems.

320 Our data support the idea that high C:N ratios may be associated with the light:nutrient-use efficiency  
321 hypothesis but not photosynthetic N or P use efficiency in arid environments, although in some cases both  
322 mechanisms may coincide. For example, our results grouped invasive and pioneer functional groups with C:N ratios  
323 that were higher than non-invasives, while BNF species differentiated in their C:P and N:P stoichiometry ratios,  
324 such that functional groups were distributed along different biogeochemical niches (Peñuelas et al. 2010; Sardans  
325 and Peñuelas 2014). For the invasive grasses buffelgrass (This study; Castellanos et al. 2010) and Lehmann  
326 lovegrass in the Sonoran Desert (Ignace et al. 2007), low foliar N concentration and high C:N stoichiometry (a  
327 proxy measure of NUE) were consistent with the resource use efficiency hypothesis for invasive success in nutrient-  
328 limited habitats (Funk 2013; Funk and Vitousek 2007), which seem to hold true also, for the native - pioneer species  
329 in the Sonoran Desert environment. We have shown that elemental biogeochemical niche hypothesis can  
330 differentiate pioneers from invasives, as well as BNF N—resource acquisition strategies in drylands environments.

331

### 332 **Conclusions**

333 In our study, the N, P and stoichiometric ratios were powerful tools to differentiate among plant functional groups  
334 and ecological strategies in drylands environments like in the Sonoran Desert. High C:N foliar ratios were able to  
335 differentiate invasive and pioneers in Sonoran Desert species, while N concentrations and N:P ratios were bigger for  
336 BNFixers than other non-legume native species. High N, C:N and N:P stoichiometry ratios may require further  
337 physiological and ecological studies to better understand their role in the differentiation of species, as they have  
338 been correlated to water, N, and P use efficiencies, and how they influence the structure and composition of dryland  
339 plant communities.

340 Stoichiometry relationships clearly differentiated biogeochemical niches of colonizing, pioneers and BNFs  
341 functional groups of Sonoran Desert species. Leaf stoichiometry ratios of dryland functional groups seem to be  
342 linked to high N and P use efficiency of their leaves and photosynthetic organs, although they may or may not be  
343 associated with higher photosynthetic performance or slow growth rates, as has been reported in non—limiting  
344 environments. Further studies linking stoichiometry to physiology in water-limited environments should help to

## Leaf C, N, P stoichiometry in drylands functional groups

345 determine how foliar nutrient concentrations and C:element (N and P) stoichiometry ratios may relate and respond  
346 to investments in photosynthetic machinery. Investments in photosynthetic performance, including photorespiration,  
347 photo-protection and respiration, and other light and energy capture processes, may increase their nutrient use  
348 efficiencies to enhance their performance and differentiate their ecological strategies. Given the different scenarios  
349 of climate change and the effects of N and P decoupling in soil, linking plant stoichiometry ratios to water, light and  
350 nutrient use efficiencies with their soil environment, may prove to be stronger tools in the future, to assess  
351 ecological strategies and species interactions in drylands ecosystems.

352

353

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Foliar C, N, P stoichiometry in drylands

598 TABLES.

599

600 Table 1. Species percentages in the group categories and their mean percent cover. Percent cover was averaged  
601 separately for the herb, shrub and tree strata. Herbs and vines were rarely sampled.

602

Group	Cover %	Species %
<i>Functional group</i>		
Vines	1.33	5
Cacti	5.00	16
Forbs	19.45	10
Herbs	12.63	19
Shrubs, non-fixing	10.38	22
Shrubs, BNF	18.61	4
Trees, non-fixing	7.80	14
Trees, BNF	15.35	10

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606 Table 2. Means and standard errors of foliar mass concentrations (mg g<sup>-1</sup>) and stoichiometric ratios of Sonoran  
607 Desert species assembled by functional group. Different letters indicate significant differences at  $p < 0.001$ .

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Functional group	C		N		P		C:N		C:P		N:P	
Trees	445.16 ± 1.97	a	25.74 ± 0.51	a	1.42 ± 0.07	b	18.26 ± 0.37	b	355.01 ± 19.05	a	19.25 ± 1.19	a
Shrubs	442.12 ± 2.94	ab	25.89 ± 0.78	a	1.50 ± 0.06	b	18.68 ± 0.62	b	332.85 ± 17.35	ac	17.72 ± 0.77	ab
Subshrubs	433.16 ± 2.69	b	25.63 ± 1.10	a	2.11 ± 0.17	a	18.71 ± 0.84	b	287.53 ± 34.85	b	15.74 ± 1.74	bc
Grasses and herbs	413.24 ± 2.16	c	15.01 ± 1.07	b	2.13 ± 0.16	a	34.72 ± 2.86	a	224.71 ± 20.66	bc	8.05 ± 1.31	d
Cacti	375.70 ± 3.36	d	11.01 ± 0.87	c	1.33 ± 0.21	b	37.8 ± 2.62	a	365.33 ± 72.04	abc	10.04 ± 1.57	cd
BNFixer	447.45 ± 2.52	a	25.63 ± 0.45	a	1.45 ± 0.08	a	18.16 ± 0.38	b	353.71 ± 17.94	a	19.36 ± 0.88	a
Non fixer	428.87 ± 1.94	b	22.74 ± 0.66	b	1.69 ± 0.07	a	23.06 ± 0.88	a	312.71 ± 16.29	b	15.71 ± 0.85	b
Evergreen leaves	447.07 ± 3.69	a	25.10 ± 0.54	a	1.35 ± 0.09	b	18.54 ± 0.47	b	380.74 ± 30.19	a	19.34 ± 1.12	a
Deciduous leaves	435.63 ± 1.52	b	24.20 ± 0.58	a	1.71 ± 0.06	a	21.11 ± 0.68	b	309.29 ± 13.21	b	16.62 ± 0.76	a
Succulent leaves	375.70 ± 3.36	c	11.01 ± 0.87	b	1.33 ± 0.21	ab	37.8 ± 2.62	a	365.33 ± 72.04	ab	10.04 ± 1.57	b
Non Invasives	441.60 ± 1.47	a	25.80 ± 0.43	a	1.56 ± 0.05	b	18.38 ± 0.33	c	333.84 ± 14.25	a	17.93 ± 0.75	a
Pioneers	424.77 ± 5.47	b	21.44 ± 1.24	b	1.70 ± 0.14	ab	23.86 ± 1.41	b	320.89 ± 28.84	a	15.12 ± 1.17	a
Invasives	409.89 ± 2.78	c	14.58 ± 1.03	c	2.05 ± 0.17	a	35.38 ± 2.74	a	224.71 ± 25.31	a	8.05 ± 1.61	b
All species	434.80 ± 1.83		23.66 ± 0.52		1.62 ± 0.06		21.43 ± 0.66		324.66 ± 13.87		16.78 ± 0.73	

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## Leaf C, N, P stoichiometry in drylands functional groups

612 Table 3. Mean differences in leaf attributes and stoichiometry ratios between legumes (N<sub>2</sub>-fixing and non-fixing)  
613 with BNF and non-fixing plant species. Significant differences at  $p < 0.001$  (\*\*) and  $p < 0.05$  (\*).  
614

Variable	$\Delta$ Legume - N <sub>2</sub> fixer	$\Delta$ Legume - Other spp
C	2.13	10.66
N <sub>mass</sub>	0.21	2.94 *
P	-0.06	-0.52 **
C:N	0.97	-2.84
C:P	19.52	71.25 *
N:P	0.47	4.57 *
N <sub>area</sub>	0.21	0.92 **

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## Foliar C, N, P stoichiometry in drylands

619 FIGURES.

620

621 Figure 1. Location of the study area (dark gray) in the Sonoran Desert (grey) (modified from Shreve and Wiggins  
622 1964).

623

624 Figure 2. Log transformed correlation of foliar nitrogen (N) with phosphorous (P) mass concentrations of nitrogen  
625 fixing (BNF) species and non-fixers. Points are means for each species ( $y=0.3792x + 1.2746$ ;  $r^2=0.152$ ;  $p=0.05$ ).

626

627 Figure 3. Log transformed correlation of foliar P mass concentration with C:N stoichiometric ratio of BNF species  
628 and non-fixers ( $y=-0.3758x + 1.3619$ ;  $r^2=0.164$ ;  $p=0.04$ ).

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630 Figure 4. Multivariate discriminant analysis for species in the functional groups. Analysis by species colonizing  
631 potential (A) and BNF plus colonizing potential (B).

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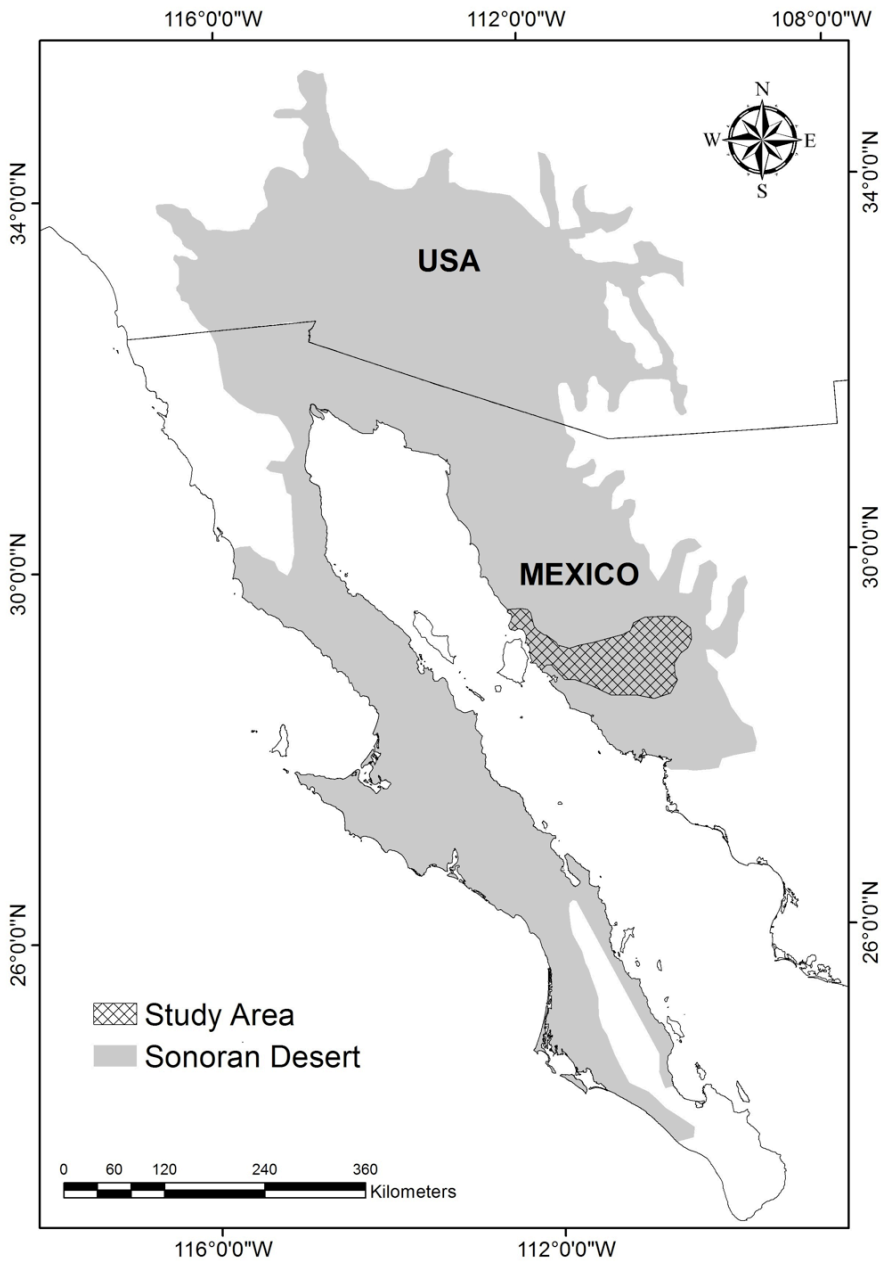
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Leaf C, N, P stoichiometry in drylands functional groups

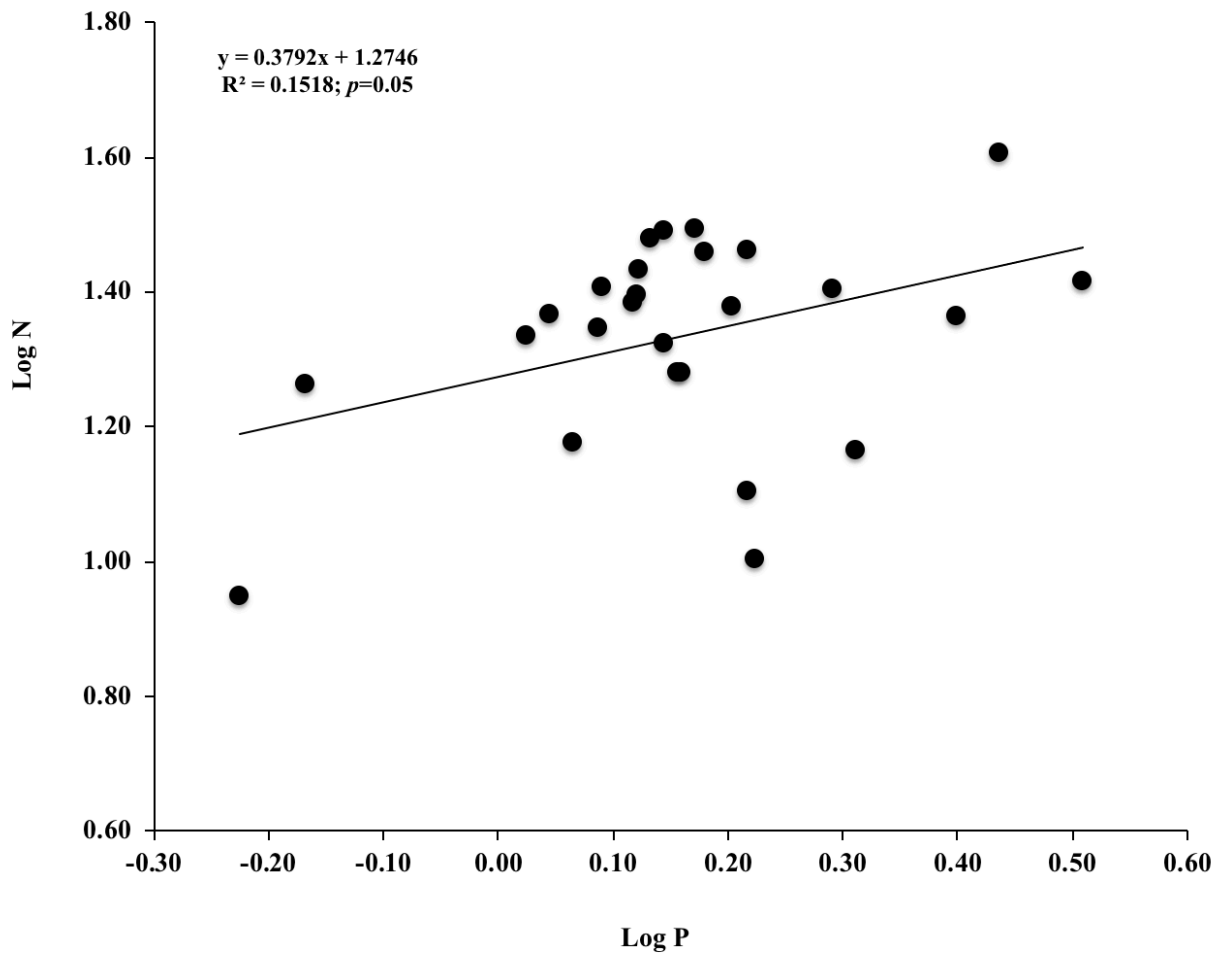
641 Figure 1.  
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Foliar C, N, P stoichiometry in drylands

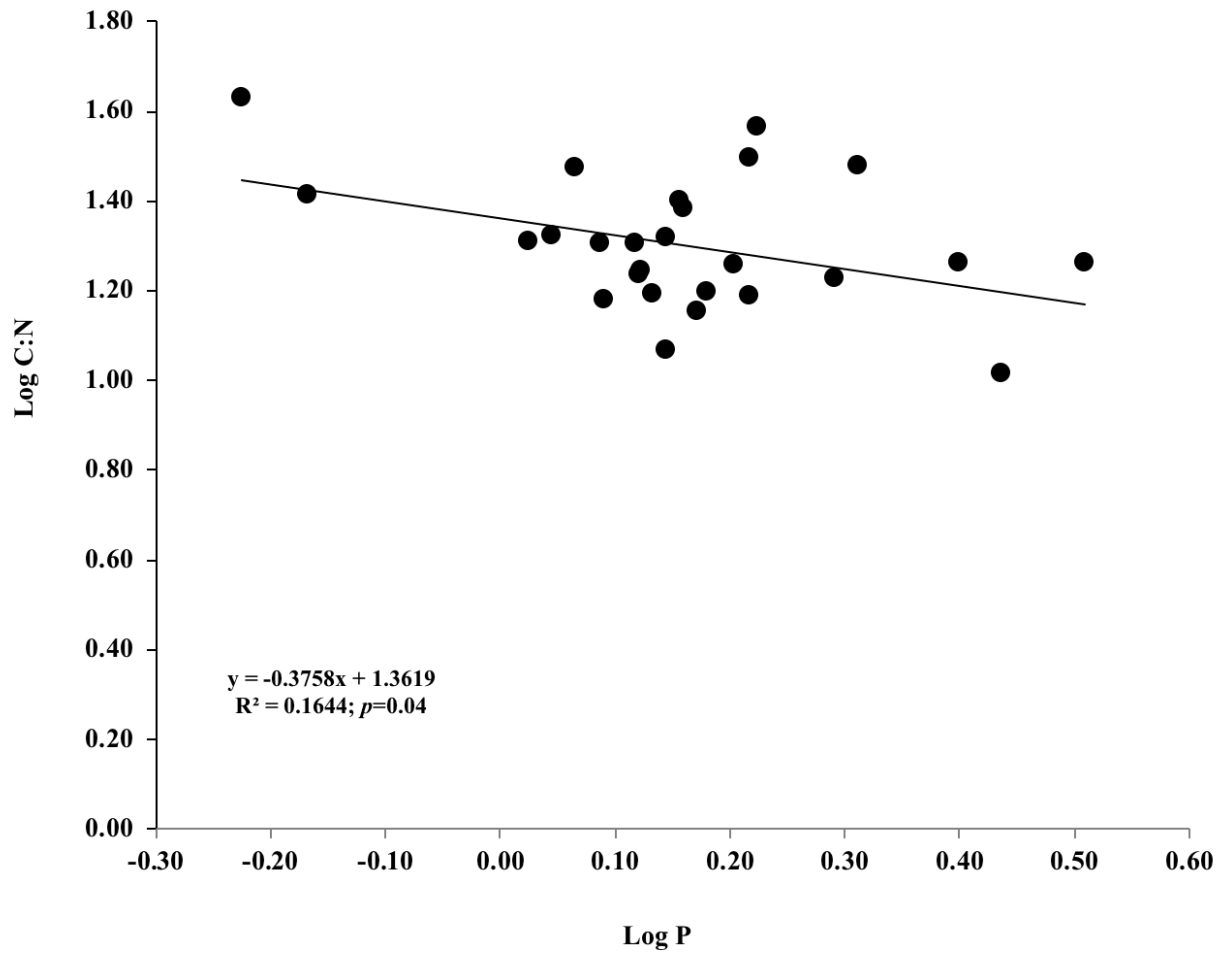
647 Figure 2.  
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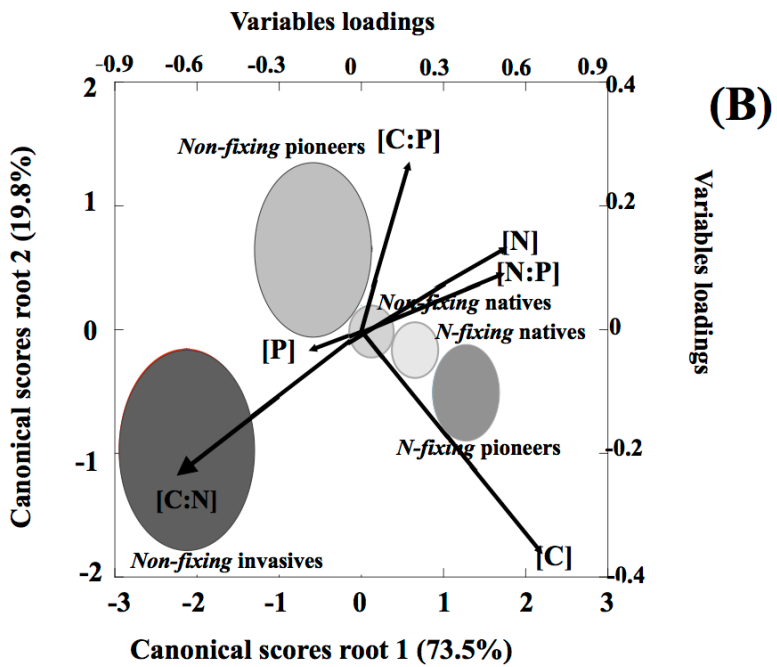
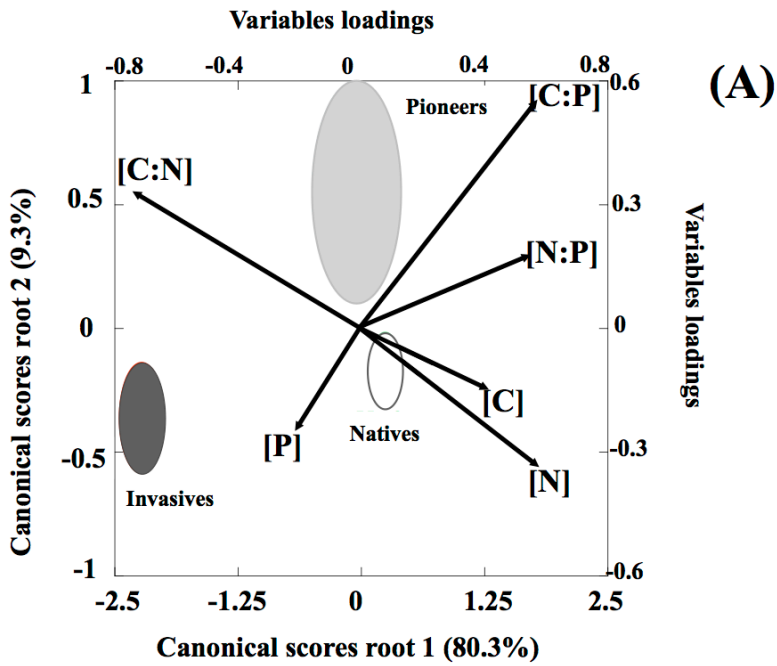
Leaf C, N, P stoichiometry in drylands functional groups

653 Figure 3.  
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Leaf C, N, P stoichiometry in drylands functional groups

663 Supplementary data Table 1. Elemental and stoichiometric ratios of the dominant species in the Sonoran Desert.

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SPECIES	N-fixing	Invasiveness	LMA	C	N	P	C:N	C:P	N:P
			g m <sup>-2</sup> ± s.d.	mg g <sup>-1</sup> ± s.d.	mg g <sup>-1</sup> ± s.d.	mg g <sup>-1</sup> ± s.d.	± s.d.	± s.d.	± s.d.
<i>Abutilon abutiloides</i>	N	NI	71.4 ± 6.9	437.6 ± 4.67	14.6 ± 0.71		30.1 ± 1.70		
<i>Acacia cochliacantha</i>	Y	PI	62.7 ± 6.5	466.5 ± 3.64	30.2 ± 1.83	1.4 ± 0.15	15.5 ± 0.94	344.9 ± 37.29	22.3 ± 3.15
<i>Acacia constricta</i>	Y	NI	99.5 ± 5.8	454.0 ± 6.05	26.8 ± 1.36				
<i>Acacia cymbispina</i>	Y	PI	73.5 ± 13.5	486.8 ± 11.55	23.4 ± 3.08	1.2 ± 0.36	21.0 ± 2.23	459.3 ± 144.92	22.2 ± 7.87
<i>Acacia greggii</i>	Y	NI	80.3 ± 30.4	465.2 ± 7.72	29.9 ± 6.12				
<i>Ambrosia cordifolia</i>	N	PI	34.7 ± 10.3	414.6 ± 14.56	40.5 ± 5.60	2.8 ± 0.48	10.4 ± 1.69	155.0 ± 36.68	15.1 ± 4.10
<i>Ambrosia deltoidea</i>	N	NI	85.1 ± 11.9	470.3 ± 7.95	26.0 ± 2.71	3.3 ± 0.44	18.3 ± 2.11	146.6 ± 17.18	8.1 ± 1.06
<i>Brassica tournefortii</i>	N	I	50.6 ± 5.2	453.6 ± 9.63	26.7 ± 7.38				
<i>Bursera fagaroides</i>	N	NI	69.7 ± 6.5	443.7 ± 4.13	18.6 ± 1.39		22.5 ±		
<i>Bursera hindsiana</i>	N	NI	85.6 ± 5.5			1.4 ± 0.08			
<i>Bursera laxiflora</i>	N	NI	54.6 ± 13.8	434.7 ± 10.71	21.2 ± 2.15	1.4 ± 0.37	19.5 ± 0.87	318.0 ± 87.11	16.4 ± 5.02
<i>Bursera microphyllum</i>	N	NI	109.0 ± 6.0			1.2 ± 0.05			
<i>Caesalpinia pumila</i>	N	PI	79.9 ± 28.0	447.3 ± 12.06	29.3 ± 7.42	1.6 ± 0.39	15.9 ± 3.21	302.7 ± 68.88	19.2 ± 2.89
<i>Celtis pallida</i>	N	NI	89.2 ± 9.2	359.8 ± 17.70	30.9 ± 1.63	1.4 ± 0.26	11.7 ± 1.04	224.0 ± 12.98	19.3 ± 1.16
<i>Cenchrus ciliaris</i>	N	I	66.8 ± 24.8	390.1 ± 119.62	14.0 ± 8.42	1.9 ± 0.77	33.4 ± 15.60	414.5 ± 633.93	17.6 ± 31.90
<i>Cercidium floridum</i>	N	NI	78.4 ± 2.9	430.2 ± 13.00	30.9 ± 4.83				
<i>Cercidium microphyllum</i>	N	NI	118.4 ± 27.7	443.8 ± 9.53	22.7 ± 5.15	1.3 ± 0.26	20.6 ± 5.62	391.0 ± 112.21	20.6 ± 8.84
<i>Cercidium praecox</i>	N	NI	71.6 ± 6.0	433.6 ± 14.68	36.0 ± 8.86				
<i>Cercidium floridum</i>	N	NI	81.0 ± 11.5	408.0 ± 22.06	29.4 ± 3.75				
<i>Croton sonora</i>	N	NI	66.8 ± 16.1	441.7 ± 18.36	31.0 ± 1.85	1.5 ± 0.29	14.3 ± 1.15	300.8 ± 62.22	21.0 ± 3.02
<i>Cylindropuntia fulgida</i>	N	PI		369.0 ± 31.96	11.2 ± 4.82	1.7 ± 0.37	33.3 ± 8.34	225.2 ± 43.49	7.1 ± 2.23
<i>Cylindropuntia versicolor</i>	N	PI		375.1 ± 7.96	9.0 ± 1.95	0.6 ± 0.06	40.9 ± 6.60	620.9 ± 67.83	15.3 ± 0.82
<i>Encelia farinosa</i>	N	PI	88.6 ± 17.9	418.2 ± 12.53	23.7 ± 5.46	2.6 ± 0.86	16.6 ± 2.42	176.9 ± 49.17	10.6 ± 2.45
<i>Eysenhardtia orthocarpa</i>	Y	NI	66.7 ± 15.4	453.4 ± 5.34	29.8 ± 4.16				
<i>Fouquieria diguetii</i>	N	NI	74.3 ± 3.9	443.7 ± 3.10	15.0 ± 2.11	1.2 ± 0.36	29.9 ± 4.52	396.3 ± 140.62	13.0 ± 2.83
<i>Fouquieria macdougalii</i>	N	NI	44.5 ± 6.2	456.6 ± 6.09	19.1 ± 2.21	1.5 ± 0.22	24.1 ± 2.84	319.2 ± 54.63	13.3 ± 2.42
<i>Guaiaecum coulteri</i>	N	NI	109.5 ± 6.1	471.1 ± 5.42	18.4 ± 2.65	0.7 ± 0.10	26.0 ± 3.73	699.4 ± 122.06	27.4 ± 6.61
<i>Ipomoea arborescens</i>	N	NI	36.6 ± 10.6	434.2 ± 18.76	32.2 ± 7.86				
<i>Jatropha cardiophylla</i>	N	NI	49.6 ± 11.2	443.0 ± 10.03	30.3 ± 9.04	1.8 ± 0.71	17.9 ± 6.32	284.9 ± 99.82	16.5 ± 5.07
<i>Jatropha cinerea</i>	N	NI	54.1 ± 2.4			1.6 ± 0.19			
<i>Jatropha cordata</i>	N	NI	41.1 ± 3.6	427.4 ± 10.41	26.0 ± 6.48	2.2 ± 0.93	17.3 ± 4.34	262.3 ± 211.01	17.0 ± 16.49
<i>Larrea tridentata</i>	N	PI	110.6 ± 21.1	477.9 ± 15.87	19.1 ± 2.13	1.5 ± 0.36	26.4 ± 3.26	349.1 ± 89.31	13.5 ± 4.27
<i>Lysiloma divaricata</i>	Y	NI	67.8 ± 30.4	430.8 ± 162.48	22.1 ± 10.20	1.4 ± 0.47	19.1 ± 5.66	383.8 ± 110.85	20.8 ± 6.74
<i>Mimosa laxiflora</i>	Y	NI	72.6 ± 16.1	416.2 ± 76.79	23.7 ± 7.30	1.7 ± 0.39	18.3 ± 3.96	287.7 ± 93.83	16.3 ± 5.91
<i>Olneya tesota</i>	Y	NI	79.9 ± 13.1	405.8 ± 95.26	23.9 ± 6.92	1.4 ± 0.51	17.9 ± 2.98	351.7 ± 161.08	19.1 ± 5.59
<i>Phaulothamnus spinescens</i>	N	NI	83.6 ± 10.7	383.0 ± 10.80	26.2 ± 7.92	1.3 ± 0.30	15.5 ± 4.40	260.1 ± 15.28	17.8 ± 5.48
<i>Prosopis velutina</i>	Y	NI	121.0 ± 24.6	472.8 ± 18.61	27.2 ± 4.15	1.4 ± 0.70	17.6 ± 2.39	368.2 ± 126.42	20.4 ± 5.30
<i>Senna pallida</i>	N	NI	59.3 ± 18.3	436.5 ± 9.54	22.6 ± 7.04	1.2 ± 0.66	23.7 ± 6.76	468.3 ± 254.27	21.3 ± 14.66
Total general			80.2 ± 30.4	427.5 ± 68.54	23.0 ± 8.98	1.6 ± 0.87	21.9 ± 9.59	344.2 ± 224.06	17.1 ± 10.98

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