1 **Effects of extreme drought on plant nutrient uptake and resorption in**

2 **rhizomatous *vs* bunch grass dominated grasslands**

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Abstract

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26 Both the dominance and the mass ratio hypotheses predict that plant internal nutrient

27 cycling in ecosystems is determined by the dominant species within plant

28 communities. We tested this hypothesis under conditions of extreme drought by

29 assessing plant nutrient (N, P and K) uptake and resorption in response to

30 experimentally imposed precipitation reductions in two semiarid grasslands of

31 northern China. These two communities shared similar environmental conditions but

32 had different dominant species – one was dominated by a rhizomatous grass (*Leymus*

33 *chinensis*), the other by a bunchgrass (*Stipa grandis*). Results showed that responses

34 of N to drought differed between the two communities with drought decreasing green

35 leaf N concentration and resorption in the community dominated by the rhizomatous

36 grass, but not in the bunchgrass dominated community. In contrast, negative effects of

37 drought on green leaf P and K concentrations and their resorption efficiencies were

38 consistent across the two communities. Additionally, in each community, effects of

39 extreme drought on soil N, P and K supply did not change synchronously with that on

40 green leaf N, P and K concentrations, and senesced leaf N, P and K concentrations

41 showed no response to extreme drought. Consistent with the dominance/mass ratio

42 hypothesis, our findings suggest that differences in dominant species and their growth

43 form (*i.e.*, rhizomatous *vs* bunch grass) play an important nutrient-specific role in

44 mediating plant internal nutrient cycling across communities within a single region.

45 **Keywords:** Dominance/mass ratio hypothesis, Dominant species, Extreme drought,

46 Nutrient cycling

Introduction

Global climatic change is predicted to alter growing season precipitation patterns, potentially increasing the risk of droughts, and in particular extreme drought events during this century (Easterling et al. 2000; Smith 2011; IPCC 2013). Despite being relatively short-term events, extreme droughts have the potential to cause significant and long-term ecological change, and thus can have impacts disproportionate to their duration (Ciais et al. 2005; Jentsch et al. 2007; Smith 2011; Lal et al. 2012; Knapp et al. 2016). As such, a better understanding of physiological and biochemical responses under these conditions is important to predict drought effects on ecosystem dynamics. Given that plant internal nutrient cycling is an important biological process and ecosystem function that can influence plant growth and productivity of terrestrial ecosystems (Wright and Westoby 2002; Reich and Oleksyn 2004), identifying the dynamics of these nutrients in response to extreme drought is important to better understand the major physiological mechanisms determining ecosystem processes under drought conditions (An et al. 2005; Silva et al. 2011, Smith 2011).

Nitrogen (N), phosphorus (P) and potassium (K) cycles can be profoundly altered by increased aridity (Chapin et al. 1988; He and Dijkstra 2014; Luo et al. 2015; Sardans and Peñuelas 2015). Generally, drought stress can depress plant growth and reproduction by affecting uptake, transport, and partitioning of nutrients (Hu and Schmidhalter 2005; Gessler et al. 2017). Reductions in soil moisture with lower precipitation may reduce plant nutrient uptake by reducing nutrient availability through a decrease in mineralization rates and/or diffusion of soil nutrients to root

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69   surfaces (Alam 1999), while reduced plant nutrient uptake capacity may also be

70   attributed to the inhibition of the nutrient translocation from below- to above-ground

71   tissues (Alam 1999; Hu and Schmidhalter 2005; Sanaullah et al. 2012). Negative

72   effects of drought stress on plant nutrient uptake affect plants' needs to resorb

73   nutrients from senescing tissues, because nutrient resorption is an important nutrient

74   conservation strategy that can reduce dependence on nutrient uptake (Kobe et al.

75   2005). Senesced leaf nutrient concentrations are expected to be reduced with drought

76   due to decreased nutrient uptake and increased nutrient resorption efficiency

77   (Killingbeck 1996), resulting in a reduction in litter quality and subsequent

78   mineralization rate (Yuan and Chen 2009; Sanaullah et al. 2012; Vergutz et al. 2012).

79   Experimentally reducing precipitation inputs into an ecosystem is a direct way to

80   examine the ecological effects of drought on ecosystem structure and function (Gilgen

81   and Buchmann 2009; Beier et al. 2012; He and Dijkstra 2014; Sardans and Peñuelas

82   2015). Over the last few decades, there has been an increasing number of

83   manipulative experiments to investigate how plant internal nutrient cycling might

84   respond to increased aridity (He and Dijkstra 2014; Gessler et al. 2017). However,

85   most research to date has focused on the effects of moderate drought (20-40%

86   precipitation reduction) on plant and soil N and P content, and on N and P availability

87   in soils (He and Dijkstra 2014; Sardans and Peñuelas 2015). Fewer studies have

88   assessed the effects of extreme drought (>60% precipitation reduction) on plant

89   nutrient composition and dynamics (Smith 2011; Hoover et al. 2014, 2015; Knapp et

90   al. 2016), which could significantly influence ecosystem functions and services.

91   Moreover, a majority of these studies are usually done at a single site and assume

92   that the plant internal nutritional responses are consistent among ecosystems or even

93   among local communities within ecosystems despite evidence to the contrary (Grime

94   et al. 2000; Knapp and Smith 2001; Wilcox et al. 2017). Thus, it is more likely that

95   drought will not uniformly affect the plant internal nutrient cycling in ecosystems.

96   Species traits or levels of diversity can affect their sensitivity and the sensitivity of

97   plant internal nutrient cycling to any given precipitation change as will the attributes

98   of ecosystems (White et al. 2000; Knapp and Smith 2001; Wilcox et al. 2017). The

99   identity and traits of dominant species will undoubtedly be important in influencing

100   the sensitivity of plant internal nutrient cycling to change, given that dominant species

101   control the majority of the resources and have disproportionate impacts on the whole

102   community (dominance/mass ratio hypothesis, Whittaker 1965; Grime 1998; Smith et

103   al. 2009). Indeed, in a chronic drought field experiment, plant community

104   composition was shown influence the effects of drought, and this effect was species-

105   specific and due to differential responses of dominant plant species (Hoover et al.

106   2014). Therefore, it is important to understand how plant internal nutrient cycles in

107   ecosystems with different dominant species may respond to future extreme

108   precipitation reduction.

109   Predicting the effects of extreme drought in grassland ecosystems is especially

110   important, as they are one of the most vulnerable ecosystems to precipitation changes,

111   and cover ~40% of the terrestrial land surface, and provide valuable ecosystem

112   services (Sala et al. 2017). The semiarid grassland region of northern China is an ideal

113 ecosystem for studying the effects of extreme drought on plant internal nutrient

114 cycling, as water availability is a primary limiting factor for plant community

115 productivity and composition in this ecosystem and the predicted effects of increased

116 aridity will likely have dramatic effects on the processes of plant nutrient cycling (Bai

117 et al. 2004; Kang et al. 2007; Luo et al. 2015, 2016b). We examined two important

118 grass communities located within a similar environmental context but that are widely

119 distributed in this semiarid ecosystem (Kang et al. 2007). The dominant grasses in

120 these communities differed in a key growth trait, one was dominated by a perennial

121 rhizomatous grass (*Leymus chinensis*, "rhizomatous grass community"), the other by a

122 perennial bunchgrass (*Stipa grandis*, "bunchgrass community") but both species co-

123 occur in each community (Bai et al. 2004).

124   These two communities provide a test-bed for assessing how the effects of extreme

125 drought on plant internal nutrient cycling are determined by differences in dominant

126 species and their growth form (Whittaker 1965; Grime 1998; Smith et al. 2009). We

127 simultaneously reduced 66% of the growing season precipitation over two-

128 consecutive years (extreme drought) across the two communities. According to the

129 dominance/mass ratio hypothesis (Whittaker 1965; Grime 1998; Smith et al. 2009),

130 we expected that the community-level responses would differ between two

131 communities due to their difference in the traits of the dominant grass species

132 (rhizomatous *vs* bunch grass, Chen et al. 2005; Lü et al. 2015). Moreover, it has been

133 widely known that drought will have the largest impact on near-surface soil moisture

134 than deeper soil moisture (Schwinning et al. 2005; Hoover et al. 2017); therefore, we

135　further hypothesized that the responses of plant nutrient uptake and resorption to

136　extreme drought will be more sensitive for rhizomatous than bunch grass

137　communities, because of the shallower root structures in the rhizomatous grass *vs* the

138　bunchgrass dominated community (Xiao et al. 1995; Wang et al. 2016).

139　**Material and methods**

140　**Study sites**

141　In 2014 (pretreatment year), two sites (*i.e.*, rhizomatous and bunch grass

142　communities) with relatively similar climatic conditions but different dominant

143　species were established in a semiarid natural grassland of northern China. The two

144　selected communities were randomly established by the invasion success of the

145　dominant species *L. chinensis* and *S. grandis* and are located at the Inner Mongolia

146　Grassland Ecosystem Research Station (IMGERS) (116°33′E, 43°32′N). These sites

147　are part of the EDGE (Extreme Drought in Grasslands Experiment) experimental

148　platform (http://edge.biology.colostate.edu/). Based on long-term (1982-2014)

149　meteorological records from a weather station located <30 km from the sites, mean

150　annual temperature is 1.9°C and mean annual precipitation is 336 mm with 74% (249

151　mm) falling during the growing season from May to August. The soil is a chestnut in

152　the China soil taxonomy classification system, equivalent to Calcicorthic Aridisol in

153　the US soil taxonomy classification. The rhizomatous grass community has been

154　fenced since 1999, which was dominated by a perennial rhizomatous grass, *L.*

155　*chinensis*, whereas the bunchgrass community has been fenced since 1979, which was

156　dominated by a perennial bunchgrass, *S. grandis* (Bai et al. 2004). *S. grandis* is a

157   subordinate species in the rhizomatrous grass community, while *L. chinensis* is a

158   subordinate species in the bunchgrass community. *L. chinensis* generally has a

159   relatively shallower root system and lower root:shoot biomass ratio than *S. grandis*

160   (Xiao et al. 1995; Wang et al. 2016).

161   These two community types represent the most widely distributed grassland

162   communities in the Eurasian steppe region, which is the largest contiguous grassland

163   area in the world (Bai et al. 2004; Kang et al. 2007). Both communities were

164   considered to be in excellent condition during the time of enclosure, representative of

165   natural and climax steppe communities. The rhizomatous and bunch grass

166   communities respectively have 86 and 61 plant species (Bai et al. 2004). The

167   aboveground net primary productivity reached the annual peak at the mid of August in

168   response to high soil water availability and temperature. The aboveground net primary

169   productivity is about 193 g m^{-2} for the rhizomatous grass community and 217 g m^{-2}

170   for the bunchgrass community (Bai et al. 2004; Kang et al. 2007).

171   **Experimental treatments**

172   At each site, an identical manipulative experiment with two treatments (untreated

173   control and extreme drought) was established in a relatively homogeneous area

174   (similar soils, vegetation, etc.). We imposed extreme drought by creating rainout

175   shelters designed to intercept 66% of ambient incoming precipitation (Fig. S1).

176   Drought shelter roofs were installed on plots from May-August growing season in

177   both 2015 and 2016. The experimental design was a randomized complete block

178   design with six replications of each treatment at each site. Experimental plots were 6

179 ×6 m and located at least 2 m from the neighboring plots. Plots were hydrologically

180 isolated from the surrounding soil matrix by aluminum flashing (buried to a depth of

181 1-m). Each plot included a 1-m external buffer to allow access to the plot and

182 minimized the edge effect associated with the infrastructure. Untreated control plots

183 without rainout shelters were set up for comparison. Rainout shelters were sloped

184 slightly towards subtle topographic gradients to allow for quick drainage of ambient

185 precipitation. Rainout shelters were 2-m above the ground surface and were not

186 closed down to the ground, allowing for near surface air exchange and minimizing

187 unwanted greenhouse effects. The effects of rainout shelters on the light environment

188 were small, permitting nearly 90% penetration of photosynthetically active radiation

189 (Yahdjian and Sala 2002). Daily mean soil moisture and temperature were

190 continuously monitored at a depth of 0-10 cm with sensors placed near the center of

191 each plot at each site.

192 **Field sampling and measurements**

193 In August 2016, a main quadrat (1×1 m) was established in each plot and four sub-

194 quadrats (50×50 cm) were set up within each main quadrat. Aboveground biomass of

195 each species was harvested by clipping at ground level of two sub-quadrats arranged

196 diagonally. All living plants were oven-dried and weighed. Species abundance was

197 calculated as the relative biomass of each species to the total aboveground biomass in

198 each plot. In the other two diagonal sub-quadrats, plant leaves were collected for the

199 most abundant species. The cumulative relative abundance of the selected species

200 reached at least 90% of the plot total abundance. Among these species, the dominant

201 species (*L. chinensis* and *S. grandis*) were present in each sub-quadrat (*i.e.*, 100%

202 frequency). Plant leaves for these species were collected again when they were fully

203 senesced in early-autumn. Green and senesced leaf samples were dried at 105°C for

204 30 min in a drying oven to minimize respiration and decomposition and were later

205 completely oven dried at 80°C to constant weight in the laboratory.

206   Five soil cores (2.5-cm in diameter and 10-cm in depth, respectively) were

207 collected after removing the litter layer in each main quadrat at both sites. Samples

208 were stored at 4°C immediately after collection for initial gravimetric moisture

209 content and soil available N (NH_4^+-N plus NO_3^--N) (fresh soils). A small subsample

210 was stored in a cloth bag at room temperature (air-dried soils).

211   Fresh soils were passed through a 2-mm sieve, and roots and rocks were removed.

212 Gravimetric moisture content was measured after drying a known amount of soil at

213 105°C for 48h. Fresh soil samples were extracted with 50 mL of 2 M KCl, and the

214 filtered soil extract was used to determine soil available [N] with a continuous flow

215 spectrophotometer (FIAstar 5000; Foss Tecator, Denmark). Air-dried soil samples

216 were sieved through a 2-mm mesh size to remove roots and rocks. Olsen [P] was

217 measured by extracting air-dried soils with 0.5 M $NaHCO_3$ (pH=8.5), which was

218 analyzed using the molybdenum blue-ascorbic acid method. The exchangeable [K]

219 was measured by extracting air-dried soils with 1 M NH_4OAc (pH=7.0) and analyzing

220 extracts for [K] by atomic absorption spectrometry (AA6800, Shimadzu, Japan). All

221 plant leaf samples and air-dried soils were ground to pass through a 1-mm sieve. Total

222 [N] in plant and soil samples were measured using an elemental analyzer (2400II

223   CHN elemental analyzer; Perkin-Elmer, USA) with a combustion temperature of

224   950°C and a reduction temperature of 640°C. Plant leaf samples were acid digested

225   with a mixture of H_2SO_4 and H_2O_2 in a microwave oven. Microwave digestion was

226   performed until the sample was dissolved into the solution. Plant [P] was analyzed

227   using the molybdenum blue-ascorbic acid method and [K] by atomic absorption

228   spectrometry (AA6800, Shimadzu, Japan).

229   **Calculation and statistical analysis**

230   In this study, statistical analyses were conducted for the two species (*L. chinensis* and

231   *S. grandis*) and for the whole plant community.

232   For each nutrient in each plot, community nutrient concentrations in green and

233   senesced leaves were calculated as the overall mean of nutrient concentrations across

234   species weighted by the relative biomass of each individual species (Kichenin et al.

235   2013):

236   Community nutrient concentrations $= \sum_{i=1}^{S}(Pi \times Ni),$ eqn 1

237   where *Pi* is the relative biomass of species *i* at the peak of growing season in the

238   plot with *S* species, and *Ni* is the nutrient concentration in green and senesced leaves

239   of species *i*.

240   Nutrient resorption efficiency was calculated as the proportion of nutrients that

241   were taken back by the plant during senescence (Van Heerwaarden et al. 2003):

242   Nutrient resorption efficiency $= \frac{Ng-Ns}{Ng} \times 100\%,$ eqn 2

243   where *Ng* and *Ns* are nutrient concentrations in plant green and senesced leaves,

244   respectively.

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245   Plant nutrient concentrations in green and senesced leaves and nutrient resorption

246   efficiency were analyzed for the two species (*L. chinensis* and *S. grandis*) and whole

247   plant community using a mixed-model analysis of variance with drought treatment

248   and community as fixed factors and block as random factor. When interactive effects

249   of drought treatment and community were significant ($p<0.05$), the mixed model

250   analysis of variance was separately applied for each community with drought

251   treatment as fixed factor and block as random factor. Similarly, soil nutrients were

252   also analyzed using the mixed models. For all analyses, any non-normal data were

253   transformed prior to analyses. All statistical analyses were performed using the *lme*

254   function in the *nlme* package of R-project (R i386 3.1.1).

Results

During the 2015 and 2016 growing seasons, the drought treatment resulted in an

extreme drought (close to the 10th percentile of the historical record) (Fig. S2). In

contrast, growing season precipitation was approximately normal in both years

(slightly lower than the 50th percentile of the historic record) for the control treatments

(Fig. S2). In this experiment, rainout shelters clearly reduced the soil moisture content

(Fig. S3), but did not significantly affect the soil temperature for each site (Fig. S4).

Senesced leaf [N] of the two common species (*L. chinensis* and *S. grandis*) and the

whole plant community was higher in the rhizomatous grass community compared to

the bunchgrass community ($p<0.05$; Table 1; Figs. 1 and 2), but senesced leaf [P] and

[K] as well as green [N], [P] and [K] and their resorption efficiencies were similar

(Table 1; Figs. 1 and 2). Total and available soil [N] were higher in the rhizomatous

grass community compared to the bunchgrass community ($p<0.05$; Table 3; Fig. 3),

but soil available [P] and [K] were similar (Table 3; Fig. 3).

Extreme drought effects on [N], [P] and [K] in green and senesced leaves and their

resorption efficiency in the common species (*L. chinensis* and *S. grandis*) and the

whole plant community were similar within rhizomatous grass or bunchgrass

communities.

The effects of extreme drought on green leaf [N] and resorption efficiency varied

between communities (all $p<0.05$; Table 1). Extreme drought had a noticeably greater

impact on green leaf [N] and resorption efficiency under extreme drought in the

rhizomatous grass community compared to the bunchgrass community (all $p<0.05$;

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277 Table 2; Figs. 1 and 2). Green leaf [N] and resorption efficiency decreased in the

278 rhizomatous grass community (all $p<0.05$) but did not show any variations in the

279 bunchgrass community (Table 2; Figs. 1 and 2).

280   In contrast, we found little evidence that the effect of extreme drought on green leaf

281 [P] and [K] and their resorption efficiencies varied between the two communities

282 (Table 1). The experimental drought negatively affected green leaf [P] and [K] (all

283 $p<0.05$); P and K resorption efficiency showed a decreased trend, although not always

284 (Figs. 1 and 2). Drought effects on [N], [P] and [K] in senesced leaves were also

285 consistent between the two communities (Table 1). These traits showed no drought

286 effect (Figs. 1 and 2). The effects of extreme drought on soil total [N] and available

287 [N], [P] and [K] were similar between the two communities. Drought increased total

288 [N] and available [P] (all $p<0.05$) but did not change available [N] and [K] (Table 3;

289 Fig. 3).

290 **Discussion**

291 Our results showed that plant green leaf [N] and resorption efficiency were more

292 sensitive to extreme drought in the rhizomatous grass community than in the

293 bunchgrass community (Table 2; Figs. 1 and 2), which is consistent with our rooting

294 depth hypothesis. This can be further corroborated by the distinct N-use strategies

295 between *L. chinensis* and *S. grandis*. Previous studies showed that *L. chinensis* as a

296 high N-demanding plant had a more flexible N acquisition strategy than *S. grandis*

297 (Zhang et al. 2004; Xu and Zhou 2006; Wang et al. 2016). In contrast, drought effects

298 on plant green leaf [P] and [K] and their resorption efficiency did not show significant

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299 differences between the two communities (Table 1). These different responses of P

300 and K compared to N may be also related to the differences in soil availability of

301 these nutrients between the rhizomatous and bunch grass community. While soil total

302 and available N concentrations were higher in the rhizomatous grass community than

303 in the bunchgrass community, soil available P and K concentrations were at the same

304 level (Table 3; Fig. 3). The higher impacts of drought on N than on P and K may be

305 also related to how these nutrients are recycled and distributed in the soil profile. In

306 this grassland, N inputs and mineralization mainly occur in the upper soil layers,

307 whereas P and K is available at deeper soil layers due to rock mineral weathering

308 (Vitousek and Farrington 1997; Sardans and Peñuelas 2014; Luo et al. 2016a).

309 Because of these differences between the N, P and K cycles, changes in plant N, P and

310 K in response to extreme drought can vary in their magnitude and direction.

311   We found that green leaf nutrients showed similar effects on nutrient resorption

312 efficiency under extreme drought in the rhizomatous and bunch grass communities.

313 Plant green leaf nutrient concentrations (except for N in the rhizomatous grass

314 community) were reduced at both the individual- and community-levels; however,

315 corresponding nutrient resorption efficiencies were not enhanced to compensate for

316 the reduced plant nutrients. In line with this result, a study in a forest ecosystem

317 showed that plant nutrient resorption was significantly lower during a drought year

318 than during a normal precipitation year, whereas such resorption behavior did not

319 correlate with plant nutrient status (Minoletti and Ralph 1994). Indeed, water

320 availability has a strong effect on nutrient resorption. Efficient transport of nutrients

321   from senesced tissues through the phloem requires adequate water from the xylem,

322   which may have been limited under extreme drought conditions (Ruehr et al. 2009;

323   Khasanova et al. 2013). Previous studies have shown that drought can impair phloem

324   loading and reduce transport velocity in sieve tubes (Plaut and Reinhold 1965; Deng

325   et al. 1990). In these communities with different dominant species, water potential

326   likely declined under extreme drought, so that the nutrient resorption rate in the

327   phloem was reduced independent of plant demand.

328   Our results demonstrated that the relationships between plant and soil nutrients

329   were similar across the rhizomatous and bunch grass communities; that is, green leaf

330   [N], [P] and [K] did not co-vary with soil N and available P and K at both individual-

331   and community-levels under extreme drought conditions. Similarly, Minoletti and

332   Ralph (1994) reported that although there were significant inter-site differences in

333   fertility in a deciduous forest, variation in foliar nutrient concentrations were not

334   consistent with site fertility in a severe drought year. Similarly, plant nutrient

335   concentrations did not co-vary with soil nutrient fertility along an aridity gradient in

336   Inner Mongolia (Luo et al. 2015, 2016b). An explanation for this pattern is the limited

337   nutrient mass flow and diffusivity within soils (Dijkstra et al. 2012; Tullus et al.

338   2012). Diffusion to the root surface is normally the rate-limiting step in nutrient

339   acquisition by plants in dry and infertile soils (Nye and Tinker 1977; Hu and

340   Schmidhalter 2005), and therefore total soil N and available N, P and K may not

341   reflect plant uptake rates of these nutrients. Chapin et al. (1988) suggested that soil

342   water flow can enhance nutrient uptake by plant roots by shortening the distance over

343   which nutrients must otherwise diffuse from the bulk soil to the root surface (Nye and

344   Tinker 1977). Thus, mass flow could be very important in overcoming the strong

345   nutrient limitation of growth and can account for the lower nutrient concentrations in

346   green leaves independent of soil nutrient supply for the two communities under

347   extreme drought conditions. Moreover, senesced leaf [N], [P] and [K] showed a

348   similar trend across the rhizomatous and bunch grass communities with constant

349   responses to two-year of extreme precipitation reduction, being inconsistent with

350   patterns of green leaf nutrients. One possible explanation for the difference in patterns

351   of nutrient concentrations related to extreme drought between green and senesced

352   leaves is that nutrient concentrations in senesced leaves were at a biochemical and/or

353   biophysical threshold of resorption (Killingbeck 1996), so that senesced leaf nutrient

354   concentrations were unrelated to variations in green leaf nutrient concentrations.

355   However, this explanation is not supported by the strong variations in senesced leaf

356   nutrient concentrations observed across the two communities (Figs. 1 and 2),

357   suggesting that nutrient concentrations in senesced leaves did not reach the minimum

358   threshold for resorption for N at the rhizomatous grass community (Killingbeck

359   1996). An alternative explanation for this pattern is that the reduced resorption

360   efficiency of nutrients, and consequently, senesced leaf nutrients did not change

361   although green leaf nutrients significantly decreased during drought.

362   **Conclusions**

363   Our study tested the dominance/mass ratio hypothesis proposed by Whittaker (1965)

364   and Grime (1998) and synthesized by Smith et al. (2009) in relation to extreme

365 drought. We showed that the structural and functional attributes of dominant grass

366 species affect responses of plant nutrient dynamics to extreme drought. Differential

367 responses of leaf nutrient concentrations and resorption with extreme drought were

368 found for N, but consistent responses for P and K between rhizomatous and bunch

369 grass communities with similar environmental context. Therefore, consistent with the

370 dominance/mass ratio hypothesis, differences in dominant species and their growth

371 form (*i.e.*, rhizomatous *vs* bunch grass) played an important role in mediating nutrient

372 cycling under climate change. However, plant N, P and K did not vary in a fully

373 coordinated manner under extreme drought conditions, presenting new evidence

374 related to the impact of climate extreme on fundamental ecological processes. Given

375 predictions of more frequent extreme drought events in semiarid grasslands in the

376 coming decades (Easterling et al. 2000; Smith 2011; IPCC 2013), our results suggest

377 that the responses of plant nutrient uptake and resorption to drought were both

378 community- and nutrient-specific. This divergent impact of extreme drought events

379 on different species and communities may result in a shift of species diversity and

380 community dynamics.

381   On the other hand, we found that green leaf nutrient concentrations were not

382 strongly linked to soil nutrient supply, and nutrient resorption efficiency changed

383 independent of green leaf nutrient concentrations with extreme drought. These results

384 suggest that extreme drought overrides expected relationships among nutrient supply,

385 uptake, and resorption and thus obscured the expected differential responses between

386 the two communities.

400 **Reference**

401 Alam SM (1999) Nutrient uptake by plants under stress conditions, in Pessarakli M

402 (eds) Handbook of Plant and Crop Stress. Marcel Dekker, New York, pp 285-313

403 An Y, Wan S, Zhou X, Subedar AA, Wallace LL, Luo Y (2005) Plant nitrogen

404 concentration, use efficiency, and contents in a tallgrass prairie ecosystem under

405 experimental warming. Glob Change Biol 11: 1733-1744 doi:10.1111/j.1365-

406 2486.2005.01030.x

407 Bai YF, Han XG, Wu JG, Chen ZZ, Li LH (2004) Ecosystem stability and

408 compensatory effects in the Inner Mongolia grassland. Nature 431: 181-184

409 doi:10.1038/nature02850

410 Beier C, Beierkuhnlein C, Wohlgemuth T, Peñuelas J, Emmett B, Körner C, Boeck H,

411 Christensen JH, Leuzinger S, Janssens IA (2012) Precipitation manipulation

412 experiments-challenges and recommendations for the future. Eco Lett 15: 899-

413 911 doi:10.1111/j.1461-0248.2012.01793.x

414 Chapin FS, Fetcher N, Kielland K, Everett KR, Linkins AE (1988) Productivity and

415 nutrient cycling of Alaskan tundra: enhancement by flowing soil water. Ecology

416 69: 693-702 doi:10.2307/1941017

417 Chen S, BaiY, Zhang L, Han X (2005) Comparing physiological responses of two

418 dominant grass species to nitrogen addition in Xilin River Basin of China.

419 Environ Exp Bot 53: 65-75 doi: 10.1016/j.envexpbot.2004.03.002

420 Ciais P, Reichstein M, Viovy N, Granier A (2005) Europe-wide reduction in primary

421 productivity caused by the heat and drought in 2003. Nature 437: 529-533

422 doi:10.1038/nature03972

423   Deng X, Joly RJ, Hahn DT (1990) The influence of plant water deficit on

424   photosynthesis and translocation of ^{14}C-labeled assimilates in cacao seedlings.

425   Physiol Plantarum 78: 623-627 doi:10.1111/j.1399-3054.1990.tb05251.x

426   Dijkstra FA, Pendall E, Morgan JA, Blumenthal DM, Carrillo Y, LeCain DR, Follett

427   RF, Williams DG (2012) Climate change alters stoichiometry of phosphorus and

428   nitrogen in a semiarid grassland. New Phytol 196: 807-815 doi:10.1111/j.1469-

429   8137.2012.04349.x

430   Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000)

431   Climate extremes: observations, modeling, and impacts. Science 289: 2068-2074

432   doi:10.1126/science.289.5487.2068

433   Gessler A, Schaub M, McDowell NG (2017) The role of nutrients in drought-induced

434   tree mortality and recovery. New Phytol 214: 513-520 doi:10.1111/nph.14340

435   Gilgen AK, Buchmann N (2009) Response of temperate grasslands at different

436   altitudes to simulated summer drought differed but scaled with annual

437   precipitation. Biogeosciences 6: 2525-2539 doi:10.5194/bg-6-2525-2009

438   Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and

439   founder effects. Journal of Ecology, 86: 902-910 doi: 10.1046/j.1365-

440   2745.1998.00306.x

441   Grime JP, Brown VK, Thompson K, Masters GJ, Hillier SH, Clarke IP, Askew AP,

442   Corker D, Kielty JP (2000) The response of two contrasting limestone grasslands

443   to simulated climate change. Science 289: 762-765

444   doi:10.1126/science.289.5480.762

445   He M, Dijkstra FA (2014) Drought effect on plant nitrogen and phosphorus: a meta-

446   analysis. New Phytol 204: 924-931 doi:10.1111/nph.12952

447   Hoover DL, Duniway MC, Belnap J (2015) Pulse-drought atop press-drought:

448   unexpected plant responses and implications for dryland ecosystems. Oecologia

449   179: 1211-1221 doi:10.1007/s00442-015-3414-3

450   Hoover DL, Duniway MC, Belnap J (2017) Testing the apparent resistance of three

451   dominant plants to chronic drought on the Colorado Plateau. J Ecol 105: 152-162

452   doi:10.1111/1365-2745.12647

453   Hoover DL, Knapp AK, Smith MD (2014) Resistance and resilience of a grassland

454   ecosystem to climate extremes. Ecology 95: 2646-2656 doi:10.1890/13-2186.1

455   Hu Y, Schmidhalter U (2005) Drought and salinity: A comparison of their effects on

456   mineral nutrition of plants. J Soil Sci Plant Nut 168: 541-549

457   doi:10.1002/jpln.200420516

458   IPCC (2013) Climate change 2013: the physical science basis. In Stocker TF, Qin D,

459   Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley

460   P M (eds) Contribution of Working Group I to the Fifth Assessment Report of the

461   Intergovernmental Panel on Climate Change. Cambridge University Press,

462   Cambridge, UK and New York, New York, USA.

463   Jentsch A., Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change

464   experiments: events, not trends. Front Ecol Environ 5: 365-374

465   doi:10.1890/1540-9295(2007)5[365:ANGOCE]2.0.CO;2

466   Kang L, Han X, Zhang Z, Sun OJ (2007) Grassland ecosystems in China: review of

467   current knowledge and research advancement. Philos T R Soc B 362: 997-1008

468   doi:10.1098/rstb.2007.2029

469 Khasanova A, James JJ, Drenovsky RE (2013) Impacts of drought on plant water

470   relations and nitrogen nutrition in dryland perennial grasses. Plant Soil 372: 541-

471   552 doi:10.1007/s11104-013-1747-4

472 Kichenin E, Wardle DA, Peltzer DA, Morse CW, Freschet GT (2013) Contrasting

473   effects of plant inter- and intraspecific variation on community-level trait

474   measures along an environmental gradient. Funct Ecol 27: 1254-1261

475   doi:10.1111/1365-2435.12116

476 Killingbeck KT (1996) Nutrients in senesced leaves: keys to the search for potential

477   resorption and resorption proficiency. Ecology 77: 1716-1727

478   doi:10.2307/2265777

479 Knapp AK, Avolio ML, Beier C, Carroll CJ, Collins SL, Dukes JS, Fraser LH,

480   Griffin-Nolan RJ, Hoover DL, Jentsch A (2016) Pushing precipitation to the

481   extremes in distributed experiments: recommendations for simulating wet and

482   dry years. Glob Change Biol 1774-1782 doi:10.1111/gcb.13504

483 Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of

484   aboveground primary production. Science 291: 481-484

485   doi:10.1126/science.291.5503.481

486 Kobe RK, Lepczyk CA, Iyer M (2005) Resorption efficiency decreases with

487   increasing green leaf nutrients in a global data set. Ecology 86: 2780-2792

488   doi:10.1890/04-1830

489   Lal R, Delgado J, Gulliford J (2012) Adapting agriculture to drought and extreme

490   events. J Soil Water Conserv 67: 162-166 doi:10.2489/jswc.67.6.162A

491   Lü XT, Freschet GT, Kazakou E, Wang ZW, Zhou LS, Han XG (2015) Contrasting

492   responses in leaf nutrient-use strategies of two dominant grass species along a

493   30-yr temperate steppe grazing exclusion chronosequence. Plant Soil 387: 69-79

494   doi: 10.1007/s11104-014-2282-7

495   Luo W, Dijkstra FA, Bai E, Feng J, Lu XT, Wang C, Wu H, Li MH, Han X, Jiang Y

496   (2016a) A threshold reveals decoupled relationship of sulfur with carbon and

497   nitrogen in soils across arid and semi-arid grasslands in northern China.

498   Biogeochemistry 127: 141-153 doi:10.1007/s10533-015-0174-4

499   Luo W, Elser JJ, Lü XT, Wang Z, Bai E, Yan C, Wang C, Li MH, Zimmermann NE,

500   Han X (2015) Plant nutrients do not covary with soil nutrients under changing

501   climatic conditions. Glob Biogeochem Cycle 29: 1298-1308

502   doi:10.1002/2015GB005089

503   Luo W, Sardans J, Dijkstra FA, Peñuelas J, Lü XT, Wu H, Li MH, Bai E, Wang Z,

504   Han X, Jiang Y (2016b) Thresholds in decoupled soil-plant elements under

505   changing climatic conditions. Plant Soil 409: 159-173 doi: 10.1007/s11104-016-

506   2955-5.

507   Minoletti ML, Ralph EJB (1994) Drought and site fertility effects on foliar nitrogen

508   and phosphorus dynamics and nutrient resorption by the forest understory shrub

509   *Viburnum acerifolium* L. Am Midl Nat 131: 109-119 doi:10.2307/2426613

510   Nye PH, Tinker PB (1977) Solute movement in the soil-root system. University of

511   California Press, Berkeley, USA.

512 Plaut Z, Reinhold L (1965) The effect of water stress on [^{14}C]sucrose transport in

513   bean plants. Aust J Biol Sci 18: 1143-1156 doi:10.1071/BI9651143

514 Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to

515   temperature and latitude. P Natl Acad Sci USA 101: 11001-11006

516   doi:10.1073/pnas.0403588101

517 Ruehr NK, Offermann CA, Gessler A, Winkler JB, Ferrio JP, Buchmann N, Barnard

518   RL (2009) Drought effects on allocation of recent carbon: from beech leaves to

519   soil CO_2 efflux. New Phytol 184: 950-961 doi:10.1111/j.1469-

520   8137.2009.03044.x

521 Sala OE, Yahdjian L, Havstad K, Aguiar MR (2017) Rangeland ecosystem services:

522   Nature's supply and humans' demand. In: Briske DD (eds) Rangeland systems:

523   processes, management and challenges. Springer, New York, pp 467-489.

524 Sanaullah M, Rumpel C, Charrier X, Chabbi A (2012) How does drought stress

525   influence the decomposition of plant litter with contrasting quality in a grassland

526   ecosystem? Plant Soil 352: 277-288 doi:10.1007/s11104-011-0995-4

527 Sardans J, Peñuelas J (2014) Hydraulic redistribution by plants and nutrient

528   stoichiometry: Shifts under global change. Ecohydrology 7: 1-20 doi:

529   10.1002/eco.1459

530 Sardans J, Peñuelas J (2015) Potassium: a neglected nutrient in global change. Global

531   Ecol Biogeogr 24: 261-275 doi:10.1111/geb.12259

532 Schwinning S, Starr BI, Ehleringer JR (2005) Summer and winter drought in a cold

desert ecosystem (Colorado Plateau) part I: effects on soil water and plant water

uptake. J Arid Environ 60: 547-566 doi:10.1016/j.jaridenv.2004.07.003

Silva EC, Nogueira RJMC, Silva MA, Albuquerque MB (2011) Drought stress and

plant nutrition. Plant Stress 5: 32-41

Smith MD (2011) An ecological perspective on extreme climatic events: a synthetic

definition and framework to guide future research. J Ecol 99: 656-663

doi:10.1111/j.1365-2745.2011.01798.x

Smith MD, Knapp AK, Collins SL (2009) A framework for assessing ecosystem

dynamics in response to chronic resource alterations induced by global change.

Ecology 90: 3279-3289 doi:10.1890/08-1815.1

Tullus A, Kupper P, Sellin A, Parts L, Sõber J, Tullus T, Lõhmus K, Sõber A, Tullus H

(2012) Climate change at northern latitudes: rising atmospheric humidity

decreases transpiration, N-uptake and growth rate of hybrid aspen. PLoS One 7:

e42648 doi:10.1371/journal.pone.0042648

Van Heerwaarden L, Toet S, Aerts R (2003) Nitrogen and phosphorus resorption

efficiency and proficiency in six sub-arctic bog species after 4 years of nitrogen

fertilization. J Ecol 91: 1060-1070 doi:10.1046/j.1365-2745.2003.00828.x

Vergutz L, Manzoni S, Porporato A, Novais RF, Jackson RB (2012) Global resorption

efficiencies and concentrations of carbon and nutrients in leaves of terrestrial

plants. Ecol Monogr 82: 205-220 doi:10.1890/11-0416.1

Vitousek PM, Farrington H (1997) Nutrient limitation and soil development:

experimental test of a biogeochemical theory. Biogeochemistry 37: 63-75

555 doi:10.1023/A:1005757218475

556 Wang R, Tian Y, Ouyang S, Xu X, Xu F, Zhang Y (2016) Nitrogen acquisition

557 strategies used by *Leymus chinensis* and *Stipa grandis* in temperate steppes. Biol

558 Fert Soils 52: 951-961 doi:10.1007/s00374-016-1128-2

559 White TA, Campbell BD, Kemp PD, Hunt CL (2000) Sensitivity of three grassland

560 communities to simulated extreme temperature and rainfall events. Glob Change

561 Biol 6: 671-684 doi:10.1046/j.1365-2486.2000.00344.x

562 Whittaker RH (1965) Dominance and diversity in land plant communities: numerical

563 relations of species express the importance of competition in community

564 function and evolution. Science 147: 250-260 doi:10.1126/science.147.3655.250

565 Wilcox KR, Shi Z, Gherardi LA, Lemoine NP, Koerner SE, Hoover DL, Bork E,

566 Byrne KM, Cahill J, Collins SL (2017) Asymmetric responses of primary

567 productivity to precipitation extremes: A synthesis of grassland precipitation

568 manipulation experiments. Glob Change Biol 23: 4376-4385

569 doi:10.1111/gcb.13706

570 Wright IJ, Westoby M (2002) Leaves at low versus high rainfall: coordination of

571 structure, lifespan and physiology. New Phytol 155: 403-416 doi:10.1046/j.1469-

572 8137.2002.00479.x

573 Xiao X, Wang Y, Jiang S, Ojima DS, Bonham CD (1995) Interannual variation in the

574 climate and above-ground biomass of *Leymus chinense* steppe and *Stipa grandis*

575 steppe in the Xilin river basin, Inner Mongolia, China. J Arid Environ 31: 283-

576 299 doi:10.1016/S0140-1963(05)80033-3

577   Xu ZZ, Zhou GS (2006) Nitrogen metabolism and photosynthesis in *Leymus*

578   *chinensis* in response to long-term soil drought. J Plant Growth Regul 25: 252-

579   266 doi:10.1007/s00344-006-0043-4

580   Yahdjian L, Sala OE (2002) A rainout shelter design for intercepting different

581   amounts of rainfall. Oecologia 133: 95-101 doi:10.1007/s00442-002-1024-3

582   Yuan Z, Chen HY (2009) Global trends in senesced-leaf nitrogen and phosphorus.

583   Global Ecol Biogeogr 18: 532-542 doi:10.1111/j.1466-8238.2009.00474.x

584   Zhang LX, Bai YF, Han XG (2004) Differential responses of N:P stoichiometry of

585   *Leymus chinensis* and *Carex korshinskyi* to N additions in a steppe ecosystem in

586   Nei Mongol. Acta Botanica Sinica 46: 259-270.

	Green leaf			Senesced leaf			Resorption		
	[N]	[P]	[K]	[N]	[P]	[K]	[N]	[P]	[K]
L. chinensis									
Drought	0.13	**<0.001**	**<0.001**	0.10	0.12	0.95	**0.02**	**<0.01**	**<0.001**
Community type	0.17	0.57	0.33	**<0.001**	0.11	0.54	**<0.001**	0.07	0.54
Drought×Community type	**<0.001**	0.06	0.17	0.79	0.50	0.78	**<0.01**	0.44	0.55
S. grandis									
Drought	0.28	**<0.01**	**0.05**	0.06	0.75	0.33	**0.02**	0.22	**0.04**
Community type	0.13	0.84	1.00	**<0.01**	0.90	0.28	**<0.01**	0.92	0.66
Drought×Community type	**<0.01**	0.88	0.42	0.47	0.57	0.62	**0.02**	0.75	0.43
Whole community									
Drought	0.06	**<0.01**	**<0.01**	0.31	0.72	0.80	**0.03**	0.11	**<0.01**
Community type	0.33	0.09	0.18	**<0.001**	0.07	0.33	**<0.001**	0.15	0.80
Drought×Community type	**<0.001**	0.62	0.26	0.69	0.30	0.92	**0.01**	0.18	0.29

592

593

594 **Table 2.** Results of mixed model analysis of variance for green leaf [N] and their

595 resorption efficiency for two grasses (*L. chinensis* and *S. grandis*) and plant

596 community at the rhizomatous and bunch grass dominated community. Drought

597 treatment was used as a fixed factor and block as a random factor. The value of p is

598 shown. Bold text indicates significance at $p<0.05$.

	[N]	Resorption
Rhizomatous community		
L. chinensis	**0.003**	0.185
S. grandis	**0.004**	**0.011**
Community	**0.001**	**0.030**
Bunch community		
L. chinensis	0.114	0.076
S. grandis	0.085	0.855
Community	0.074	0.506

599

600 **Table 3.** Results of mixed model analysis of variance for soil total [N] and available

601 [N], [P] and [K]. Drought treatment and community type were used as fixed factors

602 and block as a random factor. The value of p is shown. Bold text indicates

603 significance at $p<0.05$.

	Total [N]	Available [N]	Available [P]	Available [K]
Drought	**0.005**	0.285	**0.002**	0.741
Community type	**0.003**	**0.002**	0.702	0.142
Drought×Community type	0.146	0.502	0.287	0.947

604
605

Figures legends

607 **Fig. 1** Effects of extreme drought (C, control; D, drought) on leaf [N], [P] and [K] in

608 dominant grass species (*L. chinensis* and *S. grandis*) from two grasslands. Each point

609 represents the mean nutrient concentration with error bars indicating standard errors

610 calculated from replicate plots for each treatment. Different letters indicate significant

611 differences between the rhizomatous and bunch grass dominated community at

612 *p*< 0.05. Statistical significance of drought effect is depicted as *** *p*<0.001, **

613 *p*<0.01 and * *p*<0.05. When the responses were different between the two

614 communities, an asterisk was separately placed above each community; when the

615 responses were consistent between two communities, an asterisk was only placed in

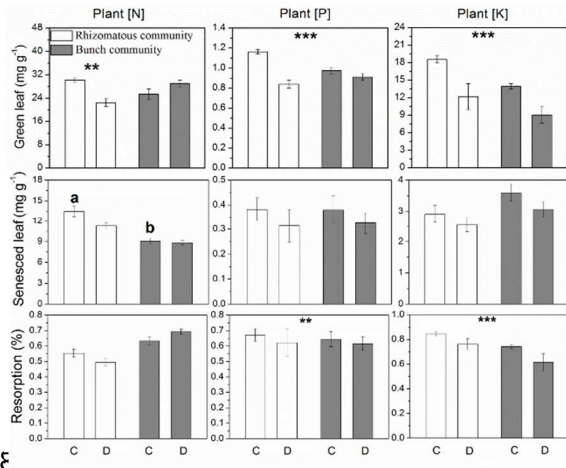616 middle of the two communities. See Tables 1 and 2 for the overall ANOVA results.

617 **Fig. 2** Effects of extreme drought (C, control; D, drought) and community type on

618 plant [N], [P] and [K] at community level. Each point represents the mean nutrient

619 concentration with error bars indicating standard errors calculated from replicate plots

620 for each treatment. Different letters indicate significant differences between the

621 rhizomatous and bunch grass dominated community at *p*< 0.05. Statistical

622 significance of drought effect is depicted as *** *p*<0.001, ** *p*<0.01 and * *p*<0.05.

623 When the responses were different between the two communities, the * was

624 separately put above each community type; when the responses were consistent

625 between two communities, the * was only put in middle of the two community types.

626 See Tables 1 and 2 for the overall ANOVA results.

627 **Fig. 3** Effects of extreme drought (C, control; D, drought) and community type on soil
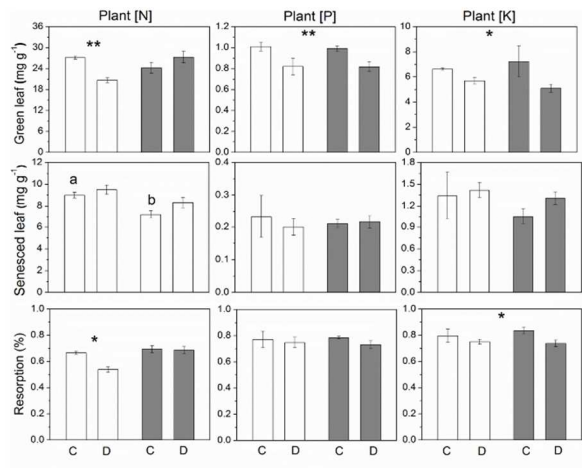
628 total [N] and available [N], [P] and [K]. Each point represents the mean nutrient

629 concentration with error bars indicating standard errors calculated from replicate plots

630 for each treatment. Different letters indicate significant differences between the

631 rhizomatous and bunch grass dominated communities at $p < 0.05$. When the responses

632 were different between two communities, an asterisk was separately placed above

633 each community type; when the responses were consistent between the two

634 communities, an asterisk was only placed in middle of the two community types.

635 Statistical significance of drought effect is depicted as *** $p<0.001$, ** $p<0.01$ and *

636 $p<0.05$. See Table 3 for the overall ANOVA results.

637

(a) *Leymus chinensis*

(b) *Stipa grandis*
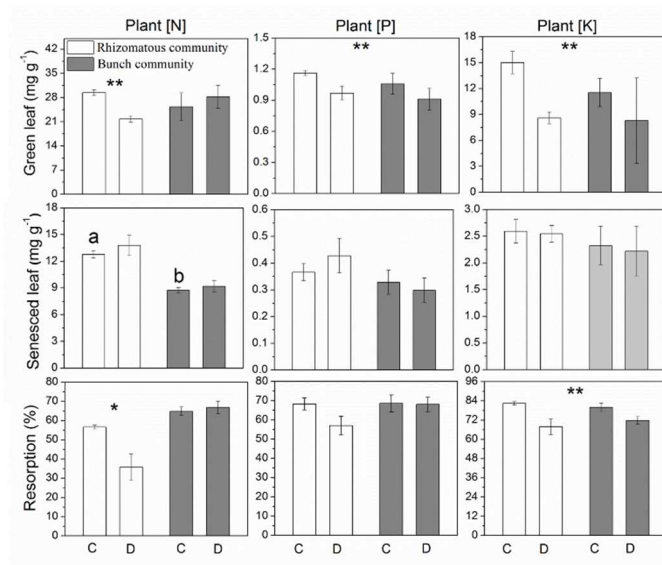
639   **Figure 1**

641
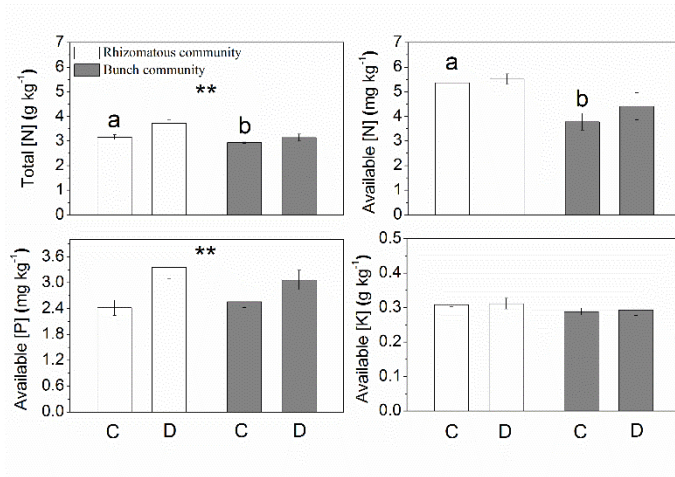
642 **Figure 2**

643

644

Figure 3