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1 **Effects of extreme drought on plant nutrient uptake and resorption in**
2 **rhizomatous vs bunch grass dominated grasslands**

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25 **Abstract**

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

47 **Introduction**

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

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

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 rhizomatous 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 $\times 6$ 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 \times 1 m) was established in each plot and four sub-
194 quadrats (50 \times 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 H₂SO₄ and H₂O₂ 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):

$$236 \quad \text{Community nutrient concentrations} = \sum_{i=1}^S (P_i \times N_i), \quad \text{eqn 1}$$

237 where P_i is the relative biomass of species i at the peak of growing season in the
238 plot with S species, and N_i 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):

$$242 \quad \text{Nutrient resorption efficiency} = \frac{N_g - N_s}{N_g} \times 100\%, \quad \text{eqn 2}$$

243 where N_g and N_s are nutrient concentrations in plant green and senesced leaves,
244 respectively.

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).

255 **Results**

256 During the 2015 and 2016 growing seasons, the drought treatment resulted in an
257 extreme drought (close to the 10th percentile of the historical record) (Fig. S2). In
258 contrast, growing season precipitation was approximately normal in both years
259 (slightly lower than the 50th percentile of the historic record) for the control treatments
260 (Fig. S2). In this experiment, rainout shelters clearly reduced the soil moisture content
261 (Fig. S3), but did not significantly affect the soil temperature for each site (Fig. S4).

262 Senesced leaf [N] of the two common species (*L. chinensis* and *S. grandis*) and the
263 whole plant community was higher in the rhizomatous grass community compared to
264 the bunchgrass community ($p<0.05$; Table 1; Figs. 1 and 2), but senesced leaf [P] and
265 [K] as well as green [N], [P] and [K] and their resorption efficiencies were similar
266 (Table 1; Figs. 1 and 2). Total and available soil [N] were higher in the rhizomatous
267 grass community compared to the bunchgrass community ($p<0.05$; Table 3; Fig. 3),
268 but soil available [P] and [K] were similar (Table 3; Fig. 3).

269 Extreme drought effects on [N], [P] and [K] in green and senesced leaves and their
270 resorption efficiency in the common species (*L. chinensis* and *S. grandis*) and the
271 whole plant community were similar within rhizomatous grass or bunchgrass
272 communities.

273 The effects of extreme drought on green leaf [N] and resorption efficiency varied
274 between communities (all $p<0.05$; Table 1). Extreme drought had a noticeably greater
275 impact on green leaf [N] and resorption efficiency under extreme drought in the
276 rhizomatous grass community compared to the bunchgrass community (all $p<0.05$;

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

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.

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587 **Table 1.** Results of mixed model analysis of variance for plant [N], [P] and [K] in
 588 green and senesced leaves and their resorption efficiency for two grasses (*L. chinensis*
 589 and *S. grandis*) and plant community. Drought treatment and community type were
 590 used as fixed factors and block as a random factor. The value of *p* is shown. Bold text
 591 indicates significance at *p*<0.05.

	Green leaf			Senesced leaf			Resorption		
	[N]	[P]	[K]	[N]	[P]	[K]	[N]	[P]	[K]
<i>L. chinensis</i>									
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
<i>S. grandis</i>									
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
<i>Rhizomatous</i> community		
<i>L. chinensis</i>	0.003	0.185
<i>S. grandis</i>	0.004	0.011
Community	0.001	0.030
<i>Bunch</i> community		
<i>L. chinensis</i>	0.114	0.076
<i>S. grandis</i>	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

606 **Figures legends**

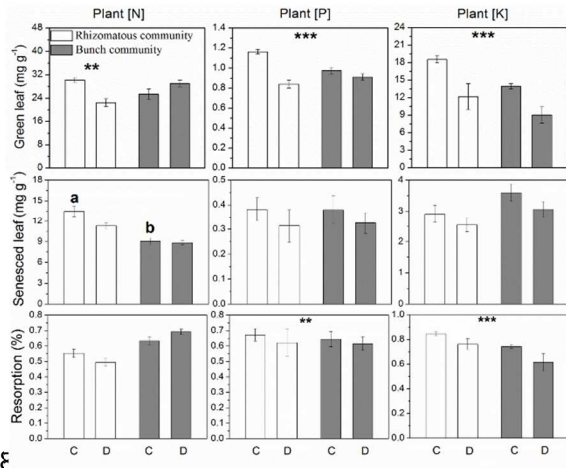
607 **Fig. 1** Effects of extreme drought (C, control; D, drought) on leaf [N], [P] and [K] in
608 dominant grass species (*L. chinensis* and *S. grandis*) from two grasslands. Each point
609 represents the mean nutrient concentration with error bars indicating standard errors
610 calculated from replicate 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.

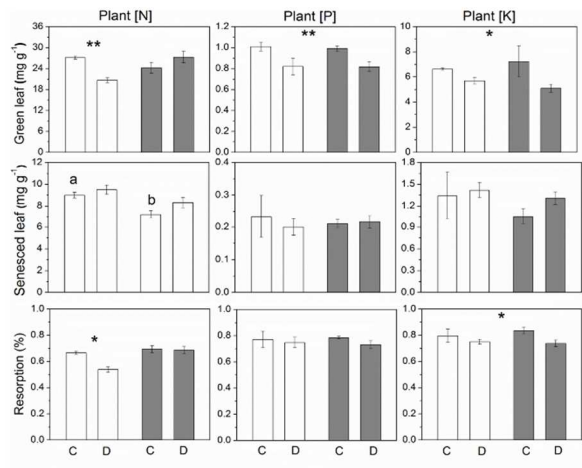
627 **Fig. 3** Effects of extreme drought (C, control; D, drought) and community type on soil

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*



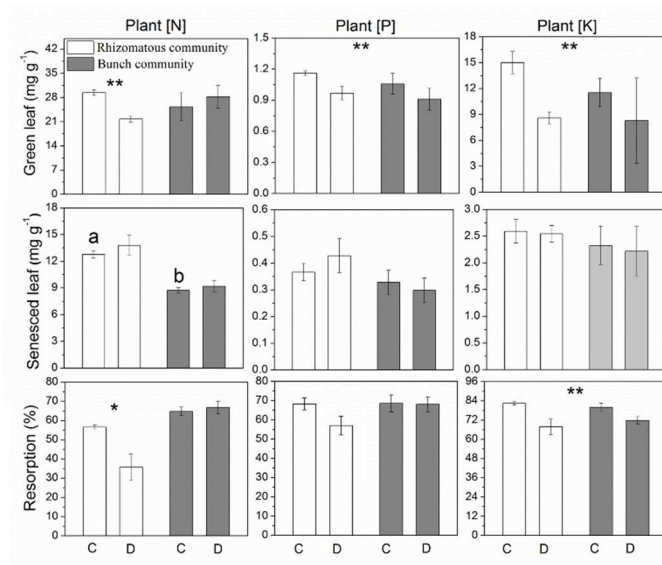
(b) *Stipa grandis*



638

639 **Figure 1**

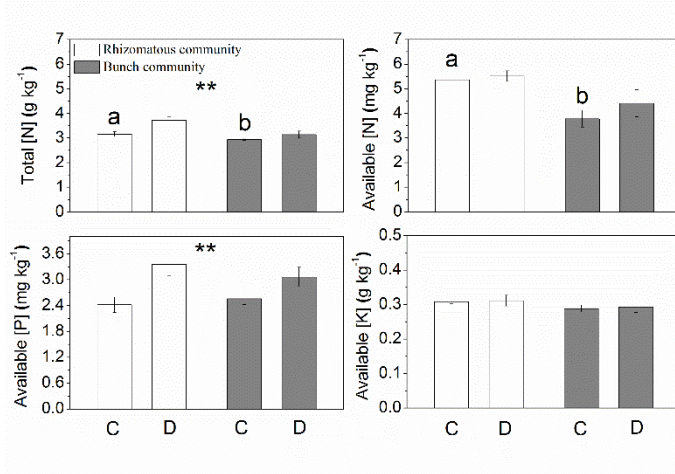
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641

642 **Figure 2**

643



644

645 **Figure 3**