Luo, Wentao; Xu, Chong; Ma, Wang; [et al.]. «Effects of extreme drought on plant nutrient uptake and resorption in rhizomatous vs bunch grass dominated grasslands». Oecologia, Vol. 188, issue 2 (Oct. 2018), p. 633-643. DOI 10.1007/s00442-018-4232-1

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

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## Abstract

Both the dominance and the mass ratio hypotheses predict that plant internal nutrient cycling in ecosystems is determined by the dominant species within plant communities. We tested this hypothesis under conditions of extreme drought by assessing plant nutrient (N, P and K) uptake and resorption in response to experimentally imposed precipitation reductions in two semiarid grasslands of northern China. These two communities shared similar environmental conditions but had different dominant species – one was dominated by a rhizomatous grass (*Leymus chinensis*), the other by a bunchgrass (*Stipa grandis*). Results showed that responses of N to drought differed between the two communities with drought decreasing green leaf N concentration and resorption in the community dominated by the rhizomatous grass, but not in the bunchgrass dominated community. In contrast, negative effects of drought on green leaf P and K concentrations and their resorption efficiencies were consistent across the two communities. Additionally, in each community, effects of extreme drought on soil N, P and K supply did not change synchronously with that on green leaf N, P and K concentrations, and senesced leaf N, P and K concentrations showed no response to extreme drought. Consistent with the dominance/mass ratio hypothesis, our findings suggest that differences in dominant species and their growth form (*i.e.*, rhizomatous *vs* bunch grass) play an important nutrient-specific role in mediating plant internal nutrient cycling across communities within a single region.

**Keywords:** Dominance/mass ratio hypothesis, Dominant species, Extreme drought, 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 surfaces (Alam 1999), while reduced plant nutrient uptake capacity may also be attributed to the inhibition of the nutrient translocation from below- to above-ground tissues (Alam 1999; Hu and Schmidhalter 2005; Sanaullah et al. 2012). Negative effects of drought stress on plant nutrient uptake affect plants' needs to resorb nutrients from senescing tissues, because nutrient resorption is an important nutrient conservation strategy that can reduce dependence on nutrient uptake (Kobe et al. 2005). Senesced leaf nutrient concentrations are expected to be reduced with drought due to decreased nutrient uptake and increased nutrient resorption efficiency (Killingbeck 1996), resulting in a reduction in litter quality and subsequent mineralization rate (Yuan and Chen 2009; Sanaullah et al. 2012; Vergutz et al. 2012).

Experimentally reducing precipitation inputs into an ecosystem is a direct way to examine the ecological effects of drought on ecosystem structure and function (Gilgen and Buchmann 2009; Beier et al. 2012; He and Dijkstra 2014; Sardans and Peñuelas 2015). Over the last few decades, there has been an increasing number of manipulative experiments to investigate how plant internal nutrient cycling might respond to increased aridity (He and Dijkstra 2014; Gessler et al. 2017). However, most research to date has focused on the effects of moderate drought (20-40% precipitation reduction) on plant and soil N and P content, and on N and P availability in soils (He and Dijkstra 2014; Sardans and Peñuelas 2015). Fewer studies have assessed the effects of extreme drought (>60% precipitation reduction) on plant nutrient composition and dynamics (Smith 2011; Hoover et al. 2014, 2015; Knapp et al. 2016), which could significantly influence ecosystem functions and services.

Moreover, a majority of these studies are usually done at a single site and assume that the plant internal nutritional responses are consistent among ecosystems or even among local communities within ecosystems despite evidence to the contrary (Grime et al. 2000; Knapp and Smith 2001; Wilcox et al. 2017). Thus, it is more likely that drought will not uniformly affect the plant internal nutrient cycling in ecosystems. Species traits or levels of diversity can affect their sensitivity and the sensitivity of plant internal nutrient cycling to any given precipitation change as will the attributes of ecosystems (White et al. 2000; Knapp and Smith 2001; Wilcox et al. 2017). The identity and traits of dominant species will undoubtedly be important in influencing the sensitivity of plant internal nutrient cycling to change, given that dominant species control the majority of the resources and have disproportionate impacts on the whole community (dominance/mass ratio hypothesis, Whittaker 1965; Grime 1998; Smith et al. 2009). Indeed, in a chronic drought field experiment, plant community composition was shown influence the effects of drought, and this effect was species-specific and due to differential responses of dominant plant species (Hoover et al. 2014). Therefore, it is important to understand how plant internal nutrient cycles in ecosystems with different dominant species may respond to future extreme precipitation reduction.

Predicting the effects of extreme drought in grassland ecosystems is especially important, as they are one of the most vulnerable ecosystems to precipitation changes, and cover ~40% of the terrestrial land surface, and provide valuable ecosystem services (Sala et al. 2017). The semiarid grassland region of northern China is an ideal ecosystem for studying the effects of extreme drought on plant internal nutrient cycling, as water availability is a primary limiting factor for plant community productivity and composition in this ecosystem and the predicted effects of increased aridity will likely have dramatic effects on the processes of plant nutrient cycling (Bai et al. 2004; Kang et al. 2007; Luo et al. 2015, 2016b). We examined two important grass communities located within a similar environmental context but that are widely distributed in this semiarid ecosystem (Kang et al. 2007). The dominant grasses in these communities differed in a key growth trait, one was dominated by a perennial rhizomatous grass (*Leymus chinensis*, "rhizomatous grass community"), the other by a perennial bunchgrass (*Stipa grandis*, "bunchgrass community") but both species co-occur in each community (Bai et al. 2004).

These two communities provide a test-bed for assessing how the effects of extreme drought on plant internal nutrient cycling are determined by differences in dominant species and their growth form (Whittaker 1965; Grime 1998; Smith et al. 2009). We simultaneously reduced 66% of the growing season precipitation over two-consecutive years (extreme drought) across the two communities. According to the dominance/mass ratio hypothesis (Whittaker 1965; Grime 1998; Smith et al. 2009), we expected that the community-level responses would differ between two communities due to their difference in the traits of the dominant grass species (rhizomatous *vs* bunch grass, Chen et al. 2005; Lü et al. 2015). Moreover, it has been widely known that drought will have the largest impact on near-surface soil moisture than deeper soil moisture (Schwinning et al. 2005; Hoover et al. 2017); therefore, we further hypothesized that the responses of plant nutrient uptake and resorption to extreme drought will be more sensitive for rhizomatous than bunch grass communities, because of the shallower root structures in the rhizomatous grass *vs* the bunchgrass dominated community (Xiao et al. 1995; Wang et al. 2016).

## Material and methods

### Study sites

In 2014 (pretreatment year), two sites (*i.e.*, rhizomatous and bunch grass communities) with relatively similar climatic conditions but different dominant species were established in a semiarid natural grassland of northern China. The two selected communities were randomly established by the invasion success of the dominant species *L. chinensis* and *S. grandis* and are located at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS) (116°33′E, 43°32′N). These sites are part of the EDGE (Extreme Drought in Grasslands Experiment) experimental platform (http://edge.biology.colostate.edu/). Based on long-term (1982-2014) meteorological records from a weather station located <30 km from the sites, mean annual temperature is 1.9°C and mean annual precipitation is 336 mm with 74% (249 mm) falling during the growing season from May to August. The soil is a chestnut in the China soil taxonomy classification system, equivalent to Calcicorthic Aridisol in the US soil taxonomy classification. The rhizomatous grass community has been fenced since 1999, which was dominated by a perennial rhizomatous grass, *L. chinensis*, whereas the bunchgrass community has been fenced since 1979, which was dominated by a perennial bunchgrass, *S. grandis* (Bai et al. 2004). *S. grandis* is a subordinate species in the rhizomatrous grass community, while *L. chinensis* is a subordinate species in the bunchgrass community. *L. chinensis* generally has a relatively shallower root system and lower root:shoot biomass ratio than *S. grandis* (Xiao et al. 1995; Wang et al. 2016).

These two community types represent the most widely distributed grassland communities in the Eurasian steppe region, which is the largest contiguous grassland area in the world (Bai et al. 2004; Kang et al. 2007). Both communities were considered to be in excellent condition during the time of enclosure, representative of natural and climax steppe communities. The rhizomatous and bunch grass communities respectively have 86 and 61 plant species (Bai et al. 2004). The aboveground net primary productivity reached the annual peak at the mid of August in response to high soil water availability and temperature. The aboveground net primary productivity is about 193 g $m^{-2}$ for the rhizomatous grass community and 217 g $m^{-2}$ for the bunchgrass community (Bai et al. 2004; Kang et al. 2007).

### Experimental treatments

At each site, an identical manipulative experiment with two treatments (untreated control and extreme drought) was established in a relatively homogeneous area (similar soils, vegetation, etc.). We imposed extreme drought by creating rainout shelters designed to intercept 66% of ambient incoming precipitation (Fig. S1). Drought shelter roofs were installed on plots from May-August growing season in both 2015 and 2016. The experimental design was a randomized complete block design with six replications of each treatment at each site. Experimental plots were 6

×6 m and located at least 2 m from the neighboring plots. Plots were hydrologically isolated from the surrounding soil matrix by aluminum flashing (buried to a depth of 1-m). Each plot included a 1-m external buffer to allow access to the plot and minimized the edge effect associated with the infrastructure. Untreated control plots without rainout shelters were set up for comparison. Rainout shelters were sloped slightly towards subtle topographic gradients to allow for quick drainage of ambient precipitation. Rainout shelters were 2-m above the ground surface and were not closed down to the ground, allowing for near surface air exchange and minimizing unwanted greenhouse effects. The effects of rainout shelters on the light environment were small, permitting nearly 90% penetration of photosynthetically active radiation (Yahdjian and Sala 2002). Daily mean soil moisture and temperature were continuously monitored at a depth of 0-10 cm with sensors placed near the center of each plot at each site.

### Field sampling and measurements

In August 2016, a main quadrat (1×1 m) was established in each plot and four sub-quadrats (50×50 cm) were set up within each main quadrat. Aboveground biomass of each species was harvested by clipping at ground level of two sub-quadrats arranged diagonally. All living plants were oven-dried and weighed. Species abundance was calculated as the relative biomass of each species to the total aboveground biomass in each plot. In the other two diagonal sub-quadrats, plant leaves were collected for the most abundant species. The cumulative relative abundance of the selected species reached at least 90% of the plot total abundance. Among these species, the dominant species (*L. chinensis* and *S. grandis*) were present in each sub-quadrat (*i.e.*, 100% frequency). Plant leaves for these species were collected again when they were fully senesced in early-autumn. Green and senesced leaf samples were dried at 105°C for 30 min in a drying oven to minimize respiration and decomposition and were later completely oven dried at 80°C to constant weight in the laboratory.

Five soil cores (2.5-cm in diameter and 10-cm in depth, respectively) were collected after removing the litter layer in each main quadrat at both sites. Samples were stored at 4°C immediately after collection for initial gravimetric moisture content and soil available N ($NH_4^+$-N plus $NO_3^-$-N) (fresh soils). A small subsample was stored in a cloth bag at room temperature (air-dried soils).

Fresh soils were passed through a 2-mm sieve, and roots and rocks were removed. Gravimetric moisture content was measured after drying a known amount of soil at 105°C for 48h. Fresh soil samples were extracted with 50 mL of 2 M KCl, and the filtered soil extract was used to determine soil available [N] with a continuous flow spectrophotometer (FIAstar 5000; Foss Tecator, Denmark). Air-dried soil samples were sieved through a 2-mm mesh size to remove roots and rocks. Olsen [P] was measured by extracting air-dried soils with 0.5 M $NaHCO_3$ (pH=8.5), which was analyzed using the molybdenum blue-ascorbic acid method. The exchangeable [K] was measured by extracting air-dried soils with 1 M $NH_4OAc$ (pH=7.0) and analyzing extracts for [K] by atomic absorption spectrometry (AA6800, Shimadzu, Japan). All plant leaf samples and air-dried soils were ground to pass through a 1-mm sieve. Total [N] in plant and soil samples were measured using an elemental analyzer (2400II

CHN elemental analyzer; Perkin-Elmer, USA) with a combustion temperature of 950°C and a reduction temperature of 640°C. Plant leaf samples were acid digested with a mixture of $H_2SO_4$ and $H_2O_2$ in a microwave oven. Microwave digestion was performed until the sample was dissolved into the solution. Plant [P] was analyzed using the molybdenum blue-ascorbic acid method and [K] by atomic absorption spectrometry (AA6800, Shimadzu, Japan).

**Calculation and statistical analysis**

In this study, statistical analyses were conducted for the two species (*L. chinensis* and *S. grandis*) and for the whole plant community.

For each nutrient in each plot, community nutrient concentrations in green and senesced leaves were calculated as the overall mean of nutrient concentrations across species weighted by the relative biomass of each individual species (Kichenin et al. 2013):

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

where *Pi* is the relative biomass of species *i* at the peak of growing season in the plot with *S* species, and *Ni* is the nutrient concentration in green and senesced leaves of species *i.*

Nutrient resorption efficiency was calculated as the proportion of nutrients that were taken back by the plant during senescence (Van Heerwaarden et al. 2003):

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

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

Plant nutrient concentrations in green and senesced leaves and nutrient resorption efficiency were analyzed for the two species (*L. chinensis* and *S. grandis*) and whole plant community using a mixed-model analysis of variance with drought treatment and community as fixed factors and block as random factor. When interactive effects of drought treatment and community were significant ($p<0.05$), the mixed model analysis of variance was separately applied for each community with drought treatment as fixed factor and block as random factor. Similarly, soil nutrients were also analyzed using the mixed models. For all analyses, any non-normal data were transformed prior to analyses. All statistical analyses were performed using the *lme* 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 $p<0.05$;

Table 2; Figs. 1 and 2). Green leaf [N] and resorption efficiency decreased in the rhizomatous grass community (all $p<0.05$) but did not show any variations in the bunchgrass community (Table 2; Figs. 1 and 2).

In contrast, we found little evidence that the effect of extreme drought on green leaf [P] and [K] and their resorption efficiencies varied between the two communities (Table 1). The experimental drought negatively affected green leaf [P] and [K] (all $p<0.05$); P and K resorption efficiency showed a decreased trend, although not always (Figs. 1 and 2). Drought effects on [N], [P] and [K] in senesced leaves were also consistent between the two communities (Table 1). These traits showed no drought effect (Figs. 1 and 2). The effects of extreme drought on soil total [N] and available [N], [P] and [K] were similar between the two communities. Drought increased total [N] and available [P] (all $p<0.05$) but did not change available [N] and [K] (Table 3; Fig. 3).

## Discussion

Our results showed that plant green leaf [N] and resorption efficiency were more sensitive to extreme drought in the rhizomatous grass community than in the bunchgrass community (Table 2; Figs. 1 and 2), which is consistent with our rooting depth hypothesis. This can be further corroborated by the distinct N-use strategies between *L. chinensis* and *S. grandis*. Previous studies showed that *L. chinensis* as a high N-demanding plant had a more flexible N acquisition strategy than *S. grandis* (Zhang et al. 2004; Xu and Zhou 2006; Wang et al. 2016). In contrast, drought effects on plant green leaf [P] and [K] and their resorption efficiency did not show significant differences between the two communities (Table 1). These different responses of P and K compared to N may be also related to the differences in soil availability of these nutrients between the rhizomatous and bunch grass community. While soil total and available N concentrations were higher in the rhizomatous grass community than in the bunchgrass community, soil available P and K concentrations were at the same level (Table 3; Fig. 3). The higher impacts of drought on N than on P and K may be also related to how these nutrients are recycled and distributed in the soil profile. In this grassland, N inputs and mineralization mainly occur in the upper soil layers, whereas P and K is available at deeper soil layers due to rock mineral weathering (Vitousek and Farrington 1997; Sardans and Peñuelas 2014; Luo et al. 2016a). Because of these differences between the N, P and K cycles, changes in plant N, P and K in response to extreme drought can vary in their magnitude and direction.

We found that green leaf nutrients showed similar effects on nutrient resorption efficiency under extreme drought in the rhizomatous and bunch grass communities. Plant green leaf nutrient concentrations (except for N in the rhizomatous grass community) were reduced at both the individual- and community-levels; however, corresponding nutrient resorption efficiencies were not enhanced to compensate for the reduced plant nutrients. In line with this result, a study in a forest ecosystem showed that plant nutrient resorption was significantly lower during a drought year than during a normal precipitation year, whereas such resorption behavior did not correlate with plant nutrient status (Minoletti and Ralph 1994). Indeed, water availability has a strong effect on nutrient resorption. Efficient transport of nutrients from senesced tissues through the phloem requires adequate water from the xylem, which may have been limited under extreme drought conditions (Ruehr et al. 2009; Khasanova et al. 2013). Previous studies have shown that drought can impair phloem loading and reduce transport velocity in sieve tubes (Plaut and Reinhold 1965; Deng et al. 1990). In these communities with different dominant species, water potential likely declined under extreme drought, so that the nutrient resorption rate in the phloem was reduced independent of plant demand.

Our results demonstrated that the relationships between plant and soil nutrients were similar across the rhizomatous and bunch grass communities; that is, green leaf [N], [P] and [K] did not co-vary with soil N and available P and K at both individual- and community-levels under extreme drought conditions. Similarly, Minoletti and Ralph (1994) reported that although there were significant inter-site differences in fertility in a deciduous forest, variation in foliar nutrient concentrations were not consistent with site fertility in a severe drought year. Similarly, plant nutrient concentrations did not co-vary with soil nutrient fertility along an aridity gradient in Inner Mongolia (Luo et al. 2015, 2016b). An explanation for this pattern is the limited nutrient mass flow and diffusivity within soils (Dijkstra et al. 2012; Tullus et al. 2012). Diffusion to the root surface is normally the rate-limiting step in nutrient acquisition by plants in dry and infertile soils (Nye and Tinker 1977; Hu and Schmidhalter 2005), and therefore total soil N and available N, P and K may not reflect plant uptake rates of these nutrients. Chapin et al. (1988) suggested that soil water flow can enhance nutrient uptake by plant roots by shortening the distance over which nutrients must otherwise diffuse from the bulk soil to the root surface (Nye and Tinker 1977). Thus, mass flow could be very important in overcoming the strong nutrient limitation of growth and can account for the lower nutrient concentrations in green leaves independent of soil nutrient supply for the two communities under extreme drought conditions. Moreover, senesced leaf [N], [P] and [K] showed a similar trend across the rhizomatous and bunch grass communities with constant responses to two-year of extreme precipitation reduction, being inconsistent with patterns of green leaf nutrients. One possible explanation for the difference in patterns of nutrient concentrations related to extreme drought between green and senesced leaves is that nutrient concentrations in senesced leaves were at a biochemical and/or biophysical threshold of resorption (Killingbeck 1996), so that senesced leaf nutrient concentrations were unrelated to variations in green leaf nutrient concentrations. However, this explanation is not supported by the strong variations in senesced leaf nutrient concentrations observed across the two communities (Figs. 1 and 2), suggesting that nutrient concentrations in senesced leaves did not reach the minimum threshold for resorption for N at the rhizomatous grass community (Killingbeck 1996). An alternative explanation for this pattern is that the reduced resorption efficiency of nutrients, and consequently, senesced leaf nutrients did not change although green leaf nutrients significantly decreased during drought.

## Conclusions

Our study tested the dominance/mass ratio hypothesis proposed by Whittaker (1965) and Grime (1998) and synthesized by Smith et al. (2009) in relation to extreme drought. We showed that the structural and functional attributes of dominant grass species affect responses of plant nutrient dynamics to extreme drought. Differential responses of leaf nutrient concentrations and resorption with extreme drought were found for N, but consistent responses for P and K between rhizomatous and bunch grass communities with similar environmental context. Therefore, consistent with the dominance/mass ratio hypothesis, differences in dominant species and their growth form (*i.e.*, rhizomatous *vs* bunch grass) played an important role in mediating nutrient cycling under climate change. However, plant N, P and K did not vary in a fully coordinated manner under extreme drought conditions, presenting new evidence related to the impact of climate extreme on fundamental ecological processes. Given predictions of more frequent extreme drought events in semiarid grasslands in the coming decades (Easterling et al. 2000; Smith 2011; IPCC 2013), our results suggest that the responses of plant nutrient uptake and resorption to drought were both community- and nutrient-specific. This divergent impact of extreme drought events on different species and communities may result in a shift of species diversity and community dynamics.

On the other hand, we found that green leaf nutrient concentrations were not strongly linked to soil nutrient supply, and nutrient resorption efficiency changed independent of green leaf nutrient concentrations with extreme drought. These results suggest that extreme drought overrides expected relationships among nutrient supply, uptake, and resorption and thus obscured the expected differential responses between the two communities.

## Acknowledgments

We thank all the people who have worked at Extreme Drought in Grasslands Experiment (EDGE) platform for assistance in carrying out the field experiment. In addition, a large thanks goes out to Inner Mongolia Grassland Ecosystem Research Station for providing long-term meteorological records. This study was supported by finding from the National Natural Science Foundation of China (41320104002, 41600302) and National Basic Research Program of China (2016YFC0500601). AKK and MDS were funded by the US National Science Foundation Macrosystems Biology program in support of the EDGE project. JS and JP were funded by the European Research Council Synergy grant ERC-SyG-2013-610028 IMBALANCE-P, the Spanish Government grant CGL2013-48074-P and the Catalan Government grant SGR 2014-274.

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

| | 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 |

**Table 2.** Results of mixed model analysis of variance for green leaf [N] and their resorption efficiency for two grasses (*L. chinensis* and *S. grandis*) and plant community at the rhizomatous and bunch grass dominated community. Drought treatment was used as a fixed factor and block as a random factor. The value of *p* is 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 |

**Table 3.** Results of mixed model analysis of variance for soil total [N] and available [N], [P] and [K]. Drought treatment and community type were used as fixed factors and block as a random factor. The value of *p* is shown. Bold text indicates 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 |

## Figures legends

**Fig. 1** Effects of extreme drought (C, control; D, drought) on leaf [N], [P] and [K] in dominant grass species (*L. chinensis* and *S. grandis*) from two grasslands. Each point represents the mean nutrient concentration with error bars indicating standard errors calculated from replicate plots for each treatment. Different letters indicate significant differences between the rhizomatous and bunch grass dominated community at $p< 0.05$. Statistical significance of drought effect is depicted as *** $p<0.001$, ** $p<0.01$ and * $p<0.05$. When the responses were different between the two communities, an asterisk was separately placed above each community; when the responses were consistent between two communities, an asterisk was only placed in middle of the two communities. See Tables 1 and 2 for the overall ANOVA results.

**Fig. 2** Effects of extreme drought (C, control; D, drought) and community type on plant [N], [P] and [K] at community level. Each point represents the mean nutrient concentration with error bars indicating standard errors calculated from replicate plots for each treatment. Different letters indicate significant differences between the rhizomatous and bunch grass dominated community at $p< 0.05$. Statistical significance of drought effect is depicted as *** $p<0.001$, ** $p<0.01$ and * $p<0.05$. When the responses were different between the two communities, the * was separately put above each community type; when the responses were consistent between two communities, the * was only put in middle of the two community types. See Tables 1 and 2 for the overall ANOVA results.

**Fig. 3** Effects of extreme drought (C, control; D, drought) and community type on soil total [N] and available [N], [P] and [K]. Each point represents the mean nutrient concentration with error bars indicating standard errors calculated from replicate plots for each treatment. Different letters indicate significant differences between the rhizomatous and bunch grass dominated communities at $p < 0.05$. When the responses were different between two communities, an asterisk was separately placed above each community type; when the responses were consistent between the two communities, an asterisk was only placed in middle of the two community types. Statistical significance of drought effect is depicted as *** $p<0.001$, ** $p<0.01$ and * $p<0.05$. See Table 3 for the overall ANOVA results.

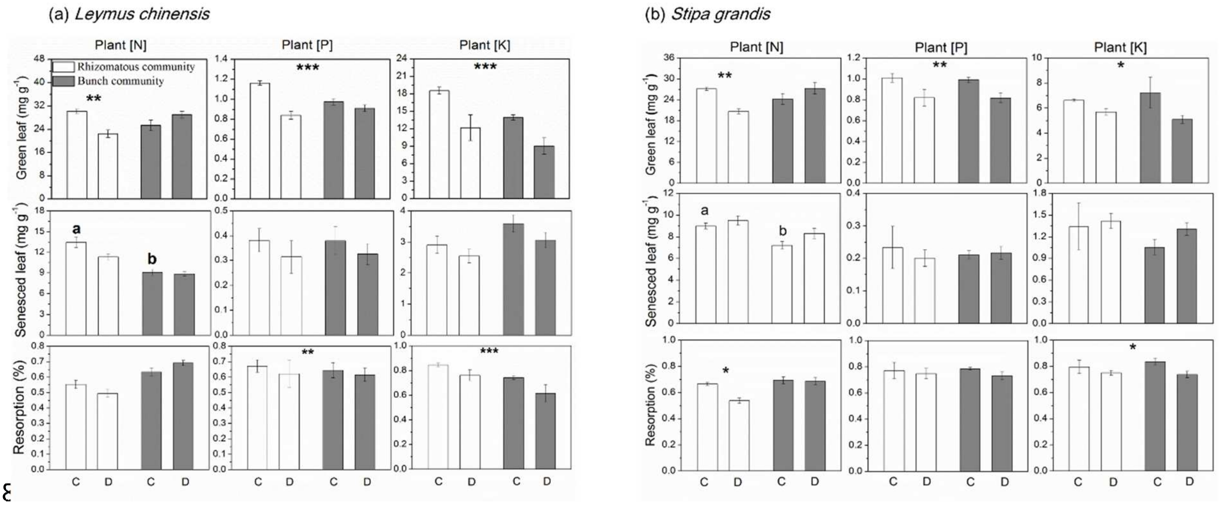
(a) Leymus chinensis
(b) Stipa grandis
Plant [N]
Plant [P]
Plant [K]
Rhizomatous community
Bunch community
Green leaf (mg g$^{-1}$)
Senesced leaf (mg g$^{-1}$)
Resorption (%)
**
***
*
a
b
C
D

**Figure 1**

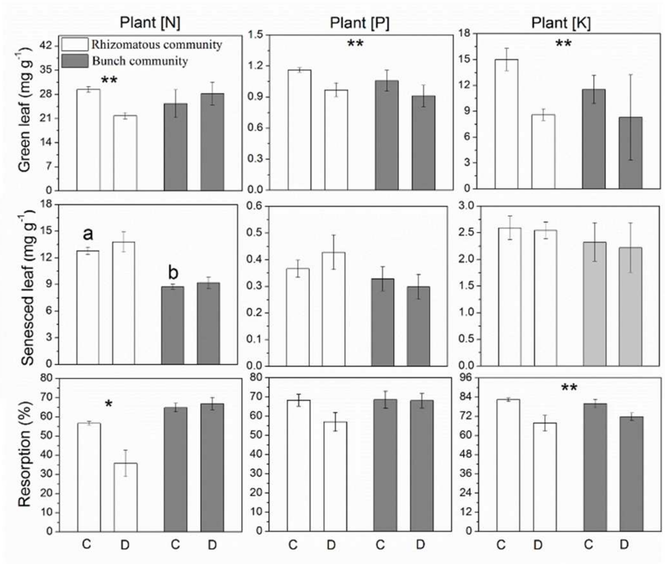
Plant [N]
Plant [P]
Plant [K]
Rhizomatous community
Bunch community
Green leaf (mg g-1)
Senesced leaf (mg g-1)
Resorption (%)
**
**
**
a
b
*
**
0 7 14 21 28 35 42
0.0 0.3 0.6 0.9 1.2 1.5
0 3 6 9 12 15 18
0 3 6 9 12 15 18
0.0 0.1 0.2 0.3 0.4 0.5 0.6
0.0 0.5 1.0 1.5 2.0 2.5 3.0
0 10 20 30 40 50 60 70 80
0 10 20 30 40 50 60 70 80
0 12 24 36 48 60 72 84 96
C D C D
C D C D
C D C D

Figure 2

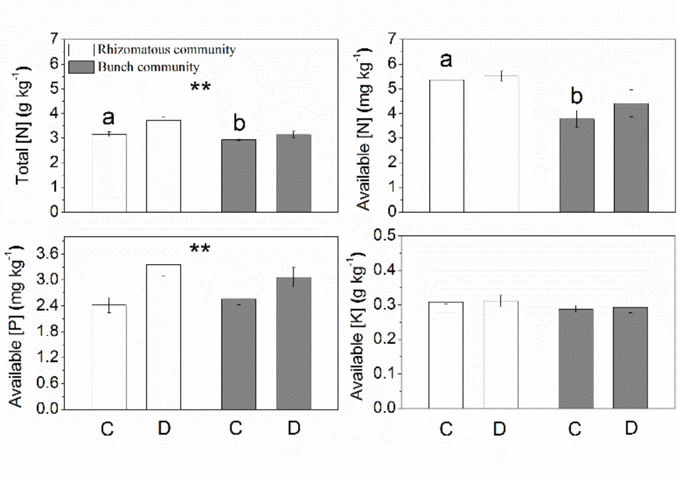
Rhizomatous community
Bunch community
Total [N] (g kg$^{-1}$)
Available [N] (mg kg$^{-1}$)
Available [P] (mg kg$^{-1}$)
Available [K] (g kg$^{-1}$)
**
a
b
**
a
b
0
1
2
3
4
5
6
7
0.0
0.6
1.2
1.8
2.4
3.0
3.6
0.0
0.1
0.2
0.3
0.4
0.5
C
D
C
D
C
D
C
D

**Figure 3**