Precipitation and nitrogen addition enhance biomass allocation to aboveground in an alpine steppe

Changbin Li1,2,3 | Zhi Zheng1,2 | Yunfeng Peng4 | Xiuqing Nie1,2,3 | Lucun Yang1,2 | Yuanming Xiao1,2,3 | Guoying Zhou1,2

Abstract

There are two important allocation hypotheses in plant biomass allocation: allometric and isometric. We tested these two hypotheses in an alpine steppe using plant biomass allocation under nitrogen (N) addition and precipitation (Precip) changes at a community level. An in situ field manipulation experiment was conducted to examine the two hypotheses and the responses of the biomass to N addition (10 g N m⁻² y⁻¹) and altered Precip (±50% precipitation) in an alpine steppe on the Qinghai-Tibetan Plateau from 2013 to 2016. We found that the plant community biomass differed in its response to N addition and reduced Precip such that N addition significantly increased aboveground biomass (AGB), while reduced Precip significantly decreased AGB from 2014 to 2016. Moreover, reduced Precip enhanced deep soil belowground biomass (BGB). In the natural alpine steppe, the allocation between AGB and BGB was consistent with the isometric hypotheses. In contrast, N addition or altered Precip enhanced biomass allocation to aboveground, thus leading to allometric growth. More importantly, reduced Precip enhanced biomass allocation into deep soil. Our study provides insight into the responses of alpine steppes to global climate change by linking AGB and BGB allocation.

Keywords
aboveground biomass, belowground biomass, nitrogen addition, precipitation changes, Tibetan alpine steppe

INTRODUCTION

Human activity-induced climate change, especially in part due to shifts in precipitation patterns, and enhanced emission of biological reactive nitrogen (N) to the atmosphere have had profound impacts on the global water and N cycle (Basto et al., 2018; Stevens, 2019; Yu et al., 2019). As water and N are the most important factors that determine the growth and survival of plant and limit the production of grassland ecosystems (Bobbink et al., 2010; Greaver et al., 2016), the altered Precip and enhanced N deposition affect grassland ecosystem functions and services that are essential for well-being of humanity (Basto et al., 2018; Liu et al., 2018). Despite numerous reports on the effects of altered Precip and enhanced N deposition grassland ecosystems (Liu et al., 2018; Ma et al., 2019; Tian et al., 2016; Yang et al., 2011), less is known with respect to how altered Precip, enhanced N deposition, and their interaction in the alpine steppe will influence aboveground and belowground biomass allocation, especially at different soil layer (Liu et al., 2018).

Aboveground and belowground biomass allocation reflected evolutionarily derived strategies for resource acquisition and
adaptation to their environment (Lambers, Chapin, & Pons, 2008).
Theoretically, plant should allocate more carbon to organs that
acquire essential and limiting resources (Johnson, Rowland, Corkidi, &
Allen, 2008). For example, as plant growth is limited by soil resources
such as nutrient and water, plant species will allocate more carbon to
root systems to acquire limiting soil resource (Johnson et al., 2008).
In contrast, in light-limited ecosystem, plant species will allocate
more carbon to leaves to intercept light and fix CO₂ for plant growth
(Hautier, Niklaus, & Hector, 2009). This leads to allometric allocations
that variations in environmental conditions affect aboveground and
belowground biomass allocation (Bloom, Chapin, & Mooney, 1985;
Chapin, Bloom, Field, & Waring, 1987). By contrast, plants rely on
their homeostasis to cope with the environment, thus leading to an
isometric allocation that aboveground biomass (AGB) scales with be‐
lowground biomass (BGB) in an isometric manner (Enquist & Niklas,
2002; Niklas, 2004). Previous studies found that, in community level
of Tibetan Plateau grassland ecosystems, AGB and BGB allocation
fitted the isometric hypothesis (McCarthy & Enquist, 2007; Yang,
Fang, Ji, & Han, 2009), while on an individual level, the allocation
fitted the allometric relationship (Wang, Niu, Yang, & Zhou, 2010), in‐
dicating that AGB and BGB allocation has strong scale dependence in
grassland ecosystems of Tibetan Plateau grassland ecosystems. Plant
growth in the alpine steppe is colimited by N and water (Hooper &
Johnson, 1999). Thus, altered Precip and enhanced N deposition
should have impacts on AGB and BGB allocation. However, we less
known how altered Precip, enhanced N deposition, and their interac‐
tion had impacts on AGB and BGB allocation relationship.
Alpine ecosystem is believed among the most sensitive eco‐
systems to global changes (Chen et al., 2013). Alpine steppe is an
integral part of the Qinghai-Tibetan Plateau. Human activities
have led to dramatic changes in Precip and atmospheric deposition
(Galloway et al., 2008; Peñuelas et al., 2013; Reay, Dentener, Smith,
Grace, & Feely, 2008). For example, during the period 1990–2003,
atmospheric N deposition has increased substantially from 8.7 to
Grace, & Feely, 2008). For example, during the period 1990–2003,
(Galloway et al., 2008; Peñuelas et al., 2013; Reay, Dentener, Smith,
have led to dramatic changes in Precip and atmospheric deposition
integral part of the Qinghai–Tibetan Plateau. Human activities
systems to global changes (Chen et al., 2013). Alpine steppe is an
37°18’N, 100°15’E, 3,286 m a.s.l.), in Qinghai
Province, China. The experiment site was located in an alpine
steppe with mean annual temperature of 0.08°C and precipitation
of 387 mm which occurs predominantly in the growing season (June
to August). The soil belongs to chestnut soil. Vegetation is an alpine
steppe community mainly dominated by Stipa purpurea, and accom‐
panied by Poa crymophila and Artemisia scoparia (Peng & Yang, 2016).

2.2 | Experimental design
The experiment was established in 2013 following exclusion of live‐
stock grazing by fencing. The manipulative experiments include six
treatments (N₁P₁: ambient N addition with reduced precipitation
50%; N₁P₂: ambient N addition with ambient precipitation; N₁P₃: am‐
ient N addition with enhanced precipitation 50%; N₂P₁: N addition
with reduced precipitation; N₂P₂: N addition with ambient precipita‐
tion; and N₂P₃: N addition with enhanced precipitation). Each treat‐
ment had five replicates, and 30 3.3 m × 2.7 m plots separated by
2-m-wide buffer strips were established in a 5 × 6 block design. The
precipitation treatment was controlled by sunlight-pervious concave
polyvinyl chloride (PVC) boards (1 mm thick) at the 15° angle above
each plot. The reduced precipitation treatment was controlled by the
nonslotted channels, and 50% of the intercepted rainwater was
collected and stored. The enhanced treatment was provided by slotted
channels that sprinkled the collected water from the reduced
plots immediately after the rain, resulting in a 50% increase relative
to ambient precipitation. The ambient precipitation treatment plots
were also installed with slotted channels. To avoid surface runoff,
metal plates were inserted to a soil depth of 20 cm with 10 cm re‐
amaining above the surface around each plot. Moreover, to simulate
ambient N deposition, NH₄NO₃ (10 g N m⁻² year⁻¹, N > 99%) was
used in N addition plots. The fertilizers were mixed with water in 1-L
water by sprinkling evenly using a sprayer to each plot. Ambient N
addition plots received equal dose of water. This N deposition rate is
higher than the current natural N deposition rate (ranging from 0.87
to 1.38 g N ha⁻¹ year⁻¹) in this region, but atmospheric N deposi‐
tion rates as high as 5.46 g m⁻² year⁻¹ in China (Xu et al., 2018). A
recent study in the same region demonstrated that N addition rate of
8 g m⁻² year⁻¹ led to N saturation in soil (Peng & Yang, 2016).

2.3 | Field sampling
Aboveground biomass was sampled in mid-August annually by clipping
all plants within three 0.25 m × 0.25 m quadrates that were randomly
placed within each plot and not overlapped spatially among years.
Briefly, shoots were cut at the soil surface and oven-dried at 65°C for
72 hr before they were weighed (Li et al., 2018). Thereafter, to assess
the effect of altered precipitation, N addition, and their interaction on
over all belowground biomass and aboveground biomass at different
soil layer, we collected belowground biomass using three 8-cm-diam‐
ter soil cores from each plot in mid-August 2016. The soil cores were
further divided into three soil layers: 0–10, 10–20, and 20–30 cm. Three
soil cores from the same layers in each plot were mixed and placed
into root bags with a mesh size of 0.5 mm and immersed in water for
24 hr. These soil cores were flushed with running water. These root
samples were picked up by manual dissection as described by Zheng,
Bai, and Zhang (2019). Then, they were oven-dried at 65°C for 48 hr weighted. Total belowground biomass was determined by pooling over three layers.

### 2.4 Statistical analysis

To investigate N and precipitation-induced changes of aboveground net primary productivity, we used date from 2013 to 2016 to assess the effect of N addition, precipitation change, and their interaction on aboveground biomass. Prior to all statistical analyses, we tested the heterogeneity of variances, and original data were normalized using log-transformation or standardization prior to statistical analysis when necessary. Firstly, an univariate analysis of variance (UNIANOVA) was used to assess treatment effects on aboveground, in which N addition, precipitation change, and year were the categorical variables, whereas aboveground biomass was
the continuous variable. For total belowground biomass, belowground biomass from different soil depth and the ratio of root to shoot (R/S), we used the data from 2016. Moreover, unpaired tests were also used to evaluate the effects of N addition, precipitation on aboveground biomass at the same year, total belowground biomass, R/S, and belowground biomass from the same soil depth. The statistical analyses above were performed in SPSS 16.0.

To examine the two allocation hypotheses allometric allocations and isometric allocation, reduced major axis (RMA) analyses were used to evaluate the relationship between log-transformed aboveground biomass and belowground biomass (Cheng & Niklas, 2006; Niklas, 2004). The slope (α) and y-intercept (log β) of the log–log linear functions were determined using the software package SMATR (Standardized Major Axis Tests and Routines; Falster, 2003; Warton, Duursma, Falster, & Taskinen, 2012) in the R Version 3.5.1 (R Development Core Team, 2018).

3 | RESULTS

3.1 | Effects of altered precipitation, N addition, and their interaction on aboveground biomass, belowground biomass, and aboveground–belowground biomass allocation

Aboveground plant biomass differed in response to N addition and altered Precip (Figure 1a–f; Table 1). For example, N addition significantly enhanced aboveground biomass by 38%, 58%, and 60% in 2014, 2015, and 2016, respectively (p < .05; Figure 1a,b). In contrast, reduced Precip led to a significant decrease in aboveground biomass by 24%, 34%, and 37% in 2014, 2015, and 2016 (Figure 1c,d), while enhanced Precip had no effect on aboveground biomass (Figure 1e,f).

In contrast to aboveground biomass responses, N addition had little impacts on overall belowground biomass (p = .20; Figure 2). Moreover, a differential response of belowground biomass to enhanced Precip and reduced Precip was observed after consecutive altered Precip for three years, such that enhanced Precip significantly increased belowground biomass by 16%, while reducedPrecip had no effect on aboveground biomass (Figure 1e,f).

In this study, N addition significantly influenced the R/S ratio (p < .05; Table 4), reducing it by 8%, 26%, and 27% for N2P1, N2P2, and N2P3, respectively (Figure 4). Compared with the N addition, the effect of Precip on R/S was not significant (p = .26; Table 4).

3.2 | Effects of altered precipitation, N addition, and their interaction on aboveground–belowground biomass allocation

Consecutive N addition and altered Precip had differential effects on aboveground and belowground biomass allocation. N addition significantly reduced the ratio of root to shoot (R/S), leading to a marked increase in aboveground biomass allocation, while altered Precip and the interaction between altered Precip and N addition had little impacts on R/S (Figure 4; Table 4).

| TABLE | Summary of univariate analysis of variance (UNIANOVA) of nitrogen addition and precipitation change on aboveground biomass from 2013 to 2016 |
| --- | --- | --- | --- | --- |
| Difference source | df | Mean square | F-value | p-value |
| Year (Y) | 3 | 180,204.48 | 44.15 | <.001 |
| Nitrogen (N) | 1 | 161,262.94 | 39.51 | <.001 |
| Precipitation (Precip) | 2 | 47,129.98 | 11.55 | <.001 |
| Y × N | 3 | 21,391.31 | 5.24 | .002 |
| Y × Precip | 6 | 12,050.97 | 2.95 | .011 |
| N × Precip | 2 | 1,965.08 | 0.48 | .619 |
| Y × N × Precip | 6 | 2,590.45 | 0.64 | .702 |

| FIGURE 2 | Effects of precipitation changes and N addition on belowground biomass (BGB) in 2016. N1 indicates ambient N, nitrogen addition (N2), 50% precipitation reduction (Precip 1), nature precipitation (Precip 2), 50% precipitation addition (Precip 3), error bars indicate the standard errors |

| TABLE | Summary of univariate analysis of variance (UNIANOVA) of nitrogen addition and precipitation change on belowground biomass (BGB) in 2016 |
| --- | --- | --- | --- | --- |
| Difference source | df | Mean square | F-value | p-value |
| Nitrogen (N) | 1 | 228,770.83 | 1.76 | .20 |
| Precip | 2 | 588,523.30 | 4.52 | .02 |
| N × Precip | 2 | 6,003.94 | 0.05 | .10 |
To further explore the relationships between N addition and altered precipitation, two allocation hypotheses were tested by testing plant biomass allocation under different N addition and precipitation condition. In natural alpine steppe, the isometric relationships between aboveground and belowground biomass allocation were observed (Figure 5a). In contrast, N addition and enhanced Precip significantly increased aboveground biomass allocation, leading to allometric allocations between aboveground and belowground biomass, while reduced Precip had no effect on the relationship between aboveground and belowground biomass allocation (Figure 5b,c).

**FIGURE 3** Effects of precipitation changes and N addition on belowground biomass (BGB) in 2016 (a, c, e) and changes (%) in belowground biomass (b, d, f) from 0–10 cm to 20–30 cm. N1 indicates ambient N, nitrogen addition (N2), 50% precipitation reduction (Precip 1), ambient precipitation (Precip 2), 50% precipitation addition (P3), p < .1, error bars indicate the standard errors

4 | DISCUSSIONS

Several manipulative experiments to simulate the changes in precipitation pattern and atmospheric N deposition have demonstrated that enhanced N input and enhanced precipitation increased aboveground plant biomass, while reduced precipitation led a marked decrease in aboveground plant biomass (Liu et al., 2018; Tian et al., 2016; Yang, Fang, Ma, Guo, & Mohammat, 2010). In the present study, we found that N addition significantly enhanced plant community aboveground biomass, while enhanced
precipitation had no effect on aboveground plant biomass and reduced precipitation significantly decreased plant community aboveground biomass (Figure 1). These findings highlight that the alpine steppe was limited by soil N availability, but not water. This might be due to the fact that cold climates in cold alpine steppe depressed N availability and water vaporization (He et al., 2006, 2008).

Another important finding is that N addition had no effect on belowground biomass (Figure 2). In long-term N-limited grassland ecosystems, their native plant species have evolved mechanisms to cope with low N availability (Chapin, 1980). Exogenous N input into soil will lead to shift from being N limited to light limited (Bobbink et al., 2010; Hautier et al., 2009). Therefore, in contrast to the response of aboveground biomass to N addition, N addition hardly led to change in belowground biomass. In contrast, we found that enhanced precipitation significantly increased belowground biomass, while reduced precipitation markedly decreased belowground biomass (Figure 2). In the field, we observed that enhanced precipitation had no effect on community structure, while reduced precipitation favored the growth of deep-root plant species, and suppressed shallow-root plants, leading to loss of shallow-root plant species (personal observation). However, we found that reduced precipitation significantly enhanced root biomass in deep soil layer, mainly due to that fact that reduced precipitation favored deep-root plant growth to enhance the efficiency of water availability.

The isometric relationships between aboveground and belowground biomass were found in the natural alpine steppe of community levels (Figure 5). Some studies have also reported an isometric relationship between aboveground and belowground biomass, for example, Yang et al. (2009) and Enquist and Niklas (2002). These consistent results indicate that coexisting plant species have evolved some mechanisms to adapt their environments and to maintain a common growth (Falster et al., 2015). For example, in long-term evolution, coexisting species occur inter- and intraspecific competition to acquire aboveground and belowground resources (Grace et al., 2016; Grime, 1974, 2006), leading to an isometric growth between shoot and root systems at the community level and allometric grow at the species level. Conversely, external resource input into soils and/or unsuitable conditions greatly affect the relationships between aboveground and belowground biomass allocations and carbon flux (Coomes, Holdaway, Kobe, Lines, & Allen, 2012; Jenkins & Pierce, 2017). In the present study, we found that N and water increment enhanced aboveground biomass allocation, leading to an allometric growth between aboveground and belowground plant biomass (Figure 5). This suggests that changes in environment will affect the balance

**TABLE 3** Summary of univariate analysis of variance (UNIANOVA) of nitrogen addition and precipitation change on belowground biomass (BGB) in different soil depth in 2016

| Difference source | df | Mean square | F-value | p-value |
|-------------------|----|-------------|---------|---------|
| 0–10 cm nitrogen (N) | 1 | 168,390.09 | 1.61 | .22 |
| 0–10 cm precipitation (Precip) | 2 | 246,407.83 | 2.36 | .12 |
| 0–10 cm N × Precip | 2 | 16,130.92 | 0.15 | .86 |
| 10–20 cm N | 1 | 54.37 | 0.01 | .95 |
| 10–20 cm Precip | 2 | 996.06 | 0.09 | .94 |
| 10–20 cm N × Precip | 2 | 823.56 | 0.07 | .93 |
| 20–30 cm N | 1 | 1,805.97 | 1.43 | .24 |
| 20–30 cm Precip | 2 | 5,225.42 | 4.15 | .03 |
| 20–30 cm N × Precip | 2 | 897.05 | 0.71 | .50 |

**TABLE 4** Summary of univariate analysis of variance (UNIANOVA) of nitrogen addition and precipitation change on changing of root: shoot ratio (R/S)

| Difference source | df | Mean square | F-value | p-value |
|-------------------|----|-------------|---------|---------|
| Nitrogen (N) | 1 | 7,959.20 | 4.30 | .049 |
| Precipitation (P) | 2 | 2,638.07 | 1.42 | .26 |
| N × P | 2 | 2,008.54 | 1.08 | .36 |

**FIGURE 4** Effects of precipitation changes and N addition on changing of R/S ratios (a) and changes (%) in R/S (b). N1P1 indicates the 50% precipitation reduction treatment, ambient precipitation (N1P2), 50% precipitation addition treatment (N 1P3), 50% precipitation reduction with nitrogen addition treatment (N2P1), the ambient precipitation without nitrogen addition (N 2P2), 50% precipitation addition with nitrogen addition (N 2P3). Error bars indicate the standard errors.
between belowground and aboveground growth. More surprisingly, we found that decrease in the precipitation had little effect on aboveground and belowground biomass, still maintaining an isometric growth. However, more biomass allocation into deep soil was observed in the present alpine steppe ecosystem (Figure 3). More root biomass in deep soil suggests that reduced precipitation stimulates root proliferation in deep soil, thus enhancing the ability to acquire water resources (Lambers et al., 2008). Therefore, future studies on impacts of altered precipitation should take root biomass from different soil layers into account in the community level.

5 | CONCLUSIONS

In summary, we demonstrated that altered precipitation and N addition led to changes in the relationship between aboveground and belowground biomass allocation. Specifically, in natural alpine steppe, aboveground and belowground biomass allocation conform to isometric hypothesis. In contrast, precipitation and N enrichment enhanced aboveground biomass allocation, leading to allometric allocation. Moreover, we demonstrated that reduced precipitation had little impacts on aboveground and belowground biomass allocation, while it enhanced more biomass into deep soil. Therefore, our finding provides a novel insight into N and precipitation-induced changes in the aboveground and belowground biomass allocation in the alpine steppe.

ACKNOWLEDGMENTS

This study is funded by Natural Science Foundation of Qinghai Province (2019-ZJ-910), and International Communication and Cooperation Project of Qinghai Province (2019-HZ-807) and Qinghai Province High-level Innovative "Thousand Talents" Program. We thank Zebing Zhong, Hechun Liu, Feng Xiong, and Yi Ning for facilitating our field surveys of the Tibetan Plateau (2014-2015) and providing laboratory assistance.

CONFLICT OF INTEREST

None declared.

AUTHORS CONTRIBUTION

C.B.L., Z.Z., X.Q.N., L.C.Y., and Y.M.X. collected the data and participated in discussions. C.B.L. analyzed the data and wrote the manuscript with Z.Z., G.Y.Z., and Y.F.P.

DATA AVAILABILITY STATEMENT

We had uploaded our data to the OSF. https://mfr.osf.io/render?url=https%3A%2F%2Fosf.io%2Fmd234%2Fdownload
REFERENCES

Basto, S., Thompson, K., Grime, J. P., Fridley, J. D., Calhim, S., Askin, A. P., & Askew, A. P., & Rees, M. (2018). Severe effects of long-term drought on calcareous grassland seed banks. *Npj Climate and Atmospheric Science*, 1(1), 1. https://doi.org/10.1038/s41612-017-0007-3

Bloom, A. J., Chapin, F. S., III, & Mooney, H. A. (1985). Resource limitation in plants—an economic analogy. *Annual Review of Ecology and Systematics*, 16(1), 363–392. https://doi.org/10.1146/annurev.es.16.110185.002051

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., ... De Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, 20(1), 30–59. https://doi.org/10.1890/08-1140.1

Chapin, F. S. (1980). The mineral nutrition of wild plants, annual review. *Annual Review of Ecology and Systematics*, 11, 233–260. https://doi.org/10.1146/annurev.es.11.110180.001313

Chapin, F. S., Bloom, A. J., Field, C. B., & Waring, R. H. (1987). Plant responses to multiple environmental factors. *Science*, 237(4819), 49–57. https://doi.org/10.1126/science.237.4819.171

Chen, H., Zhu, Q., Peng, C., Wu, N., Wang, Y., Fang, X., ... Wu, J. (2013). The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan Plateau. *Global Change Biology*, 19(10), 2940–2955. https://doi.org/10.1111/gcb.12277

Cheng, D.-L., & Niklas, K. J. (2006). Above- and below-ground biomass relationships across 1534 forested communities. *Annals of Botany*, 99(1), 95–102. https://doi.org/10.1093/aob/mcl206

Coomes, D. A., Holdaway, R. J., Kobe, R. K., Lines, E. R., & Allen, R. B. (2012). A general integrative framework for modelling woody biomass production and carbon sequestration rates in forests. *Journal of Ecology*, 100(1), 42–64. https://doi.org/10.1111/j.1365-2745.2011.01920.x

Enquist, B. J., & Niklas, K. J. (2002). Global allocation rules for patterns of biomass partitioning in seed plants. *Science*, 295(5559), 1517–1520. https://doi.org/10.1126/science.1066360

Falster, D. S. (2003). (S) MATR: Standardised major axis tests and routines. Version 1.0. Retrieved from http://www.bio.mq.edu.au/ecology/SMATR

Falster, D. S., Duursma, R. A., Ishihara, M. I., Barneche, D. R., FitzJohn, R. G., ... Várhammar, A., ... Aspinwall, M. J. (2015). BAAD: A biomass and allometry database for woody plants. *Ecology*, 96(5), 1445. https://doi.org/10.1890/14-1889.1

Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cal, Z., Freney, J. R., ... Sutton, M. A. (2008). Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science*, 320(5878), 889–892. https://doi.org/10.1126/science.1136674

Grace, J. B., Anderson, T. M., Seablom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., ... Smith, M. D. (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, 529(7586), 390. https://doi.org/10.1038/nature16524

Greaver, T. L., Clark, C. M., Compton, J. E., Vallano, D., Talhelm, A. F., Weaver, C. P., ... Haeuber, R. A. (2016). Key ecological responses to nitrogen are altered by climate change. *Nature Climate Change*, 6(9), 836. https://doi.org/10.1038/nclimate3088

Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature*, 250(5461), 26. https://doi.org/10.1038/250026a0

Grime, J. P. (2006). *Plant strategies, vegetation processes, and ecosystem properties*. Hoboken, NJ: John Wiley & Sons.

Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, 324(5927), 636–638. https://doi.org/10.1126/science.1169640

He, J.-S., Fang, J., Wang, Z., Guo, D., Flynn, D. F. B., & Gong, Z. (2006). Stoichiometry and large-scale patterns of leaf carbon and nitrogen in the grassland biomes of China. *Oecologia*, 149(1), 115–122. https://doi.org/10.1007/s00442-006-0425-0

He, J.-S., Wang, L., Flynn, D. F. B., Wang, X., Ma, W., & Fang, J. (2008). Leaf nitrogen: Phosphorus stoichiometry across Chinese grassland biomes. *Oecologia*, 155(2), 301–310. https://doi.org/10.1007/s00442-007-0912-y

Hooper, D. U., & Johnson, L. (1999). Nitrogen limitation in dryland ecosystems: Responses to geographical and temporal variation in precipitation. *Biogeochemistry*, 46(1–3), 247–293. https://doi.org/10.1007/BF01007582

Jenkins, D. G., & Pierce, S. (2017). General allometric scaling of net primary production agrees with plant adaptive strategy theory and has tipping points. *Journal of Ecology*, 105(4), 1094–1104. https://doi.org/10.1111/1365-2745.12726

Johnson, N. C., Rowland, D. L., Corkidi, L., & Allen, E. B. (2008). Plant winners and losers during grassland N-eutrophication differ in biomass allocation and mycorrhizas. *Ecology*, 89(10), 2868–2878. https://doi.org/10.1890/07.1394.1

Lambers, H., Chapin, F. S., III, & Pons, T. L. (2008). *Plant physiological ecology*. Berlin, Germany: Springer Science & Business Media.

Li, C., Peng, Y., Nie, X., Yang, Y., Yang, L., Li, F., ... Zhou, G. (2018). Differential responses of heterotrophic and autotrophic respiration to nitrogen addition and precipitation changes in a Tibetan alpine steppe. *Scientific Reports*, 8(1), 16546. https://doi.org/10.1038/s41598-018-34969-5

Liu, H., Mi, Z., Lin, L. I., Wang, Y., Zhang, Z., Zhang, F., ... He, J.-S. (2018). Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proceedings of the National Academy of Sciences of the United States of America*, 115(16), 4051–4056. https://doi.org/10.1073/pnas.1700299114

Lü, C., & Tian, H. (2007). Spatial and temporal patterns of nitrogen deposition in China: Synthesis of observational data. *Journal of Geophysical Research*, 112(D22), https://doi.org/10.1029/2006JD007990.

Ma, Q., Liu, X., Li, Y., Li, L., Yu, H., Qi, M., ... Xu, Z. (2019). Nitrogen deposition magnifies the sensitivity of desert steppe plant communities to large changes in precipitation. *Journal of Ecology*, 1–13. https://doi.org/10.1111/1365-2745.13264.

McCarthy, M. C., & Enquist, B. J. (2007). Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Functional Ecology*, 21(4), 713–720. https://doi.org/10.1111/j.1365-2435.2007.01276.x

Niklas, K. J. (2004). Modelling below- and above-ground biomass for non-woody and woody plants. *Annals of Botany*, 92(2), 315–321. https://doi.org/10.1093/aob/mcl028

Peng, Y., & Yang, Y. (2016). Allometric biomass partitioning under nitrogen enrichment: Evidence from manipulative experiments around the world. *Scientific Reports*, 6, 28918. https://doi.org/10.1038/srep28918

Peruelas, J., Poulter, B., Sardans, J., Clais, P., van der Velde, M., Bopp, L., ... Janssens, I. A. (2013). Human-induced nitrogen-phosphorus imbalances alter natural and managed ecosystems across the globe. *Nature Communications*, 4, 2934. https://doi.org/10.1038/ncomms3934

R Development Core Team (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/

Reay, D. S., Dentener, F., Smith, P., Grace, J., & Feely, R. A. (2008). Global nitrogen deposition and carbon sinks. *Nature Geoscience*, 1(7), 430. https://doi.org/10.1038/ngeo230
Stevens, C. J. (2019). Nitrogen in the environment. Science, 363(6427), 578–580. https://doi.org/10.1126/science.aav8215

Wang, L., Niu, K. C., Yang, Y. H., & Zhou, P. (2010). Patterns of above- and belowground biomass allocation in China’s grasslands: Evidence from individual-level observations. Science China Life Sciences, 53(7), 851–857. https://doi.org/10.1007/s11427-010-4027-z

Warton, D. I., Duursma, R. A., Falster, D. S., & Taskinen, S. (2012). SMART 3- An R package for estimation and inference about allometric lines. Methods in Ecology and Evolution, 3(2), 257–259. https://doi.org/10.1111/j.2041-210X.2011.00153.x

Xu, W., Zhao, Y., Liu, X., Dore, A. J., Zhang, L., Liu, L., & Cheng, M. (2018). Atmospheric nitrogen deposition in the Yangtze River basin: Spatial pattern and source attribution. Environmental Pollution, 232, 546–555. https://doi.org/10.1016/j.envpol.2017.09.086

Yang, H., Li, Y., Wu, M., Zhang, Z., Li, L., & Wan, S. (2011). Plant community responses to nitrogen addition and increased precipitation: The importance of water availability and species traits. Global Change Biology, 17(9), 2936–2944. https://doi.org/10.1111/j.1365-2486.2011.02423.x

Yang, Y., Fang, J., Ji, C., & Han, W. (2009). Above-ground and belowground biomass allocation in Tibetan grasslands. Journal of Vegetation Science, 20(1), 177–184. https://doi.org/10.1111/j.1654-1103.2009.00566.x

Yang, Y., Fang, J., Ma, W., Guo, D., & Mohammat, A. (2010). Large-scale pattern of biomass partitioning across China’s grasslands. Global Ecology and Biogeography, 19(2), 268–277. https://doi.org/10.1111/j.1466-8238.2009.00502.x

Yu, G., Jia, Y., He, N., Zhu, J., Chen, Z., Wang, Q., ... Goulding, K. (2019). Stabilization of atmospheric nitrogen deposition in China over the past decade. Nature Geoscience, 12(6), 424. https://doi.org/10.1038/s41561-019-0352-4

Zheng, Z., Bai, W., & Zhang, W.-H. (2019). Root trait-mediated belowground competition and community composition of a temperate steppe under nitrogen enrichment. Plant and Soil, 437(1–2), 341–354. https://doi.org/10.1007/s11104-019-03989-z

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Li C, Zheng Z, Peng Y, et al. Precipitation and nitrogen addition enhance biomass allocation to aboveground in an alpine steppe. Ecol Evol. 2019;9:12193–12201. https://doi.org/10.1002/ece3.5706