# Ecological biomass allocation strategies in plant species with different life forms in a cold desert, China (Postprint)

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**Date:** 2019-10-26T00:00:00+00:00

## Abstract

Biomass allocation patterns among plant species are related to their adaptive ecological strategies. Ephemeral, ephemeroid and annual plant life forms represent three typical growth strategies of plants that grow in autumn and early spring in the cold deserts of China. These plants play an important role in reducing wind velocity in the desert areas. However, despite numerous studies, the strategies of biomass allocation among plant species with these three life forms remain contentious. In this study, we conducted a preliminary quadrat study during 2014–2016 in the southern part of the Gurbantunggut Desert, China, to investigate the allocation patterns of above-ground biomass (AGB) and below-ground biomass (BGB) at the individual level in 17 ephemeral, 3 ephemeroid and 4 annual plant species. Since ephemeral plants can germinate in autumn, we also compared biomass allocation patterns between plants that germinated in autumn 2015 and spring 2016 for 4 common ephemeral species. The healthy mature individual plants of each species were sampled and the AGB, BGB, total biomass (TB), leaf mass ratio (LMR) and root/shoot ratio (R/S) were calculated for 201 sample quadrats in the study area. We also studied the relationships between AGB and BGB of plants with the three different life forms (ephemeral, ephemeroid and annual). The mean AGB values of ephemeral, ephemeroid and annual plants were 0.806, 3.759 and 1.546 g/plant, respectively, and the mean BGB values were 0.106, 4.996 and 0.166 g/plant, respectively. The mean R/S value was significantly higher in ephemeroid plants (1.675) than in ephemeral (0.154) and annual (0.147) plants. The mean LMR was the highest in annual plants, followed by ephemeroid plants and ephemeral plants, reflecting the fact that annual plants allocate more biomass to leaves, associated with their longer life span. Biomass of ephemeral plants that germinated in autumn was significantly higher than those of corresponding plants that germinated in spring in terms of AGB, BGB and TB. However, the R/S value was similar in plants that germinated in autumn and spring. The slope of regression relationship between

AGB and BGB differed significantly among the three plant life forms. These results support different biomass allocation hypotheses. Specifically, at the individual level, the AGB and BGB partitioning supports the allometric hypothesis for ephemeroid and annual plants and the isometric hypothesis for ephemeral plants.

## Full Text

Journal of Arid Land (2019) 11(5): 729–739
https://doi.org/1010.1007/s40333-019-0062-1
Science Press and Springer-Verlag

**Ecological biomass allocation strategies in plant species with different life forms in a cold desert, China**

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Received: 2018-09-08; Revised: 2019-03-13; Accepted: 2019-06-08

http://jal.xjegi.com; www.springer.com/40333

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## Abstract

Biomass allocation patterns among plant species are related to their adaptive ecological strategies. Ephemeral, ephemeroid, and annual plant life forms represent three typical growth strategies of plants that grow in autumn and early spring in the cold deserts of China. These plants play an important role in reducing wind velocity in desert areas. However, despite numerous studies, the strategies of biomass allocation among plant species with these three life forms remain contentious. In this study, we conducted a preliminary quadrat study during 2014–2016 in the southern part of the Gurbantunggut Desert, China, to investigate the allocation patterns of above-ground biomass (AGB) and below-ground biomass (BGB) at the individual level in 17 ephemeral, 3 ephemeroid, and 4 annual plant species. Since ephemeral plants can germinate in autumn, we also compared biomass allocation patterns between plants that germinated in autumn 2015 and spring 2016 for four common ephemeral species. Healthy mature individual plants of each species were sampled, and AGB, BGB, total biomass (TB), leaf mass ratio (LMR), and root/shoot ratio (R/S) were calculated for 201 sample quadrats in the study area. We also examined the relationships between AGB and BGB of plants with the three different life forms (ephemeral, ephemeroid, and annual). The mean AGB values of ephemeral, ephemeroid, and annual plants were 0.806, 3.759, and 1.546 g/plant, respectively, and the mean BGB values were 0.106, 4.996, and 0.166 g/plant, respectively. The mean R/S value was significantly higher in ephemeroid plants (1.675) than in ephemeral (0.154) and annual (0.147) plants. The mean LMR was highest in annual plants, followed by ephemeroid plants and ephemeral plants, reflecting the fact that annual plants allocate more biomass to leaves, associated with their longer life span. Biomass of ephemeral plants that germinated in autumn was significantly higher than that of corresponding plants that germinated in spring in terms of AGB, BGB, and TB. However, the R/S value was similar in plants that germinated in autumn and spring. The slope of the regression relationship between AGB and BGB differed significantly among the three plant life forms. These results support different biomass allocation hypotheses. Specifically, at the individual level, AGB and BGB partitioning supports the allometric hypothesis for ephemeroid and annual plants and the isometric hypothesis for ephemeral plants.

**Keywords:** above-ground biomass; below-ground biomass; plant life forms; herbaceous species; allometric hypothesis; isometric hypothesis; Gurbantunggut Desert

**Citation:** FAN Lianlian, DING Junxiang, MA Xuexi, LI Yaoming. 2019. Ecological biomass allocation strategies in plant species with different life forms in a cold desert, China. Journal of Arid Land, 11(5): 729–739. https://doi.org/1010.1007/s40333-019-0062-1

## Introduction

Biomass allocation, which reflects the fundamental trade-off in partitioning between above-ground biomass (AGB) and below-ground biomass (BGB) in plants, plays an important role in plant life cycles [?, ?, ?, ?]. Biomass allocation within a plant, particularly the distribution of biomass among various organs, is strongly affected by species characteristics, ontogeny, and the environment where the plants live [?]. As a result, the relative biomass representing above-ground and below-ground parts is not fixed and varies greatly under different environments or among different species [?]. Understanding the quantitative allocation of a plant' s biomass to above-ground and below-ground parts is of fundamental importance to the study of plant ecology and evolution [?, ?].

Desert vegetation, especially natural vegetation, plays an important role in reducing wind velocity [?], thus preventing or at least decreasing desertification caused by soil erosion [?]. Ephemerals (with short life span), ephemeroids (perennial plants with short life span), and annuals (with longer life span than ephemeral and ephemeroid plants) are the three dominant plant life forms comprising the herbaceous layer in the Gurbantunggut Desert in northwestern China [?]. These three types of plants usually account for more than 50% of the vegetation cover from early spring to summer and make a large contribution to the annual productivity of the desert vegetation in spring and autumn; they also act as a nutrient reservoir for other plants [?, ?]. Ephemeral and ephemeroid plants both take advantage of available water during the rainy season to complete their life cycle rapidly within a few months [?]. Furthermore, some ephemeral plants can germinate in autumn when water and temperature conditions are suitable, and then grow over winter to complete their life cycle in the following year. In contrast, annual plants grow for a longer period with less rapid vegetative growth and tend to grow under drier soil conditions than ephemeral and ephemeroid plants [?]. Given that biomass allocation is an essential process, we therefore surmise that plants with different life forms will adopt different strategies to regulate their allocation to AGB and BGB in order to adapt to environmental conditions.

According to optimal partitioning theory, plants usually allocate relatively more biomass to shoots if the limiting factors for growth are above-ground (e.g., CO and sunlight) and more biomass to roots if the limiting factors are below-ground (e.g., water and nutrients). Thus, to achieve optimal growth, plants will allocate biomass preferentially to the organ that accesses the most growth-limiting resources [?]. Several studies have reported that plants in desert ecosystems have a larger root/shoot ratio (R/S) than plants in other ecosystems, such as forest and steppe ecosystems [?]. Generally, allocating relatively more biomass to below-ground organs (roots) would allow plants to absorb more soil moisture required for growth, especially in arid regions [?, ?]. However, plants are generally less able to adjust biomass allocation than to alter organ morphology, given that leaf and root morphology must also be altered to increase the capture of limiting resources [?]. The optimal resource partitioning pattern for one species may thus not be optimal for other species [?, ?]. The high R/S of plants grown in desert environments may not be widely applicable, given that the ratio might be more closely related to plant life form or temperature than to aridity [?, ?]. Additionally, biomass allocation is strongly associated with plant life form and the niche that the plant has evolved to occupy. A precise analysis of biomass allocation patterns is thus crucial for evaluating the performance of plants living in different environmental conditions or for comparing growth among different species or life forms [?].

Biomass allocation patterns are related to the ecological adaptive strategies of plants [?]. Previous studies indicated that plant biomass allocation differed among different life forms [?, ?, ?]. Numerous studies have investigated ephemeral, ephemeroid, and annual species in desert ecosystems, focusing on their ecological contributions to ecosystems [?, ?, ?] or their physiological responses to changing environmental factors [?, ?, ?, ?]. Although detailed quantitative information about plant biomass allocation patterns is still lacking, such information is required to analyze possible ecological strategy benefits and understand the regulatory mechanisms of desert plants responding to climate change. We therefore investigated the biomass allocation patterns of 17 ephemeral species, 3 ephemeroid species, and 4 annual species in the Gurbantunggut Desert to test the hypothesis that plants with different life forms show different AGB and BGB allocation patterns. We also tested whether ephemeral plants that germinated in autumn show different biomass allocation patterns compared with those that germinated in the following spring.

### 2.1 Study Area

This study was conducted in the southern part of the Gurbantunggut Desert, with a latitudinal range from 44°33 N to 44°56 N and a longitudinal range from 87°66 E to 87°96 E. The Gurbantunggut Desert, located in the center of the Junggar Basin in Xinjiang Uygur Autonomous Region of China, is the second largest desert in China. The study area is characterized by a typical continental arid climate, with dry, hot summers and cold winters. The annual maximum temperature is 42.6°C, the annual minimum temperature is -41.6°C, and the annual mean temperature is 6.6°C. The mean annual precipitation is 70-180 mm. The desert surface is covered by about 20 cm of snow for approximately 100-160 days, starting in late November and ending in late March of the following year [**?**]. An increase in temperature in spring often results in rapid snowmelt, equivalent to high rainfall, which penetrates the soil, provides abundant soil moisture, and therefore supports the emergence and growth of many desert plants. Ephemerals, ephemeroids, and annuals are the three typical life forms in this region, accounting for more than 50% of the vegetation cover from early spring to summer [**?**].

### 2.2 Plant Sampling and Measurement

In this experiment, we randomly established 201 sample quadrats (1 m × 1 m each) in the southern Gurbantunggut Desert in 2014. Twenty-four species from 14 families were sampled, including 17 ephemeral species, 3 ephemeroid species, and 4 annual species (409 total plant samples; Table 1 ), during the period of maximum vegetation growth (from May to September). The ephemeral and ephemeroid plants were harvested in mid-May 2014, and the annual plants were harvested in mid-August 2014. For each species, 10-30 healthy mature individuals were collected. Some species with little biomass were difficult to harvest, and in these cases, 2-5 individual plants were mixed as a composite sample and the average value was calculated per plant.

According to previous research and the plant' s root morphology, we excavated a patch containing most of the root mass with a spade [**?**]. Generally, a patch with the plant at the center was excavated to a depth of 40-50 cm and a diameter of 30-40 cm [**?**]. After excavation, we carefully separated the roots from soil and other materials, and the shoots and roots were then taken to the laboratory and separated. Shoot samples were further divided into leaves and other parts to calculate the leaf biomass ratio (LMR). Root samples were washed under running tap water. The different organs from each sample were then placed in separate paper envelopes, dried at 65°C to constant mass, and weighed.

Leaf biomass (LB), stem biomass (SB), and root biomass (RB) were measured. Thus, AGB was calculated as AGB = LB + SB, BGB was equal to RB, and total biomass (TB) was calculated as TB = AGB + BGB. LMR was calculated as the ratio of LB to TB, and R/S was calculated as R/S = BGB/AGB. Generally speaking, if precipitation and temperature in July or August are suitable, ephemeral plants will germinate in autumn, continue to grow through winter, and complete their life cycle in the following year [**?**]. We therefore chose four common ephemeral species and compared the growth of plants that germinated in autumn 2015 with those that germinated in spring 2016. The sampling method was the same as described above.

### 2.3 Data Analysis

AGB, BGB, LMR, and R/S were calculated for all plant samples. Differences in biomass allocation variables (i.e., LMR and R/S) among the three plant life forms (ephemeral, ephemeroid, and annual) were analyzed by one-way parametric analysis of variance (ANOVA) using SPSS version 18.0. The relationship between AGB and BGB was log-transformed before applying linear regression analysis. The slope (represented as $a$) and y-intercept (represented as $b$) of log-log linear functions for reduced major axis were calculated using the software package Standardized Major Axis Tests and Routines [**?**].

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## 3.1 AGB, BGB, and TB of Ephemeral, Ephemeroid, and Annual Plants

There were wide variations in AGB, BGB, and TB among all 409 plants (Fig. 1 [Figure 1: see original paper]). The mean AGB values for ephemeral, ephemeroid, and annual plants showed significant differences, as did the mean BGB and TB values (Table 2 ). Generally, biomass of ephemeroid plants with perennial roots was obviously larger than that of ephemeral and annual plants.

## 3.2 LMR and R/S of Ephemeral, Ephemeroid, and Annual Plants

Both LMR and R/S differed significantly among plants with the three life forms. Annual plants generally allocated more biomass to leaves and thus had a higher LMR (0.590) than ephemeral (0.354) and ephemeroid (0.415) plants (Fig. 2a [Figure 2: see original paper]). In contrast, the R/S value for ephemeroid plants (1.675) was significantly ($P < 0.05$) higher than those for ephemeral (0.154) and annual (0.147) plants. Moreover, the R/S values for ephemeral and annual plants were not significantly different from one another (Fig. 2b [Figure 2: see original paper]).

### 3.3 Allometric Relationship Between AGB and BGB in Ephemeral, Ephemeroid, and Annual Plants

In this study, we estimated the slope (represented as *a*) and y-intercept (represented as *b*) of the relationship between AGB and BGB across the three different plant life forms through allometric analysis (Fig. 3 [Figure 3: see original paper]; Table 3 ). The relationship between AGB and BGB in plants with three different life forms (ephemeral, ephemeroid, and annual) was characterized by the linear function: $\lg(\text{AGB}) = a \times \lg(\text{BGB}) + b$. The standardized major axis was used to test slope heterogeneity at $P = 0.05$ across different plant life forms. In terms of the test for allometry, the AGB versus BGB relationship supports the isometric allocation hypothesis when $P > 0.05$, while the relationship supports the allometric allocation hypothesis when $P < 0.05$.

As shown in Figure 3 and Table 3, biomass allocations in ephemeroid and annual plants supported the allometric allocation hypothesis, with slopes of 0.985 and 1.202 for the relationship between AGB and BGB, respectively. In contrast, the relationship between AGB and BGB in ephemeral plants supported the isometric allocation hypothesis ($P > 0.05$; slope = 1.036). These results indicated that biomass allocation in ephemeroid and annual plants followed an allometric pattern, while it followed an isometric pattern in ephemeral plants.

### 3.4 Biomass Allocation Between Autumn- and Spring-Germinated Ephemeral Plants

Among the four ephemeral species, biomass of plants that germinated in autumn was significantly higher than biomass of corresponding plants that germinated in spring, in terms of AGB, BGB, and TB (Figs. 4a–c). However, there was no significant difference in R/S values between plants that germinated in spring and autumn (Fig. 4d [Figure 4: see original paper]).

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### 4.1 Biomass Allocation Patterns in Plants with Three Different Life Forms

Generally, rainfall in arid and semi-arid regions is usually low, with highly variable and unpredictable characteristics [**?**, **?**, **?**]. Individual plants living in these regions are thus usually small because of the stressful dry environment. This finding was confirmed in the current study, with 85% of all 409 plants having a dry weight of <4 g (Fig. 1 [Figure 1: see original paper]). This suggests that plants reduce their individual size to adapt to the water-limited environment.

R/S is usually considered to reflect the trade-off in investment between above-ground and below-ground organs [?, ?], and R/S values have been well-documented for plant species with different life forms. For example, the R/S value for ephemeroid species *Tulipa sinkiangensis* in the north of the Tianshan Mountains was about 1.000 [?]; nevertheless, most ephemeral species allocate less of their biomass to roots, generally resulting in low R/S values of $<0.200$ [?, ?]. LMR also represents the resources that the plant invests in photosynthetic organs, and previous studies have found that most species had LMR values of $<0.300$ [?]. In the context of our study, the R/S values of ephemeral plants (0.154) and annual plants (0.147) were significantly smaller than that of ephemeroid plants (1.675), and the LMR values of ephemeral, ephemeroid, and annual plants were approximately 0.354, 0.415, and 0.590, respectively. Both R/S and LMR differed significantly among the three different plant life forms. These differences in biomass partitioning could be explained by respective survival strategies: plants generally allocate proportionally more biomass to roots and shoots if their growth is more strongly limited by below-ground and above-ground factors, respectively [?, ?].

However, plants can adjust not only their biomass but also their leaf or root surface area per unit mass, overall morphology, and even life cycle in response to environmental limitations [?, ?]. We therefore considered that the lower R/S in ephemeral plants may be related to their opportunistic nature and short growth period. Ephemeral plants thus usually experience less water and nutrient stress when developing their individual structures [?, ?]. Furthermore, for ephemeral plants, increasing biomass allocation to above-ground parts such as leaves and flowers may promote population spread, including sexual propagation. Ephemeral plants would therefore not benefit from allocating a large proportion of their biomass to roots, as reflected by lower R/S values. Ephemeroid plants are characterized by having short-lived above-ground parts but perennial root systems, and thus they often have higher R/S values. Plants generally allocate biomass to the organs that acquire the most limiting resources [?], and annual plants, which live longer than ephemeral and ephemeroid plants, would thus tend to invest more biomass in leaves to produce more carbohydrates as an energy reservoir to allow them to adapt to harsh and highly variable desert conditions.

For most plant species, the timing of seed germination can vary among seasons to better utilize available resources and extend and expand populations [?]. In our study area, it is common for herbaceous plants to germinate in autumn when water and temperature conditions are suitable. These plants can then grow over winter to complete their life cycle in the following year. In this study, biomass of typical ephemeral plants that germinated in autumn was heavier than that of similar plants that germinated in spring, in terms of AGB, BGB, and TB. This result was consistent with the findings of Zhang et al. (2007). However, the R/S values were similar in ephemeral plants that germinated in spring and autumn, indicating that although plant size changed, the ratio of biomass allocated to above-ground and below-ground tissues remained constant. The reason for this result is that ephemeral plants that germinated in autumn had a much longer life span than corresponding plants that germinated in the following spring. Therefore, these plants can take advantage of additional time for absorbing resources to support their larger bodies.

## 4.2 Allometric Relationship Between AGB and BGB in Plants with Three Life Forms

Allocation of AGB and BGB reflects the responses of individual plants to natural selection pressures and their own developmental limitations. The isometric and allometric theory of biomass partitioning is widely accepted [?, ?, ?]. Global studies have supported the assumption that AGB scales one-to-one with respect to BGB for non-woody species across all treatments and species [?]. In addition, many studies—but not all—have supported the expectation that shoot biomass does not scale one-to-one with root biomass [?, ?, ?], as in the allometric scaling relationships between root biomass and shoot biomass of herbaceous species in Chinese grasslands [?]. In the current research, we investigated the relationships between AGB and BGB of plants with three different life forms and found that allocation patterns between AGB and BGB varied significantly among plants with different growth strategies. Specifically, ephemeral plants employed an isometric allocation pattern, while ephemeroid and annual plants adopted an allometric allocation pattern.

Biomass allocation is not only widely accepted to reflect a plant' s adaptation to diverse conditions but is also considered a trade-off between resource capture and resource utilization [?, ?]. For example, plants in water-limited or nutrient-poor ecosystems usually allocate more biomass to roots to acquire more water and nutrients from deeper soils than plants in water- and nutrient-rich ecosystems [?]. Additionally, the below-ground parts of some plants are modified into tuberous roots, rhizomes, or tubers for nutrient storage or other functions, and many species may therefore not conform to the isometric allocation relationship between AGB and BGB. This was further confirmed by our findings that cold desert plants with different life forms supported different biomass allocation hypotheses.

During their short growth period, ephemeral plants usually live in favorable hydrothermal conditions and are not limited by water or temperature resources; therefore, the distribution of biomass to above-ground and below-ground parts is isometric. Overall, cold desert plants follow specific biomass distribution models that allow them to adapt to the arid environment. Similarly, the relationship between AGB and BGB of plants in the alpine steppe and alpine meadow of the Tibetan Plateau supported the isometric allocation hypothesis [?], while biomass allocation of plants in the alpine grassland of the northern Tibetan Plateau followed the allometric allocation hypothesis [?, ?].

## Conclusions

Plant species have evolved specialized strategies to regulate their AGB and BGB allocation in order to adapt to diverse environments. The current study revealed large differences in biomass allocation patterns among plants with different life forms in cold deserts. Specifically, ephemeroid plants allocated more biomass to roots while annual plants allocated more biomass to shoots to adapt to their environments. Although ephemeral plants that germinated in autumn were larger than corresponding plants that germinated in spring, the R/S values of these plants remained the same. Furthermore, the slope of the regression relationship between AGB and BGB differed significantly among plants with different life forms. Our results support different biomass allocation hypotheses, with AGB and BGB partitioning following the allometric allocation hypothesis in ephemeroid and annual plants and the isometric hypothesis in ephemeral plants at the individual level.

**Acknowledgements**

This study was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA20020101) and the National Natural Science Foundation of China (31400394). We thank International Science Editing (http://www.internationalscienceediting.com) for editing this manuscript.

**References**

Aysajan A, Tan D Y, Omarxat T. 2012. Effects of vegetative growth, plant size and flowering order on sexual reproduction allocation of *Tulipa sinkiangensis*. Biodiversity Science, 20(3): 391-399. (in Chinese)

Barboni D, Harrison S P, Bartlein P J, et al. 2009. Relationships between plant traits and climate in the Mediterranean region: a pollen data analysis. Journal of Vegetation Science, 15(5): 635-646.

Blume-Werry G, Lindén Elin, Andresen L, et al. 2018. Proportion of fine roots, but not plant biomass allocation below ground, increases with elevation in arctic tundra. Journal of Vegetation Science, 29(2): 226-235.

Cella Pizarro L, Bisigato A J. 2010. Allocation of biomass and photoassimilates in juvenile plants of six Patagonian species in response to five water supply regimes. Annals of Botany, 106(2): 297-307.

Chen B M, Wang G X, Peng S L. 2009. Role of desert annuals in nutrient flow in arid area of Northwestern China: a nutrient reservoir and provider. Plant Ecology, 201(2): 401-409.

El-Sheikh M A, Abbadi G A, Bianco P M. 2010. Vegetation ecology of phytogenic hillocks (nabkhas) in coastal habitats of Jal Az-Zor National Park, Kuwait: Role of patches and edaphic factors. Flora-Morphology, Distribution, Functional Ecology of Plants, 205(12): 832-840.

Fan L L, Li Y, Tang L S, et al. 2013. Combined effects of snow depth and nitrogen addition on ephemeral growth at the southern edge of the Gurbantunggut Desert, China. Journal of Arid Land, 5(4): 500—510.

Fan L L, Tang L S, Wu L F, et al. 2014. The limited role of snow water in the growth and development of ephemeral plants in a cold desert. Journal of Vegetation Science, 25(3): 681-690.

Gill R A, Kelly R H, Parton W J, et al. 2002. Using simple environmental variables to estimate below-ground productivity in grasslands. Global Ecology and Biogeography, 11(1): 79-86.

Han B, Fan J W, Zhong H P. 2006. Grassland biomass of communities along gradient of the Inner Mongolia grassland transect. Journal of Plant Ecology, 30(4): 553-562. (in Chinese)

Huang G, Su Y G, Zhu L, et al. 2016. The role of spring ephemerals and soil microbes in soil nutrient retention in a temperate desert. Plant and Soil, 406(1-2): 43-54.

Lauenroth W K, Bradford J B. 2009. Ecohydrology of dry regions of the United States: precipitation pulses and intraseasonal drought. Ecohydrology, 2(2): 173-181.

Li X H, Li X L, Jiang D M, et al. 2009. A comparative study of the individual biomass and modular biomass of 70 herbaceous species found in the Horqin sandy land. Arid Zone Research, 26(2): 200-205. (in Chinese)

Li X R, Zhou H Y, Wang X P, et al. 2003. The effects of sand stabilization and revegetation on cryptogam species diversity and soil fertility in the Tengger Desert, Northern China. Plant and Soil, 251(2): 237-245.

Luo W T, Jiang Y, Lü X T, et al. 2013. Patterns of plant biomass allocation in temperate grasslands across a 2500-km transect in northern China. PLoS ONE, 8(8): e71749.

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.

Mckenna M F, Houle G. 2000. Why are annual plants rarely spring ephemerals? New Phytologist, 148(2): 295-302.

Mokany K, Raison R J, Prokushkin A S. 2006. Critical analysis of root: shoot ratios in terrestrial biomes. Global Change Biology, 12(1): 84-96.

Müller I, Schmid B, Weiner J. 2000. The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. Perspectives in Plant Ecology, Evolution and Systematics, 3(2): 115-127.

Niklas K J. 1994. Plant Allometry: The Scaling of Form and Process. Chicago: The University of Chicago Press: 1-343.

Niklas K J. 2004. Plant allometry: is there a grand unifying theory? Biological Reviews, 79(4): 871-889.

Noy-Meir I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics, 4(1): 25-51.

Oliveira N, Rodríguez-Soalleiro R, Pérez-Cruzado C, et al. 2018. Above- and below-ground carbon accumulation and biomass allocation in poplar short rotation plantations under Mediterranean conditions. Forest Ecology and Management, 428: 57-65.

Poorter H, Nagel O. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO , nutrients and water: a quantitative review. Functional Plant Biology, 27: 595-607.

Poorter H, Niklas K J, Reich P B, et al. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytologist, 193: 30-50.

Poorter H, Sack L. 2012. Pitfalls and possibilities in the analysis of biomass allocation patterns in plants. Frontiers in Plant Science, 3: 259, doi: 10.3389/fpls.2012.00259.

Qiu J, Tan D Y, Fan D Y. 2007. Characteristics of photosynthesis and biomass allocation of spring ephemerals in the Junggar Desert. Journal of Plant Ecology, 31(5): 883-891. (in Chinese)

Reich P B, Tjoelker M G, Waltes M B, et al. 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. Functional Ecology, 12(3): 327-338.

Reich P B. 2002. Root-shoot relations: optimality in acclimation and adaptation or the ° Emperor' s new clothes'' ? In: Waisel Y, Eshel A, Kafkafi U. Plant Roots, the Hidden Half. New York: Marcel Dekker Press, 205-220.

Scheck H J, Jackson R B. 2005. Mapping the global distribution of deep roots in relation to climate and soil characteristics. Geoderma, 126(1-2): 129-140.

Shipley B, Meziane D. 2002. The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. Functional Ecology, 16(3): 326-331.

Su J Q, Li X R, Li X J, et al. 2013. Effects of additional N on herbaceous species of desertified steppe in arid regions of China: a four-year field study. Ecological Research, 28(1): 21-28.

Tyree M T, Ewers F E. 1991. The hydraulic architecture of trees and other woody plants. New Phytologist, 119(3): 345-360.

Wang L, Niu K C, Yang Y H, et al. 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.

Wang X Q, Jiang J, Lei J Q, et al. 2003. The distribution of ephemeral vegetation on the longitudinal dune surface and its stabilization significance in the Gurbantunggut Desert. Acta Geographic Sinica, 58(4): 598-605. (in Chinese)

Wang X Q, Jiang J, Wang Y C, et al. 2006. Responses of ephemeral plant germination and growth to water and heat conditions in the southern part of Gurbantunggut Desert. Chinese Science Bulletin, 51(Suppl. 1): 110–116.

Weiner J. 2004. Allocation, plasticity and allometry in plants. Perspectives in Plant Ecology, Evolution and Systematics, 6(4): 207–221.

Wolf S A, Nickling W G. 1993. The protective role of sparse vegetation in wind erosion. Progress in Physical Geography: Earth and Environment, 17(1): 50–68.

Wright I J, Reich P B, Westoby M. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. Functional Ecology, 15(4): 423–434.

Wu J B, Hong J T, Wang X D, et al. 2013. Biomass partitioning and its relationship with the environment factors at the Alpine Steppe in Northern Tibet. PLoS ONE, 8(12): e81986.

Xie J B, Tang L S, Wang Z Y, et al. 2012. Distinguishing the biomass allocation variance resulting from ontogenetic drift or acclimation to soil texture. PLoS ONE, 7(7): e41502.

Yan B G, Ji Z H, Fan B, et al. 2016. Plants adapted to nutrient limitation allocate less biomass into stems in an arid-hot grassland. New Phytologist, 211(4): 1232–1240.

Yang Y H, Fang J Y, Ji C J, et al. 2009. Above- and belowground biomass allocation in Tibetan grasslands. Journal of Vegetation Science, 20(1): 177–184.

Yang Y H, Fang J Y, Ma W H, et al. 2010. Large-scale pattern of biomass partitioning across China’ s grasslands. Global Ecology & Biogeography, 19(2): 268–277.

Zeng C X, Wu J S, Zhang X Z. 2015. Effects of grazing on above- vs. below-ground biomass allocation of alpine grasslands on the Northern Tibetan Plateau. PLoS ONE, 10(8): e0135173.

Zeng X L, Liu T, Shen X Y, et al. 2011. Environment-dependence of seed germination in autumn in Gurbantonggut Desert. Chinese Journal of Ecology, 30(8): 1604–1611. (in Chinese)

Zhang T, Sun Y, Tian C Y, et al. 2007. Ecological and biological differences between spring and autumn plants of two desert ephemerals. Journal of Plant Ecology, 31(6): 1174–1180. (in Chinese)

Zhou H F, Li Y, Tang Y, et al. 2009. The characteristics of the snow-cover and snow melt water storage in Gurbantunggut Desert. Arid Zone Research, 26(3): 312–317. (in Chinese)

Zhou X B, Zhang Y M, Ji X H, et al. 2011. Combined effects of nitrogen deposition and water stress on growth and physiological responses of two annual desert plants in northwestern China. Environmental and Experimental Botany, 74: 1–8.

Zhou X B, Zhang Y M, Niklas K J. 2014. Sensitivity of growth and biomass allocation patterns to increasing nitrogen: a comparison between ephemerals and annuals in the Gurbantunggut Desert, north-western China. Annals of Botany, 113(3): 501–511.

Zong N, Chai X, Shi P L, et al. 2017. Effects of warming and nitrogen addition on plant photosynthate partitioning in an alpine meadow on the Tibetan Plateau. Journal of Plant Growth Regulation, 37(3): 803–812.

*Note: Figure translations are in progress. See original paper for figures.*