Biomass Allocation Characteristics of Erodium oxyrhynchum in Different Habitats and Germination Types: Postprint

Authors: Zhang Yuanyuan, Meng Huanhuan, Zhou Xiaobing

Date: 2022-03-28T16:36:56Z

Abstract

Ephemeral plants represent an important functional group in desert ecosystems, exhibiting diverse habitats and asynchronous germination characteristics in many species. Biomass accumulation and allocation patterns reflect plant responses and adaptive traits to environmental conditions; thus, investigating biomass allocation strategies of ephemeral plants across different environments enhances understanding of their survival strategies. This study examined spring-germinated individuals of *Erodium oxyrhinchum* from three natural biological soil crust habitats [Bare Sand-Spring Germination (BS), Algal-Spring Germination (AS), and Lichen-Spring Germination (LS)], and summer-germinated individuals from bare sand areas [Summer Germination in Bare Sand (SG)]. Using whole-plant excavation to quantify aboveground and belowground biomass, we systematically compared differences in biomass allocation and allometric relationships among the four types to explore variability and conservatism in resource allocation strategies. The results demonstrated: (1) Aboveground, belowground, and total biomass per plant of *E. oxyrhinchum* generally followed the pattern BS>AS>LS=SG, while root-to-shoot ratios exhibited SG=LS=AS>BS. (2) BS and SG plants displayed isometric relationships between aboveground and belowground biomass, whereas AS and LS habitats showed allometric relationships, though all four types shared a common allometric exponent (0.8843). (3) Root-to-shoot ratios in AS and LS habitats decreased allometrically with increasing individual size, while those in BS and SG remained relatively constant. These findings indicate that biomass allocation in *E. oxyrhinchum* is influenced by both environmental conditions and ontogeny, manifesting pronounced plasticity that reflects a trade-off between conservatism and plasticity in resource allocation strategies.

ChinaRxiv 中X

Full Text

Biomass Allocation Patterns of *Erodium oxyrhinchum* in Different Habitats and Germination Types in the Gurbantunggut Desert, China

ZHANG Yuanyuan[1,2], **MENG Huanhuan**[1,2], **ZHOU Xiaobing**[2], **YIN Benfeng**[2], **ZHOU Duoqi**[1], **TAO Ye**[2]

[1]Anhui Province Key Laboratory of Biodiversity Study and Ecology Conservation in Southwest Anhui, College of Life Sciences, Anqing Normal University, Anqing 246133, Anhui, China
[2]State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, Xinjiang, China

Abstract

Ephemeral plants represent an important functional group in desert ecosystems, characterized by diverse habitats and, in many species, isochronous germination patterns. Plant biomass accumulation and allocation reflect environmental responses and adaptive strategies; therefore, investigating biomass allocation patterns of ephemeral plants under varying environmental conditions enhances our understanding of their survival strategies. This study examined *Erodium oxyrhinchum* individuals that germinated in summer in bare sand and in spring across three natural habitats: bare sand, algal crust, and lichen crust. Using whole-plant excavation to obtain aboveground and belowground biomass, we systematically compared differences in biomass distribution and allometric growth relationships among four types—Bare Sand-Spring Germination (BS), Algal Crust-Spring Germination (AS), Lichen Crust-Spring Germination (LS), and Summer Germination in Bare Sand (SG)—to explore the variability and conservatism of their resource allocation strategies.

The results revealed three key patterns. First, individual aboveground, belowground, and total biomass generally followed the hierarchy BS > AS > LS = SG, while root-to-shoot ratios (R/S) showed the opposite pattern: SG = LS = AS > BS. Second, aboveground and belowground biomass exhibited isometric relationships in BS and SG plants, but allometric relationships in AS and LS plants; nevertheless, all four types shared a common allometric scaling exponent (0.8843). Third, the R/S ratios of AS and LS decreased allometrically with increasing plant size, whereas those of BS and SG remained relatively constant. These findings demonstrate that biomass allocation in *E. oxyrhinchum* is influenced by both external environmental conditions and individual development, exhibiting pronounced plasticity that reflects a trade-off between conservative and plastic resource allocation strategies.

Keywords: ephemeral plants; *Erodium oxyrhinchum*; biomass allocation; allometry; biological soil crust; summer germination

1. Introduction

1.1 Study Area Overview

The Gurbantunggut Desert (44°11 -46°21 N, 84°31 -90°00 E) lies in the heart of the Junggar Basin in northern Xinjiang and represents China' s largest fixed and semi-fixed desert. The region receives average annual precipitation of 70–120 mm, with approximately 150 mm in the central desert, while annual potential evaporation reaches 2000–2800 mm. Extreme temperatures exceed 30°C, with minimum temperatures dropping to -30°C. The active accumulated temperature 10°C ranges from 3000 to 3500°C, and average relative humidity varies between 50% and 60%. Dominant plant species include *Haloxylon ammodendron*, *Artemisia songarica*, *Ephedra przewalskii*, and *Haloxylon persicum*, while ephemeral and quasi-ephemeral plants constitute the primary spring vegetation. The desert surface is extensively covered by biological soil crusts, primarily algal crusts, lichen crusts, and moss crusts, which create distinct microhabitats with lower soil moisture compared to bare sand.

1.2 Field Sample Collection

Sampling was conducted in the hinterland of the Gurbantunggut Desert during two periods. Spring-germinated plants were collected in mid-April 2019 when they reached the flowering stage. Three habitat types were established: bare sand spring germination (BS), algal crust spring germination (AS), and lichen crust spring germination (LS). For each habitat, five 5 m × 5 m quadrats were set up as replicates. Several complete, healthy plants were selected from each quadrat and excavated using the whole-plant method. In late July 2019, following a substantial rainfall event, *E. oxyrhinchum* rapidly germinated, producing summer-germinated individuals (SG). To compare with spring-germinated samples, SG plants were collected in early August 2019 from bare sand habitats only, using the same sampling protocol. Autumn-germinated plants were excluded as they typically overwinter and thus fall outside the strict definition of ephemeral plants. For brevity, all *E. oxyrhinchum* plants from different habitats and germination times are collectively referred to as "four types," with "habitat" used when comparing crust types and "type" used when comparing with summer-germinated plants. Final sample sizes were 50, 45, 45, and 40 individuals for BS, AS, LS, and SG, respectively. Fresh samples were placed in labeled envelopes and transported in coolers to the laboratory for further processing.

1.3 Biomass Calculation

Fresh samples were processed by separating aboveground and belowground mature tissues into envelopes and oven-drying at 75°C for 48 hours. Dried samples were weighed using an electronic balance (precision: 0.0001 g) to determine aboveground biomass (AGB), belowground biomass (BGB), total biomass (TB), and root-to-shoot ratio (R/S). All biomass metrics are presented as means ± standard error.

---

2. Results and Analysis

2.1 Biomass Characteristics of Different Plant Types

One-way ANOVA revealed significant differences in aboveground biomass (AGB), belowground biomass (BGB), and total biomass (TB) among the four types ($P < 0.05$). The biomass hierarchy was consistently BS > AS > LS = SG. Specifically, BS plants exhibited significantly greater AGB (0.1367 ± 0.0095 g), BGB (0.0553 ± 0.0031 g), and TB (0.1920 ± 0.0125 g) compared to AS and LS plants ($P < 0.05$), while SG plants showed the lowest values (AGB: 0.0164 ± 0.0015 g; BGB: 0.0103 ± 0.0131 g; TB: 0.0267 ± 0.0145 g). Notably, SG biomass did not differ significantly from LS ($P > 0.05$). Root-to-shoot ratios (R/S) also differed significantly ($P < 0.05$), following the pattern SG = LS = AS > BS, indicating that SG, LS, and AS plants allocated proportionally more biomass to roots than BS plants.

2.2 Allometric Relationships Between Aboveground and Belowground Biomass

Allometric analysis using reduced major axis (RMA) regression revealed highly significant ($P < 0.01$) power-law relationships between aboveground and belowground biomass across all types. The allometric relationship formula Y = X^ was log-transformed to linear form for parameter estimation, where represents the scaling exponent and the normalization constant. BS and SG plants exhibited isometric relationships (95% confidence intervals for included 1.0), whereas AS and LS plants showed significant allometric relationships (< 1.0). Despite these differences, common slope tests indicated that all four types shared a common allometric exponent of 0.8843 ($P > 0.05$ for slope heterogeneity), suggesting a fundamental conservatism in resource allocation scaling despite environmental variation.

2.3 Relationship Between Biomass Allocation and Individual Size

The relationship between R/S and individual plant size (quantified as AGB, BGB, or TB) varied among types. For AS and LS plants, R/S decreased allometrically with increasing plant size, with particularly strong declines in LS ($P < 0.01$). In contrast, BS and SG plants maintained relatively constant R/S ratios across size classes, indicating size-independent allocation patterns. These results confirm that both ontogenetic drift and environmental conditions influence biomass allocation in *E. oxyrhinchum*.

---

3. Discussion

3.1 Biomass Allocation Characteristics Across Types

When environmental conditions change, plants adjust biomass accumulation and allocation, reflecting phenotypic plasticity and adaptive responses. Arid and semi-arid temperate desert ecosystems feature extreme temperatures and limited water availability, with sparse vascular vegetation and poor nutrient cycling, often resulting in biological soil crust-covered surfaces. Despite these harsh conditions, *E. oxyrhinchum* successfully colonizes crust surfaces due to its specialized diaspore morphology. Previous studies have shown that biological soil crusts can either promote or inhibit plant growth depending on water availability. Our findings that AS and LS plants had lower biomass than BS plants likely reflect reduced soil moisture in crust habitats. Long-term observations indicate that *E. oxyrhinchum* seeds germinate when soil moisture exceeds a threshold, which can occur during summer rainfall events. However, the ephemeral water supply cannot sustain the full life cycle, leading to incomplete development and significantly smaller biomass in SG plants compared to spring-germinated individuals.

Water availability emerges as the primary factor limiting *E. oxyrhinchum* growth. Kidron's research in the Negev Desert demonstrated that crust-covered soils had lower moisture than bare sand, resulting in poorer annual plant performance. Similarly, Zhuang et al. found that crust habitats in the Gurbantunggut Desert had significantly lower soil moisture, reducing biomass of *E. oxyrhinchum* and *Hyalea pulchella*. Our results align with these findings, showing that BS plants, with access to relatively abundant water from spring snowmelt, allocated less biomass to roots (lower R/S) compared to AS and LS plants that experienced greater water stress. This pattern supports the optimal allocation hypothesis, which predicts increased investment in resource-acquiring organs (roots) under limiting conditions.

3.2 Allometric Relationships Among Component Biomass

Allometric relationships reveal fundamental scaling principles governing biological traits relative to organism size. While many studies suggest universal patterns—such as isometric scaling between aboveground and belowground biomass in woody plants—others emphasize species-specific responses driven by genetic constraints and natural selection. Our results show that *E. oxyrhinchum* exhibits both isometric (BS, SG) and allometric (AS, LS) relationships between aboveground and belowground biomass, yet maintains a common scaling exponent across all types. This suggests that while environmental conditions modify the absolute rates of biomass allocation, the underlying scaling relationship remains conserved, likely reflecting species-specific genetic constraints.

The isometric relationship in BS plants indicates proportional allocation between aboveground and belowground compartments under favorable spring conditions. In contrast, the allometric relationship in AS and LS plants (< 1.0)

indicates that belowground biomass increases at a slower rate than aboveground biomass, possibly due to nitrogen fixation by algal crusts partially offsetting water stress. The shared exponent of 0.8843 across all types underscores a fundamental conservatism in biomass scaling, consistent with findings that environmental variation alters biomass ratios without changing underlying allocation patterns.

3.3 Biomass Allocation and Individual Size

Ontogenetic drift significantly influences biomass allocation, with most herbaceous plants showing decreasing root allocation as individuals grow larger. Ephemeral plants, with their compressed life cycles, typically prioritize aboveground growth and reproduction over root investment. Our results partially support this pattern: R/S ratios decreased with plant size in AS and LS habitats, particularly in LS ($P < 0.01$), indicating ontogenetic shifts in allocation. However, BS and SG plants maintained constant R/S ratios across size classes, suggesting that water availability in bare sand habitats may relax size-dependent allocation constraints.

The contrasting patterns between habitat types likely reflect differential water stress. In crust habitats, smaller plants initially allocate more biomass to roots to enhance water acquisition, while larger plants shift allocation toward aboveground structures to maximize reproductive output. In SG plants, the most severely stressed type, the R/S ratio remained size-independent, possibly because extreme environmental conditions override typical ontogenetic patterns. These findings support Hutchings and John' s conclusion that both ontogeny and environmental heterogeneity shape root:shoot partitioning.

---

4. Conclusions

Analysis of biomass allocation in four types of the ephemeral plant *Erodium oxyrhinchum* across different habitats and germination times yielded three main conclusions:

1. **Biomass hierarchy**: Individual aboveground, belowground, and total biomass followed the pattern BS > AS > LS = SG, with water stress being the primary driver of inter-type differences. *E. oxyrhinchum* adjusted R/S ratios to cope with drought, showing greater root investment in water-limited habitats.

2. **Allometric scaling**: While BS and SG plants exhibited isometric relationships between aboveground and belowground biomass, AS and LS plants showed allometric relationships with slower belowground scaling. All types shared a common scaling exponent (0.8843), indicating conserved allocation principles despite environmental variation.

3. **Ontogenetic plasticity**: R/S ratios decreased allometrically with plant size in AS and LS habitats but remained constant in BS and SG. This demonstrates that both individual development and environmental conditions influence biomass allocation, with *E. oxyrhinchum* employing plastic strategies to optimize growth under desert conditions.

These results reveal that *E. oxyrhinchum* employs flexible resource allocation strategies to adapt to heterogeneous desert environments, providing insights into the life history strategies of ephemeral plants and informing scientific management of desert ecosystems.

References

[1] Wang Xueqin, Jiang Jin, Lei Jiaqiang, et al. The distribution of ephemeral vegetation on the longitudinal dune surface and its stabilization significance in the Gurbantunggut Desert[J]. *Acta Geographica Sinica*, 2003, 58(4): 598-605.

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

[3] Tao Ye, Zhang Yuanming. Biomass allocation patterns and allometric relationships of six ephemeroid species in Junggar Basin, China[J]. *Acta Prataculturae Sinica*, 2014, 23(2): 38-48.

[4] de Kroon H, Huber H, Stuefer J F, et al. A modular concept of phenotypic plasticity in plants[J]. *New Phytologist*, 2005, 166(1): 73-82.

[5] Bloom A J, Chapin F S, Mooney H A, et al. Resource limitation in plants: An economic analogy[J]. *Annual Review of Ecology*, 1985, 16: 363-392.

[6] Yin Q L, Tian T T, Han X H, et al. The relationships between biomass allocation and plant functional trait[J]. *Ecological Indicators*, 2019, 102: 302-308.

[7] Niklas K J. Modelling below and above ground biomass for non-woody and woody plants[J]. *Annals of Botany*, 2005, 95(2): 315-321.

[8] Wang Shasha, Zhang Yuanming. Morphological characters of *Erodium oxyrrhynchum* diaspore[J]. *Chinese Journal of Ecology*, 2010, 29(5): 855-861.

[9] Lui H L, Chen Y F, Zhang L W, et al. Is the life history flexibility of cold desert annuals broad enough to cope with predicted climate change? The case of *Erodium oxyrhinchum* in Central Asia[J]. *Biology*, 2021, 10(8): 780.

[10] Li Bin, Wu Zhifang, Tao Ye, et al. Effects of biological soil crust type on herbaceous diversity in the Gurbantunggut Desert[J]. *Arid Zone Research*, 2021, 38(2): 438-449.

[11] Zhuang W W, Serpe M, Zhang Y M, et al. The effect of lichen-dominated biological soil crusts on growth and physiological characteristics of three plant species in a temperate desert of Northwest China[J]. *Plant Biology*, 2015, 17(6): 1165-1175.

[12] Wu Nan, Zhang Jing, Zhang Yuanming. Effects of snow cover and arbuscular mycorrhizal fungi network on the seedling growth of *Erodium oxyrrhynchum*[J]. *Arid Zone Research*, 2018, 35(3): 624-632.

[13] Xiao Yao, Tao Ye, Zhang Yuanming. Biomass allocation and leaf stoichiometric characteristics in four desert herbaceous plants during different growth periods in the Gurbantünggüt Desert, China[J]. *Chinese Journal of Plant Ecology*, 2014, 38(9): 929-940.

[14] Zhang Liyun, Chen Changdu. On the general characteristics of plant diversity of Gurbantunggut Sandy Desert[J]. *Acta Ecologica Sinica*, 2002, 22(11): 1923-1933.

[15] Li Xinrong, Zhang Yuanming, Zhao Yunge. A study of biological soil crusts: Recent development, trend and prospect[J]. *Advances in Earth Science*, 2009, 24(1): 11-24.

[16] Kidron G J. The negative effect of biocrusts upon annual plant growth on sand dunes during extreme droughts[J]. *Journal of Hydrology*, 2014, 508(1): 128-136.

[17] Zhuang Weiwei. Effect of lichen-dominated biological soil crusts on growth, physiology and elements uptake of herbaceous plant in Gurbantunggut Desert[D]. Beijing: University of Chinese Academy of Sciences, 2015.

[18] Song G, Li X R, Hui R, et al. Effect of biological soil crusts on seed germination and growth of an exotic and two native plant species in an arid ecosystem[J]. *Plos One*, 2017, 12(10): e0185839.

[19] Godínez-Alvarez H, Morín C, Rivera-Aguilar V. Germination, survival and growth of three vascular plants on biological soil crusts from a Mexican tropical desert[J]. *Plant Biology*, 2012, 14(1): 157-162.

[20] Li X R, Jia X H, Long L Q, et al. Effects of biological soil crusts on seed bank, germination and establishment of two annual plant species in the Tengger Desert (N China)[J]. *Plant and Soil*, 2005, 277(1-2): 375-385.

[21] Zhang Yuanming, Nie Huali. Effects of biological soil crusts on seedling growth and element uptake in five desert plants in Junggar Basin, western China[J]. *Chinese Journal of Plant Ecology*, 2011, 35(4): 380-388.

[22] Chen Y F, Zhang L W, Shi X, et al. Life history responses of spring and autumn germinated ephemeral plants to increased nitrogen and precipitation in the Gurbantunggut Desert[J]. *Science of the Total Environment*, 2019, 659: 756-763.

[23] Zang Y X, Min X J, de Dios V R, et al. Extreme drought affects the productivity, but not the composition, of a desert plant community in Central Asia differentially across microtopographies[J]. *Science of the Total Environment*, 2020, 717: 137251.

[24] Wang Yanli, Qi Xinyu, Yang Haotian, et al. Morphological structure and biomass allocation of *Echinops gmelini* in different habitats[J]. *Journal of Desert Research*, 2018, 38(4): 756-764.

[25] Zhou Bing, Yan Xiaohong, Xiao Yi' an, et al. Module biomass of *Ageratum conyzoides* populations in different habitats[J]. *Acta Ecologica Sinica*, 2015, 35(8): 2602-2608.

[26] Zhang Tao, Sun Yu, Tian Changyan, et al. Ecological and biological differences between spring and autumn plants of two desert ephemeral species[J]. *Chinese Journal of Plant Ecology*, 2007, 31(6): 1174-1180.

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

[28] Niklas K J. A phyletic perspective on the allometry of plant biomass partitioning patterns and functionally equivalent organ categories[J]. *New Phytologist*, 2006, 171(1): 27-40.

[29] Ding Junxiang, Fan Lianlian, Li Yan, et al. Biomass allocation and allometric relationships of six desert herbaceous plants in the Gurbantunggut Desert[J]. *Journal of Desert Research*, 2016, 36(5): 1323-1330.

[30] Qiu Dong, Wu Ganlin, Zhou Xiaobing, et al. Characteristics of modular traits and interrelationships of the ephemeral species *Plantago minuta*[J]. *Prataculturalural Science*, 2017, 34(4): 744-752.

[31] Xie J B, Xu G Q, Jenerette G D, et al. Apparent plasticity in functional traits determining competitive ability and spatial distribution: A case from desert[J]. *Scientific Reports*, 2015, 5: 12174.

[32] Zhong Peifang, Jia Xiangyang, Tian Yanli, et al. Effect of elevated CO and precipitation regimes on allocation patterns of above- and belowground biomass of desert shrub *Reaumuria soongorica*[J]. *Acta Agrestia Sinica*, 2019, 27(6): 1537-1544.

[33] Chen Dongliang. Plant allometric study of biomass allocation pattern and biomass production rates[D]. Lanzhou: Lanzhou University, 2007.

[34] Li Lang, Li Yibo, Ma Quanhui, et al. Aboveground biomass modeling and allometric growth characteristics of *Artemisia capillaris* Thunb. under different water availabilities[J]. *Chinese Journal of Ecology*, 2020, 39(1): 337-348.

[35] Geng Yupeng, Zhang Wenju, Li Bo, et al. Phenotypic plasticity and invasiveness of alien plants[J]. *Biodiversity Science*, 2004, 12(4): 447-455.

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

[37] Qi Y L, Wei W, Chen C G, et al. Plant root shoot biomass allocation over diverse biomes: A global synthesis[J]. *Global Ecology and Conservation*, 2019, 18: 1-14.

[38] Wilson J B. A review of evidence on the control of shoot:root ratio, in relation to models[J]. *Annals of Botany*, 1988, 61(4): 433-449.

[39] Hutchings M J, John E A. The effects of environmental heterogeneity on root growth and root/shoot partitioning[J]. *Annals of Botany*, 2004, 94(1): 1-8.

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