Effects of Stocking Rate on Resource Allocation Patterns of Artemisia frigida Populations in the Desert Steppe of Inner Mongolia (Postprint)

Authors: Gu Chen, Chen Wanjie, Du Yufan, Wang Yating, Zhao Tianqi, Zhao Mengli

Date: 2017-04-18T00:00:00+00:00

Abstract

Investigating plant resource allocation patterns to reveal mechanisms underlying responses to environmental change holds significant ecological importance. This study examined Artemisia frigida populations in the Stipa breviflora steppe of Inner Mongolia, establishing a randomized block experiment with four stocking rate levels to explore the influence patterns of stocking rate on the resource allocation pattern of this population, based on changes in aboveground, belowground, and component biomass of Artemisia frigida, thereby providing a reference for degraded grassland restoration and rational grazing management. The results showed: (1) The height of Artemisia frigida populations decreased significantly with increasing stocking rate ($P<0.05$), moderate and heavy grazing significantly reduced the coverage of this population ($P<0.05$), and light grazing significantly increased population density ($P<0.05$); (2) Aboveground, belowground, and total biomass all decreased significantly with increasing stocking rate ($P<0.05$), and the interannual effects over 3 years and the interaction effects between stocking rate and year on total, aboveground, and belowground biomass were all significant ($P<0.05$); (3) The overall pattern of biomass allocation was root > stem > leaf > flower/fruit, and the biomass of each component decreased with increasing stocking rate; (4) The biomass allocation proportions of different components responded differently to stocking rate: moderate and heavy grazing significantly increased biomass allocation to roots ($P<0.05$), stem biomass allocation increased significantly under light grazing and decreased significantly under heavy grazing ($P<0.05$), light and moderate grazing significantly promoted leaf biomass allocation ($P<0.05$), and flower/fruit biomass allocation decreased significantly with increasing stocking rate ($P<0.05$); (5) With increasing stocking rate, the sexual reproductive capacity of Artemisia frigida weakened, while its asexual reproductive capacity enhanced.

Full Text

Stocking Rates Affect the Resource Allocation Patterns of *Artemisia frigida* in the Inner Mongolian Desert Steppe

GU Chen, CHEN Wanjie, DU Yufan, WANG Yating, ZHAO Tianqi, ZHAO Mengli*

College of Ecology and Environmental Science, Inner Mongolia Agricultural University, Hohhot 010019, China

Abstract

Studying plant resource allocation patterns to reveal their response mechanisms to environmental change is of crucial ecological significance. Using *Artemisia frigida* populations in the desert steppe of Inner Mongolia as the research object, we established a randomized block experiment with four stocking rate levels to investigate how grazing intensity affects the resource allocation patterns of this species, providing a reference for degraded grassland restoration and rational grazing management. Our results indicated that: (1) Plant height decreased significantly with increasing stocking rates ($P < 0.05$), and moderate and heavy grazing significantly reduced population coverage, while light grazing remarkably increased population density ($P < 0.05$). (2) Aboveground biomass, belowground biomass, and total biomass all decreased significantly with increasing stocking rates ($P < 0.05$), and the effects of interannual variation, stocking rates, and their interactions on these biomass measures were all significant ($P < 0.05$). (3) The biomass allocation ratio of different modules responded differently to stocking rates: moderate and heavy grazing significantly increased root biomass allocation ($P < 0.05$), while stem biomass allocation increased significantly under light grazing but decreased significantly under heavy grazing ($P < 0.05$). Light and moderate grazing significantly promoted leaf biomass allocation ($P < 0.05$), whereas flower and fruit biomass allocation decreased significantly with increasing stocking rates ($P < 0.05$). (4) The overall biomass allocation pattern was root > stem > leaf > flower/fruit. (5) With increasing stocking rates, the sexual reproduction capacity of *A. frigida* decreased ($P < 0.05$), while its asexual propagation capacity increased.

Keywords: livestock grazing; *Stipa breviflora*; steppe biome; population characteristics; biomass allocation ratios

Introduction

Since Harper [1] proposed plant modular theory, studying resource allocation patterns based on module biomass has become an important focus in ecological research. The balanced growth hypothesis, optimal allocation theory, and functional equilibrium hypothesis all indicate that plants trade off biomass allocation among roots, stems, and leaves to compete for essential resources such as water and heat [2-3]. This reflects plant adaptation to environmental change to some extent. Many scholars have investigated how warming, shading, and other factors affect plant resource allocation [7-8]. Grazing is one of the main factors influencing plant resource allocation patterns, altering water, heat, and other environmental factors as well as biological factors within the grassland ecosystem [9]. The mechanisms through which grazing affects plant resource allocation are complex, and studying these effects has important ecological significance.

Artemisia frigida is a small semi-shrub in the Asteraceae family with high nutritional value and strong regeneration capacity [10], serving as a primary forage grass in winter and spring pastures and maintaining high growth and reproductive ability even under heavy grazing pressure, thus occupying an important position in livestock production [11]. In Inner Mongolian grasslands, *A. frigida* is a companion species that can become dominant during degradation succession. It acts as a positive quantitative indicator plant for grazing and can either facilitate recovery toward grassland or continue degrading and eventually disappear [11, 15]. Research on how grazing affects *A. frigida* population characteristics and biomass allocation patterns is therefore crucial for understanding community structure and function [12-14].

This study used *A. frigida* populations in desert steppe as the research object, examining changes in aboveground, belowground, and modular biomass to explore how stocking rates affect population characteristics and resource allocation patterns. We aimed to answer: (1) How do *A. frigida* population height, coverage, and density change with stocking rates? (2) How do aboveground, belowground, and total biomass vary under different stocking rates? (3) How does the resource allocation ratio of each module change with stocking rates? (4) How is the reproductive strategy of *A. frigida* affected by stocking rates? By analyzing the relationship between population characteristics, resource allocation patterns, and stocking rates, we provide references for degraded grassland restoration and grazing management.

1. Study Site Description

The experimental site is located at the Desert Steppe Experimental Base of the Inner Mongolia Academy of Agricultural Sciences in Gengtala Grassland, Siziwang Banner, northwest Ulanqab City, Inner Mongolia Autonomous Region (41°47 17 N, 111°53 46 E). The area features a temperate continental monsoon climate with flat, open terrain at an elevation of 1450 m. The mean annual temperature is 3.4°C, with the hottest month averaging 21.5–24.0°C. Annual accumulated temperature 0°C is 2500–3100°C, and 10°C is 2200–2500°C, lasting 90–115 days. Mean annual sunshine hours are 3117.7 h. Precipitation is concentrated from June to September, accounting for 70–80% of the annual total, with mean annual precipitation of 299.4 mm and high interannual variability. Annual evaporation is approximately 2300 mm, about 7.7 times the precipitation, creating arid conditions.

The vegetation type is *Stipa breviflora* desert steppe. The plant community comprises multiple species, primarily perennial herbs including *Stipa breviflora*, *Cleistogenes songorica*, *Convolvulus ammannii*, *Heteropappus altaicus*, *Allium tenuissimum*, *Allium mongolicum*, and shrubs such as *Caragana microphylla*, *Caragana stenophylla*, and semi-shrubs including *Ceratoides latens*, *Kochia prostrata*, and *Artemisia frigida*. The soil is light chestnut with low organic matter content, approximately 40–50 cm thick, with a calcic horizon that is hard and has poor permeability.

2. Methods

2.1 Experimental Design The grazing experiment was established in 2011 on a *Stipa breviflora* grassland in Siziwang Banner, Inner Mongolia. A relatively flat area was selected and fenced to create a 50 hm^2 experimental site. A complete randomized block design was used, dividing the fenced area into four blocks, each containing four stocking rate treatments: control (CK), light grazing (LG), moderate grazing (MG), and heavy grazing (HG), with stocking rates of 0, 0.91, 1.82, and 2.71 sheep units/hm^2/year, respectively. Each treatment plot was approximately 4.4 hm^2. Grazing occurred from June to November each year (six months), using local adult Mongolian wether sheep. Sheep numbers per plot were 0, 4, 8, and 12, respectively. Within each block, the four treatments were randomly arranged [Figure 1: see original paper].

2.2 Measurement Methods Before grazing began each year, three 1 m × 1 m quadrats were fenced in each plot to measure community characteristics. Field sampling was conducted in mid-August during the peak biomass period. Within the fenced quadrats, we measured the height, coverage, and density of each population. Additionally, three replicate random samples were taken from *A. frigida* monoculture patches in each plot, using a 30 cm × 30 cm × 40 cm soil core to ensure complete aboveground-belowground connection. Aboveground parts were clipped at ground level and separated into stems, leaves, and flowers/fruits. Belowground parts were placed in root bags, brought back to the laboratory, washed clean, and other plant roots and debris were removed to obtain belowground biomass. All aboveground modules and belowground parts were oven-dried at 65°C for 48 hours before weighing.

2.3 Data Analysis Experimental data were organized and charted using Excel 2013. Differences in *A. frigida* population characteristics and resource allocation patterns among treatments were analyzed using one-way ANOVA at a significance level of $= 0.05$. Differences in treatment and interannual interactions were analyzed using two-factor ANOVA with SAS 9.4.

3. Results

3.1 Effects of Stocking Rate on *A. frigida* Population Characteristics Stocking rate showed consistent effects on *A. frigida* coverage and height. Compared with the control, moderate and heavy grazing significantly reduced population height by 39% and 62%, respectively ($P < 0.05$). Light grazing did not differ significantly from the control ($P > 0.05$). Coverage was significantly reduced by moderate and heavy grazing ($P < 0.05$), while light grazing increased population density significantly ($P < 0.05$) [Figure 2: see original paper].

3.2 Effects of Stocking Rate on *A. frigida* Biomass Aboveground, belowground, and total biomass all decreased significantly with increasing stocking rates ($P < 0.05$). The control showed the highest biomass, followed by light grazing, with moderate and heavy grazing showing the lowest values. The 3-year average total biomass in control plots was approximately 3.9, 10.2, and 14.4 times that of light, moderate, and heavy grazing plots, respectively. Interannual effects and the interaction between stocking rate and year were significant for total, aboveground, and belowground biomass ($P < 0.05$) .

Stocking rate also significantly affected the biomass of each module. Stem, leaf, and flower/fruit biomass all decreased significantly with increasing stocking rates ($P < 0.05$). Control stem biomass was 2.7, 6.8, and 14.4 times that of light, moderate, and heavy grazing, respectively. Leaf biomass in control plots was 1.1, 6.3, and 19.0 times that of light, moderate, and heavy grazing, respectively. Flower/fruit biomass was 11.0, 63.4, and 190.3 times that of light, moderate, and heavy grazing, respectively. Flowers and fruits nearly disappeared under moderate and heavy grazing [Figure 3: see original paper].

3.3 Effects of Stocking Rate on *A. frigida* Resource Allocation The overall biomass allocation pattern of *A. frigida* was root > stem > leaf > flower/fruit. Stocking rate affected resource allocation to different modules differently. Root allocation ratio increased with stocking rate, reaching 61.3% under heavy grazing compared to 43.9% and 49.4% in control and light grazing, respectively ($P < 0.05$). Stem allocation ratio first increased then decreased with stocking rate, peaking at 29.7% under light grazing and reaching its lowest value of 20.2% under heavy grazing ($P < 0.05$). Leaf allocation showed a similar trend, with light and moderate grazing showing 23.65% and 22.35% allocation, respectively, compared to 17.1% (control) and 17.6% (heavy grazing). Flower/fruit allocation decreased significantly with increasing stocking rate ($P < 0.05$), from 12.7% in the control to 4.9% (light grazing), 1.9% (moderate grazing), and 1.0% (heavy grazing) [Figure 4: see original paper].

4. Discussion and Conclusion

Grazing is an important influencing factor and evolutionary driving force in natural grasslands. When climate conditions are consistent, livestock grazing becomes the dominant factor controlling grassland community characteristics, with effects exceeding other environmental factors [12]. Our results show that *A. frigida* coverage and height decreased significantly with increasing stocking rates, while light grazing significantly increased density. The prostrate degree of *A. frigida* stems increased gradually with grazing intensity, with height declining sharply. As grazing intensity increased, the proportion of tall grasses like *Stipa breviflora* decreased and community height was reduced, weakening the light competition that drives *A. frigida* elongation growth. The species' dwarfing strategy to avoid livestock herbivory represents an adaptation to overgrazing [16].

Grazing directly affects plants by consuming stems and leaves, reducing leaf area index and interfering with normal growth and development. Grazing causes photosynthetic organs to become miniaturized, disrupting carbohydrate synthesis and reducing individual biomass [17]. With increasing stocking rates, livestock consumption and trampling damage *A. frigida*, reducing photosynthetic area, regeneration capacity, and photosynthate accumulation. Additionally, excessive trampling increases soil compaction and bulk density while reducing porosity [18-19], indirectly hindering root elongation and expansion [20]. Consequently, aboveground, belowground, and total biomass decrease, reducing competitiveness and ultimately leading to population degradation [21].

Plant resource allocation is central to life history theory [22-23], with belowground biomass accumulation primarily influenced by available resources [24]. Biomass allocation to modules like stems, leaves, and fruits determines assimilative capacity, and individual growth depends on trade-offs in resource allocation among modules [22]. Plants adjust allocation patterns to respond to habitat heterogeneity and improve assimilative efficiency [2, 25]. Our study shows the overall allocation pattern is root > stem > leaf > fruit, with all module biomasses decreasing as stocking rates increase. Consistent with Wang et al. [26-27], we found grazing increased root biomass allocation, likely because livestock trampling compacts soil and promotes greater root allocation [2]. Moderate and heavy grazing significantly increased root allocation, ensuring adequate water and nutrient uptake for aboveground growth and increasing population fitness.

Stem allocation increased under light grazing but decreased significantly under heavy grazing. Light and moderate grazing promoted leaf allocation, which may help compensate for reduced photosynthesis from defoliation by prioritizing allocation to photosynthetic organs, enhancing light interception and regeneration capacity [29-30]. This represents a primary adaptation mechanism to frequent herbivory. However, heavy grazing significantly reduced allocation to stems and leaves.

Reproductive strategy reflects plant adaptation to environmental conditions and optimal resource allocation among survival, growth, and reproduction. With increasing stocking rates, *A. frigida* sexual reproduction allocation decreased, reproductive branch numbers and seed yield declined, and sexual reproduction nearly disappeared under heavy grazing. The species shifted to asexual reproduction through adventitious roots and vegetative shoots, which have higher survival rates than seedlings. This transition from combined sexual and asexual reproduction to solely vegetative propagation represents an adaptation to heavy grazing [16, 26-27, 31]. Trampling promotes adventitious root formation on prostrate branches, enhancing bud rooting and tillering, increasing vegetative shoot differentiation rates, and strengthening competitive ability, allowing *A. frigida* to expand its population and potentially replace original constructive species [11, 16, 21, 31].

References

[1] Harper J L. Population Biology of Plants. London: Academic Press, 1977.
[2] Poorter H, Niklas K J, Reich P B, Oleksyn J, Poot P, Mommer L. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytologist, 2012, 193(1): 30-50.
[3] Freschet G T, Kichenin E, Wardle D A. Explaining within-community variation in plant biomass allocation: a balance between organ biomass and morphology above vs below ground?. Journal of Vegetation Science, 2015, 26(3): 431-440.
[4] [5] [6] [7] [8] [14]
[9] Quezada I M, Gianoli E. Counteractive biomass allocation responses to drought and damage in the perennial herb *Convolvulus demissus*. Austral Ecology, 2010, 35(5): 544-548.
[10]
[11]
[12]
[13]
[15]
[16]
[17]
[18-19]
[20]
[21]
[22-23]
[24] Enquist B J, Niklas K J. Global allocation rules for patterns of biomass partitioning in seed plants. Science, 2002, 295(5559): 1517-1520.
[25]
[26-27]
[28]
[29]
[30]
[31]

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