# Impacts of grazing and mowing on reproductive behaviors of *Stipa grandis* and *Stipa krylovii* in a semi-arid area

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**Abstract:** Disturbance can affect biomass allocation of plants, but can it influence plant reproductive behavior? To address this issue, we performed field plant community investigations and explored the reproductive behaviors of *Stipa grandis* and *Stipa krylovii* in response to grazing and mowing treatments at Maodeng pasture of Xilinguole League of Inner Mongolia, China during 2007–2009. The results showed that, with a similar niche width for the two plant species under mowing and grazing treatments, mowing significantly increased the ratio of ramet to genet number of *S. krylovii* and the carbon to nitrogen ratio of *S. grandis*, and grazing significantly decreased the ratio of vegetative to reproductive tiller biomass of *S. grandis* and increased the ratio of vegetative to reproductive tiller number of *S. krylovii*. Regression analysis showed that the significantly positive effect of root to shoot biomass ratio was stronger on the ratio of vegetative to reproductive tiller number of *S. grandis* than on that of *S. krylovii*. These results indicated that grazing and mowing influenced the reproductive manner and the process of sexual reproduction of *S. grandis* and *S. krylovii*.

**Keywords:** *Stipa grandis*; *Stipa krylovii*; disturbance; Maodeng pasture; reproductive strategy

Disturbance is an important factor that influences plant growth and vegetation dynamic process (Grime, 2001). In disturbed conditions, plant traits can undergo strong environmental selective pressures (Harper, 1977; Denslow, 1980; Miao and Bazzaz, 1990; McIntyre et al., 1995). Disturbance makes plants difficult to reach an optimal resource allocation, as vegetative life-history characteristics restrain one another. To adapt to disturbance, plants adjust resource allocation and make life-history traits reach an optimization through trade-offs (Reznick, 1985; Obeso, 2002).

As for the reproductive behavior of plants, disturbance can change sprouting ability of plants (Weiher et al., 1999). Under circumstances of wind-sand, the vegetative reproduction ability of plants is subject to their strengths of resisting wind erosion and sand bur-

ial (Liu et al., 1999). After forest fire, felling and floods, the vegetative reproduction ability of plants is also readily enhanced (Chen and Song, 1997; Del Barrio et al., 1999; Pausas, 1999). However, how grazing and mowing affect the reproductive manner and the process of sexual reproduction of plants remains an issue to be explored.

Grazing and mowing, as common disturbances in grassland, usually affect the biomass distribution between plant growth and reproduction (Adler et al., 2001; Begay et al., 2011; Guo et al., 2011; N'Guessan and Hartnett, 2011; Kioko et al., 2012). This phenomenon is mainly due to changed plant growth conditions caused by grazing and mowing, which affect not only the morphology and phenology (Van Tienderen and van der Toorn, 1991; Franks et al. 2007; Reisch and Poschlod, 2011) but also the resource al-

location manner of plants (Aoyagi and Akimoto, 2009; Mao et al., 2012) of different ecological types. The way in which plants allocate their resources is one of the most important factors in determining the persistence of plant growth (Mulder and Ruess, 1998; Taisma and Herrera, 1998; Wilkins, 2002), and could also affect plant reproductive behavior.

The reproductive behavior of plant species is critically restricted by internal (e.g. size and age) and external (e.g. temperature and light) aspects (De Jong et al., 1998). Whereas the onset of reproduction is often regulated by the individual size in short-lived monocarpic plants, and the reproductive behavior of perennial polycarpic plants depends on a complex interaction between the amount of resources currently used in reproduction and the amount of resources stored for future reproduction (Brys et al., 2011), because reproduction in one year may contribute to the survival, growth and reproduction in the next (Stearns, 1992). During the reproductive stage, therefore, monocarpic plant species have only one choice in response to grazing and mowing, and they must immediately repair the injury to compensate for the lost biomass and damaged reproductive structures; while polycarpic plant species have more options than monocarpic plants (Huhta et al., 2009). Brys et al. (2011) explored the impact of herbivores on the flowering behavior of long-lived polycarpic herbs, providing an important reference for our research. In the present study, we hypothesized that, in a semi-arid area, grazing and mowing could change reproductive behaviors in the perennial grasses *Stipa grandis* and *Stipa krylovii*. Our objective was to determine the reproductive behaviors of *S. grandis* and *S. krylovii* in response to disturbance.

# 1 Materials and methods

## 1.1 Study area and plant species

The study area was in the Maodeng pasture (43°37′48″–44°15′00″N, 116°23′24″–116°28′12″E) located 50 km in the east of Xilinhot city, Xilinguole League, Inner Mongolia of China. This region has a typical semi-arid continental climate, with an annual mean air temperature of 1.7°C, a mean annual precipitation of 287 mm and a mean annual evaporation

of 1,746 mm. The soil in the study area is Kastanozem, and the vegetation is a typical steppe. *S. grandis* and *S. krylovii* are both perennial tussock grasses and are dominant species in the typical steppe of the Inner Mongolian Plateau (Inner Mongolia-Ningxia Integrated Survey Team, 1985).

## 1.2 Field sampling and measurement

In the study area, three adjacent areas with grazing, mowing and unused treatments were selected. In each treatment area, both *S. grandis* and *S. krylovii* occurred. Cattle and sheep have been fed in the grazing area for several decades. The mowing area was fenced and established in 2004, and was mowed annually at the end of each growing season. The unused area represented natural grassland free of grazing and mowing. Within each treatment, two 50 m×50 m plots were set up and dominated by *S. grandis* and *S. krylovii*, respectively. We set up six plots totally for the three treatments. To investigate how reproductive behavior was affected by grazing and mowing, 10 quadrats of 1 m×1 m were randomly laid out within each plot in late August 2007 at full maturity of grasses and before the onset of senescence. We counted the total number of genets and the number of vegetative and reproductive tillers of each genet of *S. grandis* and *S. krylovii* within each respective quadrat. The biomass of vegetative and reproductive tillers was oven-dried separately at 80°C for 48 h and weighed. For determining the carbon (C) and nitrogen (N) contents of mature plants, mixed samples (vegetative and reproductive tillers) of each quadrat for each species were oven-dried and weighed before further chemical analysis. To investigate the relationship between reproductive behavior and above- and below-ground resource allocation, in each treatment, 30 individuals of *S. grandis* and *S. krylovii* were randomly sampled in late August 2008, respectively. Each individual of both species was divided into above- and below-ground parts; the numbers of vegetative and reproductive tillers were counted; and the biomass of each part was weighed after oven drying. Plant species compositions and their community features under grazing, mowing and unused treatments were investigated in late August 2009, by randomly laying out 10

quadrats of 1 m×1 m within each plot, with a total of 60 quadrats. In each quadrat, we identified all species and measured their height, density and biomass. All biomass was weighed after oven drying to a constant weight at 80°C.

For plant C and N measurements, the oven dried mixed sample of each plant was ground with a ball mill (Retsch MM 301L, Retsch GmbH and Co KG, Haan, Germany) and weighed, and then digested in $H_2SO_4$–$H_2O_2$. The N content was determined by Semimicro–Kjeldahl method, and the C content by potassium bichromate titrimetric method (Bao, 2000). Three replicates were performed for these measurements.

### 1.3 Statistical analysis

The importance value index (IVI) represents the relative importance of a species in a given community (He et al., 2004). The IVI was defined as the sum of relative density, relative height and relative biomass. The niche width of *S. grandis* and *S. krylovii* was determined by Simpson-Yule index (Song, 2001; Liu et al., 2004): $B_i=Y_i^2/\Sigma N_i^2$, where, $B_i$ is niche width of species $i$; $N_i$ is the relative height, relative density, relative biomass and IVI for species $i$, respectively; and $Y_i$ is the sum of these indices of species $i$.

To gain insights into several aspects of the reproductive behaviors of *S. grandis* and *S. krylovii* and how they were affected by grazing and mowing, we first calculated the ratio of ramet (all tillers) number relative to genet number at a quadrat level for each species and each treatment. Additionally, we calculated the ratio of vegetative to reproductive tiller number and the ratio of vegetative to reproductive tiller biomass. To investigate the relationship between plant resources allocation and reproductive behaviors, we calculated the C to N content ratios (C:N) and root to shoot biomass ratios of both plant species. One-way analyses of variance (ANOVAs) were used to determine whether each of these variables was significantly affected by the three treatments. Statistical analysis was applied after testing for homogeneity of variance: if equal variances were indicated, the group comparison was tested by the Least Significant Difference test; then, if no equal variance was indicated, Tamhane's

T2 was used. Independent *t*-tests were used to test whether the interspecific differences were significant for every variable. All analyses were carried out with SPSS version 13.0 (SPSS Inc., Chicago, IL, USA).

## 2 Results

### 2.1 IVI and niche width

There were 30 plant species belonging to 10 families and 24 genera in the three treatment areas. The dominant families were Gramineae, Leguminosae, Liliaceae and Rosaceae. The most dominant species for all three treatments areas were *Cleistogenes sguarosa*, *Leymus chinensis*, *S. grandis*, *Agropyron cristatum* and *S. krylovii* (Table 1). Although *S. grandis* had higher IVI than *S. krylovii*, the niche width of both species was similar (Table 2).

### 2.2 Reproductive behavior

The ratio of ramet to genet number of *S. grandis* showed no significant effect among the grazing, mowing and unused treatments ($F=0.475$; $P=0.624$); however, there was a significant effect for *S. krylovii* ($F=4.182$; $P=0.020$) (Fig. 1). The ratio of ramet to genet number of *S. krylovii* differed significantly between the mowing and unused treatments, but no significance was observed between the grazing and unused treatments. The effect of the three treatments was not significant for the ratio of vegetative to reproductive tiller number of *S. grandis* ($F=1.193$; $P=0.311$), but was significant for *S. krylovii* ($F=3.953$; $P=0.025$). For *S. krylovii*, there was a significant difference between the grazing and unused treatments, but no significant difference was found between the mowing and unused treatments. However, the ratio of vegetative to reproductive tiller number for *S. grandis* showed an increasing trend from grazing, mowing to unused treatments, with ratios of 28.13±5.76, 38.19±10.23 and 46.24±8.22, respectively; however, for *S. krylovii* there was a decreasing trend with corresponding values of 5.08±1.90, 2.73±0.55 and 1.22±0.62, respectively. For the ratio of vegetative to reproductive tiller biomass, there was a significant effect of the three treatments for *S. grandis* ($F=3.511$; $P=0.036$), but not for *S. krylovii* ($F=1.758$; $P=0.182$).

**Table 1**  Plant species and importance value index (IVI) for the three treatments

| Species | Grazing | Mowing | Unused | Species | Grazing | Mowing | Unused |
|---------|---------|--------|--------|---------|---------|--------|--------|
| *Agropyron cristatum* | 0.217 | 0.270 | 0.255 | *Heteropappus altaicus* | 0.044 | 0.021 | |
| *Allium anisopodium* | 0.037 | 0.032 | 0.043 | *Iris tenuifolia* | 0.071 | 0.040 | 0.038 |
| *Allium macrostemum* | | | 0.019 | *Koeleria cristata* | 0.019 | 0.026 | 0.032 |
| *Allium tenuissimum* | 0.062 | 0.036 | 0.046 | *Leymus chinensis* | 0.792 | 0.571 | 0.691 |
| *Anemarrhena asphodeloides* | 0.019 | 0.027 | | *Melilotus suaveole* | | 0.113 | |
| *Artemisia frigida* | 0.053 | 0.110 | 0.118 | *Melissitus ruthenicus* | 0.036 | | |
| *Artemisia sieversiana* | 0.051 | 0.053 | 0.025 | *Oxytropis aciphylla* | | | 0.074 |
| *Asparagus dauricus* | | 0.031 | | *Potentilla bifurca* | 0.034 | | |
| *Astragalus galactites* | 0.026 | 0.014 | 0.134 | *Salsola collina* | 0.051 | 0.014 | 0.031 |
| *Carex korshinskyi* | 0.111 | 0.158 | 0.062 | *Saposhnikovia divaricata* | | 0.027 | |
| *Cleistogenes sguarosa* | 0.639 | 0.682 | 0.627 | *Scutellavia scordifolia* | 0.043 | 0.078 | |
| *Cleistogenes songonia* | | | 0.060 | *Serratula* spp. | 0.050 | 0.051 | 0.103 |
| *Cymbaria dahurica* | | 0.041 | | *Sibbaldia adpressa* | 0.013 | 0.014 | |
| *Elymus dahuricus* | 0.095 | | | *Stipa grandis* | 0.318 | 0.361 | 0.413 |
| *Heterobostrychus hamatipeunis* | 0.036 | | 0.018 | *Stipa krylovii* | 0.181 | 0.230 | 0.213 |

**Table 2**  Dominance and niche width of *S. grandis* and *S. krylovii*

| Index | Grazing | | Mowing | | Unused | |
|-------|---------|---------|---------|---------|---------|---------|
| | *S. grandis* | *S. krylovii* | *S. grandis* | *S. krylovii* | *S. grandis* | *S. krylovii* |
| Relative density | 0.058 | 0.031 | 0.056 | 0.012 | 0.057 | 0.022 |
| Relative biomass | 0.168 | 0.060 | 0.213 | 0.052 | 0.253 | 0.053 |
| Relative height | 0.092 | 0.090 | 0.093 | 0.165 | 0.103 | 0.138 |
| Importance value index | 0.318 | 0.181 | 0.361 | 0.230 | 0.413 | 0.213 |
| Niche width | 2.867 | 2.886 | 2.784 | 2.546 | 2.746 | 2.683 |
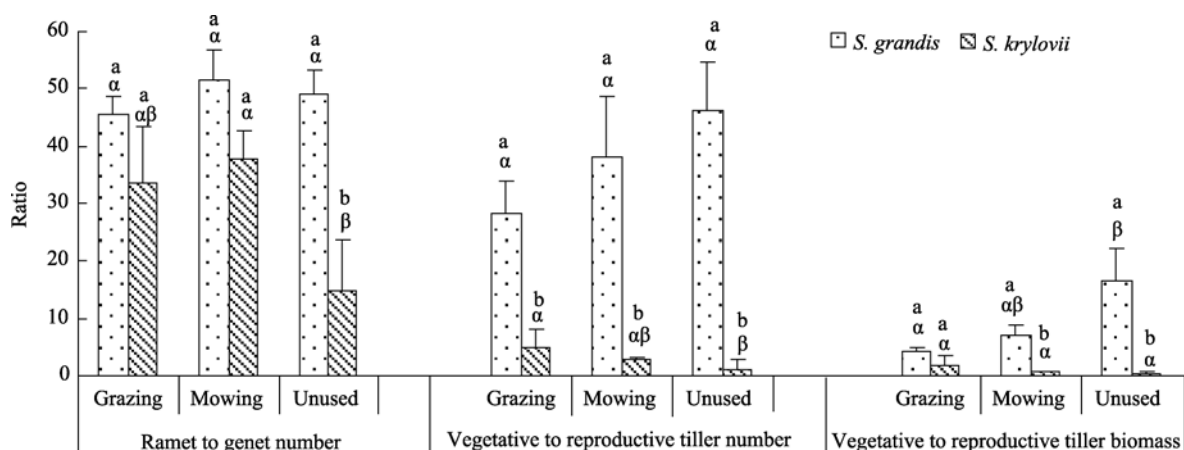


**Fig. 1**  Ratios of ramet to genet number, vegetative to reproductive tiller number and vegetative to reproductive tiller biomass for *S. grandis* and *S. krylovii* under three treatments. Significance for the three treatments is displayed with different latin letters according to one-way ANOVA, significance of differences between *S. grandis* and *S. krylovii* is displayed with lowercase letters tested by *t*-test ($p < 0.05$). Mean±SD.
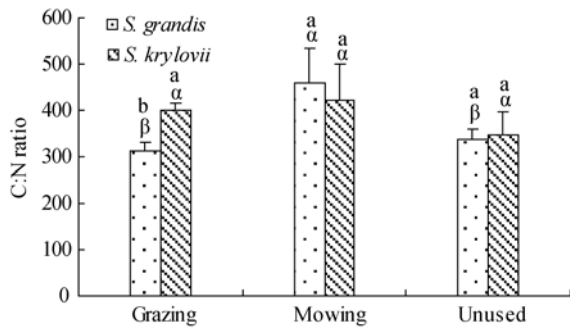
In addition, the ratio of vegetative to reproductive tiller biomass of *S. grandis* differed significantly be-
tween the grazing and unused treatments, but did not differ significantly between the mowing and unused

treatments. For the grazing, mowing and unused treatments, the ratios of vegetative to reproductive tiller biomass for *S. grandis* and *S. krylovii* showed similar trends to the changes in the ratios of vegetative to reproductive tiller number.

### 2.3 Relationship between resource allocation and reproductive behavior

The C:N ratio of *S. grandis* was significantly higher for the mowing than for the grazing and unused treatments. The C:N ratio for *S. krylovii* showed no significant differences among the three treatments. There were significantly higher C:N ratios for *S. krylovii* than for *S. grandis* in the grazing treatment; however, the differences between the two species were not significant in the mowing and unused treatments (Fig. 2).



**Fig. 2** C:N ratios of *Stipa grandis* and *S. krylovii* under three treatments. Significance representation is the same as for Fig. 1. Mean±SD.
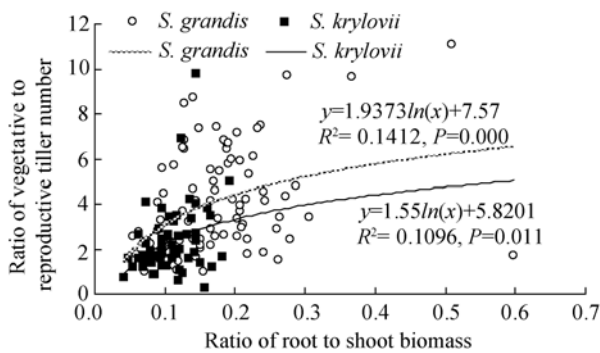


**Fig. 3** The relationships between the ratios of vegetative to reproductive tiller number and the ratios of root to shoot biomass for *Stipa grandis* and *S. krylovii*.

Regression analysis showed a significant positive logarithmic relationship between the ratios of vegetative to reproductive tiller number and the ratios of root to shoot biomass for both *S. grandis* and *S. krylovii*.

Moreover, the regression coefficient of *S. grandis* (1.9373) was greater than that of *S. krylovii* (1.55). Compared to *S. krylovii*, the root to shoot ratio of *S. grandis* had a greater effect on the ratio of vegetative to reproductive tiller number according to the regression coefficient (Fig. 3).

## 3 Discussion

Plant reproductive strategy in response to disturbance is an important theme in plant ecology (Grime, 2001). Ecologists are endeavoring to test the hypothesis of "whether plants, mainly through physiological characteristics, adapt to climate changes, or, through the reproductive characteristics, adapt to disturbances" (Liu et al., 2003; Liu, 2010). In this study, the ratios of ramet to genet number, vegetative to reproductive tiller number and vegetative to reproductive tiller biomass generally differed across the grazing, mowing and unused treatments for *S. grandis* and *S. krylovii*. The results provided an evidence of radical difference on reproductive behaviors between the two species under three treatments. The niche width of both species was similar for the three treatments. However, the grazing and mowing treatments had different influences on the reproductive behaviors of *S. grandis* and *S. krylovii*. The mowing treatment significantly affected the ratio of ramet to genet number for *S. krylovii*, but had no significant effect for *S. grandis*. Due to the greater dominance of *S. grandis* relative to *S. krylovii* in the study area, *S. grandis* could increase genet number by seeds, whereas *S. krylovii* could increase the number of ramets through changing the variability of vegetative growth, to adapt to disturbance and increase fitness. However, grazing had no significant effect on the ratios of ramet to genet number for both species. It is possible that the effect of grazing on the number of individuals and plant biomass was less than that of mowing (Wang, 1998). Thus, grazing and mowing had obviously different effects on the reproductive behaviors of *S. grandis* and *S. krylovii*.

Resource allocation to sexual reproduction is an important life-history characteristic of clonal plants (van Kleunen et al., 2002). In the long process of natural evolution, plants have formed a physiological

mechanism that prioritizes the supply of resources and energy to reproductive organs (Pan, 2001). Once plants go into the sexual reproductive period, asexual reproduction and vegetative growth would be inhibited, and the inhibition effect is not eliminated until seeds mature (Yang et al., 2001; Yang and Zhang, 2006). In fact, disturbance can effectively influence the sexual reproductive process of plants. The present study indicated that compared to the unused treatment, grazing significantly decreased the ratio of vegetative to reproductive tiller biomass and the ratio of vegetative to reproductive tiller number of *S. grandis*. However, grazing significantly increased the ratio of vegetative to reproductive tiller number and the ratio of vegetative to reproductive tiller biomass of *S. krylovii*. The effect of mowing on these two ratios was also consistent with the effect of grazing for both species, and the differences were not significant. Seemingly, the results were not consistent with those of the reproductive behaviors described above, but in essence, they did not conflict. This was because that the ramet number of plants was the sum of vegetative (no-flowering) clone number and flowering clone number in the statistics of the ratio of ramet to genet number. However, in the statistics of the ratio of vegetative to flowering tiller number, the total ramet number was divided into vegetative tiller number and flowering tiller number, i.e. the latter distinguished the process of sexual reproduction of *S. grandis* and *S. krylovii*, and so led to the difference. Our results indicated that the effects of grazing and mowing on the flowering behaviors of *S. grandis* and *S. krylovii* were more complicated than had been assumed, and also reflected the strong reproductive plasticity of both species under disturbance.

Plant C and N metabolism is coordinated with each other on the plant C sources, energy, enzymes, the reducing power of common requirements, ATP and carbon skeletons (Sugiharto and Sugiyama, 1992). The degree of coordination directly affects plant growth rate, and hence the process of sexual reproduction of individual plants. We found that both *S. grandis* and *S. krylovii* had the highest C:N ratios for the mowing treatment, and *S. krylovii* also had a relatively higher C:N ratio for the grazing treatment than for the unused treatment. Long-term mowing and grazing removed part or a large amount of plant biomass, and thus increased the C:N ratio in plants, which promoted asexual reproduction and resulted in more vegetative tillers. However, biomass removal by mowing and grazing could lead to the increase of root to shoot biomass ratio of plants. We found logarithmic incremental relationships between the ratios of vegetative to reproductive tiller number and the ratios of root to shoot biomass for both *S. grandis* and *S. krylovii*, and this relationship was stronger in *S. grandis* than in *S. krylovii*. This implied that the increased root to shoot biomass ratio would promote the formation of vegetative tillers. Thus, for the mowing and grazing treatments, the higher C:N ratios and the larger root to shoot biomass ratios of *S. grandis* and *S. krylovii* plants promoted their asexual reproduction and delayed their sexual reproductive process.

# 4 Conclusion

The mowing and grazing treatments could influence the carbon to nitrogen ratio of *S. grandis* and *S. krylovii*, while the carbon to nitrogen ratio was an important factor influencing plant root to shoot biomass ratio. Our results suggested that the root to shoot biomass ratio had a significantly positive effect on the vegetative to flowering tiller number ratio of *S. grandis* and *S. krylovii*. Our results revealed that the mowing treatment affected the ratio of ramet to genet number (i.e. the reproductive behavior) of *S. krylovii*,; while the grazing treatment notably affected the ratios of vegetative to reproductive tiller number and the ratios of vegetative to reproductive tiller biomass of *S. grandis* and *S. krylovii* (i.e. prevented them from entering the sexual reproductive process). Thus, the grazing and mowing treatments affected the reproductive behaviors of *S. grandis* and *S. krylovii*. The present study will be available to explain plant adaptive mechanisms to mowing and grazing disturbances, especially to verify plant adaptation to disturbance by means of reproductive behaviors.

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