

Growth and production characters of *elymus cylindricus* in different shortening heading time

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Abstract. Ramet modules in a certain population differ in terms of functions, which accounts for different contributions of the same ramets. Shortening heading time brings about different contributions of such modules. Ramets heading one after another were treated as a continuum in respective cohorts of *Elymus cylindricus* aged two. The reproductive ramets that head earlier were marked with tags every four days during the whole heading stage from the beginning to the end, after which all the labeled ramets at the maturity period were gathered. The results showed that, the height and biomass of ramets, the length and biomass of inflorescences, percentage of inflorescence length to ramet height, percentage of inflorescence biomass to ramet biomass, the number and biomass of seeds, seed-setting rate, and percentage of seed biomass to ramet biomass declined with the increasing intensity of heading time shortening as displayed with linear or quadratic function. Ramet characteristics weakened remarkably when shortened heading time added up to 17 days. The biomass distribution in relation to inflorescence and seed maintain a stable rate at the early heading stage and dwindled quickly at the near-end stage, but the biomass of ramets remain constant throughout the entire heading stage. The ramets with earlier heading time make greater contribution to the survival of population than the shortened heading time in this species of bunchgrass.

Keywords: Perennial herb; Allocation strategy; Phenotypic plasticity; Irregular heading; Ramet reproduction.

INTRODUCTION

Given the fact that the bunchgrass have no full-grown rhizome to expand growing space, ramet reproduction plays a vital role in the whole life of bunchgrass population, for the whole population relies on sexual reproduction and seed production to survive normally (Reekie & Bazzaz, 1987; Albert et al., 2015; Benevides et al., 2015). Irregularity of reproduction occurs among plants as a common

phenomenon (Bawa, 1983; Amanda et al., 2016). It is just such irregular reproduction that raises concerns of those researchers in both experimental and theoretical field (Bienau et al., 2015; Saino et al., 2017).

Quite a few studies have focused their attention on the causes underlying irregular reproduction arising among plants. Plant reproduction depends mainly on genetic factors (Marcello & Single, 1971; Hof et al., 1999), while other factors are responsible for the phenotypic plasticity of plants. Martin & Willis (2007) speculated that the irregular reproduction of *Mimulus nasutus* may result from the excessive rate of flowering, or the responses to complex surroundings. Markin & Yoshioka (1996) suggested that the environmental factors such as temperature, light availability, and distribution and genetic polymorphism lead to varying reproduction time of a population, as what happens to herbs. As is often the case, the reproduction of trees does experience irregularity as well (Durand et al., 2017). The study conducted by Singh & Kushwaha (2006) showed that, the synchronous reproduction of tropical trees mainly hinges on the prevailing climate of the seasons, while the irregularity in population embodies the myriad characteristics of individual plants. Modules and tissues in individual plants compete for the absorption of water and nutrients (Ashman & Schoen, 1997), which contributes further to the differences of reproduction time (Singh & Kushwaha, 2006). Moreover, temperature and soil humidity also exert influence on differing reproductive time (Llorens & Penuelas, 2005; Gordo & Sanz, 2010). Laube et al. (2014) carried out a test to discover the effect that low temperature and photoperiod had on the phenology of trees, which revealed the fact that abnormally low temperature in winter was held accountable for the delay and the variations of time series of germination. So far as cluster grass is concerned, it is still not clear what factors can trigger the irregularity of heading time in the reproductive stage.

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In previous series of studies, no conclusion was reached concerning whether irregular reproduction is beneficial to plant population. Some researchers asserted that the irregularity of reproductive time may have positive influence on plant population (Simons & Johnston, 1997), and the study with *Lupinus lepidus* as the subject showed that the population featuring asynchronous individuals bore more fruits than those synchronous ones (Bishop et al., 1998). The asynchronous flowering of *Pilosocereus leucocephalus* contributed to the reproduction of population (Munguia-Rosas & Sosa, 2010). On the contrary, advocates equipped with evolutionarily stable strategy theory assumed that the competition for resource among plants caused a threat to the survival of juvenile individuals and the characteristics of appearing in the irregularity of plants can be conducive to plants in their adapting to complex environment (Iwasa, 1991; Ezoe, 1995). Other researchers claimed that the more irregular individuals' flowering is, the fewer potential exchange genes individual plants carry forward to their next generation during the reproduction period (Bronstein, 1990). Nevertheless there exist fuzzy ideas circling the issue of whether and how this very irregular reproduction contributes to bunchgrass.

A cohort of *Elymus cylindricus* was recruited in our study, during which heading ramets were marked every four days throughout the whole heading stage. Measurements were conducted aiming to obtain data about ramets' flowering and seeding features in populations aged 2 and 3. The goals of our study were as follows: (1) to discover the regularity of various modules in terms of heading time of the population; (2) to explore the differences of reproductive modules in the aspect of shortening heading time; (3) to confirm the positive or negative influence that irregular heading has on the survival of cluster grass.

MATERIALS AND METHODS

Study area. The experiment was conducted at Grassland Ecology Research Station of Northeast Normal University situated in Changling in western Jilin Province, China (44°45'N, 123°45'E). Topography of this area is characterized by flat and wild field, where the climate is semi-arid, semi-humid and continental monsoonal with average daily temperature being 4.9 °C. Annually accumulated temperature over 10 °C adds up to 2920 °C. The mean annual precipitation spanning June and September is 470.6 mm. Annual evapotranspiration is three times more than annual precipitation and the frost-free period is about 150 days (Li et al., 2015).

Subject species *Elymus cylindricus* is a perennial bunchgrass growing widely in China's Inner Mongolia Autonomous Region, Hebei, Sichuan, Qinghai and Xinjiang Province with remarkable adaptability to soil salinization. Appealing to livestock because of its high palatability, grass of this kind is usually cultivated and grown on some grassland serving as a forage base. Being a winter grass, this plant begins to flower in its second growth cycle. In our study site, the natural population of this grass heads in the middle of

June, and the ultimate seed maturity terminates in late July and this grass experiences its peak production periods in the 2nd and 3rd year of its life with the output shrinking by a wide margin in 4th growing year (Chen & Jia, 2002).

Experiment method. The seeds of *Elymus cylindricus* were collected from the Hulun Buir League experiment station in Inner Mongolia Region (49°16'N, 119°35'E) in the year of 2014 and stored in a dry room with desirable ventilation condition. Established in May of the year of 2015, the experiment field served as an ideal grass-growing space in the previous year. In the same field, seeds were placed for experiment use, prior to which the vegetation on the surface of the ground together with those underground roots was removed. Each experimental plot was 2 m*3 m with rows 0.3 m apart and plants 0.3 m apart. Five plots were earmarked for the experiment and they were separated from each other by plots for other experiments. The first seven days after sowing seeds witnessed the plots irrigated daily to ensure the early growth of seedlings. Then each sowing point of seedlings was thinned to a single plant, upon which no further human-involved interferences were imposed afterwards.

In the mid-June of the year of 2016, at the early heading stage of a 2-year-old *Elymus cylindricus* cohort, the reproductive ramets were randomly marked with plastic tag every four days. Each plot had six or seven reproductive ramets selected and marked. The date of marking fell on 16 June, 20 June, 24 June, 28 June, 2 July, 6 July and 10 July respectively. All the labeled ramets were harvested at dough stage on 11 August. Accordingly, the identical methods were employed in the mid-June of 2017, when a 3-year-old *Elymus cylindricus* cohort grew at early heading stage and the reproductive ramets were randomly tagged every four days, and seven ramets in each plot were labeled as well. The marking dates included 18 June, 22 June, 26 June, 30 June, 4 July, 8 July and 12 July. All tagged ramets were also harvested at dough stage on 13 August. Since some of the tagged ramets were damaged by strong wind or heavy rain in growing period, a total of 200 ramets were harvested in 2016 and 203 ramets in 2017.

The early heading stage of reproductive ramets was defined by flag leaves measuring approximately 1 cm the drawing out of inflorescence. Every plant had only its parts above the ground of gathered, and the ramet height, inflorescence length and the number of seeds were measured. Then those ramet plants collected were dissected into inflorescences, seeds, and the rest part (stems and leaves), each part of which were heated and dried at 80 °C for 48 hours to acquire a constant weight.

Data Analysis. All statistical analyses were conducted by means of SPSS 20.0 software package. Dates were presented in mean±S.E. Pending the analysis, the data was conducted Kolmogorov-Smirnov test for assumptions of normality, and Levene's test for homogeneity of variance. Significant level was $P < 0.05$. As all variables conformed with the tests, One-way ANOVA (Tukey's multiple comparison test) was used to analyze the differences of ramet parameters during shortening heading time in each age. Those data were related with ramet height, biomass of ramets, inflorescence length, biomass of inflorescences, percentage of inflorescence length

to ramet height, percentage of inflorescence biomass to ramet biomass, number of seeds, biomass of seeds, seed-setting rate, and percentage of seed biomass to ramets biomass.

A regression analysis was undertaken to analyze the relationships between quantity-wise characteristics of reproductive ramets and the shortening of heading time in a two-year growth period of an *Elymus cylindricus* cohort. Linear, quadratic, exponential and power functions were used for the analysis. By using AICc (Akaike information criterion), the best curve in conformity with each relationship was pinpointed (Sugiura, 1978; Hurvich & Tsai, 1991).

In the year of 2016, the heading period began on 16 June through 11 July with heading occurring each day. As was shown in the diagram, we added one day to every tagged date in order to avoid deducting zero day on the first day of heading stage and not including zero in the curve. Differing from the first day of heading, every marked day found its expression as shortening 1d, 5d, 9d, 13d, 17d, 21d, 25d in sequence. In the year of 2017, as the interval time between tagged dates remains unchanged, the sequence of shortening heading time was the same as that of 2016.

RESULTS

Ramet Growth and Biomass

Over the two years, with the accumulated shortened heading time increasing in terms of amount, both the height and biomass of ramets decreased linearly (Fig. 1, Table 1). Ramet height and biomass of ramets aged 3 were higher than those of the 2-year-old ones. The ramet height went lower remarkably from 13d (Fig. 1A), and the biomass of ramets decreased greatly from 5d (Fig. 1B). Compared with shortening 25d, the ramet height through shortening 1d was 1.26 times and 1.33 times higher respectively in 2-year-old and 3-year-old ramets, the ramet biomass through shortening 1d was 1.98 times and 1.77 times higher in 2-year-old and 3-year-old ramets respectively.

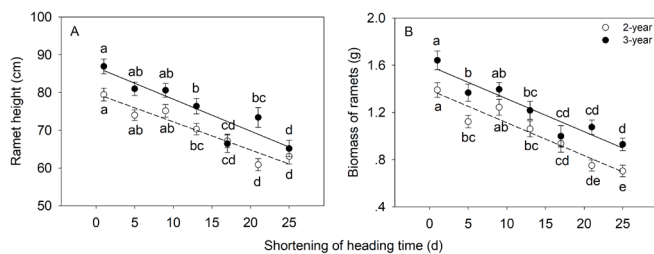


Fig. 1. Regression analysis and differences among irregular heading time on (A) ramet height, (B) biomass of ramets in 2-year-old and 3-year-old *Elymus cylindricus* cohort. Shortening of heading time are 1d, 5d, 9d, 13d, 17d, 21d, 25d respectively. Data are means $\pm$ S.E. Different letters for the same year mean significant difference among irregular heading time ($P < 0.05$). The regression equations are from regression analysis and AICc. Hollow circles represent 2-year ramets (dashed lines); black crosses represent 3-year ramets (solid lines). Lines are drawn from regression analysis.

Inflorescence Growth and Allocation

With the increase of time shortened from early heading time, inflorescence length, the biomass of inflorescences on two-year old plants and percentage of inflorescence length to ramet height in 2-year-old ones of *E. cylindricus* decreased as shown by means of quadratic functions (Figs. 2A, 2C, 2D, Table 1). But the percentage of inflorescence biomass to ramet biomass descended linearly (Fig. 2B, Table 1). The inflorescence length and biomass of inflorescences of 2-year-old ramets decreased by a wide margin, which started from 17d (Fig. 2A), and decreased significantly from 13d in 3-year-old ramets (Fig. 2B). The percentage of inflorescence length to ramet height and that of inflorescences biomass to ramets biomass lowered greatly at 17d, 21d or 25d (Figs. 2C and 2D).

Compared with shortening 25d, the inflorescence length, biomass of inflorescences, percentage of inflorescence length to ramet height, percentage of inflorescence biomass to ramet biomass for shortening 1d were 1.51 times, 2.84 times, 1.43 times and 1.20 times higher respectively in 2-year-old ramets, and were 1.54 times, 2.64 times, 1.50 times and 1.13 times higher respectively in 3-year-old ramets.

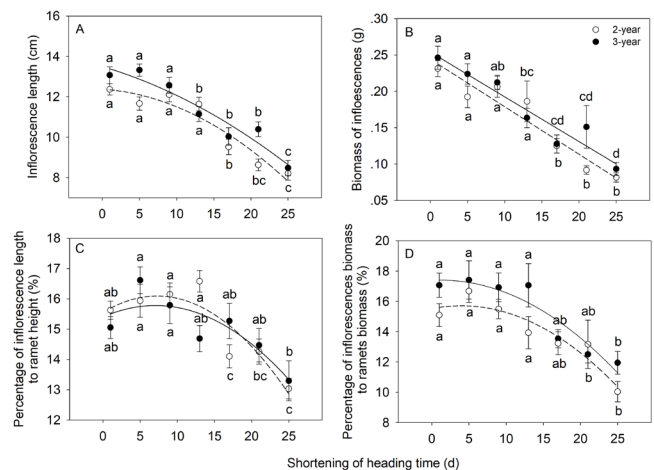


Fig. 2. Regression analysis and differences related to irregular heading time on (A) inflorescence length, (B) biomass of inflorescences, (C) percentage of inflorescence length to ramet height, and (D) percentage of inflorescence biomass to ramet biomass in 2-year-old and 3-year-old *Elymus cylindricus* cohort. Amount of shortened heading time are 1d, 5d, 9d, 13d, 17d, 21d, 25d, respectively. Data are means $\pm$ S.E. Different letters for the same year stand for significant differences of irregular heading time ($P < 0.05$). The regression equations are based upon regression analysis and AICc. Hollow circles represent 2-year-old ramets (dash lines); black crosses signify 3-year-old ramets (solid lines). Lines are also based upon regression analysis.

Seed Production and Reproductive Allocation

With the increase of the amount of time shortened from heading time, the number of seeds, setting rate in two aged ramets and biomass of seeds in 3-year-old ramets decreased linearly (Figs. 3A, 3B, 3C, Table 1), but biomass of seeds in

Table 1. Regression equations among quantified features of reproductive ramets and shortening heading time in *Elymus cylindricus* cohort. Shortened time from heading time is 1d, 5d, 9d, 13d, 17d, 21d, 25d respectively (n=7).

Quantitative characters	Growing years	Function	R ²	P
Ramet height (cm)	2	$y=79.68-0.74x$	0.915	0.010
	3	$y=86.689-0.845x$	0.840	0.040
Biomass of ramets (g)	2	$y=1.391-0.028x$	0.913	0.010
	3	$y=1.594-0.028x$	0.905	0.001
Inflorescence length (cm)	2	$y=12.377-0.023x-0.06x^2$	0.916	0.007
	3	$y=13.5-0.108x-0.003x^2$	0.925	0.006
Biomass of inflorescences (g)	2	$y=0.244-0.007x$	0.911	0.010
	3	$y=0.254-0.006x$	0.918	0.001
Percentage of inflorescence length to ramet height (%)	2	$y=15.550+0.149x-0.010x^2$	0.826	0.030
	3	$y=15.399+0.107x-0.008x^2$	0.740	0.068
Percentage of inflorescences biomass to ramets biomass (%)	2	$y=17.387-0.027x-0.011x^2$	0.894	0.011
	3	$y=15.519+0.96x-0.012x^2$	0.888	0.013
Number of seeds	2	$y=13.599-0.612x$	0.782	0.008
	3	$y=15.555-0.751x$	0.837	0.004
Biomass of seeds (g)	2	$y=0.137-0.02x-5.915E-005x^2$	0.955	0.020
	3	$y=0.162-0.05x$	0.946	0.000
Setting rate (%)	2	$y=12.064-0.527x$	0.613	0.037
	3	$y=17.136-0.828x$	0.841	0.040
Percentage of seeds biomass to ramets biomass (g)	2	$y=10.165+0.02x-0.007x^2$	0.970	0.010
	3	$y=9.675+0.042x-0.01x^2$	0.951	0.020

2-year-old ramets and percentage of seeds biomass to ramet biomass decreased significantly as shown by quadratic functions (Figs. 3B and 3D, Table 1). The number of seeds in 3-year-old ramets, biomass of seeds and setting rate in ramets of two years decreased significantly from 13d (Figs. 3A, 3B, 3C). The number of seeds in 2-year-old ramets, percentage of seeds biomass to ramet biomass of two aged ramets decreased significantly from 17d and 25d respectively (Figs. 3A and 3D).

Compared to shortening 25d, the biomass of seeds and percentage of seeds biomass to ramet biomass for shortening 1d were 3.23 times and 1.63 times higher in 2-year-old ramets, and was 3.66 times and 2.09 times higher in 3-year-old ones respectively. The number of seeds and seed-setting rate declined to zero from where shortening 17d arose in 2-year-old ones and from where shortening 21d took place in 3-year-old ones.

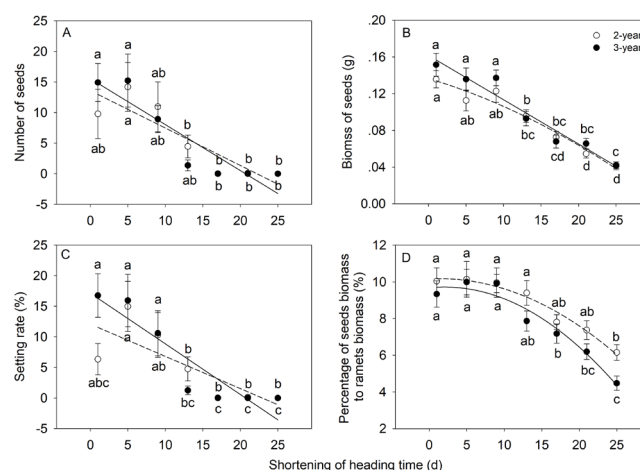


Fig. 3. Regression analysis and difference among various irregular heading time on (A) number of seeds, (B) biomass of seeds, (C) seed-setting rate and (D) percentage of seeds biomass to ramets biomass in 2-year-old and 3-year-old *Elymus cylindricus* cohort. Amount of time shortened from heading time are 1d, 5d, 9d, 13d, 17d, 21d, 25d respectively. Data are means±S.E. Different letters for the same year mean significant differences among irregular

heading time ($P < 0.05$). The regression equations come from regression analysis and AICc. Hollow circles represent 2-year-old ramets (dash lines); black crosses represent 3-year-old ramets (solid lines). Lines are based upon regression analyses.

DISCUSSION

Bunchgrasses, both annual and perennial, are characterized by the capability of vegetative propagation (Albert et al., 2015). The ramets in the same cluster usually differ from each other because of the differences of occurrence time and their positions (Miner et al., 2005). The earlier the ramets appear, the better space resources the ramets can have access to, which contributes to different microenvironments in the vicinity of the ramets (Gao et al., 2014). The ramet of individual plant of *Elymus cylindricus* tassel and flower irregularly, and florets on the same inflorescence flower irregularly as well. The heading stage of the natural population of this grass can last for up to one month (from mid-June to mid-July) in our study station. During our two-year study, changes in terms of the ramet height, biomass of ramets, inflorescence length, biomass of inflorescences, percentage of inflorescence length to ramet height, percentage of inflorescences biomass to ramets biomass, number of seeds, biomass of seeds, seed-setting rate, and percentage of seeds biomass to ramets biomass contributed to the confirmation of growth plasticity and all quantified features declined with the increase of time amount of heading time shortening. Based on the published results of relevant studies and our experimental observations, there may be two reasons for growth variation resulting from irregular heading time. One is related to the climate change and microenvironment differences during the formation of ramets (Zhou et al., 2003; Gao et al., 2014). The other one is related to the different growth strategy of ramets which head at different time.

In China's Songnen Plain, the ramet height, inflorescence length, and the number of florets in flowering ramets of *E. cylindricus* individuals are all determinate growth. Once the growth cycle is complete, those biological characteristics will stop changing (Chen & Jia, 2002). Although it is relatively time-consuming for ramets to accumulate their biomass of both plants and inflorescence, the overlapping time in the process of shortening heading time is also long accordingly (Sun et al., 2009). The climatic condition in the growing season developing gradually, the climate fluctuations between two adjacent points of heading time were insignificant. To conclude, what is mentioned above can serve as the reason that accounts for the nuance in terms of specific characters between every two neighboring points of heading time.

Whether the florets can bear fruits or not and how many seeds are produced in the maturity stage are not only related to the quality of ovule and the number of pollen grains within the population, but also related to the growth situation of ramet and the habitat (Post et al., 2001). In terms of growth

and pollination condition, early-flowering ramets gained a preemptive advantage over others and took up more favorable growth space than those which flowered later, and during peak flowering period the pollen was plentiful enough to have florets fertilized easily (Primack, 1987; Ehrlen et al., 2015; Li et al., 2015), while the ramets which flowered later deprived themselves of the accessibility to better growing space and pollination condition (Li et al., 2015). Furthermore, only if the substance output as a result of the production of ramets was constrained, the substance transfer to fertilized grains was often terminated (Vondras et al., 2016). To secure the normal growth of ramets, individuals of a certain population adopted some expedient strategies to counteract negative influence of a certain special situation, which gave occasion to a phenomenon where most adjacent seeds headed more or less differently in terms of specific time.

The subdivisions of inflorescences of bunchgrass being spikelet, one or more florets usually grow on a spikelet. As a result of the different arrangement orders, there are two types of spikelet-panicle and spike (Chen & Jia, 2002). Even on the same spikelet of some, different florets flower at different time, for they take shape at differing time and disparities exist in terms of the order of nutrient transport. Therefore, it needs a span of time for the inflorescence to flower. In the case of a bunchgrass population, the different shape-taking time of ramets and inflorescence keep the heading and flowering stage lasting for a long time. Two main reasons underlie the irregular heading time of *Elymus cylindricus* reproductive ramets. Firstly, this bunchgrass in the study area will go through a relatively long budding period to take in sufficient nutrients after seed ripening. Budding period usually stretches from late June to mid-September, and the buds grow into winter juvenile ramets. Therefore, when it comes to spring seedlings and ramets, winter ones outlast spring ones in terms of growing time. Ims (1990) revealed that older genepersentagens can avail themselves of more resources, but the likelihood to suffer more disastrous events will also increase. Therefore, individual plants are supposed to optimize themselves to be able to seek out a counterpoise point where the time is desirably distributed between reproduction and heading and it is possible to maximize the reproductive output and further reduce the negative interference to the minimum degree, thus establishing a strategy of irregular reproductive time (Eric et al., 2001). Secondly, the differences of micro-topography within and between clusters lead to the distinctions of reviving period and light resource. The earlier the ramets enters reviving period, the earlier the ramets head (Li et al., 2018). Those two reasons can speak for the differences which arise on bunchgrass when they begin heading at different time and irregularly.

The quantitative traits at heading stage are shown in the form of index by means of the mean values of large samples, through which the characteristics of reproductive ramets aged two all declined with the increase of amount of shortened heading time. That outcome was acquired by analyzing data out of observing the samples heading in regular sequence of time as a continuum (Mbeau-Ache &

Franco, 2011). The analysis of the parameters of the fitting equation offered us an insight into the functions of the ramet population (Zhang et al., 2015). As discovered in the figures concerning the properties of the individual plants, linear decline was a process at a constant speed, while quadratic decline was a process of varying speed with a sharper and higher rate at the end-approaching stage. Accordingly the features of reproductive ramets were different as dupercentagen of shortening heading time differed in the series. At the terminal stage of heading period, inflorescence length, percentage of inflorescence length to ramet height, percentage of inflorescence biomass to ramet biomass, and that of seed biomass to ramet biomass all declined at a greater speed. The changes of quantified characteristics reflected an allocation strategy that the biomass adopted to keep a relatively high level of distribution to inflorescences and seeds at the early heading stage, and declined sharply and quickly even to zero at the near-the-end heading stage. However, the other modules of reproductive ramet, such as the biomass of ramet or seed-setting rate were kept at a lower rate of gradual reduction.

CONCLUSIONS

In Songnen Plain of China, with the increase of amount of heading time shortening in *Elymus cylindricus* cohort over the two years, the height and biomass of ramets, the length and biomass of inflorescences, percentage of inflorescence length to ramet height, percentage of inflorescence biomass to ramets biomass, the number and biomass of seeds, seed-setting rate, and percentage of seed biomass to ramets biomass declined as shown in the form of linear or quadratic functions. Those data all shrank significantly when the heading time was cut by about half of a month in ramets aged two, especially the number of seeds and seed-setting rate. In the plasticity growth of individuals, the ramets kept stable the allocation to inflorescence biomass and seed biomass, but declined rapidly at the terminal heading stage. Reproductive ramets declined at a constant rate throughout the heading stage. Early heading and reproduction have greater contribution than others for bunchgrass survival.

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