

Different regrowth patterns after repeated clipping in two Mongolian pasture species

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Abstract

We investigated changes in the regrowth patterns of two grass species on the Mongolian steppe, *Agropyron cristatum* and *Stipa krylovii*, in response to repeated clipping and used a growth analysis to identify the factors responsible for differences in their regrowth patterns. Plants grown in pots were clipped every 3 weeks, and leaf area, dry mass, and N and crude fiber contents were measured. Aboveground biomass recovered to the same level as that before clipping in both species even after 3 clipping–regrowth cycles, but the mechanisms behind their regrowth abilities differed. In *A. cristatum*, a decrease in biomass allocation to aboveground parts with repeated clipping was fully compensated by the positive effect derived from the increase in growth rate due to increased leaf area expansion associated with an increase in specific leaf area (SLA). In *S. krylovii*, a decrease in SLA reduced leaf area but at the same time increased N content per unit leaf area and consequently photosynthetic ability, leaving the growth rate unchanged. The values of growth parameters involved in regrowth after clipping changed with repeated clipping, and those changes differed between species. In particular, the difference in the response of SLA to repeated clipping contributed greatly to the difference in regrowth patterns. These results imply that changes in leaf morphology as plant strategies against grazing can contribute to plants' regrowth patterns.

Introduction

Pastoralism is a key industry in Mongolia, where 75% of the land area is used for livestock grazing (FAO 2020). Pastoralism in Mongolia is mainly nomadic and livestock feed mostly pastures naturally growing on grasslands. The number of livestock in Mongolia has increased during the past three decades, resulting in grassland deterioration such as a decrease in grassland productivity and spread of unpreferable plants for livestock feeding. Plants in grasslands used for grazing experience repeated cycles of herbivory and regrowth during the growing season (Oosterheld and McNaughton 1988, 1991). Therefore, to maintain grassland productivity for sustainable livestock production, it is essential to understand the regrowth characteristics of major pasture species.

Clipping aboveground plant parts is commonly used to mimic grazing in investigations of the regrowth of pasture species. Modifying the frequency of clipping allows the grazing tolerance of plants to be tested. For example, in mixed-grass prairie in South Dakota, USA, aboveground net primary production was not decreased by clipping once a month but was decreased by clipping once every 2 or 1 weeks (Green and Detling 2000); similar results were obtained in an experiment in West Africa (Leriche et al. 2003). Clipping of five rhizomatous grassland species every 4 weeks decreased aboveground biomass production in *Carex divisa*, *Juncus articulatus*, and *Elytrigia repens*, but did not affect *Eleocharis palustris* or *J. gerardii*, indicating species differences in grazing tolerance (Esmaeili et al. 2009). In a repeated clipping experiment with two Mongolian grassland species, *Stipa krylovii* and *Leymus chinensis*, regrowth capacities differed mainly as a result of the difference in net assimilation rate (NAR), which represents photosynthetic ability (van Staaldin and Anten 2005). Such experiments with repeated clipping have contributed greatly to the elucidation of the regrowth of pasture species after grazing.

Most previous studies analyzed regrowth patterns such as relative contributions of photosynthates and belowground reserves to aboveground regrowth through growth variables averaged or integrated over the experimental period (Anten and Ackerly 2001; van Staaldin and Anten 2005; van Staaldin et al. 2010). However, regrowth patterns may change with clipping–regrowth repetitions. As aboveground regrowth depends on belowground reserves and on photosynthetic products of newly growing leaves (Chapin et al. 1990; Fulkerson and Donaghy 2001), clipping repetitions may gradually deplete belowground reserves (Wang et al. 2012, 2013), thus increasing regrowth dependency on leaf photosynthesis. Moreover, changes in regrowth patterns due to clipping repetitions may differ among species because the dependency of regrowth on belowground reserves differs among species (Thornton et al. 1993). To date, no studies have investigated changes in regrowth pattern with clipping repetitions or interspecific differences in such changes. Elucidating the changes in regrowth patterns by clipping repetitions can improve our understanding of how to use grazing land sustainably.

Here, we investigated changes in the regrowth patterns of two grass species, *Agropyron cristatum* and *S. krylovii*, in response to repeated clipping. These two species are widely distributed in the semi-arid grasslands of Inner Mongolia and Mongolia (Cheng et al. 2008; Yoshihara et al. 2009), and are highly palatable to livestock (Undarmaa et al. 2018). They have different growth forms—*A. cristatum* is rhizomatous and *S. krylovii* is caespitose—and thus are expected to respond differently to clipping. In semi-arid grasslands, as grazing pressure increased, caespitose species were replaced by rhizomatous species (Fernandez-Gimenez and Allen-Diaz 2001), and rhizomatous *L. chinensis* had a greater regrowth ability than caespitose *S. krylovii* because of its higher photosynthetic ability (Van Staaldin and Anten 2005). Thus, we expected that *A. cristatum* would maintain better regrowth ability than *S. krylovii* with repeated clipping. Plants grown in pots were clipped repeatedly and the changes in regrowth patterns were analyzed. N and crude fiber contents of aboveground parts were investigated to test changes in the nutritive value of the grasses due to altered leaf traits associated with regrowth. N content relates positively to the amount of crude protein and fiber content negatively to the digestibility of pasture (Schönbach et al. 2009; van Soest 1994). We posed the following questions: (1) How do the regrowth patterns of the two species change with repeated clipping? (2) Do differences in those changes depend on growth form? (3) How do changes in leaf traits with regrowth affect the nutritive value of the aboveground parts?

Materials And Methods

Plant materials

Agropyron cristatum and *Stipa krylovii* are widely distributed in dry grasslands of Eurasia and are highly palatable to livestock (Undarmaa et al. 2018). Seeds were collected in 2014 from the semi-arid grasslands of Bayan-Unjuul (47°02.77'N, 105°57.08'E), Mongolia, and stored at 5°C in a refrigerator until the experiment.

On 07 July 2020, 150 seeds of each species were prepared: the seed coats were removed, and the seeds were sterilized in ethanol (10 s) and rinsed in tap water. They were then sown on dampened filter papers in Petri dishes and held at 20°C under red light (660 nm) in an incubator. More than 80% of seeds had germinated by 10 July. Each germinated seed was then transplanted into a 1.5-L plastic pot filled with washed dune sand, and the pots were placed in a greenhouse at Tottori University (35°30'N, 134°10'E). The monthly mean temperature in the greenhouse during the experiment was 24.8°C in July, 30.6°C in August, 24.9°C in September, 18.1°C in October, and 13.8°C in November. All plants emerged by 18 July. From 27 July, plants received 50 mL of 1/100-strength commercial nutrient solution (Hyponex, NPK 6-10-5; Hyponex, Osaka, Japan) every week. Plants were watered with tap water every evening.

Clipping experiment

On 25 July, 90 plants of each species were selected and divided into 6 groups of 15 plants each. On 31 August, 1 plant from each group (total of 6 plants) was harvested in each species (first harvest, H_1). Harvested plants were divided into aboveground and belowground parts. We defined leaf blades as leaves and the remaining aboveground parts as stems, and measured the leaf area by leaf area meter (Li-3100; Li-Cor, Lincoln, NE, USA). After oven-drying at 70°C for 2 days, the dry mass was determined. Immediately after H_1 , the aboveground parts of the remaining plants were clipped with scissors at ground level, collected, dried, and weighed. Three weeks later, following the first regrowth period (R_1), H_2 followed by the second clipping was carried out on 21 September. Three weeks later, following R_2 , H_3 followed by the third clipping was carried out on 12 October. Three weeks later, following R_3 , H_4 followed by the third clipping was carried out on 2 November.

Nitrogen and fiber contents of aboveground parts

The contents of N and crude fiber in the aboveground parts were measured. To ensure enough material for measurement, we combined the aboveground parts from the harvested plants and the clipped plants within each group. The samples were ground in a mill. The N content was measured with an NC analyzer (JM1000CN; J-Science Lab, Kyoto, Japan). Crude fiber was extracted by a FibreBag System (FBS6; Gerhardt, Königswinter, Germany). Grinded samples were washed with acetone, and then boiled first with 1.25% sulfuric acid and then with 1.25% sodium hydroxide sequentially. Extracts were dried and weighed and then ashed in a muffle furnace (NHK-120BS-1; Nitto Kagaku, Aichi, Japan) at 600°C for 1 h. Crude fiber content was calculated by subtracting the dry mass of ash from that of the extracts.

Leaf N content was calculated as leaf dry mass $\times$ N content per unit dry mass of aboveground parts, as leaves accounted for > 85% of the aboveground biomass.

Growth analysis

Traditional growth analysis (Hunt 1990) with some modification was used to analyze the regrowth patterns of the two species. As aboveground parts were entirely removed by clipping treatment, we defined aboveground biomass at harvest 3 weeks after clipping as the amount of regrowth. The rate of

aboveground regrowth (S , daily increase in aboveground biomass) in each 3-week regrowth period i ($R_1 - R_3$) was calculated as:

$$S(R_i) = \frac{SW(H_{i+1})}{21}$$

1

where $SW(H_i)$ is aboveground dry mass at the i th harvest. S was analyzed as plant growth rate in R_i (G , daily increase in plant biomass) $\times$ the fraction of G that was allocated to the aboveground parts (U , no dimension):

$$S(R_i) = G(R_i) \times U(R_i)$$

2

where $G(R_i)$ and $U(R_i)$ are G and U of R_i . $G(R_i)$ was calculated as:

$$G(R_i) = \frac{W(H_{i+1}) - [W(H_i) - SW(H_i)]}{21}$$

3

where $W(H_i)$ is whole plant dry mass at H_i . $U(R_i)$ was calculated as $S(R_i) \div G(R_i)$.

G was analyzed as mean leaf area (MLA) $\times$ net assimilation rate (NAR, daily increase in plant biomass per unit leaf area) in R_i :

$$G(R_i) = \text{MLA}(R_i) \times \text{NAR}(R_i)$$

4

where $\text{MLA}(R_i)$ and $\text{NAR}(R_i)$ are MLA and NAR in R_i calculated as:

$$\text{MLA}(R_i) = \frac{LA(H_{i+1})}{2}$$

5

$$\text{NAR}(R_i) = \frac{W(H_{i+1}) - [W(H_i) - SW(H_i)]}{21} \times \frac{2}{LA(H_{i+1})}$$

6

where $LA(H_i)$ is plant leaf area at H_i .

MLA was analyzed as mean leaf weight (MLW) × mean specific leaf area (SLA, leaf area per leaf mass) in R_i :

$$MLA (R_i) = MLW (R_i) \times SLA (R_i)$$

7

where $MLW(R_i)$ and $SLA(R_i)$ are MLW and SLA in R_i calculated as:

$$MLW (R_i) = \frac{LW (H_{i+1})}{2}$$

8

$$SLA (R_i) = \frac{LA (H_{i+1})}{LW (H_{i+1})}$$

9

where $LW(H_i)$ is plant leaf dry mass at H_i .

NAR was analyzed as leaf N productivity (LNP, daily increase in plant biomass per unit leaf N) × mean leaf N per unit leaf area (N_A) in R_i :

$$NAR (R_i) = LNP (R_i) \times N_A (R_i)$$

10

where $LNP(R_i)$ and $N_A(R_i)$ are LNP and N_A in R_i calculated as:

$$LNP (R_i) = \frac{W (H_{i+1}) - [W (H_i) - SW (H_i)]}{21} \times \frac{2}{LN (H_{i+1})}$$

11

$$N_A (R_i) = \frac{LN (H_{i+1})}{LA (H_{i+1})}$$

12

where $LN(H_i)$ is plant leaf N content at H_i .

N_A was analyzed as mean leaf N per unit leaf mass (N_M) × leaf mass per area (LMA, = 1/SLA) in R_i :

$$N_A (R_i) = N_M (R_i) \times LMA (R_i)$$

where $N_M(R_i)$ and $LMA(R_i)$ are N_M and LMA in R_i ; $N_A(R_i)$ was calculated as:

$$N_M(R_i) = \frac{LN(H_{i+1})}{LW(H_{i+1})}$$

All growth variables were calculated for each of the 6 groups in each species.

Statistical analysis

Differences in dry mass, N content, and fiber content among harvests and in growth variables among regrowth periods were tested by Tukey's multiple comparison test ($P < 0.05$) in GraphPad Prism 9 software (GraphPad Software, San Diego, CA, USA).

Results

Biomass production

Aboveground biomass just before first clipping (H_1) was 0.102 g in *A. cristatum* and 0.125 g in *S. krylovii* (Fig. 1). That at H_2 , H_3 , and H_4 was not significantly different from that at H_1 in either species. On the other hand, belowground biomass increased with periodic clipping in both species.

Growth analysis

S in each 3-week recovery period did not change significantly with the number of clipping repetitions in either species (Fig. 2a). In *A. cristatum*, G increased and U decreased with clipping repetitions, though the changes from R_2 to R_3 were small (Fig. 2b, c). In *S. krylovii*, there was no clear tendency in the effect of increasing clipping repetitions, with G increased only in R_2 and U unchanged.

In *A. cristatum*, MLA increased with clipping repetitions, but NAR did not change (Fig. 3a, b). In *S. krylovii*, NAR increased with the number of clipping repetitions, while MLA decreased from R_2 to R_3 , offsetting the increase in NAR.

In *A. cristatum*, MLW tended to increase (Fig. 4a), and SLA increased significantly with clipping repetitions (Fig. 4b). In *S. krylovii*, MLW did not change with clipping repetitions and SLA decreased significantly from R_2 to R_3 .

In *A. cristatum*, neither LNP nor N_A changed significantly (Fig. 5a, b), but N_M increased significantly with clipping repetitions (Fig. 5c). In *S. krylovii*, LNP temporarily increased only in R_2 , but N_A increased with clipping repetitions, significantly from R_2 to R_3 . N_M increased significantly with clipping repetitions.

Nitrogen and crude fiber contents

Aboveground N content per unit mass at H₁ was 3.21% in *A. cristatum* and 3.03% in *S. krylovii*, and increased with clipping repetitions in both species (Table 1). The crude fiber content of aboveground parts was 28.7% in *A. cristatum* and 23.2% in *S. krylovii* at H₁, and decreased with clipping repetitions in both species.

Table 1

Nitrogen and crude fiber contents of aboveground parts of *A. cristatum* and *S. krylovii* before clipping and after 3-week regrowth. H₁, harvest just before first clipping; H₂, harvest 3 weeks after H₁ and just before second clipping; H₃, harvest 3 weeks after H₂ and just before third clipping; H₄, harvest 3 weeks after H₃. Values with the same letter are not significantly different among harvests within each species ($P < 0.05$, Tukey's multiple comparison test)

	<i>A. cristatum</i>				<i>S. krylovii</i>			
	H ₁	H ₂	H ₃	H ₄	H ₁	H ₂	H ₃	H ₄
Nitrogen (%)	3.21 ^a	3.98 ^b	4.51 ^c	5.04 ^d	3.03 ^a	3.91 ^b	4.48 ^c	5.01 ^d
Crude fiber (%)	28.7 ^d	26.3 ^c	24.4 ^b	21.3 ^a	23.2 ^c	19.7 ^b	18.8 ^b	16.3 ^a

Discussion

S during the 3-week recovery period did not change with repeated clipping in either species (Fig. 2a), but the underlying mechanisms differed between them. In *A. cristatum*, the increase in *G* with clipping repetitions was canceled by the decrease in *U*, whereas in *S. krylovii*, there was no clear trend in *G* or *U* (Fig. 2b, c). These results indicate that changes in the regrowth pattern in response to clipping repetitions vary among species. It was unclear why the increase in *G* was accompanied by the decrease in *U* in *A. cristatum*, but it may relate to the limitation of the number of tillers produced: successive tiller production by the development of axillary buds allows persistent biomass production of perennial grasses (Flemmer et al. 2002; Jewiss 1972), and therefore, tiller number commonly correlates positively with aboveground biomass (Boe 2007; Boe and Beck 2008; Boe and Casler 2005; Zarroug et al. 1983). In perennial grasses, the number of buds and tillers remains almost constant even after repeated clipping (Busso et al. 1989, 2011), which is likely to be the case in our two species. Thus, in *A. cristatum*, the regrowth of aboveground biomass may be limited by the number of tillers, and consequently *U* may have decreased with the increase in *G*. The decrease in *U* would thus contribute to the growth of belowground parts, including rhizomes (Bai et al. 2010; Wan et al. 2011).

We attribute the difference in the response of *G* to clipping repetitions between species to the responses in MLA and NAR: MLA increased but NAR did not change with clipping repetitions in *A. cristatum*, but MLA decreased and NAR increased in *S. krylovii* (Fig. 3). This contrasting MLA response between the two species was due to the increase in SLA in *A. cristatum* but the decrease in *S. krylovii* with repeated clipping (Fig. 4b). SLA is recognized as an indicator of leaf morphology and toughness, and changes in

SLA in response to defoliation are associated with strategies of grass species against grazing (Cingolani et al. 2005; Cunningham et al. 1999). Leaves with lower SLA are tougher (avoiding damage by grazing), while leaves with higher SLA have larger photosynthetic area (allowing rapid compensatory growth for grazing tolerance) (Cingolani et al. 2005; Díaz et al. 2001; Jardine et al. 2020). Moreover, leaves with higher SLA generally have shorter expansion times (Moles & Westoby 2000), which also can contribute to grazing tolerance. Thus, in our study, *A. cristatum* reinforced its strategy to tolerate grazing, while *S. krylovii* strengthened its strategy to avoid grazing.

NAR increased with repeated clipping only in *S. krylovii* (Fig. 3a), and the increase was due mainly to the increase in N_A (Fig. 5b). A similar increase in N_A in response to clipping has been reported in other grass species (Anten and Ackerly 2001; An and Li 2014; Zheng et al. 2011). In contrast, N_M increased with clipping repetitions in both species (Fig. 5c). These results indicate that the difference in the response of N_A to repeated clipping between the species was due to the contrasting response of SLA between them (Fig. 4b). The decrease in SLA in *S. krylovii* corresponds to increased leaf thickness or tissue density with repeated clipping, which may have increased the amount of chloroplasts per unit leaf area and consequently improved the photosynthetic ability (NAR, Fig. 3b). Photosynthetic capacity correlates positively with leaf thickness (Jurik 1986), and thicker leaves have larger spaces along cell walls where chloroplasts can be accommodated to achieve higher photosynthetic capacity (Oguchi et al. 2003). Thus, our results indicate that a decrease in SLA with defoliation can contribute positively to the regrowth potential through improvement of photosynthetic ability.

Contrary to our expectation, rhizomatous *A. cristatum* did not show higher regrowth ability than caespitose *S. krylovii* (Figs. 1, 2a), possibly because of the suppression of regrowth of *A. cristatum* by certain factors. Water availability has been suggested as a factor limiting the compensatory growth of rhizomatous species. For example, van Staalduijn and Anten (2005) showed that rhizomatous *L. chinensis* exhibited high compensatory growth after clipping under wet conditions but less under drought stress, while caespitose *S. krylovii* exhibited low compensatory growth irrespective of water availability. Similar results were found in another study of two rhizomatous and two caespitose species (Zhang et al. 2018). In our study, plants were watered every day, but the pot was relatively small (1.5 L vs. 5 L in van Staalduijn and Anten 2005); therefore, plants might have been susceptible to water deficit, and consequently the regrowth of rhizomatous *A. cristatum* was not enhanced. This speculation should be carefully considered, because very few studies have compared regrowth between rhizomatous and caespitose grasses, and one study showed conversely that the tiller growth rate after defoliation was higher in caespitose *Hesperostipa comata* than in rhizomatous *Pascopyrum smithii* (Broadbent et al. 2017). Clearly, more studies are needed to understand the difference in regrowth ability between rhizomatous and caespitose species.

In both species, the N content of the aboveground parts increased and the crude fiber content decreased with clipping repetitions (Table 1). Aboveground N content is positively related to the amount of crude protein, and fiber content is negatively related to digestibility (Schönbach et al. 2009; van Soest 1994). Thus, our results indicate that the two grass species improved their nutritive value with increasing

clipping repetitions. Such improvement after grazing is commonly observed (Green and Detling 2000; McCarthy et al. 2013; Miao et al. 2015; Sasaki et al. 2012; Schönbach et al. 2012). The increase in the nutritive value observed here may be partly related to the change in the ratio of leaves to stems in the aboveground parts leaves generally have a higher protein content and a lower fiber content than stems (Chaves et al. 2006), and as grazing intensity increases, the proportion of stems in aboveground parts decreases and consequently the nutritive value improves (Chapman et al. 2014). In our study, the ratio of stem to aboveground biomass was decreased with repeated clipping (from 8.2% at H₁ to 5.1% at H₄ in *A. cristatum*, and from 14.5% at H₁ to 3.6% at H₄ in *S. krylovii*, Fig. 1), which may have contributed to the improvement of the nutritive value of the aboveground parts.

Conclusion

Both *A. cristatum* and *S. krylovii* maintained their aboveground biomass even after repeated clipping, but the mechanisms underlying the consistent recovery performance differed between the species. In *A. cristatum*, a decrease in biomass allocation to aboveground parts with increasing clipping repetitions canceled the increase in growth rate due to increased leaf area expansion derived from the increase in SLA. In *S. krylovii*, a decrease in SLA reduced leaf area but at the same time increased N content per unit leaf area, which increased photosynthetic ability, so growth rate remained unchanged. The N content of aboveground parts increased and the fiber content decreased with repeated clipping in both species. These results imply that both species can maintain the amount of grass even after repeated clipping and improve nutritional value. In addition, we clarified that the values of growth parameters involved in the regrowth after clipping change with repeated grazing–regrowth, and that those changes differed between species. Differences in the response of SLA to repeated clipping contributed greatly to the interspecific differences in regrowth pattern. We conclude that plant strategies against grazing through leaf morphological changes may strongly contribute to the plants' regrowth patterns.

Declarations

Author contributions

RH and TK designed and performed the experiments. RH analyzed the data, RH and TK wrote the manuscript. BG helped with the collect of plant seeds in 2014. YY provided editorial advice.

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Competing interests

We have no competing interests.

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Figures

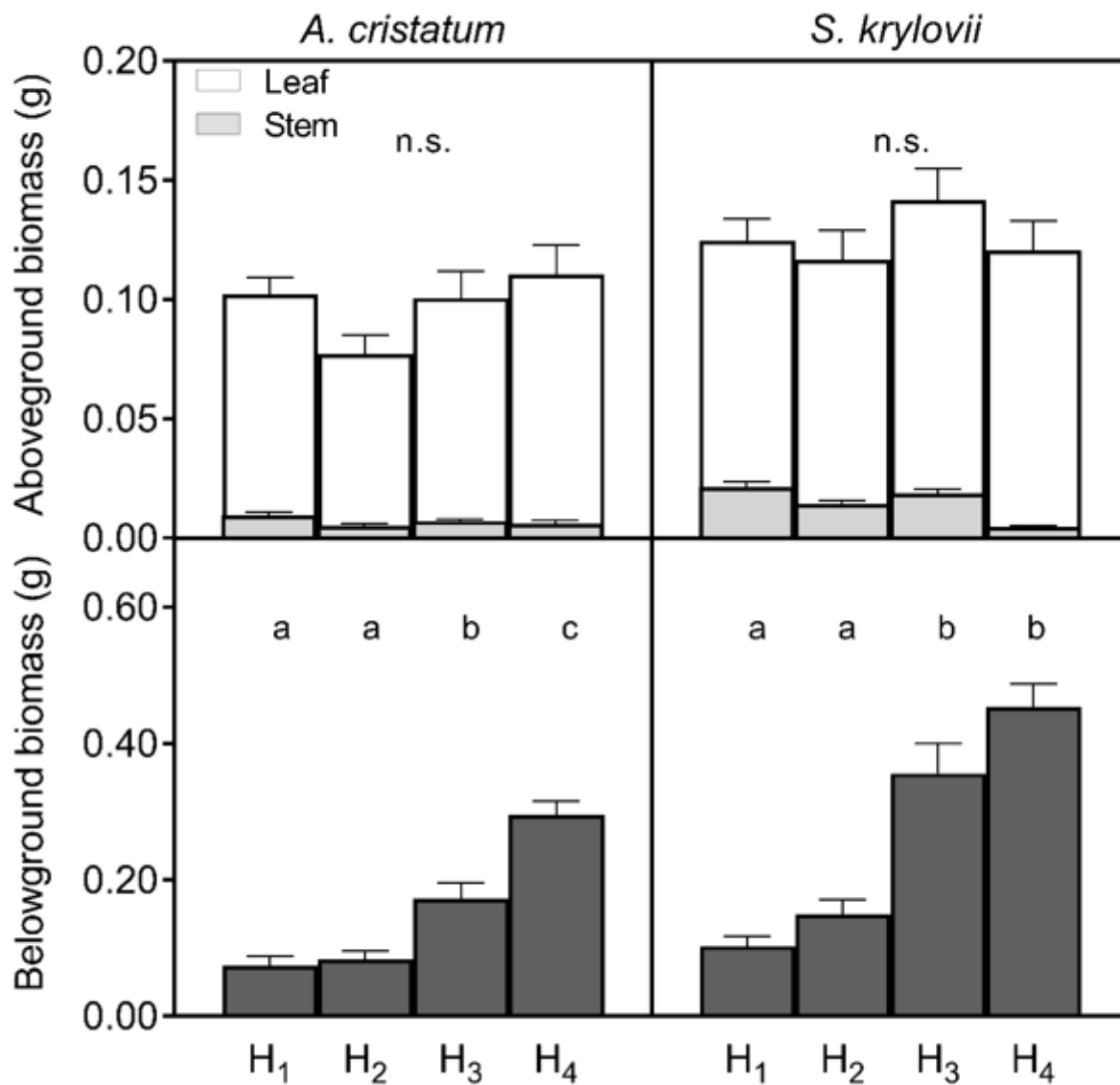


Figure 1

Dry mass of above- and belowground parts of *A. cristatum* and *S. krylovii* before clipping and after 3-week regrowth. H₁, harvest just before first clipping; H₂, harvest at 3 weeks after H₁ and just before second clipping; H₃, harvest at 3 weeks after H₂ and just before third clipping; H₄, harvest 3 weeks after H₃. The same letter above columns indicates no significant difference among harvests within each species ($P < 0.05$, Tukey's multiple comparison test). n.s., not significant. Error bars indicate SE ($n = 6$)

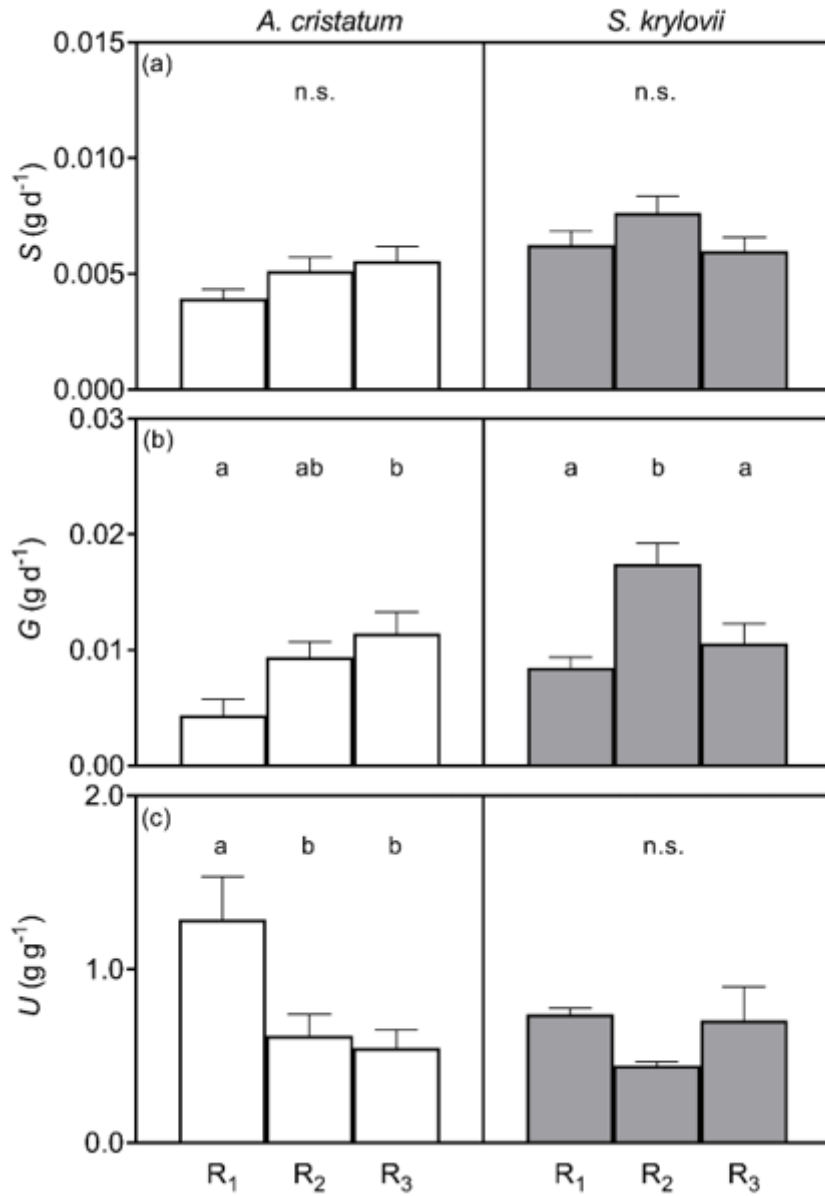


Figure 2

(a) Rate of aboveground regrowth (S), (b) plant growth rate (G), and (c) fraction of G that was allocated to aboveground parts (U) in *A. cristatum* and *S. krylovii* during 3-week regrowth after clipping. R₁, R₂, and R₃ indicate 3-week regrowth after the first, second, and third clippings. The same letter above columns indicates no significant difference among regrowth periods within species ($P < 0.05$, Tukey's multiple comparison test). n.s., not significant. Error bars indicate SE ($n = 6$)

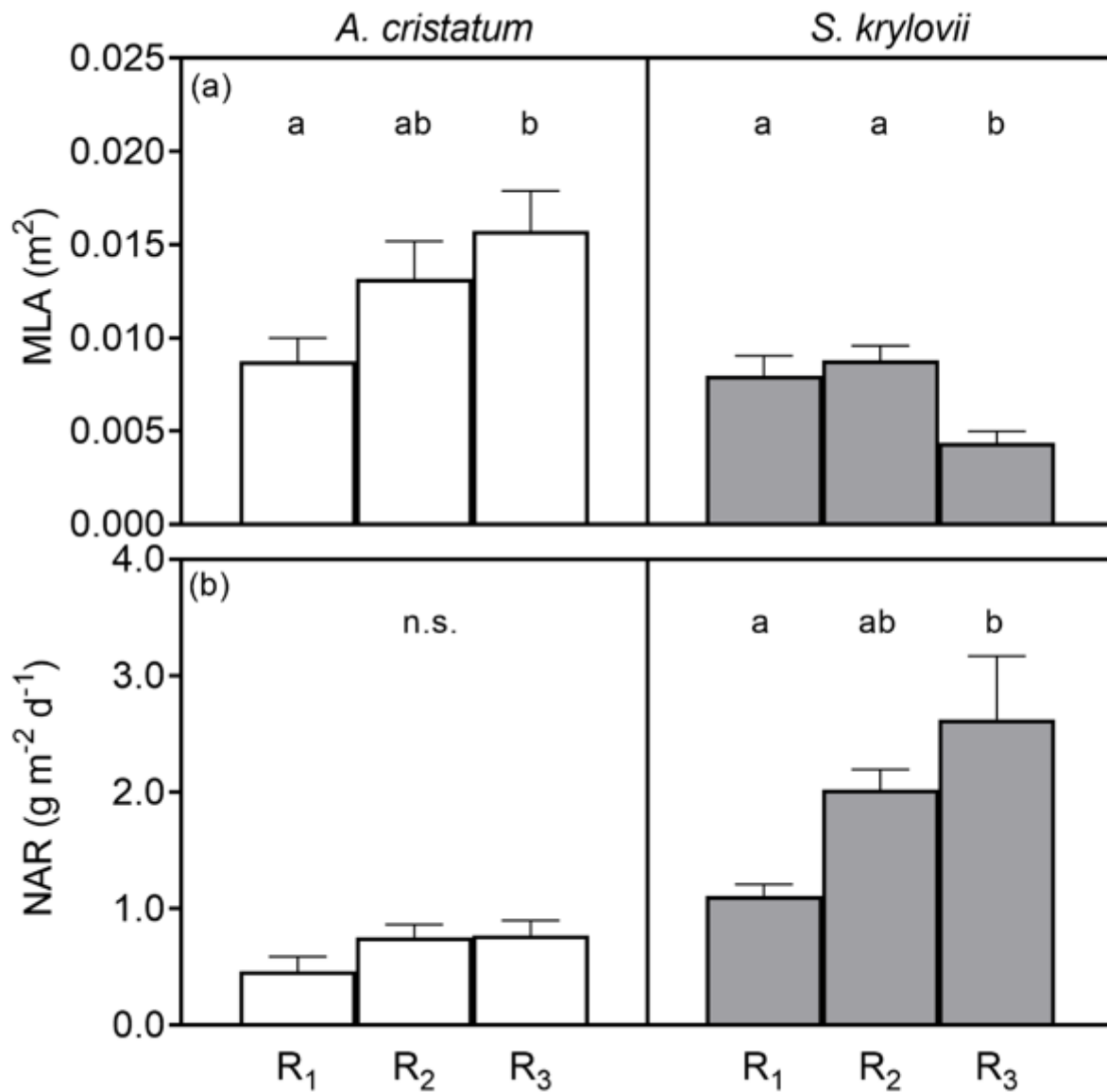


Figure 3

(a) Mean leaf area (MLA) and (b) net assimilation rate (NAR) of *A. cristatum* and *S. krylovii* during 3-week regrowth after clipping. R₁, R₂, and R₃ indicate 3-week regrowth after the first, second, and third clippings. The same letter above columns indicates no significant difference among regrowth periods within species ($P < 0.05$, Tukey's multiple comparison test). n.s., not significant. Error bars indicate SE ($n = 6$)

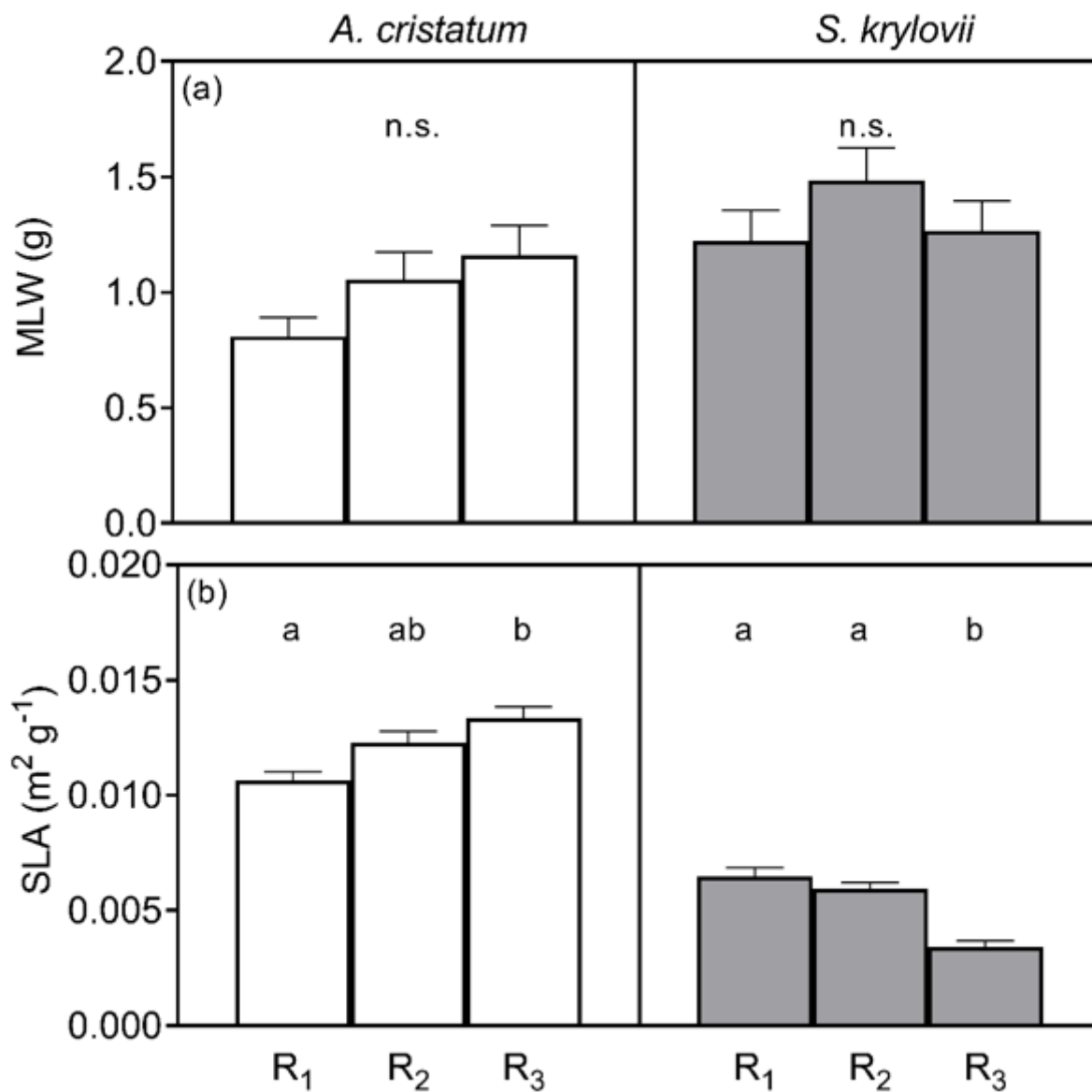


Figure 4

(a) Mean leaf weight (MLW) and (b) specific leaf area (SLA) of *A. cristatum* and *S. krylovii* during 3-week regrowth after clipping. R_1 , R_2 , and R_3 indicate 3-week regrowth after the first, second, and third clippings. The same letter above columns indicates no significant difference among regrowth periods within species ($P < 0.05$, Tukey's multiple comparison test). n.s., not significant. Error bars indicate SE ($n = 6$)

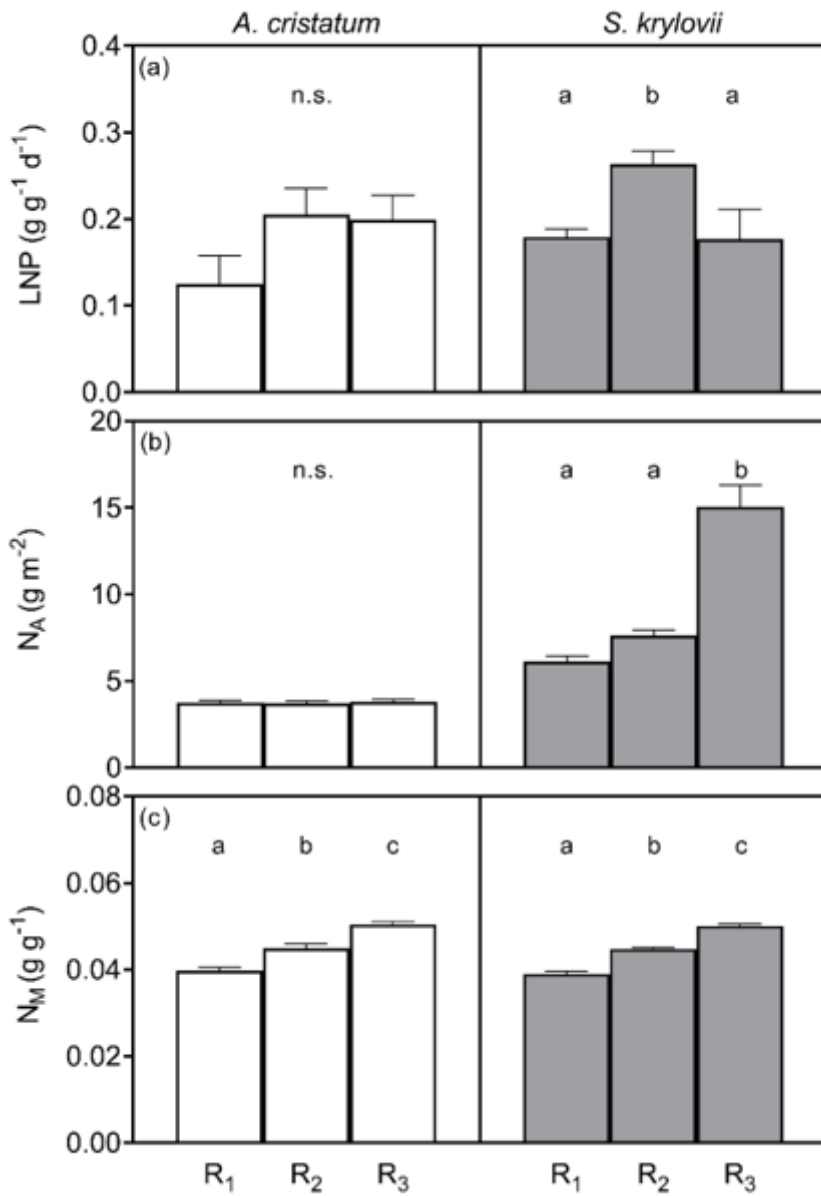


Figure 5

(a) Leaf N productivity (LNP), (b) leaf N per unit leaf area (N_A), and (c) leaf N per unit mass (N_M) of *A. cristatum* and *S. krylovii* during 3-week regrowth after clipping. R₁, R₂, and R₃ indicate 3-week regrowth after the first, second, and third clippings. The same letter above columns indicates no significant difference among regrowth periods within species ($P < 0.05$, Tukey's multiple comparison test). n.s., not significant. Error bars indicate SE ($n = 6$)