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Kin recognition benefits clonal offspring performance of historically grazed *Leymus chinensis*: insights for grassland management

Zhen Zhang^{1,2*}, Xiliang Li², Junjie Duan² and Juan Sun¹

Abstract

Background: Individual plants can identify their neighbors and adjust their biomass investment to avoid competing with their relatives or jointly cope with external stresses. Maternal effects can improve their offspring adaptability under external stresses. However, how grazing-induced maternal effects influence plant kin interactions remain unknown.

Methods: Clonal offspring of *Leymus chinensis* grown under multi-year grazing and non-grazing conditions were used for this study. A greenhouse experiment was conducted to evaluate the performance of focal plants in the presence of kin and stranger neighbors, with the aim of analyzing the interaction between maternal effect and kin relatedness.

Results: Kin relatedness of neighboring plants affected the biomass production and allocation of focal plants, demonstrating the presence of kin recognition in *L. chinensis*. Moreover, grazing-induced maternal effects significantly enhanced kin recognition in the species. Consequently, the presence of stranger neighbors significantly improved the growth potential of grazed offspring. Specifically, the total biomass of clonal offspring increased by 73.1% compared to the kin group, potentially buffering grazing-induced plant productivity declines.

Conclusions: This study shows that historical grazing enhances kin recognition in *L. chinensis*. Thus, introducing multi-genotypic plants can increase the productivity of grasslands. The findings of this study enhance our understanding of intraspecific plant–plant interactions in clonal species and provide new insights into sustainable grassland management.

Keywords: Clonal plant, Intraspecific interaction, Livestock grazing, Maternal effects

Introduction

Some plants can distinguish between self and non-self in relation to other plants (Pierik et al. 2013), and even kin and stranger individuals (Bais 2015; Dudley and File 2007; File et al. 2012) by root exudates or plant volatiles. These kin recognitions cause significant adjustments in plant morphology, physiology, and biochemical characteristics

to facilitate cooperation or competition with neighboring plants (Broz et al. 2010; Pierik et al. 2013). The ability to recognize and respond to close relatives may reduce biomass allocation in competing organs, such as roots and leaves, increasing fitness when coexisting with closely related plants (Dudley 2015; Meier et al. 2013; Mercer and Eppley 2014).

Kin interactions enable plants to jointly cope with external stresses, such as low soil fertility, high soil salinity, and low light availability, to improve fitness (Anten and Chen 2021; Chen et al. 2015; Karban and Shiojiri 2009). For example, leaves of *Arabidopsis thaliana* can

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resume horizontal orientation towards empty spaces to reduce mutual shading among plants (Crepy and Casal 2016). Similarly, plants grown in nutrient-rich or poor soils decrease mutual shading by shoots or increase nutrient absorption efficiency by roots to leverage kin benefits (Li et al. 2018; Palmer et al. 2016). Studies have found that early-warning responses are more effectively induced in neighboring kin plants than in unrelated plants when plants experience biotic stresses, such as a herbivore-induced mechanical injury (Burns and Strauss 2011; File et al. 2012). Most studies on the effects of biotic stress on kin recognition have mainly focused on herbivory by insects (Kalske et al. 2019; Karban et al. 2013). However, the interaction mechanism between grazing by large herbivores and kin recognition remains largely unknown.

Grasslands occupy more than 30% of the global land area (Hufkens et al. 2016). However, most grasslands have undergone intense overgrazing by livestock over the past several decades (Zhang et al. 2013). Recent studies postulate that overgrazing can trigger clonal maternal effects in the grasses, allowing their asexually propagated offspring to rapidly adapt to recurrent browsing or related changes in the microhabitats of degraded grasslands (Li et al. 2015a; Wang et al. 2016). Maternal effects result from imprinting by the environment via changes in epigenetic inheritance or quality of propagules (Dyer et al. 2010; Wang et al. 2016). The regeneration capacity and tolerance of clonal plants affected by herbivory can be enhanced and passed to their vegetative offspring (Dong et al. 2017). Studies on perennial grass *Leymus chinensis* (Trin.) Tzvel., a dominant species in the eastern Eurasian steppe, has shown that maternal effects can manifest as reductions in plant size, stem elongation, and photosynthesis of clonal offspring of grazed plants (Li et al. 2015a, b; Ren et al. 2017).

Approximately 90% of the intergenerational turnover of individual plants on semi-arid grassland depends on vegetative propagation mediated by bud banks (Benson and Hartnett 2006). Because of their limited dispersal distance, ramets of grassland plant species, such as *L. chinensis*, always grow close to their clonal siblings, and overgrazing increases the probability of encountering close relatives (Masclaux et al. 2010). Therefore, kin recognition is of great ecological interest in grasslands. A previous study found that maternal effects affect the growth and population dynamics of *L. chinensis* (Li et al. 2015b). However, kin recognition and maternal effect are usually studied separately, and their potential linkage is relatively unexplored (Bilas et al. 2021; Dudley et al. 2013; Yin et al. 2019; Zhang et al. 2019). Indeed, the influence of maternal effects on plant population dynamics has only been investigated using a single genotype (Dong

et al. 2017; Segura et al. 2015). Thus, information regarding the relationship between maternal effects and kin interactions remains scanty.

To determine how grazing-induced maternal effects influence kin recognition in a clonal species, we investigated the interactions between plants with kin and stranger genetic relatedness from clonal offspring that originated from long-term grazed and non-grazed populations of *L. chinensis*. This study had two specific objectives: (i) to determine whether clonal plants growing in the same space can distinguish their kin from unrelated plants; (ii) to explore how maternal effect and heavy grazing can influence kin interactions in *L. chinensis*.

Methods

Field grazing experiment

A field experiment was conducted at the research station of the Chinese Academy of Agricultural Sciences, Hohhot, Inner Mongolia, China, located in an agropastoral transition zone. This region is characterized by semi-arid, temperate, and continental climates, with a mean annual precipitation of 400 mm, elevation of 1060 m, and mean annual temperature of 7.4 °C. The bulk density and pH of the topsoil (20-cm depth) in the investigated region is approximately 1.25 g cm⁻³ and 8.6, respectively. In 2008, we established a 14-ha artificial grassland plot with a mix of five plant species, including three species of grasses (*L. chinensis*, *Elymus sibiricus* L. and *Elymus nutans* Griseb) and two legumes (*Lespedeza daurica* (Laxm.) Schindl. and *Medicago sativa* L.). Sheep grazing experimental plots used in the present study were established in 2009. The plots were divided into three treatments, including control with no anthropogenic activities (CK), rotational grazing (RG), and continuous grazing (CG). Each treatment had three replications and were distributed based on a randomized block design. One CK plot, five RG plots, and one CG plot were included in each block, resulting in 21 plots in this experiment. Each plot was 81.67 m × 81.67 m. Only the CK and CG treatments were used, and the stocking rate was 9 sheep per ha. The duration of sheep grazing has been from June 1 to October 31 since 2009. Therefore, at the time of bud sampling for the kin interaction experiment in 2018, the field grazing experiment had been ongoing for ten years, and the grassland was dominated by *L. chinensis* (relative biomass > 70%).

Genetic relatedness of *L. chinensis* individuals

Original rhizome buds of *L. chinensis* were collected from the field plots of a long-term grazing experiment. The buds were picked from March 1 to March 5, 2018, before the end of the bud bank dormancy (early April in Hohhot). At least six buds connected by a complete

rhizome were selected as each experimental group to meet the demand of the experiment. The rhizome buds from the plots were cleaned with distilled water to remove impurities from their surface.

The clonal offspring of *L. chinensis* in CK and CG plots were collected to study grazing-induced maternal effects. Four soil blocks were selected from each experimental plot (three non-grazed plots and three continuously grazed plots), resulting in 24 soil blocks. Notably, an average of 76 and 102 rhizomes were previously included in the non-grazed and continuously grazed soil blocks (30 cm (length) × 30 cm (width) × 25 cm (height)), respectively. Thus, the number of rhizomes met the needs of the experiment.

To study kin recognition, we maintained a distance of 40 m between each soil sampling point in the same plot to ensure that the clonal offspring of *L. chinensis* from two soil blocks were not genetically related (Semchenko et al. 2017).

Kin interaction experiment

Kin interaction experiment was designed as follows: two paired buds were cultivated in each hydroponic pot. The buds were attached to black biochemical cotton, separated by approximately 5 cm. Two buds from the same mother were used for each kin treatment. Although the cloned offsprings were genetically identical to the parents, they were considered kin treatment because they are two individuals. Meanwhile, two buds from different mothers were used in stranger treatments (Fig. 1) (Godard et al. 2020; Pezzola et al. 2019). Hydroponic environment provides adequate water and nutrient for plants, thus, plant growth rate mainly depends on heredity, cell characteristics, and physiological vigor of buds. Therefore, we set up a hydroponic system to evaluate the performance of the focal *L. chinensis* plants in the presence of different neighbor plants (kin and stranger). The plants were grown in 10.5 cm (diameter) × 14.5 cm (height) plastic pots wrapped in opaque polyethylene. The plastic pots contained 900 mL of Hoagland nutrient solution (Additional file 1: Table S1), which was replaced every 5 days to ensure sufficient nutrient supply to the plants. All the pots were arranged in a phytotron according to a randomized block design. Growth conditions were 27 °C with a 14 h:10 h (day:night) cycle. The blocks comprising three pots were readjusted every ten days to limit the effects of light heterogeneity.

During the experiment, plant height was measured four times, at 30, 37, 44, and 60 days. Plants were harvested after 60 days. Agronomic data, which included net photosynthetic rate, total tiller number, leaf length, and maximum root length, were measured before harvesting. Net photosynthetic activity was measured

using the LI-6400 system. The third leaf from the base of each *L. chinensis* plant was measured at an air-flow rate of 500 $\mu\text{mol}\cdot\text{s}^{-1}$ with a photosynthetic photon flux density of 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

The number of plants in each pot was recorded as tiller density. Flag leaf length and root length of the plants were measured using a scan meter (WinRHIZO) on the last day of the experiment. The tiller density, leaf length, and root length of the plants in each pot were recorded. The plants were divided into leaf, stem, and belowground parts and oven-dried at 65 °C for 48 h before biomass measurements.

Data analysis

The aboveground biomass, total biomass, and biomass ratios were calculated from the stem, leaf, and root biomass. The effects of grazing history and kin relatedness among various treatments were tested using two-way analysis of variance (ANOVA). To assess whether the clonal offspring of non-grazed and grazed *L. chinensis* plants responded differently to neighbor identity, we calculated the log response ratio ($\text{LRR}_{\text{identity}}$), a dimensionless index (Kalske et al. 2019) as follows:

$$\text{LRR}_{\text{identity}} = \ln (X_{\text{stranger}}/X_{\text{kin}}), \quad (1)$$

where X_{stranger} and X_{kin} are the variables of a focal plant that coexists with a stranger or kin plant. X_{stranger} is the response value for biomass of focal plant when grown with stranger neighbor, while X_{kin} is the response value for biomass of focal plant when grown with kin neighbor. $\ln (X_{\text{stranger}}/X_{\text{kin}}) > 0$ represents clonal offspring of focal plant with larger biomass when grown with stranger plant than kin plant. $\ln (X_{\text{stranger}}/X_{\text{kin}}) < 0$ represents focal plant with smaller biomass when grown with stranger neighbor than kin neighbor, and $\ln (X_{\text{stranger}}/X_{\text{kin}}) = 0$ represents clonal offspring with the same biomass allocation. Further, we tested the statistical significance of the effect of grazing history on the log response ratios of *L. chinensis* offspring using ANOVA. The relationship between LRRs in non-grazed and grazed *L. chinensis* offspring was analyzed using the Pearson method. Kolmogorov–Smirnov test was adopted to assess the normality of the data before subsequent analyses. All data analyses were performed using SPSS statistical software (version 24.0).

Results

Biomass response to kin recognition was significantly regulated ($P < 0.05$) by grazing-induced maternal effects (Table 1). The biomass of the non-grazed offspring was significantly higher ($P < 0.05$) than that of grazed offspring when grown with kin neighbors (Fig. 2). However,

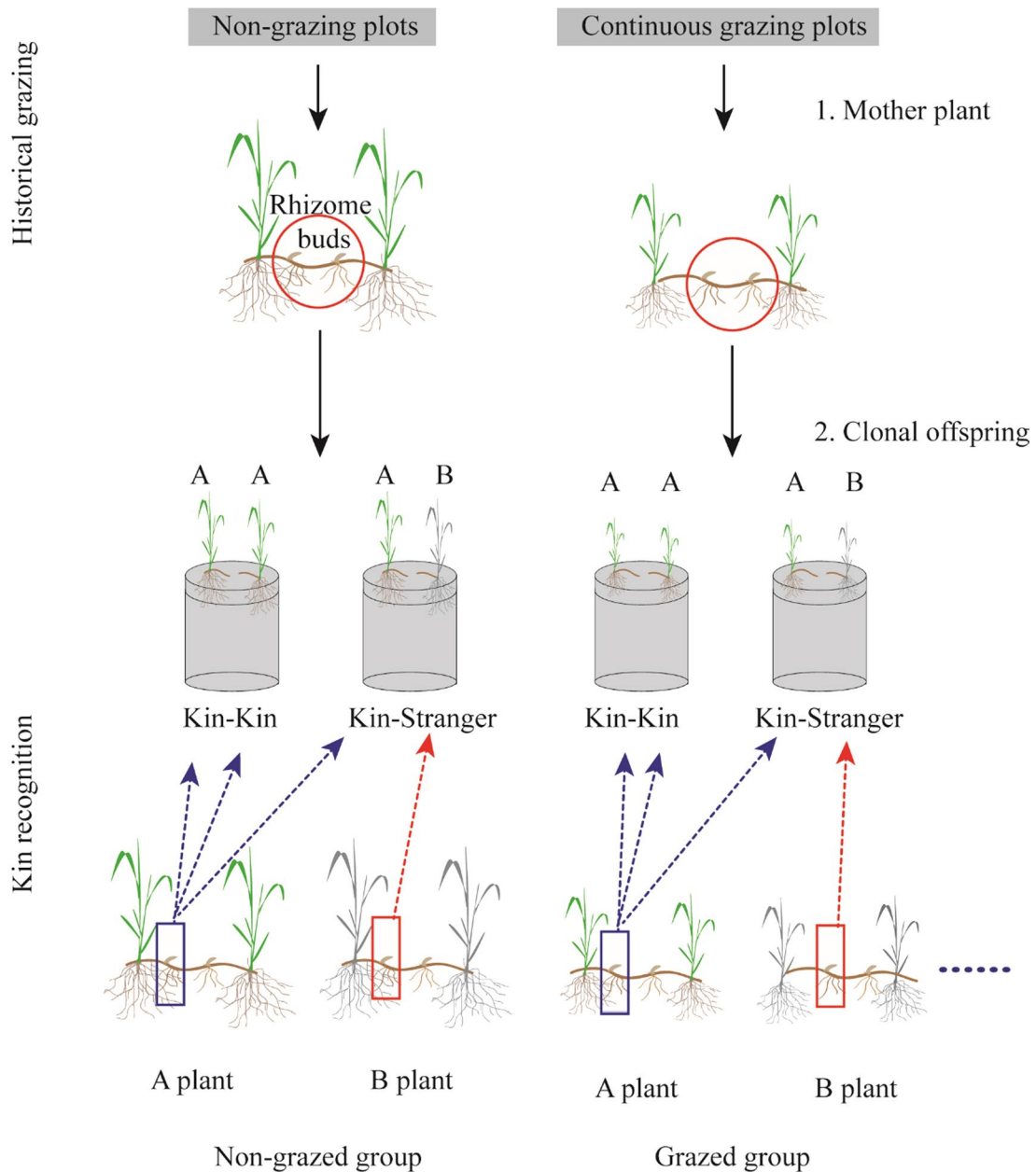


Fig. 1 Schematic diagram of the experimental design. The clonal offspring of *Leymus chinensis* that had experienced either a 9-year period of continuous grazing or non-grazing were used. The same letters indicate kin group *L. chinensis* offspring from the same plant. Kin plants were the clonal siblings from the same mother as the focal *L. chinensis* plant, whereas stranger plants were from different mothers

the aboveground and total biomass did not differ significantly between non-grazed and grazed offspring when they were grown with stranger neighbors (Fig. 2). Notably, LRRs dramatically varied among the 13 measured variables related to shoots and roots. The LRRs to neighbor identity of the 13 measured variables average related to shoots and roots decreased by 0.08 in non-grazed plants and increased by 0.36 in grazed plants

(Additional file 1: Fig. S1). In non-grazed groups, most of the indexes exhibited lower performance in offspring grown with stranger neighbors compared to those grown with their siblings (Fig. 3). Comparatively, ramet-level biomass of leaf and stem tissues had the lowest LRRs in non-grazed offspring (Fig. 3). In contrast, offspring in the grazed group generally exhibited a more robust growth when coexisting with kin neighbors, except in root length

Table 1 Results of linear models assessing the effects of neighbor identity and maternal effect induced by grazing on aboveground biomass (ABM), belowground biomass (BBM), total biomass (TBM), stem biomass (SBM), leaf biomass (LBM), leaf biomass of a single plant (SLBM), stem biomass of a single plant (SSBM), and aboveground biomass of a single plant (SABM)

Variables	ABM		BBM		TBM		SBM		LBM		SSBM		SSLBM		SABM	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Neighbor identity (NI)	0.03	ns	0.05	ns	0.04	ns	0.06	ns	0.01	ns	0.74	ns	0.68	ns	0.72	ns
Maternal effect (ME)	4.39	ns	9.36	**	6.14	**	1.19	ns	9.16	**	0.33	ns	4.24	*	2.05	ns
NI × ME	3.18	*	3.55	*	3.64	*	3.17	*	2.96	ns	4.6	**	3.87	*	4.28	*

* $P < 0.05$; ** $P < 0.01$; ns, $P > 0.05$

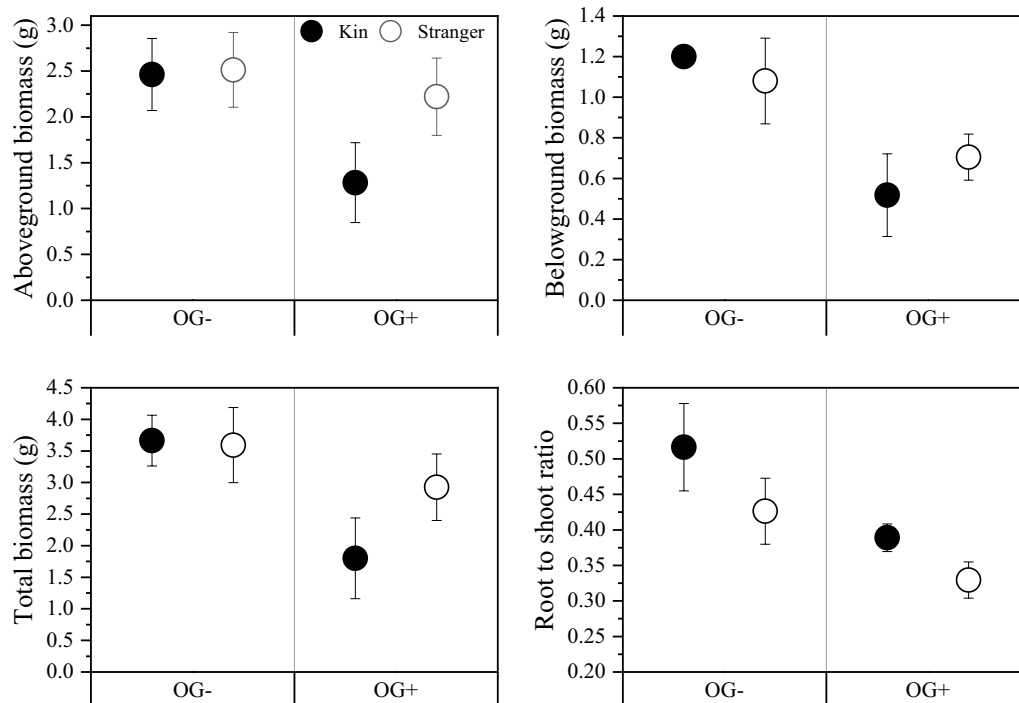
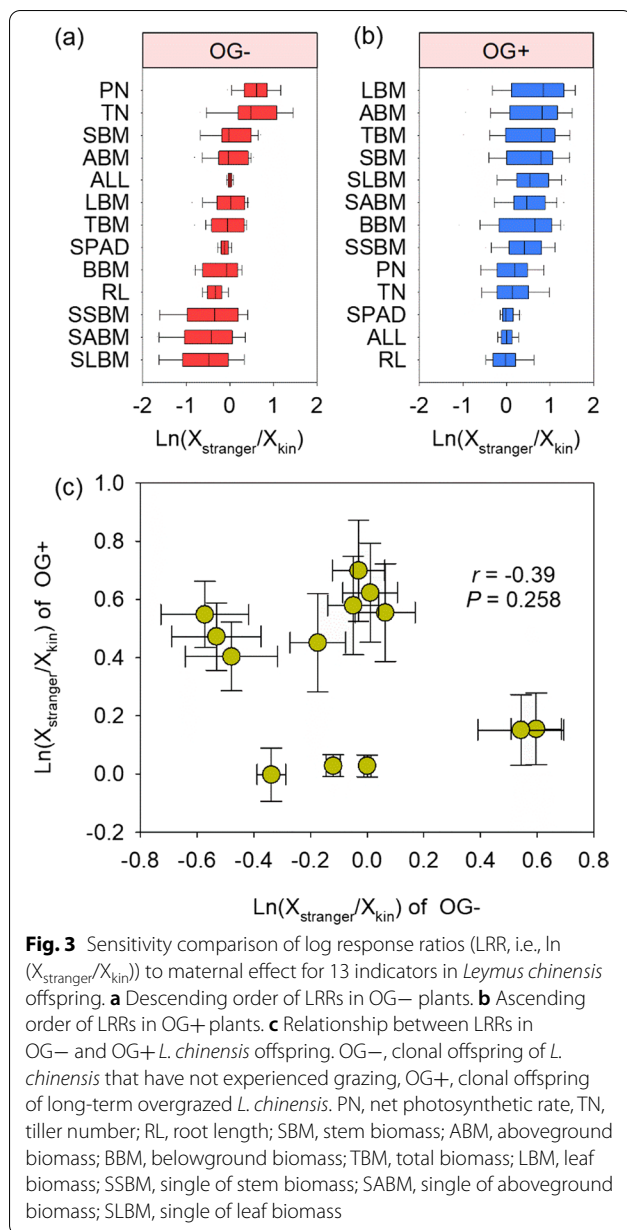


Fig. 2 Effects of neighbor identity and grazing history of grazing on aboveground biomass, belowground biomass, total biomass, and the root–shoot ratio of *Leymus chinensis* offspring. OG–, offspring of *L. chinensis* that have not experienced grazing, OG+, offspring of long-term overgrazed *L. chinensis*

(Fig. 3). Biomass-related variables, especially the biomass of the aboveground portion, had higher responses than other variables, such as photosynthesis, chlorophyll content, and root length in grazed groups (Fig. 3). However, no significant correlations were observed in LRRs between the non-grazed and grazed groups ($r = -0.39$, $P > 0.05$; Fig. 3), indicating that maternal effects altered the response sensitivity both in shoots and roots of offspring (Fig. 3).

Compared with the non-grazed groups, the LRRs of the grazed offspring increased significantly from 0.01 to 0.62 in aboveground biomass and -0.17 to 0.63 in belowground biomass (Fig. 4a). Moreover, *L. chinensis* offspring had a higher shoot biomass allocation when

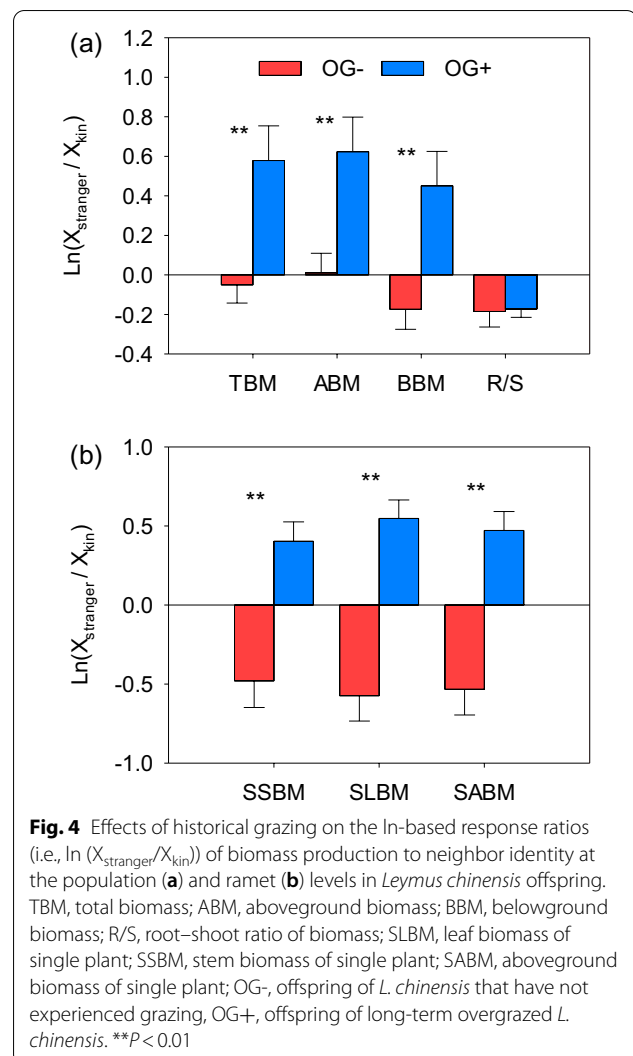
grown with stranger neighbors and a lower root biomass allocation when grown with kin neighbors (Additional file 1: Fig. S2). Compared with kin, the tiller number of non-grazed offspring increased by 73.08%, whereas grazed offspring increased by 8.00% when grown with stranger neighbor (Additional file 1: Fig. S3). LRRs of biomass per offspring were significantly reversed from negative to positive by grazing-induced maternal effect (Fig. 4b). Compared to the offspring grown with kin, the decreases and increases in LRRs were, respectively, detected in the ramet biomass and height of non-grazed and grazed offspring when grown with stranger neighbors (Additional file 1: Figs. S4, S5). These results imply that grazing experience can



mediate the interaction of *L. chinensis* offspring with different but related neighbors.

Discussion

In this study, the biomass of grazed focal plants was significantly affected by neighbor identity and increased considerably when grown with stranger neighbors, whereas non-grazed focal plants were not affected. This indicates that grazing history can induce observable maternal effects on plant kin recognition. Contrary to the strong response of grazed clonal offspring to neighbor identity, the responses of the offspring from a non-grazed habitat were relatively weak. Indeed, kin



recognition in clonal plants plays a crucial role in grasslands, where clonal species are always the dominant plant community (Benson and Hartnett 2006). The aggregation of clonal offspring from the same genotype is commonly observed in grasslands owing to their diffusional limitation (Maestre et al. 2009). Moreover, grazing can dramatically decrease the intraspecific genotype diversity of clonal plants to enhance the clustering of plant populations with closer kinship (Wang et al. 2014). Therefore, the productivity and stability of populations may be dramatically affected by the identity of neighboring plants in grazing grasslands. In the present study, LRRs of *L. chinensis* offspring biomass significantly increased in grazed groups compared with non-grazed groups. These findings show that the overall effect of neighbor identity on biomass production was relatively weak. However, there were significant interactive effects of maternal effect and neighbor identity on plant biomass.

How kin recognition affects biomass partitioning in competitive organs of plants remains controversial, but is thought to be dependent on external environmental factors (Biedrzycki and Bais 2010; Dudley and File 2007). Most studies have explicitly shown that plants tend to decrease root biomass investment when coexisting with close relatives (Biedrzycki and Bais 2010; Biersnaskie 2011). However, some studies have found that the response to neighbor identity is mainly achieved through changes in root morphology rather than changes in biomass allocation (Semchenko et al. 2014). In the present study, biomass allocations were associated with neighbor identity rather than grazing history and interactive effects. In general, the biomass allocation in the above-ground plant parts, rather than belowground parts, increased when focal plants were grown with stranger plants. This contrasts with the previous studies that have postulated that greater root allocation is a consequence of an increase in belowground competitive ability (Dudley and File 2007; Mercer and Eppley 2014). The focal species in this study, *L. chinensis*, is a clonal perennial plant. Therefore, the individual siblings of this species share the same root system, allowing them to effectively benefit from nutrient competition with other coexisting species (Ren et al. 2017). Moreover, in non-grazed and grazed groups, there was lower root biomass allocation in plants grown with stranger neighbors than those grown with kin neighbors. Various adaptation strategies in the aboveground organs, such as increased stem elongation and specific leaf area for light capturing, are essential for acquiring more resources. Specifically, *L. chinensis* has a high light compensation and light saturation points (Liu et al. 2019; Murphy and Dudley 2009). In this study, historically grazed plants had higher leaf biomass allocation when grown with stranger neighbors than when grown with kin (increasing from 32.67% to 36.90%), which is consistent with the findings of previous studies. However, biomass allocation to stems rather than leaves increased considerably in *L. chinensis* when grown with stranger neighbors in the non-grazed group.

In this study, the interaction effects between maternal effects and neighbor identity were enhanced at the ramet level compared to pot-level responses. This was indirectly mediated by the tillering capacity of clonal *L. chinensis*. Size–density tradeoffs are species dependent and commonly underlain by external factors (Carneiro da Silva et al. 2021; Marquard et al. 2009). Herein, non-grazed clonal offspring had a higher increase in tiller capacity than grazed offspring. Consequently, compared to *L. chinensis* grown with kin, decreases, and increases in biomass were detected in the ramet of non-grazed and grazed offspring, respectively, when grown with stranger neighbors. Specifically, grazing-induced maternal effects

significantly reversed the LRRs of kin relatedness. Comparatively, the pot-level responses to kin relatedness were much greater than those at the ramet level, especially among non-grazed *L. chinensis* offspring. These findings suggest that size–density tradeoff played a central role in regulating the plant biomass production and allocation response to land use history and neighbor identity in *L. chinensis*. Of note, we also found the ramet-level responses to neighbor identity changed over time in both non-grazed and grazed groups. For a period of 2 months, plant size was measured four times (using vertical height as a proxy), and the results revealed that the differences between the heights of *L. chinensis* grown with kin and strangers gradually narrowed, suggesting that kin interaction plays a crucial role in determining the population dynamics during the early stage of plant growth.

The disturbance history of maternal plants can dramatically determine offspring fitness. Ren et al. (2017) proposed that over 30 years of overgrazing can lead to significant maternal effects on *L. chinensis*, manifesting as legacy effects on plant performance. Consistent with the previous study, grazing for 9 years significantly decreased the total biomass, leaf biomass, and below-ground biomass of clonal offspring at the pot and ramet scale in the present study.

In this study, significant differences in the above- and below-ground biomass were observed between non-grazed and grazed *L. chinensis* offspring grown with their kin. In contrast, offspring grown with stranger neighbors exhibited no significant difference in plant performance between non-grazed and grazed offspring. These findings indicate that maternal experiences of large herbivore grazing can remarkably increase the growth potential of offspring via positive phenotypic plasticity in the presence of heterogeneous genetic lineages (Segura et al. 2015; Singh et al. 2017).

Our findings revealed that grazing-induced maternal effects could be partially offset by the surrounding neighbor identity when plants are grown with stranger plants from a different mother, which is consistent with the results reported previously (Li et al. 2015a; Ren et al. 2017). According to the stress gradient hypothesis, facilitation becomes more important with increasing external stresses, such as overgrazing in the grassland ecosystem (Maestre et al. 2009; Malkinson and Tielbörger, 2010). In this study, grazing-induced dwarf phenotypes were rapidly restored in plants coexisting with stranger neighbors, implying that the facilitation ability of neighboring plants was improved by increasing the biomass of individual plants under grazing. Increased intraspecific genotypic diversity has been verified to facilitate population stability and biomass accumulation (Abbott et al. 2017; Fukano et al. 2019; Wilkinson et al. 2010). Therefore, the results

of the present study can be adopted for practical application in grassland reseeded to increase genotypic diversity of degraded grasslands.

Conclusion

To the best of our knowledge, this is the first study to report that plant maternal effects induced by grazing can significantly affect intraspecific kin recognition. Our results demonstrated that *L. chinensis* plants recognized neighbor identity and distinguished their clonal siblings from stranger neighbors. Consequently, the plants were able to adjust their growth strategies by enhancing their aboveground biomass investment. Notably, the clonal offspring of the non-grazed *L. chinensis* exhibited a weak response to neighbor identity. On the contrary, the historically grazed *L. chinensis* offspring increased significantly in biomass when grown with stranger neighbors compared to when they were grown with their clonal siblings. These findings suggest that maternal grazing can increase kin recognition ability of clonal offspring, further implying that genotype-aggregated reseeded may accelerate grassland restoration in *L. chinensis*. The discovery of kin recognition and maternal effects in clonal plant, as well as a further understanding of its potential mechanisms in response strategies and the improved effects of the interaction of kin recognition and maternal effects on grassland produced, could lead to new insight into grassland restoration at the end of grazing.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-022-00377-x>.

Additional file 1. Fig. S1. Overall effect of historical grazing on the \ln -based response ratios (i.e., $\ln(X_{\text{stranger}}/X_{\text{kin}})$) to neighbor identity for 13 indicators in *Leymus chinensis* offspring. OG-, clonal offspring of *L. chinensis* that have not experienced grazing, OG+, clonal offspring of long-term overgrazed *L. chinensis*. **Fig. S2.** Biomass allocations to leaf, stem, and root tissues in *Leymus chinensis* according to neighbor identity and grazing history. OG-, offspring of *L. chinensis* that have not experienced grazing, OG+, offspring of long-term overgrazed *L. chinensis*. **Fig. S3.** Effects of neighbor identity and grazing history of grazing on pot-scale tiller number and single of aboveground biomass in *Leymus chinensis*. OG-, offspring of *L. chinensis* that have not experienced grazing, OG+, offspring of long-term overgrazed *L. chinensis*. **Fig. S4.** Effects of neighbor identity and grazing history on leaf biomass of a single plant (SLBM), stem biomass of a single plant (SSBM), and aboveground biomass of a single plant (SABM) in *Leymus chinensis*. OG-, offspring of *L. chinensis* that have not experienced grazing, OG+, offspring of long-term overgrazed *L. chinensis*. **Fig. S5.** Temporal variation in the response of plant height to neighbor identity and grazing history in *Leymus chinensis*. OG-, offspring of *L. chinensis* that have not experienced grazing, OG+, offspring of long-term overgrazed *L. chinensis*. **Table S1.** The composition and concentration of each chemical substance used in the hydroponic experiment. **Table S2.** Results of linear models assessing the effects of neighbor identity and grazing-related maternal effects on biomass allocation.

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Author contributions

ZZ conducted field collections, conducted field collections, analyzed and interpreted the data, and wrote the manuscript. XL contributed to project design, processed and assisted with data analysis and interpretation. XL, JD and JS provided supervision and reviewed the final draft of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Not applicable.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable. All authors agreed and approved the manuscript for publication in *Ecological Processes*.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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