

## Research Article

# *Leymus chinensis* Tolerates Mowing Disturbance by Maintaining Photosynthesis in Saline-Alkali Heterogeneous Habitats

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*Leymus chinensis* is a perennial rhizomatous clonal plant with strong tolerance to mowing, grazing, drought, and salt-alkali. However, with patchy soil environment, how mowing affect the photosynthesis of *L. chinensis* in heterogeneous patches is largely unknown. In this experiment, we tested the effects of mowing intensity (0, 35%, and 70% removal of aboveground biomass) on plant photosynthesis under different heterogeneous patches with different saline-alkali soil. We found that moderate concentrations of salt-alkali under heterogeneous patches have no significant effect on the photosynthesis of *L. chinensis*. Moderate mowing can maintain photosynthesis under no heterogeneity soil and moderate salt-alkali patch condition. In addition, heavy mowing and high salt-alkali soil under heterogeneous patches both inhibited net photosynthetic rate ( $P_N$ ) and transpiration rate ( $E$ ), reduced leaf area, and plant height. *L. chinensis* responded to extreme soil conditions and strong disturbance by increasing water-use efficiency (WUE), reducing relative water content (RWC), and changing stomatal conductance (Gsw). Therefore, our results imply that moderate grazing or mowing can be used to maintain the productivity and economic benefits of grassland when the soil heterogeneous patches with moderate saline-alkali conditions.

## 1. Instruction

Salinization and alkalization of soil is a major environmental problem worldwide [1–3]. Soil salinization represents an increasing environmental problem [4], and the salinities are heterogeneously distributed in natural habitats. There are about 932 million hectares of saline-alkalized land in the world, and about  $10 \times 10^6$  hm<sup>2</sup> of irrigated farmland is abandoned every year [5]. There are many reasons for the formation of saline-alkalized land in the natural environment. In addition to the natural environmental factors, the formation of saline-alkali land has human causes [6, 7] and mainly refers to the overuse of grassland resources among them. In the Songnen Plain of Northeast China, about 70% of the natural grassland has been seriously degraded due to soil salinization and alkalization, and this trend is still increasing [8, 9].

It is generally considered that saline-alkali stress inhibits plant growth by water deficiency or ion toxicity, high concentrations of salts in the soil make it harder for roots to extract water, and high concentrations of salts within the plant can be toxic [4]. But in salt-tolerant species (e.g., *L. chinensis*), plant growth is only moderately inhibited, or even stimulated at certain levels of salinity [10]. Tolerance to osmotic stress is a feature of most clonal plants; it has been suggested to be perceived partly by stretch-activated channels. The integration by clonal plant may cause a reduction in leaf area and a development in clonal growth, which allows plant to conserve soil moisture and prevent an escalation in the salt concentration in the soil [4]. Early studies demonstrated that cloned plants have the ability to modify their morphology in response to habitat heterogeneity habitat which is one kind of phenotypic plasticity [11, 12]. The morphological plasticity

of *L. chinensis* simultaneously occurs at above- and below-ground; these responses to stimuli most in a way by compensatory growth or shoot and root biomass allocation. In addition, saline-alkali stress also affects the physiological characteristics of plants.

Saline-alkali stress affects every stage of plant growth and development [13]. It can also slow down the growth rate of plant, reduce individual size, decrease leaf area, and decrease root activity and yellowing leaves, resulting in the reduction of biomass accumulation and other physiological characteristics [14]. Photosynthesis of plants is sensitive to salinity and alkali stress and can be used as one of the important indicators of plant response to stress [15]. The photosynthesis of tomato seedlings was inhibited by salt-alkali stress [16]. The net photosynthetic rate and stomatal conductance of barley were also inhibited under salt-alkali stress [17]. But there are many plants having tolerance to saline-alkali. Some studies have shown that clonal plants have high tolerance to adverse habitats (e.g., saline-alkali, low nutrition, and drought) due to the presence of stolon and rhizomes [18–20]. *L. chinensis*, a clonal plant, showed good tolerance to saline-alkali environment [21]. It evades and resists the damage caused by saline-alkali environment by selectively distributing, expanding, and utilizing rhizomes for clonal integration [11, 22]. And low concentration of saline-alkali can also promote the growth of *L. chinensis* [10]. The main challenge to be solved is to unravel the relationship between morphological and physiological characteristics of cloned plants under heterogeneous saline-alkali conditions.

In natural communities, the resource distributions within environment (i.e., light, water, and nutrients) are usually heterogeneous in a spatial and temporal pattern. Previous studies have shown that clonal plants possess a particularly foraging behavior of rhizome or stolon responses to heterogeneity, such as higher proportional allocation of biomass to stolon under low light patches [23], greater production of ramet, and above-ground biomass in the nutrient-rich environment [19]. Plants should maximize benefits and minimize costs subject to certain constraints. The experimental evidences are still lacking to understand the mechanisms of clonal plant adaptability under heterogeneous environment. A number of studies have shown that connections among ramets of clonal plants by rhizome allow transport of photosynthates, water, and nutrients from established genet (parent plant) to developing ramet (daughter plant) [22, 24, 25]. However, the photosynthesis of plant would explain more on the physiological responses.

Moreover, grazing and mowing are the two major ways of grassland utilization [26]. It is generally believed that grazing and mowing have many adverse effects on plant growth by defoliation and indirectly by modifying growth allocation (e.g., enhancing total production, altering relative growth rate, and enhancing tiller compensatory growth due to leaf removal) and resource availability (e.g., altering water uptake and redistribution of nutrients) [23, 27]. With the increase of grazing intensity, in order to better adapt to grazing, plants not only change morphological indicators but also change physiological indicators such as photosynthesis and redistribution of nutrients in plants [28, 29]. Grazing reduces the leaf area of plants, directly affects photosynthesis [30], and even

directly impairs some functions of plants [31]. In addition, grazing can affect the water situation in plants, thus changing the relationship between net photosynthetic rate and water, leading to the decline of net photosynthetic rate [30]. However, many studies have found that moderate grazing and mowing can stimulate plants to produce compensatory growth, thus restoring their lost biomass, and even produce more biomass. In the study of *Festuca arundinacea*, the result suggested that moderate grazing could promote its quality and yield [32]. Similar results were also found in the experiment of cutting *L. chinensis*, under mild and moderate mowing intensities, overcompensatory growth appeared, and aboveground biomass accumulation, relative growth rate, and root tillering were all higher [18]. Particularly under the condition of sufficient resources, both mild and moderate mowing can promote the accumulation of biomass and the growth of buds of *L. chinensis* [24]. Grazing can stimulate plants and compensate them, thus promoting photosynthesis [33, 34]. Photosynthesis affects productivity and is important for grazing and mowing; studies in Hunshandak Sandland showed that moderate grazing intensity promoted photosynthesis [29]. However, some studies have also found that grazing has little effect on plants and no changes in physiological indicators such as photosynthesis [35].

Previous studies on the effects of salinity and grazing on the clone growth and photosynthesis of *L. chinensis* almost have not considered the interaction between these two factors. However, in the salinized grassland, these two kinds of stress exist simultaneously. In addition, most experiments in the field have difficulty distinguishing the growth, expansion, and biomass distribution of belowground roots of rhizome clones, especially in heterogeneous habitats with large numbers of other species. Therefore, we conducted to set pot experiments in greenhouse, to explore the changes of photosynthetic characteristics and resistance mechanism of *L. chinensis* under saline-alkali heterogeneous patches and mowing disturbance.

## 2. Materials and Methods

**2.1. Species and Site Description.** The experiment was conducted in a greenhouse located at the Research Station of Shenyang Agricultural University (41°50'N, 123°34'E). The station base belongs to temperate semihumid continental climate with average annual temperature of 8.1°C and average annual precipitation of 721.9 mm. The greenhouse was controlled with natural photoperiod, 42%/69% day/night relative humidity and 26°C/20°C day/night temperature, and an average day/night vapor-pressure deficit of 1.75/0.35 kPa. The total experimental period of this study was 120 days and was conducted from mid-May to the end of September. We chose the clonal plant *L. chinensis*, which seeds were collected from the natural grasslands of the Songnen Plains, as our experimental material. *L. chinensis* is a typical rhizomatous perennial Gramineae clonal plant [20] distributed in the eastern part of the Eurasian steppe, including the northern and eastern parts of the Mongolian People's Republic, the Lake Baikal region of Russia, the North China Plain, the Inner Mongolia Plateau, and the Northeast Plain [36, 37]. It is rich

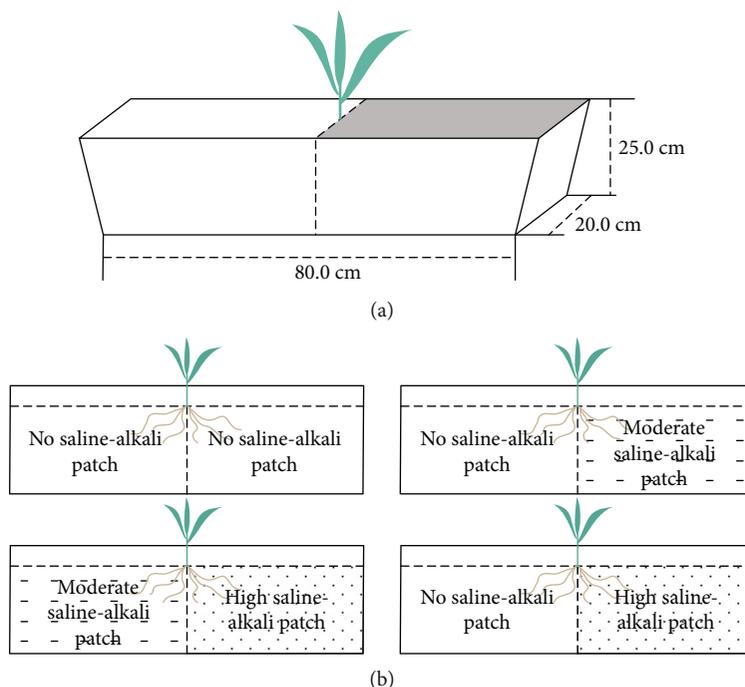


FIGURE 1: The planting configuration of the plants. Each long trough pot has one plant, which is planted in the middle of the pot (directly above the baffle), and the plant roots can grow left and right. Schematic representation of saline-alkali stress treatments given to different patches.

in protein, minerals, and carbohydrates, with strong palatability, drought resistance, cold tolerance, barren tolerance, and high tolerance to saline-alkali soil. It is also resistant to mowing and grazing, commonly known as “alkali grass” in Northeast China [38]. It has strong ecological adaptability and plasticity. As the dominant species in this area, it has great significance for grassland restoration.

**2.2. Experimental Design.** A  $3 \times 4$  factorial, completely randomized design was used with three mowing levels and four heterogeneity patches. There were three levels of mowing treatment: no mowing (NM), moderate mowing (MM) which was 35% of aboveground biomass harvested, and heavy mowing (HM) which was 70% of aboveground biomass harvested. Four heterogeneity patches was conducted with sand as culture medium and long trough pot (80 cm length  $\times$  20 cm width  $\times$  25 cm depth), as shown in Figure 1(a), these containers were used to ensure that the clonal growth of *L. chinensis* individuals was not limited by the size of the pot, and the new ramets can find enough space to establish and grow. A baffle retaining was placed into the center of each trough pot to blocking the lower 2/3 of a culture medium layer, and remaining the super 1/3 to allowing the plants root system grow. Therefore, the install baffle of each long trough pot divided the container into two patches. Similar or different concentrations of saline-alkali solution were added into both patches of one same pot to simulate homogeneous or heterogeneous soil saline-alkali habitats. There are four combinations of soil saline-alkali heterogeneity patches: nonheterogeneity (no saline-alkali on both patches, recorded as NS-NS), heterogeneity (no saline-alkali and moderate saline-alkali patches, recorded as NS-MS;

moderate saline-alkali and high saline-alkali patches, recorded as MS-HS; no saline-alkali and high saline-alkali patches, recorded as NS-HS), such as Figure 1(b). Saline-alkali stress was realized by using different concentrations of compound saline-alkali solution with varying salinity and pH, which was set as three gradients: non-saline-alkali (NS), moderate saline-alkali (MS), and high saline-alkali (HS). Two neutral salts ( $\text{NaCl}$  and  $\text{Na}_2\text{SO}_4$ ) and two alkaline salts ( $\text{NaHCO}_3$  and  $\text{Na}_2\text{CO}_3$ ) were selected based on the salt components in the extent saline-alkali soil of northeast China [10]. The medium concentration of moderate saline-alkali was 100 mmol/L, the high concentration of saline-alkali was 200 mmol/L, and the ratios of four salts were  $\text{NaCl}:\text{Na}_2\text{SO}_4:\text{NaHCO}_3:\text{Na}_2\text{CO}_3 = 1:1:1:1$  [1, 10].

At the beginning of the experiment, *L. chinensis* seeds were germinated in seedling trays for four weeks. At about 30-day age, each long trough pot was transplanted with one *L. chinensis* seedling, which was placed into the middle of the pot directly perpendicular above the baffle. By this design, the root system of plant could grow random direction of the long pot. The saline-alkali solution and nutrient liquid were added into culture medium from the either side edges of each long trough to ensure the solution not confused. There are total 36 long troughs with 12 treatments, 3 replications for each treatment. Saline-alkali and mowing treatments were carried out at intervals of 30 days. Indicators were measured and sampled at 20 days after treatment. Total three times of mowing and saline-alkali additions were implemented from June to August in 2019. A total of about 29.286 g and 58.572 g solid salt mixture were added into each moderate and high salt-alkaline patch, respectively. Water availability was controlled by the water capacity test (Moisture

TABLE 1: Statistical summary of two-way ANOVA evaluating the effects of salt-alkali heterogeneity of soil and clipping their combined effects on the net photosynthetic rate ( $P_N$ ), intercellular  $\text{CO}_2$  concentration ( $C_i$ ), ambient  $\text{CO}_2$  concentration ( $C_a$ ), intercellular  $\text{CO}_2$ /ambient  $\text{CO}_2$  ( $C_i/C_a$ ), stomatal conductance ( $G_{sw}$ ), and stomatal limitation (LS) of *L. chinensis*. Values are  $F$  ratios and their significance for effects.

Treatment	df	$P_N$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )		$C_i/C_a$		$C_i$ ( $\mu\text{mol mol}^{-1}$ )		$C_a$ ( $\mu\text{mol ol}^{-1}$ )		$G_{sw}$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )		LS (%)	
		$F$	$P$	$F$	$P$	$F$	$P$	$F$	$P$	$F$	$P$	$F$	$P$
Mowing (M)	2	14.867	<0.001**	1.871	0.176	4.903	0.016*	24.934	<0.001**	0.389	0.682	1.871	0.176
Saline-alkali heterogeneity (S)	7	3.262	0.039*	2.638	0.073	1.360	0.279	10.321	<0.001**	4.104	0.017*	2.638	0.073
S×M	14	5.709	0.001**	4.664	0.003**	6.173	0.001**	6.679	<0.001**	1.893	0.123	4.664	0.003**

$F$  values and significance levels (\*\* $P < 0.01$ ; \* $P < 0.05$ ) are given.

Meter type HH2, Delta-T Devices Ltd., UK) of trays every 2 days and by adding tap water until a prefixed sand water content was reached (75% of field capacity for well-watered). During the experiment, all pots received adequate fertilized of Hoagland's nutrient solution once a week. The experiment was started on May 5, 2019, and harvested on September 25, 2019.

**2.3. Measurements and Calculations.** The individual height of each genet plant and daughter plants was measured every week and was averaged for each pot. The clipped biomasses after each time of mowing treatment as well as the final living biomass were collected and oven-dried at first 1 h at  $105^\circ\text{C}$  and then  $65^\circ\text{C}$  for 48 h to determine the accumulated aboveground biomass. The leaf area was measured by a portable laser leaf area meter (CI-202, USA). Leaf mass per area (LMA) was calculated as leaf biomass/leaf area.

**2.4. Leaf Relative Water Content.** Weigh the fresh leaves (about 0.1 g) to obtain the fresh weight (FW), then immerse the leaves in distilled water, put them under  $4^\circ\text{C}$ , stay overnight in the dark, weigh their apparent turgid fresh weight (TW) the next day, and finally put them in the oven, dry them to constant weight at  $65^\circ\text{C}$ , and weigh their dry weight (DW). The relative water content (RWC) of leaves is  $\text{RWC} = [(FW-DW)/(TW-DW)] \times 100\%$ .

**2.5. Leaf Gas Exchange.** Photosynthesis-related indexes were measured from 8:00 to 11:00 in a clear morning, included the net photosynthetic rate ( $P_N$ ), intercellular  $\text{CO}_2$  concentration ( $C_i$ ), ambient  $\text{CO}_2$  concentration ( $C_a$ ), intercellular  $\text{CO}_2$ /ambient  $\text{CO}_2$  ( $C_i/C_a$ ), stomatal conductance ( $G_{sw}$ ), transpiration rate ( $E$ ), water-use efficiency (WUE), and stomatal limitation (LS), by a portable photosynthesis system (LI-6800, USA).

**2.6. Plant Height.** After 20 days of the third treatment, 3 pots were randomly selected for each treatment, and 5 *L. chinensis* plants for each pot were randomly selected for plant height determination.

**2.7. Statistical Analysis.** For plant photosynthesis, variables performed two-way ANOVA to evaluate the effects of mowing, saline-alkali, and their interaction. Data were further analyzed within each factor when the interaction was not significant. *Post hoc* tests (Tukey's HSD test) were performed to

compare the means between clipping treatments at each saline-alkali intensity levels. All statistical analyses were performed using the SPSS statistical package.

### 3. Result

**3.1. Gas Exchange.** The net photosynthetic rate ( $P_N$ ) was significantly affected by mowing and soil saline-alkali heterogeneity and their interaction ( $P < 0.05$ , Table 1). Without mowing, the heterogeneity patches of different soil saline-alkali concentrations had no significant effect on  $P_N$ . Under moderate mowing treatment,  $P_N$  were significantly decreased in MS-HS and NS-HS patches. The  $P_N$  of *L. chinensis* with heavy mowing showed a similar pattern as no mowing (Figure 2(a)).

The intercellular carbon dioxide concentration ( $C_i$ ) was significantly affected by mowing and the interaction between mowing and saline-alkali patches ( $P < 0.05$ ). In NS-NS and NS-MS patches, the  $C_i$  was significantly increased with heavy mowing. Furthermore, under heavy mowing, the  $C_i$  in NS-HS patches was significantly lower than that of other soil patches (Table 1, Figure 2(b)).

Mowing treatment, soil saline-alkali heterogeneity, and their interaction have significant effects on the concentration of ambient carbon dioxide ( $C_a$ ) ( $P < 0.05$ ). The  $C_a$  in NS-NS and NS-MS was similar as  $C_i$ ; it was significantly higher under heavy mowing than moderate and no mowing treatments. However, in NS-HS patches, the  $C_a$  was significantly lower only under no mowing condition (Table 1, Figure 2(c)).

The  $C_i/C_a$  was only significantly affected by the interaction of soil saline-alkali heterogeneity and mowing ( $P < 0.05$ , Table 1). In homogeneous environment (NS-NS), heavy mowing was significantly increased  $C_i/C_a$ . Under heavy mowing, the  $C_i/C_a$  was significantly decreased in NS-HS patches, Figure 2(e). The limiting value of stomata (LS) followed an opposite pattern to the  $C_i/C_a$  (Figure 2(f)) and was significantly affected by the interaction of soil saline-alkali heterogeneity and mowing (Table 1). The stomatal conductance ( $G_{sw}$ ) was only affected by the heterogeneity of soil saline-alkali patches (Table 1) and significantly decreased in NS-HS patches (Figure 2(d)).

**3.2. Moisture Change.** The soil saline-alkali heterogeneity and the interaction between saline-alkali and mowing had a significant effect on transpiration rate ( $E$ ) ( $P < 0.05$ , Table 2).

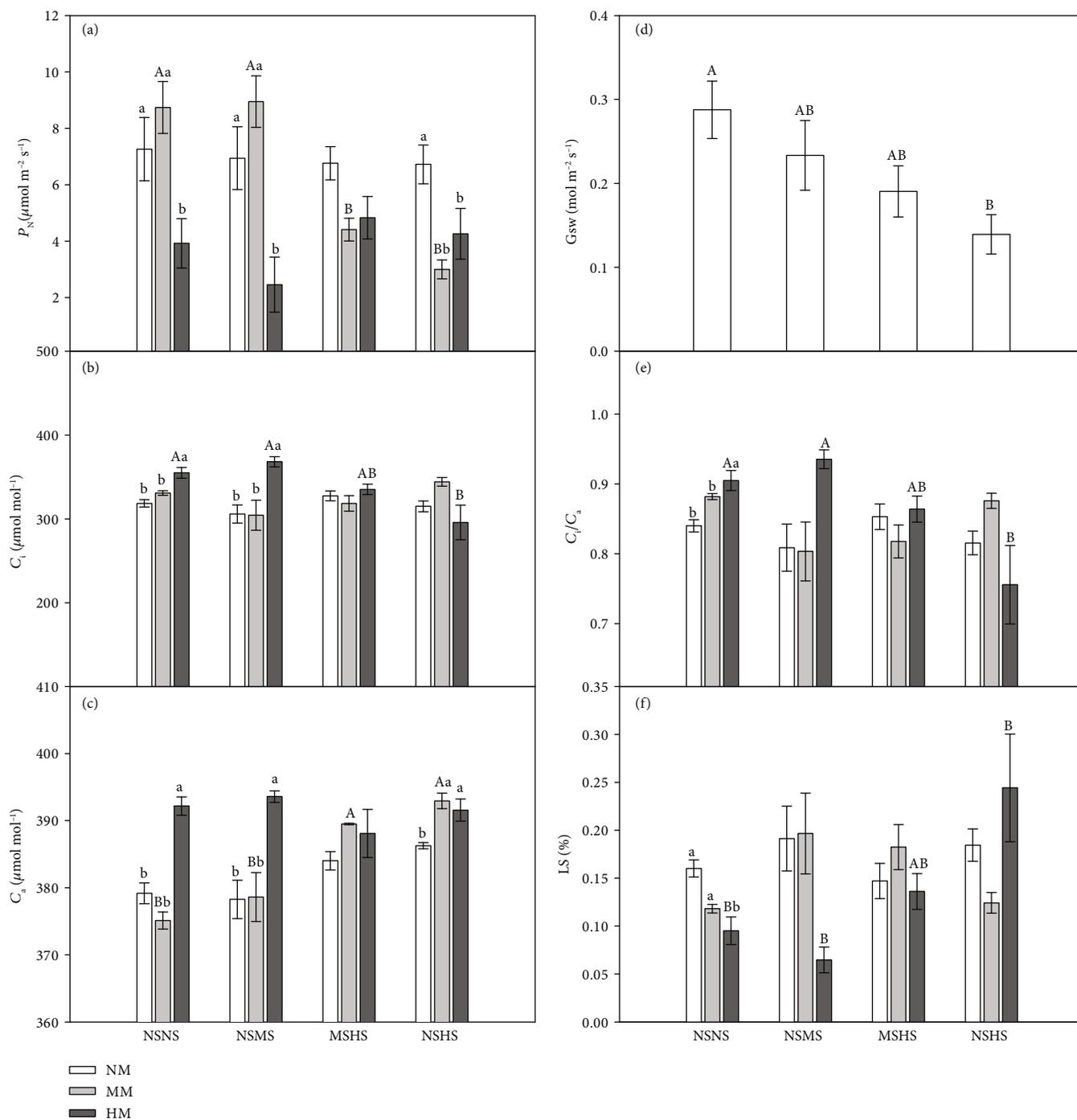


FIGURE 2: Effects of saline-alkali and clipping stress on the net photosynthetic rate ( $P_N$ ), intercellular  $\text{CO}_2$  concentration ( $C_i$ ), ambient  $\text{CO}_2$  concentration ( $C_a$ ), the intercellular  $\text{CO}_2$ /ambient  $\text{CO}_2$  ( $C_i/C_a$ ), stomatal limitation (LS), and stomatal conductance ( $G_{sw}$ ) of *L. chinensis*. Different lowercase letters represent significant difference ( $P < 0.05$ ) among the saline-alkali and clipping treatments.

In homogeneous environment (NS-NS), the transpiration rate under moderate mowing was significantly higher than that of no mowing and heavy mowing. Meanwhile, the transpiration rate was also significantly decreased in saline-alkali heterogeneous patches NS-MS under moderate mowing (Figure 3(b)).

Water-use efficiency (WUE) was significantly affected by the interaction between soil saline-alkali heterogeneity

and mowing ( $P < 0.05$ , Table 2). Under heavy mowing, WUE in NS-HS patches was significantly higher than other patches (Figure 3(a)). There were no significant effects of mowing and soil saline-alkali heterogeneity and their interaction on relative water content (RWC, Table 2).

3.3. Growth Situation. The plant height of *L. chinensis* only showed significant difference in different mowing treatments

TABLE 2: Statistical summary of two-way ANOVA evaluating the effects of salt-alkali heterogeneity of soil and clipping their combined effects on the transpiration rate ( $E$ ), water-use efficiency (WUE), leaf area, leaf mass per area (LMA), relative water content (RWC), and plant height of *L. chinensis*. Values are  $F$  ratios and their significance for effects.

Treatment	df	$E$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )		WUE ( $P_N/E$ )		Leaf area ( $\text{cm}^2$ )		LMA ( $\text{g/cm}^2$ )		RWC (%)		Plant height (cm)	
		$F$	$P$	$F$	$P$	$F$	$P$	$F$	$P$	$F$	$P$	$F$	$P$
		Mowing (M)	2	2.003	0.157	1.614	0.220	22.746	<0.001**	0.015	0.985	0.859	0.436
Saline-alkali heterogeneity (S)	7	5.667	0.004**	3.709	0.025*	5.063	0.007**	0.647	0.592	0.608	0.617	1.281	0.304
S×M	14	2.518	0.049*	4.492	0.003**	1.161	0.359	0.735	0.626	2.507	0.050	1.594	0.192

$F$  values and significance levels (\*\* $P < 0.01$ ; \* $P < 0.05$ ) are given.

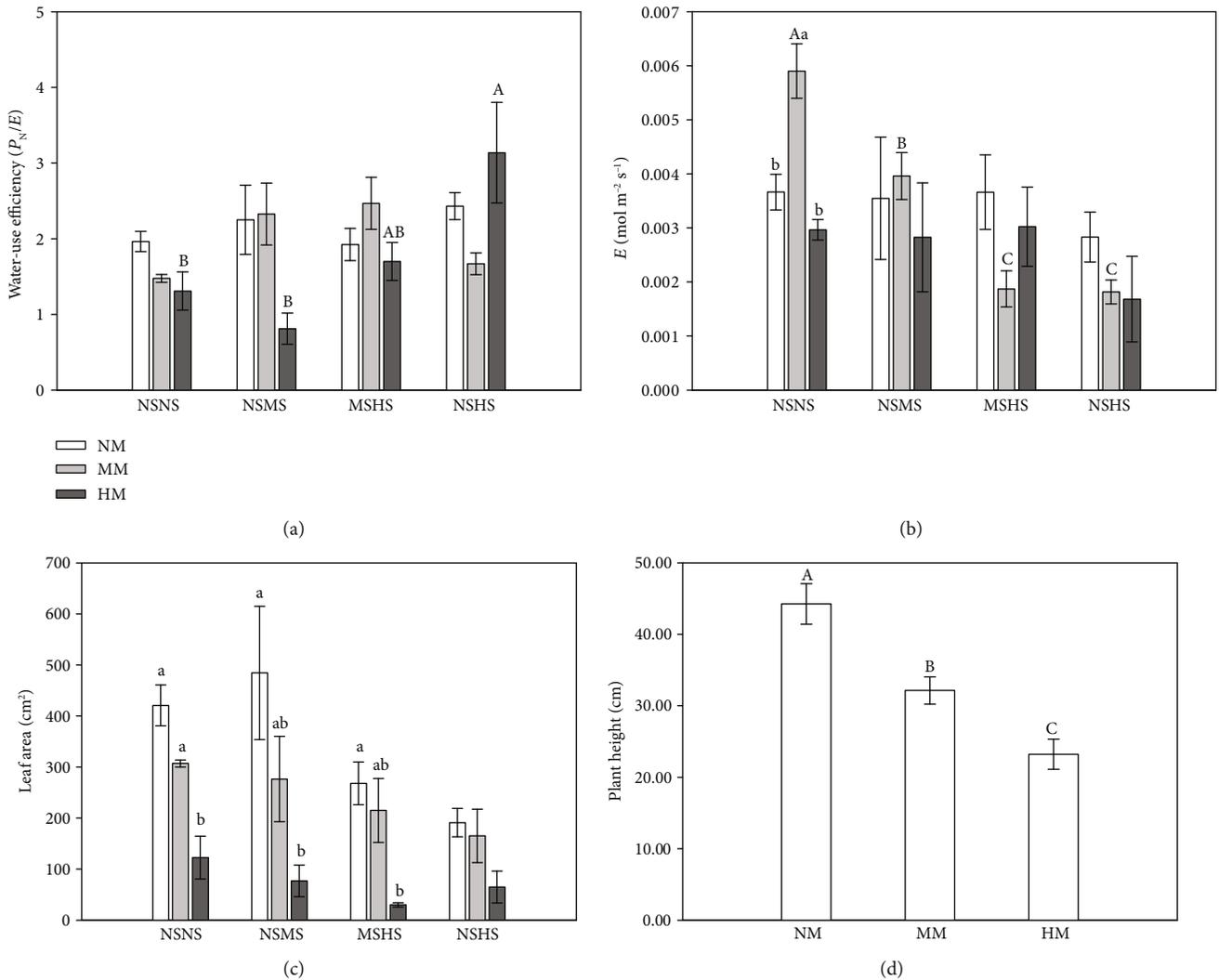


FIGURE 3: Effects of saline-alkali and clipping stress on the leaf area, plant height, transpiration rate ( $E$ ), and water-use efficiency (WUE) of *L. chinensis*. Different lowercase letters represent significant difference ( $P < 0.05$ ) among the saline-alkali and clipping treatments.

( $P < 0.05$ ). With the increase of mowing intensity, plant height decreased gradually (Table 2, Figure 3(d)).

Mowing treatment and soil saline-alkali heterogeneity had a significant effect on the leaf area of *L. chinensis* ( $P < 0.05$ ). Under each patches, with the increase of cutting

intensity, the leaf area decreased, and HM significantly reduced the leaf area, except the NS-HS patches which mowing have no effect on the leaf area (Table 2, Figure 3(c)). There was no significant effect on the leaf mass per area (LMA) of *L. chinensis* under different treatments (Table 2).

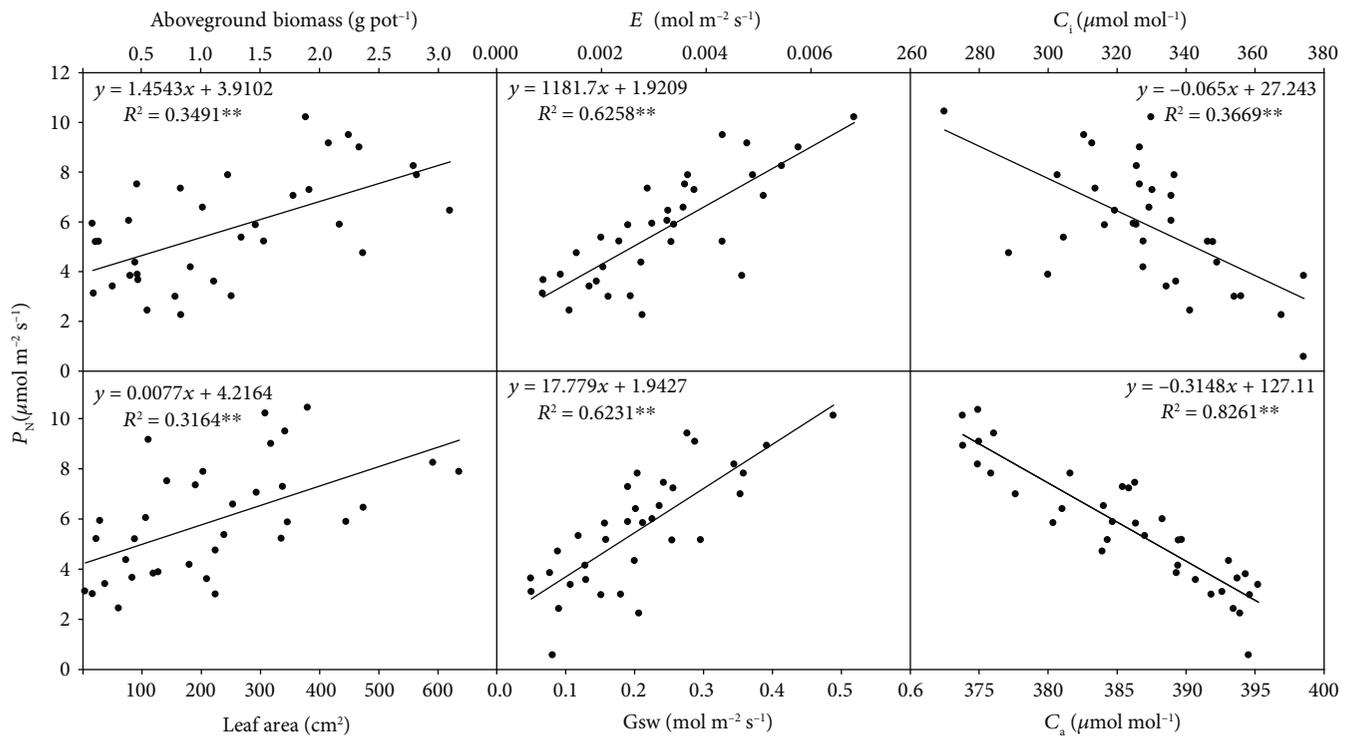


FIGURE 4: Correlation of aboveground biomass, leaf area, and gas exchange parameters of *L. chinensis*.

**3.4. Correlation of Gas Exchange.** The  $P_N$  of *L. chinensis* was positively correlated with aboveground biomass, leaf area, transpiration rate ( $E$ ), and stomatal conductance ( $G_{sw}$ ) and negatively correlated with intercellular  $\text{CO}_2$  concentration and ambient  $\text{CO}_2$  concentration (Figure 4).

## 4. Discussion

Photosynthesis can fix the solar energy, which is an important physiological activity of plants, affects the growth and development of plants, and determines the productivity of plants [39]. The results showed that under moderate mowing, *L. chinensis* could maintain the net photosynthetic rate ( $P_N$ ) and transpiration rate in the NS-NS and NS-MS of soil saline-alkali patches (Figures 2(a) and 3(b)). This was similar to Yan et al. who study on *Stipa baicalensis* in Grassland of Hulun Buir, Inner Mongolia [40]. This may be due to the reduction of leaf area by mowing, and in order to compensate for defoliation losses, *L. chinensis* chose to increase the photosynthetic rate to compensate, which is in line with the statement that the loss of leaf area will increase photosynthesis found in other studies [18, 32]. And photosynthesis has a significant positive correlation with aboveground biomass (Figure 4), so the photosynthesis is maintained and the aboveground biomass is maintained. Our experiment found that the compensation of aboveground biomass may be through the compensation of leaf area. The results showed that there was a significant positive correlation between leaf area and net photosynthesis (Figure 4). Moreover, there is no significant difference between the leaf area of moderate mowing (MM) and that of no mowing (NM) when there is no salt-alkali (NS-NS) or low salt-alkali (NS-MS) content in

soil patches (Figure 3(c)). This proves that the growth of leaf area is compensated. The reason for this compensatory growth may be related to mowing or grazing promoted the growth of the rhizome of *L. chinensis* [41]. It is also possible that moderate mowing or grazing promoted tiller growth and increased bud number of *L. chinensis*, resulting in compensatory growth of daughter plant and increased photosynthetic rate [42]. As the place where photosynthesis takes place, the compensation of leaf area will also ensure the progress of photosynthesis. There are many conditions for photosynthesis to go on normally, one of which is the opening degree of stomata. Stomata are the channels of gas exchange between leaves and the outside world, which can supplement  $\text{CO}_2$  for photosynthesis and affect transpiration rate. Our results show that photosynthesis is negatively correlated with intercellular  $\text{CO}_2$  concentration and ambient  $\text{CO}_2$  concentration, positively correlated with transpiration (Figure 4). If the stomatal opening degree is low, the transpiration rate is reduced and the carbon dioxide outside the cell cannot enter the cell normally; photosynthesis will be inhibited. The stomatal conductance reflects the degree of stomatal opening, so as our results, there is a significant positive correlation between stomatal conductance and net photosynthesis (Figure 4).

When the salt concentration of soil saline-alkali patches is high (MS-HS and NS-HS), compared with the other two saline-alkali environments, the compensation growth disappears and the net photosynthetic rate decreases significantly when cutting moderately (Figure 2(a)). We speculate that high concentration of salt and alkali has an overwhelming adverse effect on plant growth. This may be due to the high concentration of salt and alkali plaque on the plant to produce osmotic stress or affect the ion balance around the root

system, so as to reduce the photosynthetic rate [1]. One study of the photosynthetic characteristics of cotton seedlings found that the main reason for the decline of photosynthesis under saline-alkali stress was the stomatal factor, but when the saline-alkali concentration increased or the effects lasted for a long time, the influencing factors gradually became nonstomatal factors [43]. Our results showed that the stomatal conductance decreased with the increase of saline-alkali stress concentration (Figure 2(f)). This is consistent with the positive correlation between the stomatal conductance and the index of plant assimilation ability found by Drake et al. [44]. Therefore, under the stress caused by the saline-alkali concentration, the main factor limiting the photosynthesis of *L. chinensis* might be a stomatal factor. Stomata closing forced by saline-alkali stress, which reduced the stomatal conductance, hindered CO<sub>2</sub> from entering the leaves and also reduced the evaporation of water, thus reducing the transpiration rate and net photosynthetic rate. However, the change of stomatal limit (LS) value did not increase with the increase of saline-alkali concentration. This changing trend was different under different mowing treatments, which may be due to the influence of nonstomatal factors on photosynthesis under the combined stress of saline-alkali stress and mowing treatment [45]. The results of this experiment showed that the stomatal limit value was low (Figure 2(f)), but the net photosynthetic rate was low as well (Figure 2(a)), which may be because under these conditions, the nonstomatal factors have more prominent influence on the photosynthetic rate. As some studies have found that there is a nonlinear relationship between net photosynthetic rate and stomatal conductance, that is, the net photosynthetic rate increases with the increase of stomatal conductance, but the increase rate decreases gradually, which may be due to the aggravation of nonstomatal factors on photosynthetic rate [46]. Under heavy mowing, the leaf area, plant height, transpiration rate, and net photosynthetic rate of *L. chinensis* decreased significantly (Figures 3(c) and 3(d)). Mowing greatly reduced leaf area and plant height, resulted in loss of photosynthetic organs, thus reduced photosynthetic rate, which is similar to the results of Rhodes et al. [33]. Moreover, photosynthesis has a significant positive correlation with aboveground biomass (Figure 4), so the decrease of photosynthesis may reduce aboveground biomass, thus plant height. Water-use efficiency (WUE) refers to the amount of organic matter assimilated by plants in time of losing unit water [47], which can reflect the water consumption and adaptation of plants to stress [48]. The results showed that the water-use efficiency of NS-HS soil salt and alkali patches increased under heavy mowing (Figure 3(a)). This may be due to the existence of mowing treatment which reduces water-use efficiency, or it may be that these treatments have made *L. chinensis* unable to survive. Some studies have shown that there is a positive correlation between net photosynthetic rate and water-use efficiency of *L. chinensis* after grazing. It improved water-use efficiency by increasing net photosynthetic rate and reducing transpiration rate and adapted to grazing stress [29, 49]. However, with the continuous grazing time, perennial grasses can survive by reducing water-use efficiency to respond to stress [28, 50]. Moreover,

under saline-alkali stress, plants will limit water loss, improve water-use efficiency, and fix more CO<sub>2</sub> but reduce the overall growth rate [51].

## 5. Conclusion

Maintaining photosynthetic characteristics is the primary integration strategy by clonal plants to tolerated or escaped highly stresses. In moderate saline-alkali heterogeneity site, moderate mowing or grazing can maintain photosynthesis, resulting in the promotion of compensatory growth. However, high saline-alkali patches have an overriding detrimental impact on plant compensatory growth and extremely inhibit net photosynthetic rate. In the future research, we should focus on the nonstomatal factors limiting photosynthesis and combined with the biomass distribution model of plant in field experiments, to explore the photosynthetic characteristics and growth strategy of *Leymus chinensis* under mowing and soil saline-alkali heterogeneity environments, so as to provide effective reference for the rational utilization of grassland.

## Data Availability

All materials used in this paper are public, and the data used to support the results of this study are available on request from the corresponding author.

## Conflicts of Interest

The authors declare that there is no conflict of interests regarding the publication of this paper.

## Authors' Contributions

Nan Lu and Luhao Qu are joint first authors.

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