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Regrowth, yield and nutrition of *Leymus chinensis* and *Hordeum brevisubulatum* in response to defoliation intensity and frequency

Rebrote, rendimiento y nutrición de *Leymus chinensis* y *Hordeum brevisubulatum* en respuesta a la frecuencia e intensidad de defoliación

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Abstract. The effects of different defoliation intensities and frequencies were studied on regrowth and herbage mass of *Leymus chinensis* and *Hordeum brevisubulatum* in northeast China for two years. Plants were defoliated to 6, 8 or 10 cm stubble height by removing about 40% of growth down to each designated defoliation height. In the first year, *L. chinensis* was defoliated 22, 17 or 13 times, and in the second year was defoliated 21, 15 or 15 times to reach 6, 8 or 10 cm stubble height treatments, respectively. *H. brevisubulatum* was defoliated 26, 21 or 15 times in the first year, and 28, 23 or 21 times in the second year to reach the 6, 8 or 10 cm stubble, respectively. *L. chinensis* was more productive than *H. brevisubulatum*, but *H. brevisubulatum* showed a better forage quality than *L. chinensis* because *H. brevisubulatu*m showed a higher leaf to stem ratio and crude protein concentration than *L. chinensis*. Both species produced the highest yield, but the lowest quality when defoliated to 10 cm stubble. There were no significant differences in water soluble carbohydrate (WSC) concentrations in below-ground culm and rhizome tissues between defoliation heights, but *L. chinensis* had a higher WSC concentration than *H. brevisubulatum*.

Keywords: Defoliation frequency; Pasture quality; Rhizomatous grass; Songnen grassland; Stubble height.

Resumen. Se estudiaron los efectos de diferentes intensidades y frecuencias de defoliación sobre el rebrote y la producción de biomasa de *Leymus chinensis* y *Hordeum brevisubulatum* en el noreste de China durante 2 años. Las plantas fueron defoliadas a 6, 8 ó 10 cm de altura desde el nivel del suelo de forma de remover un 40% del crecimiento hasta la altura de defoliación correspondiente. En el primer año, *L. chinensis* fue defoliado 22, 17, ó 13 veces, y en el segundo año fue defoliado 21, 15 ó 15 veces de forma de alcanzar los 6, 8 ó 10 cm de altura desde el nivel del suelo, respectivamente. *H. brevisubulatum* fue defoliado 26, 21 ó 15 veces en el primer año, y 28, 23 ó 21 veces en el segundo año para alcanzar los 6, 8 ó 10 cm de altura, respectivamente. *L. chinensis* fue más productivo que *H. brevisubulatum*, pero *H. brevisubulatum* mostró una mejor calidad de forraje que *L. chinensis*. Esto fue debido a que *H. brevisubulatum* mostró una mayor relación hoja/tallo y concentración de proteína bruta que *L. chinensis*. Ambas especies produjeron el mayor rendimiento pero la menor calidad de forraje cuando fueron defoliadas a 10 cm de altura desde el nivel del suelo. No hubo diferencias significativas en la concentración de carbohidratos solubles en agua en los tallos subterráneos y tejidos de rizomas entre las alturas de defoliación, pero *L. chinensis* tuvo una mayor concentración de carbohidratos solubles en agua que *H. brevisubulatum*.

Palabras clave: Frecuencia de defoliación; Calidad de la pastura; Gramínea rizomatosa; Pastizal de Songnen; Altura de tallos remanentes.

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INTRODUCTION

Songnen Plain is one of the most productive grasslands in northeast China. More than 40% of Songnen grasslands are dominated by *Leymus chinensis* (Wang & Ripley, 1997). *L. chinensis* is an important perennial grass, well adapted to high pH (8.5–11.5) in sodic soils (Jin et al., 2006), because of its good quality and growth (Wang & Ripley, 1997). It is regarded as one of the best pasture grass species for the rangeland industry in northern China (Baoyin et al., 2015). *Hordeum brevisubulatum* is another commonly found perennial grass in the region, which originated from western Turkey (Von Bothmer et al., 1995). It has good tolerance to salt, cold and low soil fertility. It commonly occurs in moist environments, usually growing in meadows where the soil pH is at least 8.0 (Dong et al., 1992; Suhayda et al., 1997). It grows in rather dense tufts, with either short or long subterranean runners, and it has a good ability for tillering and regrowing after grazing and trampling. In short, both *L. chinensis* and *H. brevisubulatum* are widely grown in northeast China (Dong *et al.*, 1992). Both *L. chinensis* and *H. brevisubulatum* are rhizomatous grasses with typical clonal propagation, and both are suitable for grazing or cutting for hay (Yang & Li, 2003; Wang & Zhou, 2004).

Defoliation characteristics have to be appropriate for an adequate grassland management (Tälle et al., 2016). The effect of defoliation on plant yield, regrowth and nutrition mainly depend on the frequency, intensity and timing of defoliation (Kaensombath & Frankow-Lindberg, 2012; Shen et al., 2013). In Songnen grassland, it is recommended to cut *L. chinensis* once a year in late July (Zhang, 1993). Defoliation twice or more per year would significantly reduce the production of the *L. chinensis* grassland (Li et al., 2000; Li & Liu, 2000). However, previous studies have determined that the defoliation stubble height was most often at 5–6 cm from the soil surface, giving relatively little attention to both defoliation intensity and frequency. For *H. brevisubulatum*, most research focused on the seed maturity and harvesting time (Wang et al., 2006), leaf growth pattern (Yang & Li, 2003), and photosynthesis and transpiration (Wang & Zhou, 2004). There are a few studies on the impact of soil nutrition or defoliation on yield of *H. brevisubulatum*. Overall, the information on the response of *H. brevisubulatum* to defoliation intensity and frequency is very limited.

The objectives of this research were (a) to determine the yield potential and plant nutritional value of *L. chinensis* and *H. brevisubulatum*, and (b) to study the effects of defoliation intensity and frequency on the regrowth, to optimize herbage mass while maintaining feed quality.

Table 1. Monthly rainfall and mean monthly air temperature at the study site in 2005 and 2006.
Tabla 1. Lluvia mensual y temperatura del aire mensual promedio en el sitio de estudio en 2005 y 2006.

	Rainfall (mm)		Temperature (°C)	
	2005	2006	2005	2006
May	5.0	11.3	19	19
June	85.8	62.2	22	22
July	131.5	154.9	25	25
August	15.9	80.2	23	25
September	22.9	8.2	19	18

MATERIALS AND METHODS

Study site. The experiment was undertaken at the Songnen Grassland Ecological Research Station of Northeast Normal University, Jilin Province, PR China (44° 45' N, 123° 45' E, elevation, 140 m) over two growing seasons, namely from May to September in 2005 and 2006. The study area has a semi-arid, continental climate. The May to September rainfall was 261 mm in 2005 and 317 mm in 2006, and the mean monthly air temperature ranged between 18 and 25 °C from May to September (Table 1).

Pot preparation. In May 2005, sods (350 mm long x 350 mm wide and 350 mm deep) were dug from two mature swards (7 year old) containing either *L. chinensis* or *H. brevisubulatum* - 12 sods from each species. Both swards were maintained as pure stands by hand weeding. All sods were then carefully trimmed to fit into pots with 320 mm diameter and 320 mm depth. The pots were buried outdoors with the upper surface level at the ground surface. All above-ground parts were cut to 50 mm for a uniform start. All pots were watered to field capacity immediately after transplanting and watered twice in May-June 2005 to ensure survival. No additional irrigation was applied during the rest of the experiment. Fertilizer (N:P:K 26:10:12) was applied at 46 kg/ha twice, in June and August 2005 and again in June and August 2006.

Experimental design and treatments. The experiment used a completely randomized design with two species (*L. chinensis* and *H. brevisubulatum*) and three defoliation intensities (heavy, medium and light defoliation), replicated 4 times. The defoliation stubble height was 6, 8 and 10 cm for the heavy, medium and light defoliations, respectively. The defoliation frequency was determined by plant regrowth. Plants were cut every once they reached 10, 13.3 and 16.7 cm for heavy, medium and light defoliation treatments, respectively. This represented 40% removal of the herbage when cut to the respective stubble height treatments. No cutting was performed after the growing season finished in September, when pastures were cut to ground level. In total, *L. chinensis* was cut 22, 17, 13 times in the first year, and 21, 15, 15 times in the second year, and *H. brevisubulatum* was cut 26, 21, 15 times in the first, and 28, 23, 21 times in the second year for the heavy, medium and light defoliation treatments, respectively.

Data collection. Herbage mass, yield components and protein content. All herbage above each defoliation stubble height was collected from each pot at each cutting time. A subsample was taken to dissect into leaf, stem, and ears if present. All samples were dried for 24 h at 65 °C and weighed. Dried samples were ground to pass through a 1 mm sieve in preparation for analysis of nitrogen (N) concentration using an automatic Kjel-Foss apparatus (2300, FOSS Tecator AB, Höganäs, Sweden) (Bao 2005). Crude protein (CP) was calculated from N content (N x 6.25).

Tiller dynamics. All tillers, including dead tillers, in each pot were marked with a colored wire loop and counted before each cutting. Plant height was recorded and tiller density (tillers/m^2) counted at each harvest.

Water soluble carbohydrate content. At the end of growing season in 2006, a 150 x 150 mm sod was taken from each pot and washed free of soil. The samples, that included below-ground culms and rhizomes, were dried for 24 h at 65 °C, and then ground to pass a 1 mm sieve for analysis of water soluble carbohydrate (WSC) content using the laboratory methods described by Teixeira et al. (2007).

Statistical analyses. All studied variables were analyzed using general linear models. Repeated measures ANOVA were used to test the response variables of growth rate, herbage mass, leaf to stem ratio, tiller number, and CP concentration. The within-subjects variables were month or year, and the between-subjects variables were species and stubble height. Two way ANOVAs were performed to test the effects of species, stubble height, and their interactions on WSC content in below-ground culms and rhizomes. Treatment means were statistically compared by Duncan Post Hoc Test at the 5% probability level. All statistical analyses were performed using SPSS 13.0 (SPSS Inc., Chicago, USA).

RESULTS

Regrowth. In the first year, the regrowth rate was significantly affected by month, the interactions of month x species, month x height, and month x species x height (Table 2). The regrowth rate of *L. chinensis* was faster than that of *H. brevisubulatum* ($P<0.05$) (Fig. 1a b, Table 2). For both species, regrowth rates increased as cutting height increase. The 10 cm cutting height treatments had the highest regrowth rate (Fig. 1a, b). The regrowth rates of both species were greatest during the months of June and July for all stubble height treatments ($P<0.05$).

In 2006, the regrowth rate was significantly affected by month and the interaction of month x species x height, but it was not affected by the interactions of month x species and month x height. There was no cutting height effect within either species. Rates of regrowth during the growing season in 2006 were highly variable amongst cutting height treatments (Fig. 1c, d). Both species had the highest rates of regrowth at the beginning of the growing season and there was no regrowth from *L. chinensis* cut at 8 or 10 cm in September.

Herbage mass. The accumulated herbage mass was significant different between the two years (Table 2). In 2005, there were significant differences between stubble heights in accumulated herbage mass on *L. chinensis* (Fig. 2a). Whereas *L. chinensis* produced increasingly more herbage mass as stubble height increased, this trend was not significant for *H. brevisubulatum* (Fig. 2a, b; Table 2). *Leymus chinensis* had the highest mass at the 10 cm cutting height treatment which was 305.2 g/m^2.

In 2006, *L. chinensis* was again more productive than *H. brevisubulatum* but there was no stubble height effect for either species (Table 2). The herbage mass was about 350 g/m^2 for *L. chinensis* and 240 g/m^2 for *H. brevisubulatum*.

Leaf to stem ratio. The leaf to stem ratios were significantly different between 2005 and 2006 (Table 2). Species, stubble height and their interactions affected significantly the leaf to stem ratio (Table 2). In 2005, *L. chinensis* had a higher ratio at the 6 cm than at the 8 or 10 cm stubble height (Fig. 2c). *Hordeum brevisubulatum* had a similar ratio amongst stubble heights but at the 10 cm stubble height the leaf to stem ratio of *H. brevisubulatum* was higher than that in *L. chinensis*.

In 2006, *L. chinensis* cut to 10 cm had a lower leaf to stem ratio than when it was cut to 6 cm, but this similar trend was not significant for *H. brevisubulatum* (Fig. 2d). There was higher leaf to stem ratios at both 8 and 10 cm heights in *H. brevisubulatum* than at these heights in *L. chinensis* in 2006 (Fig. 2c, d). In general, the leaf to stem ratio in *L. chinensis* was always lower than that on *H. brevisubulatum* in both 2005 and 2006 (Fig. 2c, d).

Tiller dynamics. In 2005, the tiller numbers were significantly affected by the month, the interactions of month x species, and month x height, but it was not significantly affected by the interaction of month x species x height (Table 2). During the growing season, except the tiller numbers of *H. brevisubulatum* in September, tiller numbers increased with time in both species at all stubble heights, with the highest tiller numbers in August and September (Fig. 3a, b). *Leymus chinensis* had higher tiller numbers at 10 than at 6 or 8 cm stubble height. Overall, *L. chinensis* had more tillers than *H. brevisubulatum* ($P<0.05$, Fig. 3a, b).

In 2006, tiller numbers were significantly affected by month,

Table 2. Tests of within-subjects and between-subjects effects of regrowth rate, herbage mass, leaf to stem ratio, tiller number, and crude protein by repeated measures ANOVAs.
Tabla 2. Pruebas de los efectos dentro y fuera de los organismos sobre la tasa de rebrote, biomasa de forraje, relación hoja/tallo, número de macollas y proteína bruta por ANOVA de medidas repetidas.

	Within-subjects effects		Between-subjects effects	
Variable	**Source**	**F**	**Source**	**F**
Regrowth rate	month	139.432(4)***		
(2005)	month*species	14.35(4)***	species	6.984 (1)*
	month*height	4.612(8)***	height	15.873 (2) ***
	month*species*height	8.664(8)***	species*height	5.22 (2) *
Regrowth rate	month	34.738 (4)***		
(2006)	month*species	1.743 (4) n.s.	species	0.569 (1) n.s.
	month*height	1.699 (8) n.s.	height	0.753 (2) n.s.
	month*species*height	2.522 (8)*	species*height	5.053 (2) *
Tiller number	month	391.321 (4) ***		
(2005)	month*species	5.143 (4) ***	species	61.208 (1) ***
	month*height	3.442 (8) **	height	1.076 (2) n.s.
	month*species*height	0.789 (8) n.s.	species*height	0.942 (2) n.s.
Tiller number	month	54.829 (4) ***		
(2006)	month*species	18.272 (4) ***	species	1.729 (1) n.s.
	month*height	3.344 (8) **	height	0.883 (2) n.s.
	month*species*height	2.868 (8) **	species*height	1.057 (2) n.s.
Crude protein	month	161.255 (4) ***		
	month*species	119.788 (4) ***	species	438.198 (1) ***
	month*height	51.31 (8) ***	height	119.21 (2) ***
	month*species*height	37.863 (8) ***	species*height	28.774 (2) ***
	Error			
Herbage mass	year	69.851 (1)***		
	year*species	1.8 (1) n.s.	species	44.018 (1) ***
	year*height	1.197 (2) n.s.	height	3.255 (2) n.s.
	year*species*height	2.343 (2) n.s.	species*height	0.523 (2) n.s.
Leaf to stem ratio	year	6.023 (1)*		
	year*species	2.841 (1) n.s.	species	18.35 (1) ***
	year*height	1.48 (2) n.s.	height	17.278 (2) ***
	year*species*height	0.594 (2) n.s.	species*height	4.517 (2) *

* P<0.05; ** P<0.01; *** P<0.001; n.s., not significant. The subscript in the parentheses was degrees of freedom.

the interactions of month x species, month x height, and month x species x height (Table 2). However, the species, height, and their interaction had no significant effect on tiller numbers (Table 2). *Leymus chinensis* had more tillers at 6 and 8 cm than at 10 cm stubble height (Fig. 3c, d). By contrast tiller numbers in *H. brevisubulatum* were lower when cutting was at 8 than at 6 or 10 cm stubble height. In general, *H. brevisubulatum* had more tillers than *L. chinensis* from June to August 2006. During the growing season, tiller number in all treatments increased until July, then gradually decreased in August and September in *H. brevisubulatum*, at remained at a similar density in *L. chinensis* (Fig. 3c, d).

Water soluble carbohydrate content. WSC of below-

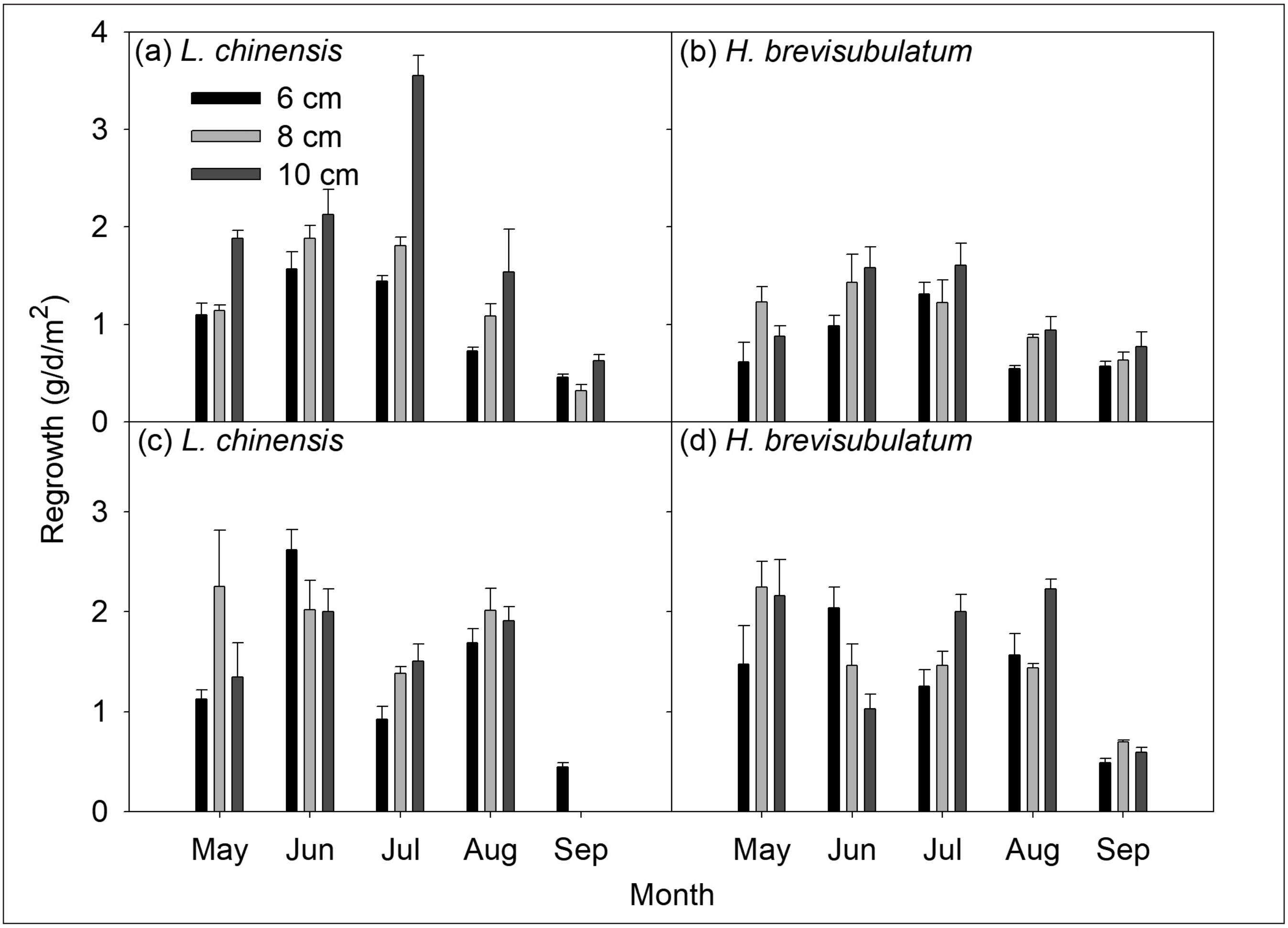

Fig. 1. Effect of defoliation on regrowth rate (g/d/m^2) of *L. chinensis* and *H. brevisubulatum* cut to stubble heights of 6, 8, or 10 cm. (a) *L. chinensis* in 2005, (b) H. brevisubulatum in 2005, (c) *L. chinensis* in 2006, and (d) *H. brevisubulatum* in 2006. Error bars are SE of the means.

Fig. 1. Efecto de la defoliación sobre la tasa de rebrote (g/d/m^2) de L. chinensis and *H. brevisubulatum* cortados a una altura remanente de 6, 8 ó 10 cm. (a) *L. chinensis* en 2005, (b) *H. brevisubulatum* en 2005, (c) *L. chinensis* en 2006, y (d) *H. brevisubulatum* en 2006. Las barras verticales indican el error estándar de los promedios.

ground culms and rhizome were both affected by species, but it was not affected by stubble height in 2006 (Table 3). However, there was significant interaction in WSC of rhizomes between species and stubble height, and there were no significant interaction in WSC of below-ground culm (Table 3). *L. chinensis* had a significantly higher WSC concentration in both underground stem (P<0.05) and rhizome (P<0.01) compared to *H. brevisubulatum* (Table 3, Fig. 2e, f).

Crude protein concentration. The concentration of CP varied significantly through the growing season (P<0.001, Table 2), and time, species, stubble height, and their interaction significantly affected on CP (Table 2). Concentration of CP was higher in *H. brevisubulatum* than in *L. chinensis* (P<0.01) and in forage cut at 6 cm than at 8 or 10 cm stubble height (P<0.01) (Fig. 4, Table 2). For both species, CP was highest in September (more than 26%) and lowest in June (about 14%).

DISCUSSION

Leymus chinensis and *H. brevisubulatum* are widely grown as the most productive perennial pasture species in northeast China where there is high salinization in the soil. *Leymus chinensis* produced 30% more herbage than *H. brevisubulatum* in both years (Fig. 2a, b). However, *H. brevisubulatum* had better quality than *L. chinensis*, attributed to its greater CP concentration and higher leaf to stem ratio.

A high leaf to stem ratio is consistently associated with a greater forage quality, because leaf is more nutritious and more palatable to livestock than stem (Hurley et al., 2009). Thus, the increasing CP concentration with the more severe defoliation treatments mirrors the trend with leaf to stem ra-

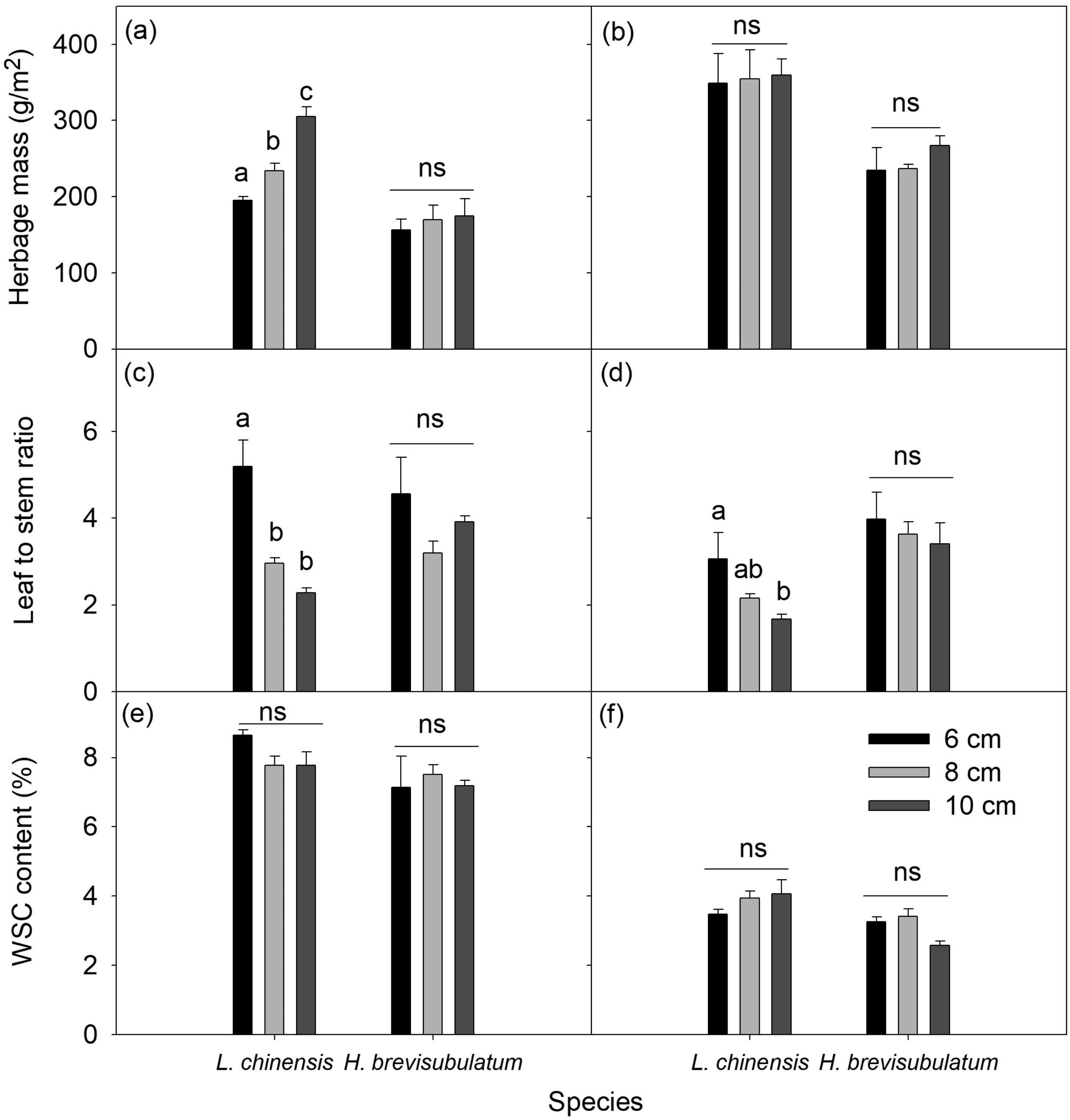

Fig. 2. The herbage mass in (a) 2005 and (b) 2006, leaf to stem ratio in (c) 2005 and (d) 2006, and water soluble carbohydrate concentration in (e) below-ground culms and (f) rhizomes in 2006 of *L. chinensis* and *H. brevisubulatum* cut to 6, 8, or 10 cm stubble heights. Error bars are SE of the means. Different letters on the same species are significantly different at 0.05 level, ns: none significant means.

Fig. 2. Biomasa de forraje en (a) 2005 y (b) 2006, relación hoja/tallo en (c) 2005 y (d) 2006, y concentración de carbohidratos solubles en agua en (e) tallos subterráneos y (f) rizomas en 2006 de *L. chinensis* y *H. brevisubulatum* cortadas a una altura de 6, 8 ó 10 cm. Las barras verticales indican el error estándar de los promedios. Letras diferentes sobre la misma especie son significativamente diferentes a un nivel de 0,05; ns: promedios no significativos.

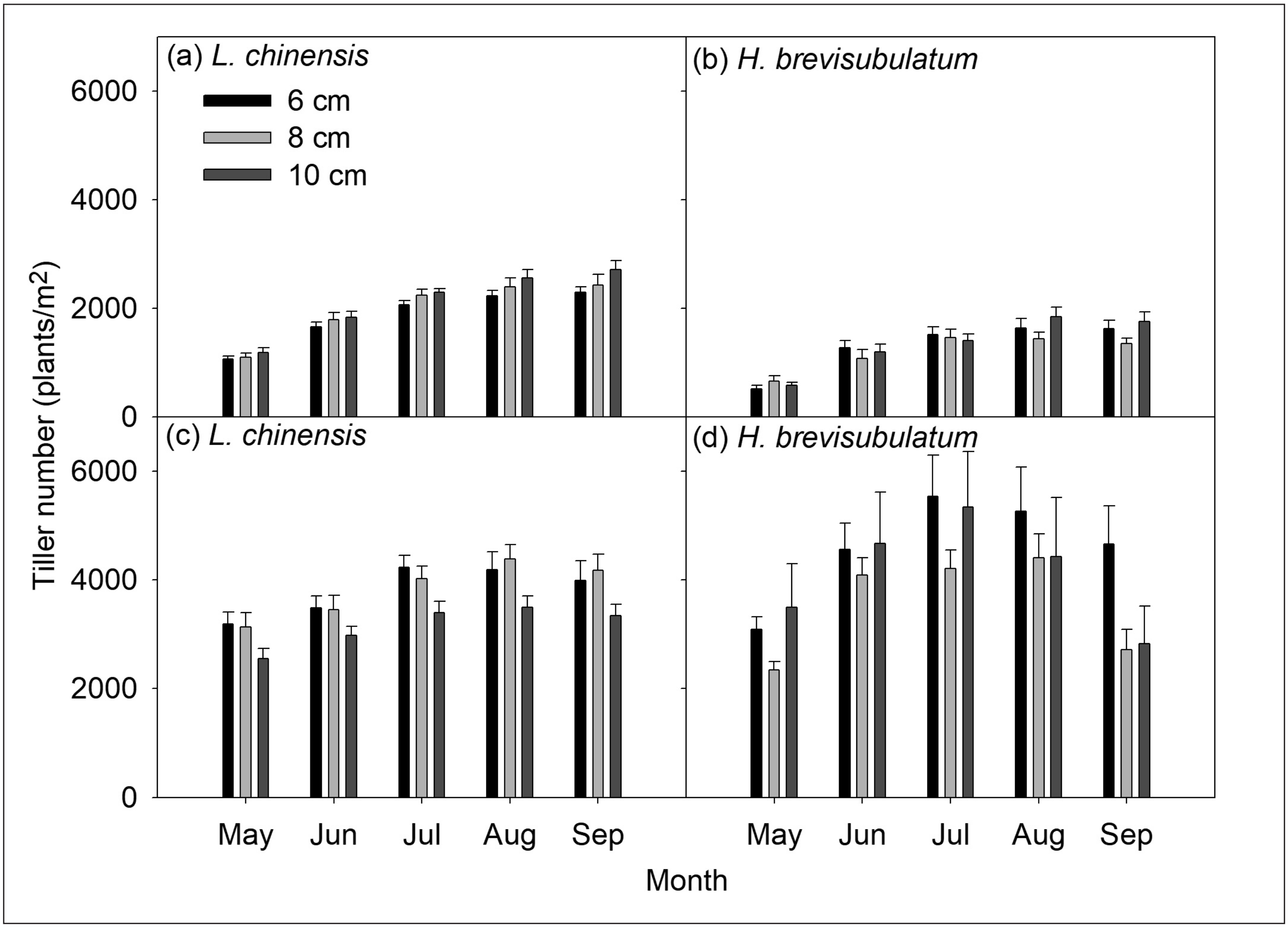

Fig. 3. Monthly tiller numbers initiated from *L. chinensis* and *H. brevisubulatum* plants defoliated at stubble heights of 6, 8, or 10 cm. (a) *L. chinensis* in 2005, (b) *H. brevisubulatum* in 2005, (c) *L. chinensis* in 2006, and (d) *H. brevisubulatum* in 2006. Error bars are SE of the means.

Fig. 3. Número de macollas por mes iniciadas de plantas de *L. chinensis* y *H. brevisubulatum* plants defoliadas a una altura de corte de 6, 8 ó 10 cm. (a) *L. chinensis* en 2005, (b) *H. brevisubulatum* en 2005, (c) *L. chinensis* en 2006, y (d) *H. brevisubulatum* en 2006. Las barras verticales indican el error estándar de los promedios.

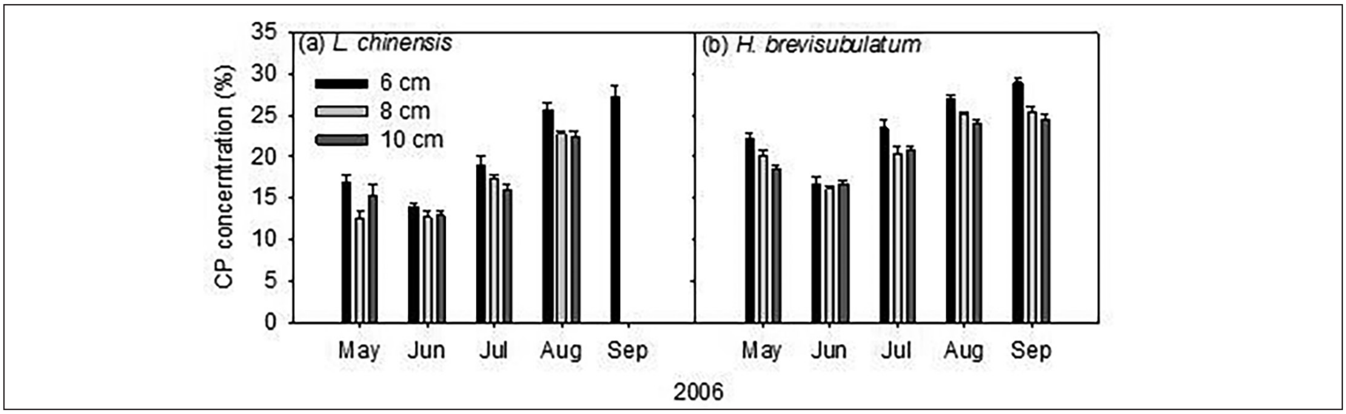

Fig. 4. Crude protein concentration of (a) *L. chinensis* and (b) *H. brevisubulatum* cut to stubble heights of 6, 8, and 10 cm in 2006. Error bars are SE of the means.

Fig. 4. Concentración de proteína bruta de (a) *L. chinensis* y (b) *H. brevisubulatum* cortadas a 6, 8 y 10 cm en 2006. Las barras verticales indican el error estándar de los promedios.

Table 3. Two way ANOVAs of water soluble carbohydrate concentration in below-ground culms and rhizomes affected by species, stubble height and their interactions.
Tabla 3. ANOVA de dos vías de la concentración de carbohidratos solubles en H_2O en los tallos subterráneos y rizomas afectados por la especie, la altura de tallos remanente luego de la defoliación y sus interacciones.

Index	Source	Type III sum of squares	df	Mear square	F	Sig.
WSC in below-ground culms	species	3.699	1	3.699	4.698	0.044
	height	0.685	2	0.342	0.435	0.654
	species*height	1.665	2	0.833	1.057	0.368
	Error	14.174	18	0.787		
WSC in rhizomes	species	3.278	1	3.278	16.597	0.001
	height	0.6	2	0.3	1.518	0.246
	species*height	1.783	2	0.891	4.513	0.026
	Error	3.555	18	0.198		

tio (Fig. 4). This is because severe defoliation has a shorter plant regrowth interval that limits stem growth and increases leaf fractions.

Both *L. chinensis* and *H. brevisubulatum* have a large proportion of leaves in the total above-ground dry matter (Wang & Zhou, 2004). Yang & Li (2003) indicated that the two species had similar leaf growth processes and patterns. Both species have strong tillering capability. When the tillers begin to regrow following defoliation, they will firstly invest energy into leaf growth, and then to stem and root growth (Yang & Li, 2003; Abraham et al., 2009). Our results confirmed that frequent (heavy) defoliation maintained the plants in a vegetative phase during a longer period, and delayed the reproductive phase, thereby resulting in a higher leaf to stem ratio than in the other cutting treatments (Table 2). Fulkerson and Slack (1995) reported an increasing leaf to stem ratio of Napier grass as defoliation frequency increased. It was also found in species such as *Dactylis glomerata* (Abraham et al., 2009) and Berseem clover (Giambalvo et al., 2011).

Defoliation intensity and frequency had effects on herbage mass production of *L. chinensis* and *H. brevisubulatum.* In general, herbage mass production increased as stubble height increased for both species (Fig. 2 a, b). In previous grass studies, hard and frequent defoliation have reduced above-ground biomass (Abraham et al., 2009, Tessema et al., 2010). Defoliation removes standing herbage mass but also reduces the residual photosynthetic area (Giambalvo et al., 2011). The residual leaf area of *H. brevisubulatum* and *L. chinensis* was greater when plants were defoliated at 10 cm compared with 6 cm, potentially providing plants with a greater capacity for photosynthesis, and therefore rate of regrowth (Nelson & Booysen, 1975; Lee et al., 2008) (Fig. 1). In addition, light defoliation with a longer time period to regrow until the subsequent harvest, was less frequently defoliated than with heavy defoliation. Therefore, plants with light defoliation will accumulate more dry matter of lower quality than plants that are frequently and heavily defoliated.

Hordeum brevisubulatum showed a short vegetative grass shoot with enough leaves remaining after defoliation to adequately meet post defoliation demands for regrowth and respiration through photosynthesis. However, *L. chinensis* is a tall vegetative grass and the few leaves remaining after severe defoliation may be unable to produce enough energy for regrowth (Wang & Zhou, 2004). Accordingly, we conclude that *L. chinensis* is more sensitive to defoliation height than *H. brevisubulatum* following defoliation, especially under unfavorable conditions.

Previous research demonstrates that WSC reserves are linearly related to plant regrowth following defoliation, and that light defoliation of these species leads to greater WSC assimilation during the subsequent recovery period (Loaiza et al., 2016; Loaiza et al., 2017). In this study, stubble height treatment had no effect on WSC concentrations in below-ground culm and rhizome (Fig. 2e, f). Wang (2007) indicated that WSC content in below-ground culms of *L. chinensis* were a little more stable than in above-ground shoots due to different defoliation frequencies. Wang et al. (2007) also emphasized that WSC content in rhizomes of *L. chinensis* was not significantly different between the defoliations at the 5, 10 and 15 cm stubble heights, but it was significantly higher than at 2 cm stubble height in a meadow steppe in the eastern edge of the Inner Mongolia Plateau. Those results suggested that plants defoliated at 2 cm likely had insufficient WSC reserves to initiate and sustain rapid plant growth immediately following defoliation, whereas our plants cut to 6 cm were unaffected in this respect.

The WSC in below-ground culms were greater than in rhizomes of both *L. chinensis* and *H. brevisubulatum*. This was opposite to a previous research finding with *L. chinensis* defoliated at different frequencies (Wang, 2007). This was possibly caused by more frequent defoliation during the growing season in our study in 2006. Rhizomes are the important organs for WSC reserves and vegetative propagation in *L. chinensis* in Songnen grassland (Yang & Li, 2003; Wang & Zhou, 2004), but frequent defoliation will deplete WSC reserves in rhizomes (Wang, 2007). Conversely, the lowest WSC content in rhizomes was under our light defoliation on *H. brevisubulatum*.

Tiller regrowth following grazing (defoliation) is important for the persistence of a grassland (Gatti et al., 2016). Under increasing grazing pressure or defoliation frequency, grass populations tend to adjust their structure so that there is a high density of small tillers per unit land area (Interrante et al., 2010). In 2005, our results were consistent with this expectation, whereby the heavy defoliation had more tillers than the light defoliation (Fig. 3a, b). However, Wang et al. (2004) reported that tiller number of *L. chinensis* fell as defoliation stubble height increased in a semi-arid zone. Our results in 2006 agreed with that study (Fig. 3c, d). Buds of rhizomatous grasses are classified by the presence of shoot buds or rhizome buds. These buds have high plasticity as they can transform from one form to the other if the growing environment changes (Yang & Li, 2003; Zhang et al., 2009). In our experiment, the energy reserves were likely to have stimulated shoot buds first, following a heavy defoliation under drought conditions. The rhizome forming buds remained dormant until the conditions were suitable for above-ground regrowth. Light defoliation could have increased energy reserves stimulating more shoot bud regrowth due to a greater photosynthesis by the new leaves.

Rainfall, especially in July and August, was the primary limiting factor for pasture production based on the correlation analysis between yield and climatic factors, using data from 1978 to 1990 in the Songnen grassland (Guo & Zhu, 1994). At our study site, the rain from May to September in 2006 (317 mm) was more favorable for plant regrowth than that in 2005 (261 mm). As a result, herbage yield of *L. chinensis* and *H. brevisubulatum* was higher in 2006 than that in 2005 (Fig. 2a, b). However, rainfall during May to September in both years was lower than the mean annual (1980-2000) rainfall (392 mm) during the same period. There was a significant difference between defoliation height and production of *L. chinensis* between stubble height treatments. This suggests that the influence of defoliation on this less leafy species is more susceptible to dry conditions than that of the more leafy *H. brevisubulatum* (Fig. 2a, b).

CONCLUSIONS

Defoliation intensity and frequency had a greater effect on plant quality than dry matter yield of *L. chinensis* and *H. brevisubulatum* in the present study. Results showed that *L. chinensis* showed a higher production but a lower quality than *H. brevisubulatum.* Both species had the highest production at the 10 cm defoliation height and the best quality at the 6 cm stubble height treatment. *Hordeum brevisubulatum* was also more tolerant to defoliation than *L. chinensis*. Results showed that the optimum defoliation height to stimulate tillering was 6 cm. In general, it is recommended that the defoliation height to maximize yield and quality of the two species in Songnen grassland is 6 cm in a normal year; however, the stubble height should be slightly higher in a drought year.

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