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Morphological and reproductive response of *Caragana microphylla* to different stocking rates

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Abstract

Understanding the effect on host plants of defending against herbivores is important in grazing ecology and grassland management. In this study, the morphological and reproductive responses of *Caragana microphylla* Lam. to grazing sheep were investigated using a 15-year grazing experiment with six stocking rates in the Inner Mongolia steppe of China. Plant height, rachis length, leaflet size, and number of pods decreased significantly, whereas spine density and length increased significantly with increased stocking rate. Significant negative correlations were observed between production of vegetative and reproductive organs and defensive organs, indicating that it is costly for *C. microphylla* to defend against herbivores and that morphological miniaturization and a tradeoff between production and defense were main responses of *C. microphylla* to herbivores.

Keywords: *Caragana microphylla*; Herbivory; Inner Mongolia steppe; Physical defense

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1. Introduction

Thorns and prickles are common physical defenses and effective deterrents against herbivory (Young, 1987). When browsed, plants show higher thorn density and longer spines (Young, 1987; Milewski et al., 1991) and reduce their limited resources toward growth (Teague, 1989; Belovsky et al., 1991; Takada et al., 2001). These phenomena show that defensive responses can reduce harmful effects caused by herbivores and increase plant fitness (Paige, 1992; Takada et al., 2001). The response of host plants to different stocking rates during long-term grazing and the relationship between plants' physical defenses and reproduction have seldom been studied.

Caragana microphylla Lam. is a widely distributed shrub species in the northern steppe and agro-pastoral ecotone of China. It has compound leaves and spines in the stem (Liu et al., 2004). *C. microphylla* has a great ecological and economic value in the region in the following ways: (1) it plays a key role in vegetation succession from active dune to sandy grassland (Zhang, 1994) and forms shrub shelterbelts for crops or artificial grassland; (2) it is a typical C_3 legume shrub and helps restore degraded land by fixing atmospheric nitrogen; and (3) it can serve as a supplemental livestock forage with higher nutrient value (Liu et al., 2004). Grasslands in northern China are heavily degraded due to over-utilization (Zhu and Liu, 1988; Wang et al., 2004). However, *C. microphylla* shows great resistance to grazing animals (Xiong et al., 2003).

The present study explored the response of the shrub *C. microphylla* to different stocking rates based on a 15-year grazing experiment in the Inner Mongolia steppe. The study sought to answer following research questions: (1) How does *C. microphylla* adapt to herbivory? (2) Is there a tradeoff between development of defensive organs and vegetative and reproductive organs?

2. Materials and methods

2.1. Study site

The grazing experimental field was established by the Inner Mongolia Grassland Ecosystem Research Station in 1989 and was located at 43°37′N, 116°43′E, mostly at an elevation of 1000 m above sea level or more (Li et al., 1999). The regional climate is continental, with a 30-year average annual rainfall of approximately 350 mm (200–500 mm), 60–70% of the total occurring from June to August. Annual mean temperature is −0.4 °C and average monthly temperature is −23 °C in January and 17.9 °C in July. There are 150–180 days for supporting plant growth. The predominant plant species of the field are *Artemisia frigida* and *Cleistogenes squarrosa* (Wang et al., 2001).

Grazing plots were set up using a randomized complete block design with 6 stocking rates (0, 1.33, 2.67, 4.00, 5.33, and 6.67 sheep hm^{-2}) with 3 blocks (100 m × 100 m) per treatment. The six stocking rates were named as follows: no grazing (0 sheep hm^{-2}); light grazing (1.33 and 2.67 sheep hm^{-2}); medium grazing (4.00 sheep hm^{-2}); heavy grazing (5.33 sheep hm^{-2}); and over grazing (6.67 sheep hm^{-2}), respectively (Wang et al., 1998). Inner Mongolia fine sheep were used in the experiment every year during the warm season, from 20 May to 5 October.

2.2. Experimental design and plant measurements

C. microphylla was randomly distributed in the experimental plots. Ten shrubs and five branches per shrub were randomly chosen within three blocks of each treatment to measure plant size, spine traits, and pod numbers in 2004. Plant size included plant height (from the bottom to the top of the shrub), rachis length (mature leaves), and leaflet length and width (the second leaflet at the top of the compound leaf). Spine traits included the length and density of the ripe spines (density is the number of spines within 10 cm length of mature stem), and inclination between stem and spines. The plant height was measured on 18th May. Rachis length, leaf size, and number of pods were measured on 20th August of 2004.

2.3. Data analysis

All data were statistically analysed using one-way ANOVA procedure of the SPSS version 10.0 (Chicago, IL, USA). To estimate the difference in morphological traits among different stocking rates, post hoc multiple comparisons were performed using least significant difference (LSD). Means were considered significant at $P<0.05$. Unless otherwise stated, all results are presented as mean plus standard error of the mean ($n = 3$). Correlative efficiencies of traits were calculated using partial correlation.

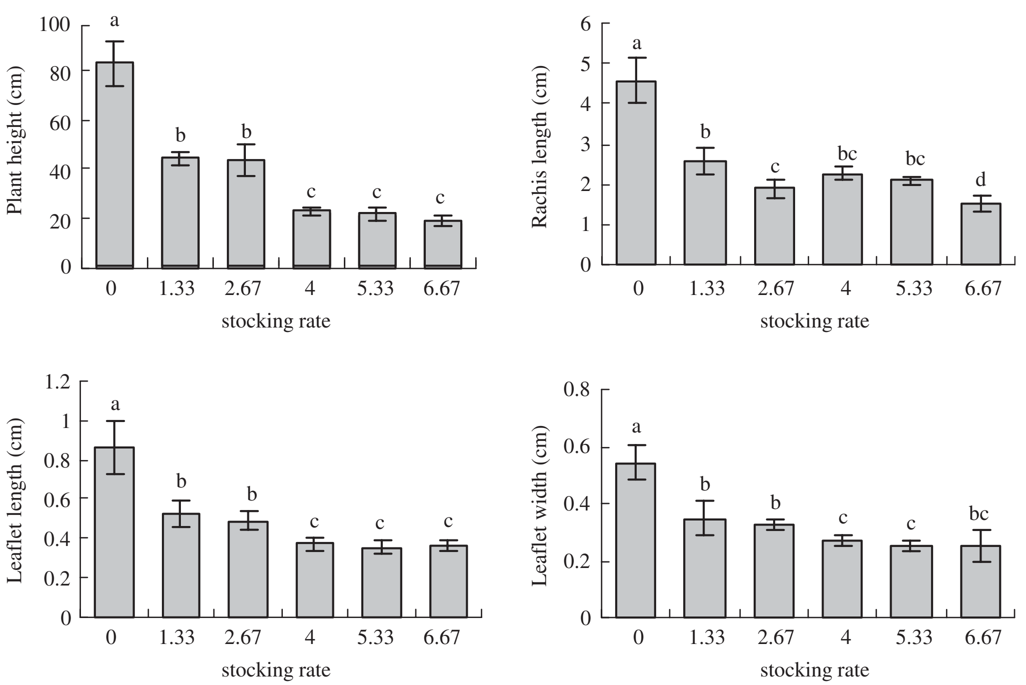

Fig. 1. Means of plant size of *C. microphylla* in six stocking rates (sheep hm^{-2}). Bars are standard errors. The treatments with the same letter are not significantly different at $P = 0.05$.

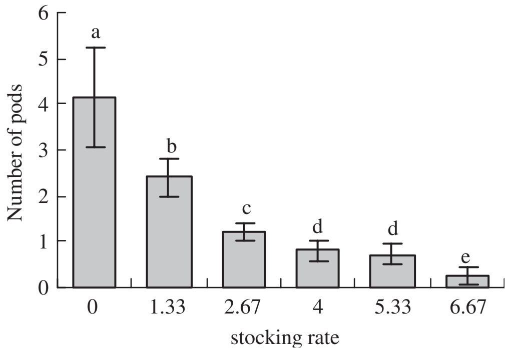

Fig. 2. Means of the number of pods in six stocking rates (sheep hm^{-2}). Bars are standard errors. The treatments with the same letter are not significantly different at $P = 0.05$.

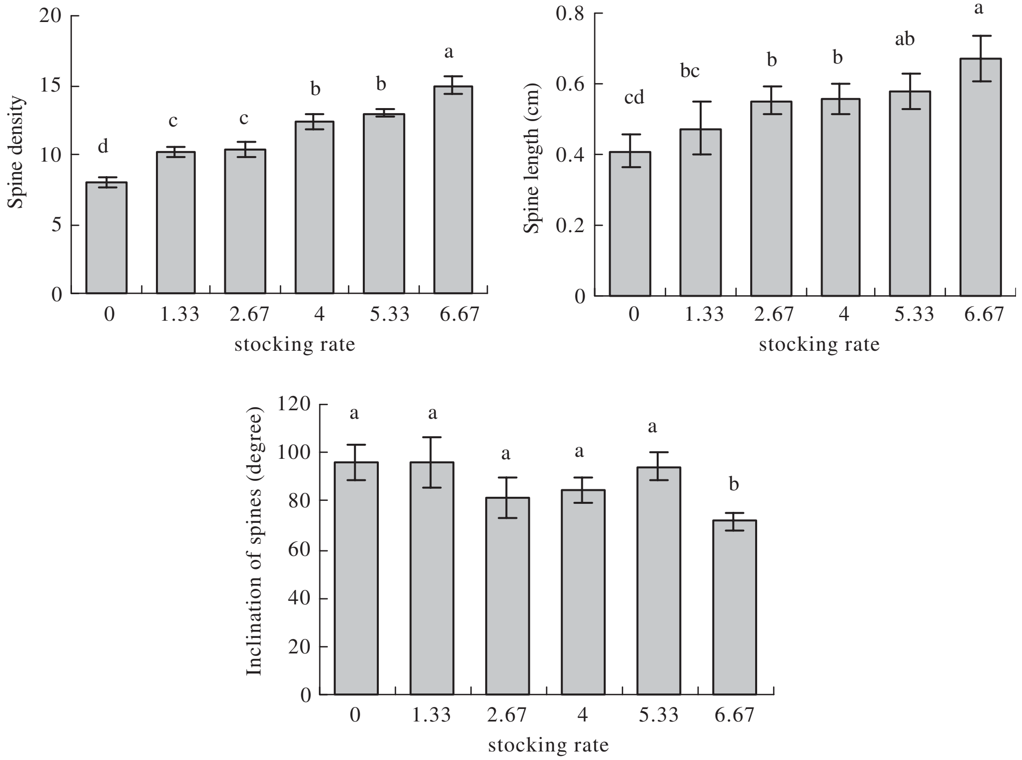

Fig. 3. Means of spine traits of *C. microphylla* in six stocking rates (sheep hm^{-2}). Bars are standard errors. The treatments with the same letter are not significantly different at $P = 0.05$.

3. Results

Plant height, leaf size, and number of pods decreased significantly with increasing stocking rate (Figs. 1 and 2). Plant height was almost two times higher for the no-grazing

Table 1
Partial correlation matrix between all pairings of eight characters for *C. microphylla* with the different stocking rates

	Plant height	Rachis length	Leaflet length	Leaflet width	Spine density	Spine length	Inclination of spine
Rachis length	0.042						
Leaflet length	−0.034	0.428*					
Leaflet width	0.028	0.467**	0.700**				
Spine density	−0.186	−0.313*	−0.185*	0.373*			
Spine length	−0.007	−0.272*	−0.317*	−0.315*	0.037		
Inclination of spine	−0.365*	−0.061	0.082	−0.212	−0.060	−0.025	
Number of pods	0.283	−0.028	−0.275	−0.364*	−0.319*	−0.266*	−0.038

*Correlation is significant at the 0.05 level.
**Correlation is significant at the 0.01 level.

treatment than for other treatments, but there were no significant differences among medium-grazing, heavy-grazing, and over-grazing treatments ($P > 0.05$). Significant differences in leaf sizes (including rachis length, leaflet length, and leaflet width) were observed only between the no-grazing and over-grazing treatments ($P < 0.001$). There was a significant negative correlation between pod numbers and stocking rate ($R^2 = 0.49$, $P < 0.001$). Density and length of spines increased linearly with increasing stocking rate (Fig. 3). Spine density and length in the over-grazing treatment area increased by almost 100% and 40%, respectively, compared with the no-grazing treatment. A significant difference in spine inclination was found only between over-grazing and other treatments.

The correlations between the eight morphological traits were shown by the partial correlation coefficients (Table 1). Thirteen of the 28 paired comparisons were significantly correlated ($P < 0.05$) and 9 of these comparisons involved either spine density or spine length. Furthermore, spine density and length had a significant negative correlation with rachis length, leaflet length and width, and pod numbers.

4. Discussion

Many researchers have found that grazing-resistant species are shorter with smaller leaves (Diaz et al., 2001; Takada et al., 2001). This individual miniaturization has been proposed to be a defensive strategy of plants against herbivores (Wang et al., 2000). In our study, the host plant also showed miniaturization as stocking rates increased during the 15-year grazing period.

Thorn length is sensitive to herbivore pressure (Young, 1987) and spines of browsed plants are mainly characterized by longer and denser thorns (Milewski et al., 1991; Takada et al., 2001). There were significant differences in spine length between over-grazing and other grazing treatments in the present study, but spine inclination was not affected by stocking rate. Thorns may affect browsing rates and thus reduce the biomass consumed by herbivores (Trlica and Rittenhouse, 1993; Gowda, 1996; Hutchings and Gordon, 2001; Gowda and Palo, 2003), because sharp spines may penetrate mouth parts and long spines may restrict the lateral mouth movement that strips branches (Cooper and Owen-Smith, 1986; Milewski et al., 1991; Takada et al., 2001).

The number of pods is an important trait of the sexual reproduction of plants (Hartnett, 1989). The number of pods of *C. microphylla* decreased rapidly with increasing stocking rate, and there were significant differences among stocking rates (Fig. 2). One important reason could be the limited resources host plants have for reproduction, which is an important sink of carbohydrates (Gowda and Palo, 2003). Herbivores may induce host plants to invest more resources in defending against browsing (Simms and Rausher, 1987).

The optimal defense can reduce the growth and reproduction of individual plants (Gowda and Palo, 2003). To diminish the impact of herbivores, plants have to develop a variety of defensive mechanisms (Cornelissen and Fernandes, 2001). In our study, the spine traits (except inclination of spines) had significant negative correlations with leaf size (rachis length, leaflet length, and leaflet width) and number of pods. The results were similar to *Acacia tortilis*, namely, increasing densities of spines corresponded with decreasing leaf size (Gowda, 1996). Furthermore, Belovsky et al. (1991) found woody plants with thorns had proportionally less leaf mass at a given twig diameter than did plants without thorns. The production of spines might be costly in terms of energy or nutrients, retarding the accumulation of leaf mass (Belovsky et al., 1991) and reproduction (Gowda and Palo, 2003). On the other hand, the smaller leaf size may be a second defensive strategy employed by the thorned plants (Belovsky et al., 1991).

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