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COMPETITIVE INTERACTIONS BETWEEN PALATABLE AND UNPALATABLE GRASSES: EFFECTS OF SELECTIVE DEFOLIATIONS OF THE PALATABLE GRASSES

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ABSTRACT

Selective herbivory of the palatable species appears to be a dominant mechanisms contributing to species competitive replacement in grasslands. Selective herbivory of the palatable species allows unpalatable species to realize a competitive advantage within the community. To test this hypothesis we compare the competitive ability of the unpalatable grasses *Stipa trichotoma* or *S. gyneriodes* in the presence of nondefoliated and defoliated plants of the palatable grass *S. clarazii*. The three species are native to a temperate semiarid grassland of Argentina. The response variables estimated in *S.trichotoma* and *S.gynerioides*, at both plant and tiller levels, were higher ($P < 0.05$) in the presence of defoliated than in the presence of undefoliated plants of *S.clarazii*. These results support the hypothesis that selective herbivory of the palatable species confers unpalatable species a competitive advantages, contributing to species competitive replacement within the community.

KEYWORDS

Competitive ability, grass competition, palatable/unpalatable grasses, selective grazing, grass-grazer interactions, grassland ecology, Argentina native grasslands, *Stipa spp*.

INTRODUCTION

Grazing by domestic livestock is commonly associated with certain degree of change in species composition in grasslands throughout the world (e.g. Westoby *et al*., 1989; Milchunas and Lauenroth, 1993; Milton *et al*., 1994). These compositional changes frequently involve the replacement of palatable grasses by unpalatable grasses (Noy-Meir and Walker, 1986). In temperate semiarid grasslands of central Argentina, palatable grasses commonly give way to the increase of cover or even the invasion of unpalatable grasses under conditions of continuous heavy grazing (Llorens, 1995; Distel and Bóo, 1996).

Selective herbivory of the palatable species appears to be a dominant mechanism contributing to species competitive replacement (Anderson and Briske, 1995). Selective herbivory of the palatable species allows unpalatable species to realize a competitive advantage within the community. The objective of this study was to test this hypothesis in palatable and unpalatable grasses native to temperate semiarid grasslands of Argentina. Our approach was to compare the competitive ability of the unpalatable grasses *Stipa trichotoma* or *S. gynerioides* in the presence of nondefoliated and defoliated plants of the palatable grass *S. clarazii*.

MATERIALS AND METHODS

Study site and species. A field study was conducted on an upland site of a native grassland located in the central part of Argentina (38° 45' S; 63° 45' W). The climate is temperate, semiarid. Mean annual temperature is 15°C, and mean annual rainfall 400 mm. Precipitations peak in March and October. During the experimental period precipitations were 363 mm and 267 mm, in 1994 and 1995, respectively. Dominant soils are Calciustolls, of coarse texture. A petrocalcic horizon is commonly found at depths of 60 to 80 cm. The potential physiognomy of the vegetation is grassland with isolated woody plants. The palatable grass *Stipa clarazii* is one of the late-seral dominant grasses. In uplands with a long history of heavy grazing the occurrence of patches dominated by unpalatable grasses is common. Two of the more abundant unpalatable species are *S.gynerioides* and *S.trichotoma*. The palatable grasses are higher in protein and lower in fiber than the unpalatable grasses (Moretto and Distel, unpublished data). These differences in chemical composition are reflected in the high acceptability of the palatable species and the low acceptability of the unpalatable species by grazing animals (Cano, 1975; Bóo et al., 1993).

Field experiment. Forty pairs of plants were randomly selected in the study site, in February, 1994. Pairs were composed of one individual of *S.clarazii* (palatable) and one individual of *S.trichotoma* (unpalatable) that were growing close together. Plants were protected from grazing by a small exclosure of mesh wire (60 cm diameter by 40 cm tall). The rest of the vegetation within the exclosure was removed. In 20 pairs the individuals of the palatable species were periodically defoliated during the growing season, whereas the individuals of the unpalatable species remained undefoliated. Defoliations were carried out with hand clippers, in a way that simulates the heavy grazing by cattle that is normal in these grasslands. In the other 20 pairs neither the palatable species nor the unpalatable species were defoliated, and served as controls. Five tillers were marked with colored wire in 20 unpalatable plants of each treatment in early April of 1994, to estimate total length of green blade, dry mass and recruitment. In early December of 1994 and 1995 (end of the growing season) the aboveground biomass was clipped at 3 cm above the soil surface. In the laboratory the material was weighed after oven drying at 60° C for 48 hours. Since initial plant size was not completely uniform, end-of-season shoot production of the unpalatable species was expressed relative to basal area.

Greenhouse experiment. Plants of *S.clarazii* (palatable) and *S.gynerioides* (unpalatable) were grown in five liter pots in paired mixtures of four plants. Pots were filled with 5 kg of soil (1.5% organic matter; 0.12% total nitrogen; 9.4 ppm extractable phosphorous; 458 ppm potassium) and sown in April, 1994. Both soil and seeds were from the study site. The water content of the soil was kept at 14% (soil field capacity) along the experimental period by weighing the pots twice weekly and supplying the required amount of water. The first year plants were allowed to establish. During the second year (1995), in half of the pots the individuals of the palatable species were periodically defoliated, whereas the individuals of the unpalatable species remained undefoliated. Defoliations were carried out with hand clippers at 3-5 cm above soil surface, each time the plants reached 10-15 cm tall (4 defoliations during the growing season). In the rest of the pots neither the palatable nor the unpalatable species were defoliated, and served as controls. Each treatment was replicated 10 times. Five tillers were marked with colored wire in 10 unpalatable plants of each treatment in early April of 1995 to estimate total green blade length, dry mass and recruitment. In October of 1995 the aboveground biomass was clipped at 3 cm above the soil surface and the material weighed after oven drying at 60° C for 48 hours. Shoot production of the unpalatable species was expressed as grams per pot.

RESULTS AND DISCUSSION

The response variables estimated in *S.trichotoma* (field experiment, Table 1) and *S.gynerioides* (greenhouse experiment, Table 2), at both plant and tiller levels, were higher ($P < 0.05$) in the presence of

defoliated than in the presence of nondefoliated plants of *S.clarazii*. In the field experiment, the relatively low shoot production in 1995 was associated with scarce precipitations. These results provide an explanation to the increase in size and abundance of unpalatable grasses in areas formerly dominated by palatable grasses, in spite of the greater competitive ability of the latter in the absence of grazing (Moretto and Distel, unpublished). Similar results were recently reported by Anderson and Briske (1995) for a mesic grassland in Texas (USA).

Worth mentioning is the common observation that once unpalatable grasses attain a high level of dominance it is extremely difficult to reverse the change, even if all grazing is removed (Noy-Meir and Walker, 1986). This behavior may be related to the poor litter quality of unpalatable grasses (Wedin, 1995), which translates into decreased nutrient turnover and reduced soil nutrient availability (Berendse, 1994; Jones *et al*., 1994; Wedin, 1995; Aerts, 1995). In the study area nitrogen and phosphorus availability were 50% and 600% higher in patches dominated by palatable grasses than in patches dominated by unpalatable grasses (Moretto and Distel, unpublished). Moreover, the high accumulation of litter may represent an important constraint for seedling establishment of palatable grasses (Facelli and Pickett, 1991).

Our results support the hypothesis that selective herbivory of the palatable species confers on unpalatable species a competitive advantage, contributing to species competitive replacement within the community. Therefore, for palatable species to maintain their competitive position in the community, grazing strategies should be developed to reduce herbivory intensity on the palatable species and/ or to reduce herbivore selective behavior.

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Table 1

Productive responses in a field study of the unpalatable grass *Stipa trichotoma* in the presence of undefoliated or defoliated plants of the palatable grass *Stipa clarazii*. Means in a column followed by a different letter are statistically different ($P < 0.05$)

Treatment	Shoot production		Tiller total green blade length			Tiller recruitment	Tiller dry mass
	1994	1995	Apr.	Jul.	Nov.		
	g / cm^2 basal area			cm		# / parental tiller	mg
Stipa clarazii Nondefoliated	0.31 a	0.15 a	26.3 a	20.4 a	72.0 a	2.4 a	23 a
Stipa clarazii Defoliated	0.58 b	0.22 b	35.0 a	33.0 b			

Table 2

Productive responses in a greenhouse study of the unpalatable grass *Stipa gynerioides* in the presence of undefoliated or defoliated plants of the palatable grass *Stipa clarazii*. Means in a column followed by a different letter are statistically different ($P < 0.05$)

Treatment	Shoot production	Tiller total green blade length			Tiller recruitment	Tiller dry mass
		Apr.	Jul.	Nov.		
	g / pot		cm		# / parental tiller	mg
Stipa clarazii Nondefoliated	2.0 a	33.4 a	29.5 a	37.0 a	2.8 a	11 a
Stipa clarazii Defoliated	4.9 b	34.5 a	36.8 b	48.0 b	3.6 b	12 b