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ORIGINAL ARTICLE

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Rodent seed predation on tree invader species in grassland habitats of the inland Pampa

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Abstract Woody plant invasion in grassland ecosystems is a worldwide phenomenon, and biotic interactions as competition and predation have been invoked as a possible barrier to woody encroachment in many ecosystems. We evaluated the role of rodents as seed predators in Pampean grasslands, and we assessed the differences in removal by rodents between one native species, *Prosopis caldenia* (Caldén) and one exotic species, *Gleditisia triacanthos* (Honey locust). The experiment was conducted at different phases of the rodent population cycle in two grassland communities, a remnant of a native grassland and a post agriculture grassland (old field). The amount of seed loss caused by predation was estimated by a bait-removal experiment in foraging stations. We estimated the frequency of foraging stations with consumption, the overall amount of seed predation and the individual rate of seed predation. The total amount of seed removal and the individual rate of seed removal were higher for *P. caldenia* than for *G. triacanthos*, in the native grassland than in the old field, and in autumn when rodent density was maximum. Overall, the role of rodents on woody seed removal varied according to the plant species and depending on the local conditions that vary through time and space.

Keywords Grassland · Rodents · Seed predators · Woody invaders

Introduction

Biotic exchanges among ecosystems are a major component of global changes brought about by modern human activity (Chapin et al. 1997; Mack et al. 2000). Species' range expansions occurring at both regional and intercontinental scales reflect the influence of human-mediated transport as well as the impact of altered disturbance or stress regimes on community invasibility (Hobbs and Huenneke 1992; Alpert et al. 2000). Several factors may contribute to community resistance against invasion by novel, exotic, or native plant species, including physical stress, competition from established species, attack by natural enemies, and lack of suitable mutualists (Elton 1958; Crawley 1987; Maron and Vilá 2001; Levine et al. 2004). Among the mechanisms adding to biotic resistance, competition between invader and resident species has received the most attention (Levine et al. 2004), whereas the role of generalist consumers as a biotic barrier to invasion has been less frequently studied (Parker et al. 2006; Nuñez et al. 2008; Pearson et al. 2011).

Seed predation may greatly affect recruitment dynamics of seed-limited plant species (Edwards and Crawley 1999), such as is the case of many invaders in a variety of systems (Clark et al. 2007; Simberloff 2009). Thus, generalist seed predators might operate as a significant mechanism of biotic resistance (Maron and Vilá 2001; Pearson et al. 2011). If this were so, we would need better knowledge on resident granivores' preferences for

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different 'novel' seed types and overall seed predation rates in different invasion-prone habitats (e.g., Vilá and Gimeno 2003). Rodents are the prominent post-dispersal seed consumers in many herbaceous plant communities, where they can produce substantial seed losses (Mittelbach and Gross 1984; Edwards and Crawley 1999; Howe and Brown 2000; Manson et al. 2001; Anderson and Mac Mahon 2001). However, the realized impact of rodent granivores on exotic seed survival will depend on habitat factors such as vegetation cover and alternative food availability (Brown 1988; Manson et al. 2001). Further, granivory rates may be highly species-specific, reflecting target seed size and nutritional quality (Moles et al. 2003; Xiao et al. 2006), relative to rodent body size and energetic needs, which may vary widely across seasons (Bilenca and Kravetz 1998).

Grassland ecosystems worldwide are increasingly threatened by land-use changes and alien plant invasions (Gibson 2009). Woody species encroachment is of particular concern, with negative implications for habitat conservation and provisioning of grassland ecosystem services (Richardson et al. 1994; Jackson et al. 2002; Asner et al. 2004; Simberloff et al. 2010). Woody plant invasions may involve range expansions by native species across biomes (Jackson et al. 2002; Briggs et al. 2005) as well as the introduction of exotic life forms (trees, shrubs) into geographically distant regions (Richardson and Rejmánek 2011). The success of invasive tree species in grasslands has been associated with competitive release via disturbance of the resident grass cover (Lamarque et al. 2011). In contrast, granivores have been neglected as agents of biotic resistance, despite seed predation being known to suppress tree colonization in various contexts (De Steven 1991; Nepstad et al. 1996; Nuñez et al. 2008; Mazía et al. 2010). Tree seeds arriving in grassland patches represent a distinctive food item, which may be differentially handled by resident consumers in a context-dependent fashion, according with habitat productivity, vegetation structure, and rodent population densities (Manson et al. 2001). Therefore, granivory rates on invading trees should vary with seed species identity and across grassland communities.

The Pampas of east-central Argentina encompass some of the largest remaining areas of temperate grasslands (Gibson 2009). Notwithstanding, native grasslands are shrinking rapidly, being fragmented and replaced by crop fields and semi-natural pastures at various stages of post-agricultural succession (Ghersa and León 1999; Baldi et al. 2006). Disturbed grassland remnants and abandoned fields are often colonized by invasive tree species (Facelli and León 1986; Mazía et al. 2001, 2010; Ghersa et al. 2002; Chaneton et al. 2004), which can establish dense woody stands with reduced herbaceous diversity (see Zalba and Villamil 2002). In this system, tree encroachment is limited by seed dispersal from nearby forested patches and landscape corridors (Ghersa et al. 2002), and also by competition from established perennial grasses (Mazía et al. 2001). Overall, undisturbed remnants of native tussock grassland appear to be more resistant to tree invasions than old-field communities dominated by exotic forbs and grasses (Chaneton et al. 2004; Mazía et al. 2010). Evidence suggests that native rodents can substantially decrease seed survival in these agroecosystems (Cittadino et al. 1994; Fraschina et al. 2009), especially in tussock grassland patches (Murillo et al. 2007). Little is yet known about the impact of rodent granivores on tree seed species in these grasslands (Mazía et al. 2010).

Here we examine the potential role of granivorous rodents as a biotic obstacle to tree species invasion in grassland communities of the Inland Pampas, Argentina. Our specific objectives were: (1) to assess seed predation rates on two leguminous trees: one exotic, the large-seeded (100–200 mg) *Gleditsia triacanthos* L. (honey locust) and one native, smaller-seeded (30 mg) *Prosopis caldenia* Burk. (Caldén); (2) to compare the patterns of seed predation between a native tussock grassland relict and a midsuccessional old-field grassland and (3) to assess seasonal variations in rodent seed removal in order to evaluate the importance of the natural fluctuations of the rodent population and resources on seed granivory. *G. triacanthos* is an exotic tree species that became invasive throughout the Pampas, while *P. caldenia* is native to the drier savannas bordering the Inland Pampas (Mazía et al. 2001; Ghersa et al. 2002). Seed consumption by rodents was evaluated both under field conditions and in feeding trials with caged animals. Overall, we expected predation to be more intense on the small-seeded tree species (*Prosopis* > *Gleditsia*), because of the small size of predators in the area. In addition, we expected tree seed predation to be higher in the C_4 grass-dominated tussock grassland, where there is generally less food available to granivorous rodents, than in the most productive old-field grassland community. We also expected a higher seed removal in autumn, when rodent population densities are higher, with respect to the summer and winter.

Methods

Study site and studied species

The study was conducted at the Department of Carlos Casares (36°S, 61°05′W), Buenos Aires, Argentina. Mean annual precipitation is 1,016 mm (SD = 216 mm, 1976–2005); mean temperatures range between 8.2°C in July (winter) and 23°C in January (summer). Rainfall is distributed throughout the year, but with peaks in spring and autumn; winter is often the drier season. The region was originally occupied by mesic perennial grasslands, and there were no trees (Cabrera 1976; Soriano et al. 1992). The Inland Pampas have been extensively transformed to row-crop agriculture and livestock grazing. Native grassland communities are presently confined to small relict fragments and narrow corridors (Ghersa and León 1999), being often dominated by tall-tussock grasses (Mazía et al. 2010). Old-field grassland communities develop on abandoned agricultural areas and sown pastures, and become typically dominated by exotic forage grasses after several years of succession (Facelli et al. 1988; Tognetti et al. 2010).

The study grasslands correspond to (1) a native tussock-grass community located within a 400-m-long by 60-m-wide corridor extending for 10 km of an abandoned railway line. It is dominated by *Paspalum quadrifarium* Lam., a C_4 native bunchgrass, which accounts for 90% of the standing biomass, and (2) a 25-year-old successional field located in a 4-ha exclosure built in 1979 on a formerly grazed pasture. It comprises an intricate mix of exotic species, and has a fine-grained structure with no bare ground left (Facelli et al. 1988). The distance between study sites was 6 km.

Seed predators in the study area comprise birds, ants, and small mammals (mean body mass < 45 g). Common rodent species include the native sigmodontines *Akodon azarae, Calomys musculinus*, *Calomys laucha*, *Bolomys obscurus*, *Oligoryzomys flavescens*, and *Oxymycterus rufus*, the pampa cavy *Cavia aperea*, and the introduced murines *Mus musculus*, *Rattus rattus*, and *Rattus norvegicus* (Miño et al. 2007). Sigmodontine rodents are omnivorous consumers feeding on invertebrates, green plant parts, and seeds of both grasses and forbs, while the pampa cavy is considered as strictly herbivorous (Bilenca et al. 1992; Ellis et al. 1998). Rodent population densities vary seasonally, with peak numbers in late autumn–early winter and lowest numbers in spring. These dynamics reflect seasonal changes in temperature and precipitation, which affect both food availability and energy requirements by rodents (Busch and Kravetz 1992; Cittadino et al. 1994).

G. triacanthos is a tall deciduous tree native to eastern North America, which was presumably introduced to Argentina in the early 1800s as an ornamental and shade plant, and was also used to build living fences. It is the most aggressive woody invader in the study region (Mazía et al. 2001; Ghersa et al. 2002). *G. triacanthos* produces large legume fruits containing up to 20 seeds (mass $\sim$200 mg seed^{-1}), between late December (summer) and May (autumn). Seeds are readily dispersed by cattle and probably by native fauna (e.g., foxes, armadillos). The other tree species *P. caldenia* is native to the "Espinal" open woodlands and savannas of central Argentina (Cabrera 1976), and is known to invade drier grasslands in the western Inland Pampa (Peláez et al. 1992; de Villalobos et al. 2005). *P. caldenia* produces fruits with relatively small seeds (mass $\sim$30 mg seed^{-1}) between January and April (summer–autumn) and is also dispersed by livestock (Peinetti et al. 1991). Its seeds fall within the range of medium-sized (15–30 mg) seed species from documented woody invaders in the Pampas (e.g., *Robinia pseudoacacia*; Ghersa et al. 2002). There is evidence of a high pre-dispersal impact of insects of the family Bruchidae on *Prosopis* seed production, while the effect of post-dispersal predators is unknown (Villagra et al. 2002). Small mammals appeared to consume at least a proportion of the seeds offered in bait-removal experiments, while there is no evidence of consumption by birds (Villagra et al. 2002).

Data collection

Fieldwork to assess rodent consumption of seeds was conducted during 2004 at different seasons that corresponded to different phases of the rodent population cycle: summer (March), reproductive season with low abundance, autumn (May), non-reproductive season with high density and winter (August), non-reproductive season with decreasing density.

In order to assess the rodent community, we set in each habitat three lines of 15 trap stations spaced at 10 m. The distance between lines was at least 20 m, depending on the dimensions of the habitat. Two Sherman live traps baited with a mix of rolled oat, bovine fat, and peanut butter were placed at each station, while at every 20 m we placed an additional cage trap in order to capture the pampa cavy. Traps were checked every morning during three consecutive days. Animals captured were identified to species, and were given an individual mark before being released at the site of capture.

Rodent density index (RDI) was estimated for each species with the proportion of trap nights with capture (without considering recaptures within a trapping session):

$$\mathrm{RDI} = (\text{number of individuals captured}/\text{number of traps} \times \text{number of nights})$$

Differences in rodent RDI among sampling seasons and habitats were assessed by means of a test of difference between proportions (using the proportion of trap nights with capture).

The amount of seed loss caused by predation was estimated by a bait-removal experiment (Villagra et al. 2002). We placed foraging stations in transects located in the same habitats where we conducted the rodent sampling, but at a distance that avoided interference with traps. Foraging stations in each transect were separated by 10 m. In order to allow consumption of small rodents and cavies, two plastic bottles were placed 1 m apart at each foraging station (one bottle of 500 cm^3, length 21 cm, and diameter 5 cm, and the other of 2,250 cm^3, with 30 cm in length and 10 cm in diameter at the base). In each bottle, we placed ten seeds of each plant species, mixed with an artificial substrate. The artificial substrate consisted of small pieces of rubber (diameter 0.5 cm, thickness 0.01 cm) that resembled pieces of plant remains that are frequent in the natural habitat. We mixed seeds with an artificial substrate in order to mimic the natural conditions in which rodents encounter seeds. We did not use the natural substrate of the study area because this would have made it difficult to recover the remaining seeds and therefore to assess consumption.

The total number of foraging stations depended on the dimensions of the habitats, and because some bottles were lost, the total number analyzed varied among seasons in each habitat ($n = 11$ in the native grassland for summer, autumn, and winter, and $n = 19$, 16, and 16 in the old-field in summer, autumn, and winter, respectively). Each bottle had a lateral opening that allowed rodent access to seeds, but prevented the access of birds. The openings of the foraging bottles were covered by an adhesive tape to trap rodent hairs and to prevent the access of ants and other insects. It also made it possible to detect if birds had access by the recovery of feather remains. Foraging bottles were collected in the morning each day during a 3-day period, and were replaced by another bottle with the initial number of seeds.

Seed removal was estimated as the difference between the initial number (10 of each species) and the number remaining after each foraging night. For each bottle we registered the presence of rodent hairs and feces.

We conducted a controlled experiment with rodents in cages to confirm consumption of *G. triacanthos* and *P. caldenia* seeds in absence of alternative food, and in conditions that make sure that the disappearance of seeds was due to rodent consumption. We offered a known number of seeds to caged individuals of *A. azarae* (the most abundant species) captured in the study area. Captured individuals were placed in individual cages with either 20 seeds of *P. caldenia* (15 rodents) or ten *G. triacanthos* seeds (13 individuals). We added ten seeds of *G. triacanthos* to account for their larger size, relative to those of *P. caldenia*. Animals were maintained in the cages during one night, after which we recovered and counted the remaining seeds.

Data analysis

We compared the frequency of foraging stations with seed removal (number of foraging stations with at least one removed seed with respect to the total number of foraging stations) according to the habitat, plant species, and season, by means of a log-linear analysis (Zar 1996). To analyze the effect of habitat, plant species and season on the overall amount of seed removal, the mean number of seeds removed per foraging station over the 3-day period was used in statistical comparisons, with foraging stations as replicates. The individual rate of seed removal was estimated as the mean number of seeds removed divided by the RDI of rodents in each habitat and season. In both cases, we compared the amount of seed removal according to plant species, season, and habitat by a three-way ANOVA with two within subject factors (season and plant species), and habitat as a between subjects factor. Post hoc pairwise comparisons were carried out with Tukey HSD tests (honestly significant differences). The proportion of seeds consumed by animals in cages were compared between plant species by means of a Mann–Whitney *U* test (Zar 1996). Values of $p < 0.05$ were considered to be significant in all analyses.

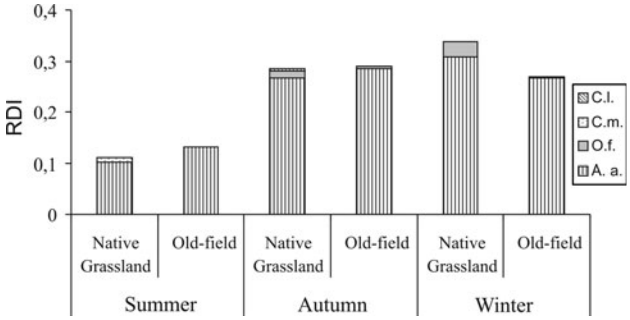

Fig. 1 Relative density indexes (RDI) of rodents in the native grassland and in the old-field. C.l., *Calomys laucha*; C.m., *Calomys musculinus*; O.f., *Oligoryzomys flavescens*; A.a., *Akodon azarae*

Results

Field experiment

We captured a total of 325 rodents with a trapping effort of 2,052 trap nights. We did not capture cavies in any sampling, and although it is a conspicuous species, we did not observe individuals in the area along the study. The RDI of small rodents ranged from 0.11 to 0.35 and was similar in both habitats in summer and autumn, while in winter density was higher in the native grassland (test for difference between proportions, $p = 0.003$, Fig. 1). *A. azarae* was the most abundant species in all samplings in both habitats (Fig. 1). In the native grassland, *A. azarae* represented 89.1% of the total captures (124 individuals). Other minor species were *O. flavescens* (7.6%), *C musculinus* (2.3%), and *C. laucha* (1.0%). In the old field, *A. azarae* represented 99.1% of the captures, and the remaining 0.9% was *O. flavescens*.

Seed removal

There was seed consumption in 32.2% ($n = 27$) of the foraging stations. The proportion of stations with seed removal did not vary significantly between habitats and species ($p > 0.10$), while the proportion of foraging stations with seed removal was higher in the old-field in winter (habitat × season: $p = 0.031$, Table 1; Fig. 2).

The mean percentage of seed removal per foraging station varied between 5.7% in summer and 21.6% in autumn for *P. caldenia*, and between 3.1 and 7% for *G. triacanthos*. There was a significant effect of species and season on overall seed removal (Table 1), but there was a significant interaction between these factors (Table 1). Differences between seasons were significant for *P. caldenia* ($F = 16.489$, $p = 0.012$), with more consumption in autumn than in summer and winter (Fig. 3), while *G. triacanthos* seed removal did not change according to

Table 1 Summary of statistical results for the percentage of foraging stations with consumption (log-linear analysis), and amount of seed removal (overall and individual rates, three-way ANOVA) for the effect of habitat, species and season

Model parameter	df	Stations with consumption (%)		Overall seed removal		Individual seed removal	
		χ^2	*p*	*F*	*p*	*F*	*p*
Habitat	1	1.235	0.266	0.734	0.400	*4.071*	*0.055*
Species	1	2.388	0.122	*26.643*	*0.000*	*31.026*	*0.000*
Season	2	3.539	0.170	*5.280*	*0.008*	0.503	0.608
Habitat × species	1	0.429	0.512	3.562	0.071	*5.995*	*0.022*
Species × season	2	3.168	0.205	*4.172*	*0.021*	1.243	0.297
Habitat × season	2	*6.924*	*0.031*	0.952	0.393	0.202	0.818
Habitat × species x Season	2			1.468	0.240	0.356	0.709

Significant values are in *italics*

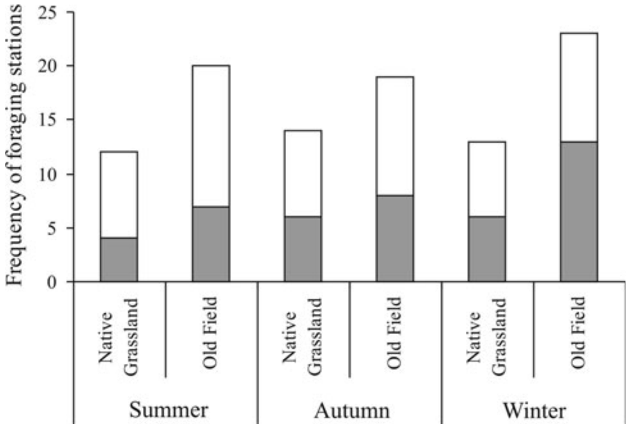

Fig. 2 Frequency of foraging stations with consumption of at least one seed for each plant species (*grey*, *P. caldenia*; *white*, *G. triacanthos*)

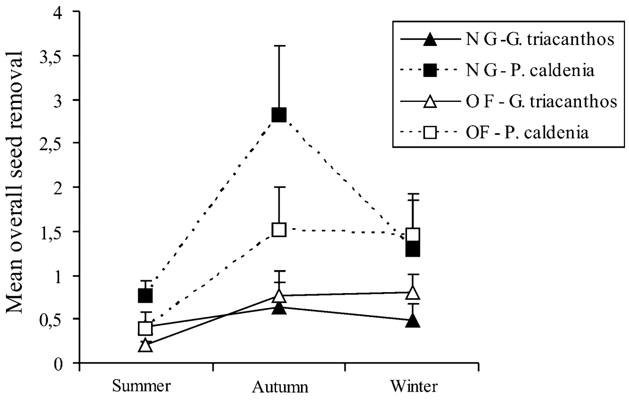

Fig. 3 Mean overall seed removal (mean + SE) in the native grassland (*NG*) and in the old-field (*OF*)

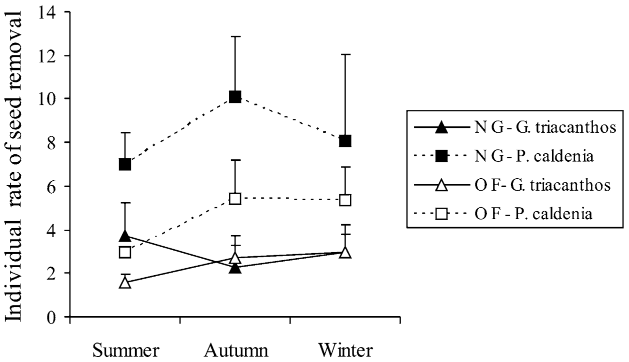

Fig. 4 Individual rate of seed removal (mean + SE) in the native grassland (*NG*) and in the old field (*OF*)

the season ($F = 1.1125, p = 0.0505$). *P. caldenia* showed a higher seed removal than *G. triacanthos* in autumn and winter ($F = 28.298$, $p = 0.00016$ and $F = 7.156$, $p = 0.013$, respectively), but in summer there were no differences between species in seed removal ($F = 1.055$, $p = 0.314$). There was no effect of habitat on the overall seed removal.

The individual rate of removal was affected by species and habitat (Fig. 4, $p < 0.0001$ and 0.0545, respectively), but there was an interaction between these factors ($p = 0.0217$, Table 1). In both habitats, there were differences in removal between species ($F = 27.126$, $p < 0.0001$, and $F = 5.979$, $p = 0.0219$ for the native grassland and the old field, respectively) with more consumption of *P. caldenia* seeds (Fig. 4), but differences between habitats were significant for only *P. caldenia* seeds removal ($F = 16.249$, $p = 0.005$ for *P. caldenia* and $F = 0.323$, $p = 0.2245$ for *G. triacanthos*), *P. caldenia* was more consumed in the native grassland than in the old field (Fig. 4). There was no effect of season on the individual rate of seed removal (Table 1).

Although there was a higher consumption of *P. caldenia* seeds, in terms of biomass, there was a higher intake of *G. triacanthos* (Table 2) because of the higher weight of seeds (150 mg for *G. triacanthos* and 30 for *P. caldenia*).

Cage experiments

The proportion of *A. azarae* individuals that consumed at least one tree seed in non-choice feeding trials was 0.46 ($n = 6$) for *G. triacanthos* and 0.80 ($n = 12$) for *P. caldenia*, but these figures were not statistically different ($p = 0.07$). On the other hand, the proportion of *G. triacanthos* seeds consumed per individual rodent was significantly lower than that of *P. caldenia* seeds ($Z = 3.36$, $p < 0.0001$).

Discussion

According to our results, seed removal by rodents varies according to the plant species, habitat, and season. These variations may be related to the characteristics of seeds as size, to alternative food availability, as well as to rodent density. In the field experiment, rodents removed

Table 2 Mean consumption in terms of biomass (mg) for *G. triacanthos* and *P. caldenia* according to habitat and season

	G. triacanthos			*P. caldenia*		
	Summer	Autumn	Winter	Summer	Autumn	Winter
Native grassland	613.63	954.54	715.91	231.82	845.45	388.6
Old field	302.63	1,140.63	1,195.31	115.79	453.13	435.94

We considered a mean weight of 150 mg for *G. triacanthos* and of 30 mg for *P. caldenia*

up to 21% of seeds of *P. caldenia*, while their effect on *G. triacanthos* seeds was low. At least in the presence of alternative seeds (or other food items) *G. triacanthos* is scarcely removed, and in consequence, rodent seed predation might not have a significant demographic effect on this species. The differential removal between the two plant species may have been related to their differences in seed size, because *G. triacanthos* seeds are too large to be eaten by small rodents without being broken, and the thick coat makes it difficult. Although we found differences between species in the amount of seed removal, this effect disappeared when we examined the frequency of foraging stations with at least one seed removed. This result suggests that rodents proved both types of seeds, but they selected the small seed (*P. caldenia*) to be eaten, or that they need to consume a small number of *G. triacanthos* seeds because of their larger size.

In natural conditions, seeds are probably wet and softer than those which we offered, and consumption of *G. triacanthos* seeds may have been underestimated by our experiment, while *P. caldenia* seeds may be consumed independently of the water content because of their smaller size. On the other hand, if we consider the mass of seeds removed in the 3 months, there was a higher removal of *G. triacanthos* than *P. caldenia*, and from the consumer point of view, there was a higher intake of biomass from *G. triacanthos* consumption than from *P. caldenia*. According to the chemical composition, *G. triacanthos* seeds are probably not a profitable item for rodents because they have a great proportion of highly indigestible compounds for non-ruminant herbivorous (Manzi et al. 1979), while for seeds of the genus *Prosopis* (*P. juliflora*) Marangoni and Alli (2006) described 35% of crude proteins, and a relatively high proportion of unsaturated fatty acids.

Seasonal variability in seed removal seemed to be positively related to rodent density, because it was higher in the seasons of higher density (autumn and winter), but the season effect disappeared when we considered the individual rate of consumption. A similar result was found by Predavec (1997), who observed an overall increase in the rate of seed removal with increased population numbers of rodents in desert habitats of Australia, while individual rates of seed removal were independent of population density.

Individual seed removal differed between habitats, possibly because of differences in alternative food availability. Food availability was probably higher in the old field, which had a higher plant cover and productivity (Machera 2006) and where seeds of *G. triacanthos* were also available from the production of established trees. Overall, seed removal in each habitat and season may have been the consequence of the interaction between rodent density (increasing overall removal, higher in the old field) and alternative food availability (decreasing individual removal, and also higher in the old field).

The effect of seed predation will depend on the availability of seeds, because seed losses by granivory will only affect plant recruitment at low seed input (Crawley 1987). Previous works made in Pampean grasslands have shown that woody plant invasion is constrained by seed and microsite availability (Mazía et al. 2001), but seed availability changes depending on the stage of invasion. The relationship between seed predation and availability may be high at the beginning of the invasion (when there is no local production of seeds) or when seed sources are far from the site. In the case of *G. triacanthos* and *P. caldenia*, it also depends on the movement of cattle. Invasion will be more successful in sites where human activities cause a reduction in seed predators, as live stock and crop fields in the Pampean region, where agrarian labors increase rodent mortality (Cavia et al. 2005; Hodara and Busch 2006).

In order to assess the potential effect of rodent predation on the demography and recruitment success of the studied plant species, not only the effects at the seed stage reported in this work must be considered but also the effects on seedlings and small plants, since rodents present in the study area are also herbivorous (Bilenca et al. 1992; Bilenca and Kravetz 1998; Ellis et al.1998). On the other hand, it is also possible that rodents affect survival and germination of seeds that are not removed, but are handled when they try to eat them. Finally, we conducted the study during only 1 year, and probably the magnitude of rodent seed predation varies among years according to environmental fluctuations that affect resource supply. For example, during dry periods when green parts of plants are less available, rodents may increase the consumption of seeds, but when alternative resources are abundant, seed predation would decrease.

We used seed removal as a surrogate for seed predation or loss, although some potential predators could have only relocated and not consumed a proportion of the seeds removed (Villagra et al. 2002). In consequence, we consider that seed removal was associated with seed loss and not to relocation or dispersal. We also assumed that seed removal was mainly due to rodent activity, since we found rodent feces and hair remains. Foraging bottles did not allow the access of ants, and we neither observed feather remains nor birds consuming seeds from the soil. These results were confirmed by the experiments in cages, where the disappearance of seeds could only have been caused by rodent consumption, and where we found similar or higher percentages of seeds consumption than those observed in the field experiment.

In summary, we conclude that rodents removed both types of seeds, but their effect was largely higher on *P. caldenia*. The role of seed predation by rodents in decreasing woody plant recruitment would depend on particular local conditions, as seed limitations of the woody plants, alternative food availability for rodents, food requirements, and rodent density that may vary through time and space. Human activities, which are increasingly changing habitat conditions and probably decreasing rodent abundance in rural habitats because of the application of agrochemicals and the agrarian labors, may favor the release of these biotic barrier to woody plant invasions, while the livestock favors their spread.

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