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Effects of grazing on seedling establishment: the role of seed and safe-site availability

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Abstract. The first objective of this paper was to assess the effects of grazing on seedling establishment of two species whose relative abundance at the adult stage is affected by grazing in a contrasting fashion. Second, we evaluated the relative importance of seed versus safe-site availability in explaining the effect of grazing on seedling establishment. We monitored seedling establishment on a grazed area, on two areas which had not been grazed for two and seven years, and on plots which had been experimentally defoliated. The species compared were *Danthonia montevidensis*, a native perennial grass which dominates both grazed and ungrazed communities, and *Leontodon taraxacoides*, an invading exotic rosette species from the *Compositae* family.

Continuous grazing enhanced seedling establishment of both species through its effect on the availability of safe sites. Seed availability accounted for only one, but very important, grazing effect: the lack of response by *L. taraxacoides* to the defoliation in the seven-year old exclosure. Its seed supply was depleted by exclusion of grazing and, consequently, its short-term regeneration capacity after disturbance was lost.

Keywords: *Danthonia*; Germination; *Leontodon*; Pampa; Seed bank.

Nomenclature: Cabrera & Zardini (1978).

Introduction

Effects of grazing on species composition of plant communities include demographic changes. Particularly, seedling establishment is considered as a crucial process in determining species composition of plant communities (Grubb 1977; Harper 1977) and their response to grazing and other disturbances (Noble & Slatyer 1980; Willems 1983; McNaughton 1983; Watt & Gibson 1988). Seedling establishment depends on the density of both germinable seeds and safe-sites (Harper 1977; Fowler 1988). Grazing may affect both factors through its effect on seed production and a variety of factors in the soil and in the vegetation canopy (Silvertown 1980; Fenner 1980; McNaughton 1983; Watt & Gibson 1988).

Grasslands of the Flooding Pampa, Argentina, evolved under a light grazing regime (Webb 1978), but they have been heavily grazed by domestic animals for more than two centuries (León, Rusch & Oesterheld 1984). Grazing is an important determinant of the present vegetation structure (Sala et al. 1986). Although grazing did not significantly affect total leaf area index and total cover, it drastically modified their vertical and horizontal distribution. Under grazing, leaves were concentrated in the 0 - 5 cm layer of the canopy, whereas in ungrazed areas the same leaf area was evenly distributed up to 40 cm high. Under protection from grazing, small and numerous individuals were replaced by few large tussocks. These structural effects of grazing were partially the result of changes in species composition. Dicots, which accounted for an important fraction of the cover (35%) in grazed areas, virtually disappeared after four years of no grazing. Simultaneously, grasses and a sedge increased from 65 % to 95 % of total cover (Sala et al. 1986). When these ungrazed areas were subjected again to grazing, a lag of at least four years was observed before the establishment of exotic species took place (Facelli 1988).

The overall objective of this paper is to explore the mechanisms which may account for the changes in species composition observed as a result of grazing in the Flooding Pampa. The first specific objective was to assess the effect of grazing on seedling establishment of two species whose relative abundance at the adult stage is differentially affected by grazing: *Danthonia montevidensis*, a perennial, native grass which doubled its basal cover from 1.8 to 3.8 % after four years of exclosure, and *Leontodon taraxacoides*, an exotic (European) rosette species from the *Compositae* family with an opposite response to grazing; it had a basal cover of 0.8 % under grazing conditions and it disappeared after four years of exclosure (Sala 1988). Our second objective was to evaluate the relative importance of seed vs. safe-site availability in accounting for the effect of grazing on seedling establishment.

Methods

The study was carried out in a native grassland community defined phytosociologically by León (1975) as the community of *Piptochaetium montevidensis, Ambrosia tenuifolia, Eclipta bellidioides* and *Mentha pulegium*. The climate of the flooding pampa region is temperate; annual mean precipitation is 924 mm, and mean monthly temperatures range from 6.8 °C in August to 21.8 °C in January.

Four grazing treatments were compared: continuous grazing, 2-yr old exclosure, 7-yr old exclosure, and spring defoliation in the same 7-yr old exclosure. This exclosure corresponds to the native community dominated by perennial grasses (Sala et al. 1986), whereas the defoliation treatment simulated a pulsed reintroduction of grazing. Defoliation in the exclosure was carried out mechanically at 5 - 10 cm and the material cut was immediately removed. The continuous grazing treatment corresponded to heavy grazing. Finally, the 2-yr old exclosure was included in order to assess the time constant of the response of seedling establishment to grazing exclusion. Five 15 × 20 m randomly established permanent plots were studied in each grazing treatment. The plots for the continuous grazing treatment were located about 200 m from both exclosures.

Three densities of seed addition were evaluated in each grazing treatment: 0, 20, and 40 seeds per dm^2 for *L. taraxacoides* and 0, 45, and 90 seeds per dm^2 for *D. montevidensis*. For each species and seed addition treatment, five subplots (5 × 20 cm) were randomly established in each of the 15 × 20 m plots. Seeds were collected in the study area in November and December and immediately sown on the subplots simulating natural shedding. Thus, each combination of species, grazing, and seed addition treatments had five distinct subreplicates in each of five plots.

Subplots in which seeds were not added had an unknown background seed density and provided information regarding our first objective, the study of the effect of grazing on seedling establishment. Subplots in which seeds were added provided information about the mechanisms underlying the effect of grazing: at maximum density of seed supply, safe sites were expected to be saturated with seeds and seedling density would be a reliable indicator of safe-site density. Here we understand the concept of safe site in its broadest sense (Harper 1977, p.112): a zone in which a seed finds the stimuli required for breakage of seed dormancy, the conditions and resources required for the germination processes to proceed, and protection from specific hazards such as predators, competitors, and pathogens. Given the time scale of our study, we extend this concept beyond the process of germination itself and include the seedling establishment stage.

Although this design is 'pseudoreplicated' (Hurlbert 1984) for the grazing treatments, we think this is unlikely to be a problem for two reasons. First, the micro-spatial scale at which the processes studied in this paper are controlled suggests that all the heterogeneity is represented inside each exclosure. Second, the exclosures were established in floristically homogeneous sites, occupied by the same plant community as defined by León (1975).

Seedling density per subplot was recorded three times between May and September 1985 (late fall and winter). The first sampling was done ca. 20 days after germination started. By the time of the last sampling, differentiation of seedlings from adults was still easy. At each sampling date, up to 10 seedlings per subplot were identified by means of colored plastic markers (Chester & Shaver 1982; Rapp & Rabinowitz 1985). The limit on the maximum number of seedlings that were marked was set in order to minimize the effect of the markers on the structure of the community inside the subplots. Markers made it possible to obtain an estimate of percent seedling mortality between dates and, thus, to know the proportion of the current seedling density that was the result of recent emergence of previously unrecorded seedlings. Seedling emergence between any two sampling dates was then considered as the number of seedlings at the second date in excess to what it would have been expected from the values of average percent mortality between dates and the density at the first date. Some plastic markers were lost at the end of the sampling period because of cattle trampling in the continuous grazing treatment. As a consequence, seedling mortality in that treatment was underestimated.

Treatments were statistically compared by a two-way analysis of variance (grazing and seed addition) for each date and species. Density and mortality data were square root and angular transformed respectively, but figures show untransformed data.

Results

Grazing exclusion significantly decreased recruitment of *Danthonia montevidensis* and *Leontodon taraxacoides* (Fig. 1). Although grazing did not affect initial seedling density of *D. montevidensis* (Fig. 1a), a significant reduction of seedling density in the oldest exclosure was observed later in the season (Fig. 1b, c). Seedling establishment of *L. taraxacoides* was also

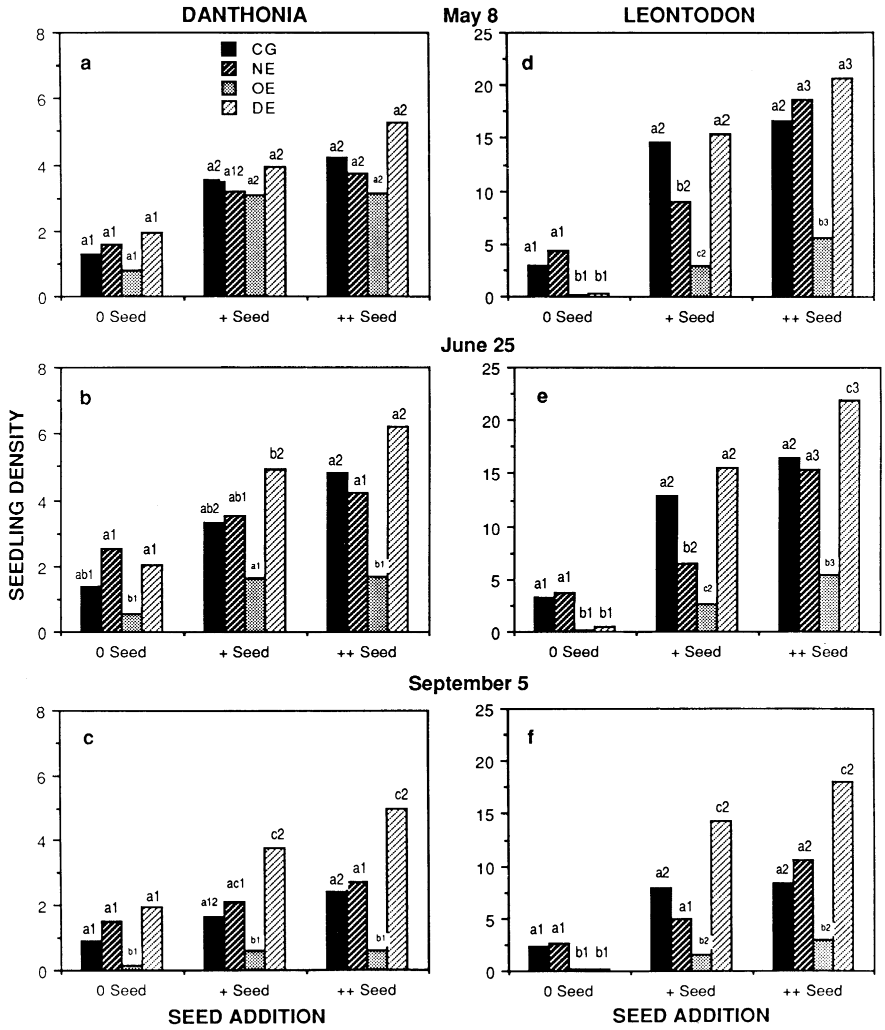

Fig. 1. Effect of grazing and seed addition treatments on seedling density (individuals / dm^2) of *Danthonia montevidensis* (Fig. 1a - c) and *Leontodon taraxacoides* (Fig. d - f) at different times after an initial germination pulse (Fig. 1a - d, May 8; Fig. 1b - e, June 25; Fig. 1c-f, September 5). CG = continuous grazing; NE = new, 2-yr exclosure; OE = old, 7-yr exclosure; DE = defoliation experiment in 7-yr exclosure; 0 seed = control; + seed = addition of seeds at medium density; ++ seed = high density. Different letters indicate significant differences between grazing treatments for the same seed addition treatment. Different numbers indicate significant seed addition effect for a given grazing treatment.

minimal at the old exclosure, but in contrast to *D. montevidensis*, *L. taraxacoides* did not respond positively to mechanical defoliation in the exclosure unless seeds were artificially supplied (Fig. 1d, e, f).

Seed availability limited seedling recruitment of both species in all grazing treatments (Fig. 1). In *D. montevidensis*, the effect of seed addition progressively declined with time (Fig. 1a, b, c); by the end of the sampling period, seed addition had a significant effect only under continuous grazing and after defoliation. In *L. taraxacoides*, the decline of the seed addition effect with time was less apparent (Fig. 1d, e, f); seed addition increased seedling density, but this increase was much larger in the defoliated exclosure.

Since seedling mortality (expressed as percentage) was not affected by seed addition ($P < 0.25$), only the main effects of grazing on mortality are shown (Fig. 2). Mortality of *D. montevidensis* was significantly higher in the old exclosure than in the other grazing treatments. Mortality of *L. taraxacoides* was also higher in the old exclosure, but there were additional significant differences (new exclosure > continuous grazing > defoliated exclosure). Emergence of new seedlings after the first sampling was detected only for *D. montevidensis*. It was minimal in the old exclosure, maximal in the defoliated exclosure, and intermediate in the other two grazing

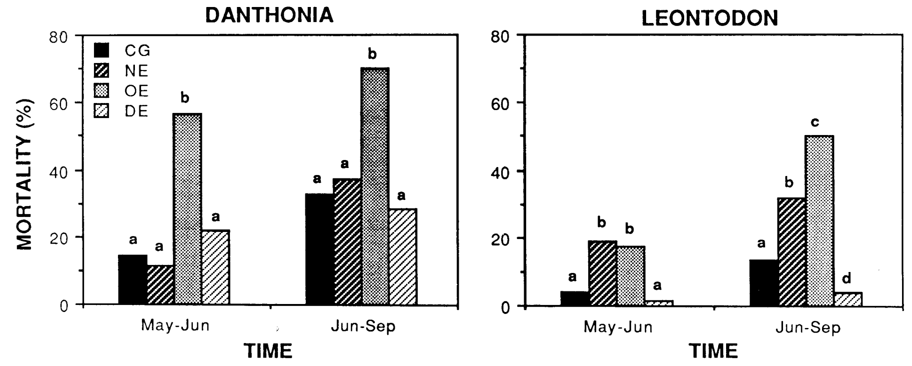

Fig. 2. Seedling mortality of *Danthonia montevidensis* and *Leontodon taraxacoides* under different grazing treatments for two periods after an initial germination pulse. Different letters indicate difference between grazing treatments for each period. Grazing treatments as in Fig. 1.

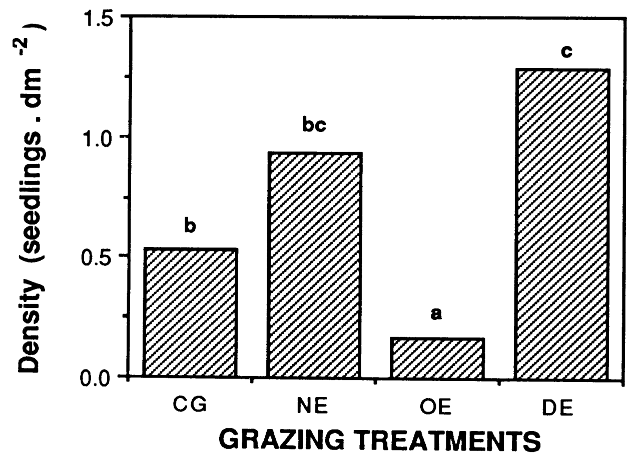

Fig. 3. Density of seedlings of *Danthonia montevidensis* emerged between May and June sampling dates. Grazing treatments as in Fig. 1.

treatments (Fig. 3). Seed addition had no effect on this late germination pulse ($P < 0.32$).

Discussion

Our results indicate that grazing increased recruitment of both species, the perennial grass and the rosette herb. The major difference between the two species ris found in the way they responded to the experimental defoliation of the old exclosure: a sharp increase of the density of grass seedlings and no response of the exotic rosette. Disturbance in general and grazing in particular promote seedling establishment in a variety of environments (Miles 1972, 1973; Gross 1984; Keeley 1987; Rusch 1988; but see Goldberg & Werner 1983; Rapp & Rabinowitz 1985; McConnaughay & Bazzaz 1987 for a discussion on the role of scale of disturbance). Potential mechanisms for grazing effect are enhancement of germination through breaking of canopy-induced dormancy (Silvertown 1980), reduction of seedling mortality because of reduced adult-seedling competition (Fenner 1978), and long-term changes in seed bank composition through the combined effect on seed rain, seed death, and germination (Williams 1984).

Our results do not fully explain the changes in species composition brought about by grazing in the Flooding Pampa. The increase in cover of *D. montevidensis* as a result of grazing prevention is not accounted for by an increase in the recruitment of new individuals. In fact, recruitment was higher under grazing. Therefore, we are led to the conclusion that the prolonged grazing exclosure must have increased the longevity and/or vegetative reproduction of *D. montevidensis*. On the contrary, continuous grazing must have resulted in a higher turnover rate. Higher recruitment and lower longevity under continuous grazing would result in the observed structural response to grazing: few and large individuals in the exclosures and more numerous, smaller individuals under continuous grazing (Sala et al. 1986). In contrast to *D. montevidensis*, the effect of grazing on seedling establishment of *L. taraxacoides* may partially explain its adult population levels. Seedling establishment under continuous grazing was much larger than after seven years of grazing exclusion.

Safe-site density, estimated from seedling density values at the highest level of seed supply, and seed availability accounted for the grazing effects in a complex way. The validity of our approach to estimate safe-site density is supported by the lack of significant differences between the two levels of artificial seed supply. This indicates that in most cases safe-sites were saturated by our seed addition treatments. Moreover, the lack of effect of seed addition on mortality rates shows that these high levels of seed addition were not high enough to create a considerable competition between seedlings of the same species.

The decrease in seedling recruitment of both species after seven years of prevented grazing was mainly accounted for by a reduction in the density of safe sites. This was largely due to higher mortality in the old, intact exclosure. Our grazing treatments brought about changes in canopy structure and light environment at soil level which had profound physiological effects on adult plants (Deregibus et al. 1985) and might account for the higher seedling mortality.

After seven years of protection from grazing seed availability was drastically reduced only in the case of *L. taraxacoides*. This was the major difference between species and may further explain their adult population levels. Defoliation in the old exclosure created a number of favorable microsites for germination, but the period of grazing exclusion had depleted the seedbank of *L. taraxacoides*, and no germination occurred unless seeds were experimentally supplied. Absence of grazing eliminated not only the adult individuals of this species, but also its regeneration capacity once the canopy was re-opened. Since the exclosure was surrounded by a grazed community where *L. taraxacoides* was abundant, this result also indicated a poor dispersal ability for this species. These observations suggest a mechanism for the lag in the invasion of *L. taraxacoides*, and other exotic species when protected native grasslands are reopened to cattle grazing (Facelli 1988).

Values of seedling establishment of both species in the two-year old exclosure were similar to the values observed under continuous grazing. This suggests that changes in the biotic and abiotic factors regulating recruitment are slow during the first two years of exclusion and become apparent only after several years.

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