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Continuous grazing disrupts desert grass-soil seed bank composition under variable rainfall

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Abstract Long-term field studies help unveil mechanisms of grass soil seed bank (SSB) persistence and resilience. We wonder whether grazing is a disruptive force that changes grass SSB composition and size, while heavy rainfall is a positive bottom-up force that restores the grass SSB in grazed areas of the Monte desert, Argentina. We used core sampling to study the grass SSB in cattle-free (17 year) and grazed (10 year) grasslands. The SSB size in cattle-free sites usually responded in a continuous positive fashion to rainfall, and the proportion of palatable grasses in the SSB was similar among years. Most grass species formed a transient SSB, but the presence of a stand of perennial plants would prevent their local extinction. In contrast, the SSB size in the grazed habitats showed a threshold response to rainfall (i.e. it did not increase under low-moderate rainfall), the seeds of palatable grasses were always scarce, and the proportion of seeds of less palatable grasses increased under extreme rainy conditions. Seed production from grasses that grew tillers from axillary buds during a drought was zero, suggesting that the bank of plants could have a role in the replenishment of the grass SSB only in mesic years. Within the time span assessed here, continuous heavy grazing together with scarce as well as heavy rainfall were disruptive forces that reduced the number and proportion of seeds from palatable grasses in the SSB, which are also the species preferred by seed-eating animals.

Keywords Long-term study · Soil seed bank persistence · Vegetation soil-seed bank correlation · Semiarid rangelands · Plant regrowth · Post-dispersal seed-eaters

Introduction

Continuous cattle grazing in desert grasslands and rangelands changes the composition and reduces the size of the soil seed bank (SSB) through the selective consumption of the preferred grass species (Pol et al. 2014). Drought may increase the negative impact of grazing on the grass SSB, whereas occasional heavy rains are expected to mitigate this impact by promoting tillering and seed production of the extant plants, and/or by enhancing seed germination and recruitment of new reproductive plants (Westoby et al. 1989; O'Connor 1994).

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Seeds in the SSB represent the main means of recovery of several grass species after habitat disturbance in deserts, where seed scarcity may limit plant recruitment (O'Connor 1991, 1994; Bisigato and Bertiller 2004; Rotundo and Aguiar 2004; Tessema et al. 2016). A bet-hedging strategy may then raise community resilience or the speed with which a community returns to its former state after it has been disturbed and displaced from that state. However, the disturbance might alter the composition and persistence of the SSB in the habitat, whereas the efficacy of the bet-hedging strategy is limited by the combined effect of seed predation (Marone et al. 2008) and pathogen attack (Marone et al. 2000). Given the complexity of the interacting factors, the effect of grazing, rainfall, and seed consumption on the long-term persistence of the grass SSB could be better unveiled by multiyear studies (Meserve et al. 2003; LaForgia et al. 2018; Chytry et al. 2019).

Seed production of herbaceous plants in deserts depends heavily on appropriate rainfall (Schwinning and Sala 2004; Pol et al. 2010). Perennial grasses produce most of their seeds during the onset of effective rain pulses (Schwinning and Sala 2004). A strong bottom-up control of grass seed production and SSB size occurs in the central Monte (Pol et al. 2010) and other South American deserts (Marone et al. 2000; Meserve et al. 2003). Although grass seed production may respond to current year rainfall, rainfall of the current and previous years combined might yield better predictions of seed production and SSB size in perennial grasses (Sherry et al. 2012; Dudney et al. 2017), since drought severely reduces the tuft size and affects seed set. Lagged effects of rains, carried over from previous environmental conditions, on the replenishment of the SSB may be, therefore, expected (O'Connor and Pickett 1992; O'Connor 1994).

Rainfall (bottom-up) and grazing (top-down) forces interact in several ways affecting the grass SSB in the central Monte desert (Pol et al. 2014). As reported in other deserts, heavy rains could blur the negative effect of grazing and allow SSB recovery, but severe drought could interact with grazing negatively (Westoby et al. 1989; O'Connor 1994). Moreover, domestic grazers primarily consume the same grass species as those with seeds that are selected and preferred by seed-eating birds (Marone et al. 2008, 2017; Camín et al. 2015) and some ants (Pirk et al. 2009; Pol et al. 2014, 2017). The effects of all these factors should be considered simultaneously to test the long-term persistence of the grass SSB in disturbed and undisturbed habitats.

We assessed the multiyear dynamics of the grass SSB to see whether rainfall is a bottom-up force buffering changes provoked by grazing in its species composition. Do occasional heavy rains promote community resilience by restoring palatable (for herbivores) and preferred (for granivores) species in the grass SSB of the central Monte desert? We also assessed whether the composition of the aboveground vegetation and the grass SSB were similar under contrasting grazing conditions, which can also favour resilience if the seed bank drives the stability of vegetation composition and the vegetation drives the stability of SSB composition.

Grass cover in the central Monte desert suffers interdecadal fluctuations. In ungrazed fields, mean total grass cover was 28.33 ± 14.86 (mean ± SD) in 1997, 35.8 ± 15.36 in 2002, 32.2 ± 14.63 in 2007, 28.35 ± 15.98 in 2012, and 1.9 ± 3.56 in 2019, and the mean cover of palatable grasses was about 25, 22, 24, 29, and 0%, respectively (F. Milesi and J. Lopez de Casenave, unpublished data). A similar abrupt decline in grass cover was observed in grazed fields during 2018–2019 (R. Pol and L. Marone, pers. obs.). Such serious reduction gave us the opportunity to test another source of grass community resilience. Does during severe drought a bud bank exist that allows the restoration of the SSB of perennial grasses through the quick development of reproductive tillers even after moderate rains (Ott et al. 2019)?

Material and methods

Study areas

We studied the grass SSB in the Biosphere Reserve of Ñacuñán, central Monte desert, Argentina (34° 03′ S, 67° 54′ W), which has been excluded from domestic grazers for the last 47 years, and also in cattle ranches located adjacent to the reserve and subject to continuous grazing. Domestic grazing is the most widespread economic activity in the central Monte. The general habitat is desert rangeland or grassland made up of scattered *Prosopis flexuosa* and *Geoffroea decorticans* trees, within a matrix of tall and low shrubs (*Larrea divaricata*, *Atriplex lampa*, *Capparis* *atamisquea*, *Condalia microphylla*, *L. cuneifolia*, *Lycium* spp., *Verbena aspera* and *Acantholippia seriphioides*). Most of the forb species in the reserve are annual. The habitat usually has an important grass layer (25–50% cover) mostly composed of perennial and palatable C_4 species like *Trichloris crinita*, *Pappophorum* spp., *Setaria leucopila*, *Digitaria californica*, *Diplachne dubia* and *Chloris castilloniana*. *Sporobolus cryptandrus* is also a C_4 perennial species with forage value but, owed to its loose and scarce foliage, it contributes barely to cattle diet. Less palatable C_4 (*Neobouteloua lophostachya*, *Aristida mendocina*) and C_3 species (e.g. *Jarava ichu*) are also present, along with a group of less abundant, usually less palatable, annual exotic (*Eragrostis cilianensis*, *E. pilosa*) or native grasses (*Bouteloua aristidoides*, *B. barbata*) (Roig 1981). Finally, *Schismus barbatus* is an annual exotic species which can be consumed by cows during a short vegetative stage. Given its very ephemeral foliage, this currently scarce but with highly invasive potential species (Pucheta et al. 2011) is considered of little forage value (Cunningham et al. 1992). Information about grass species palatability for domestic cattle follows Roig (1981) and authors cited therein, and it is mainly based on quantitative nutritional information, and the experience of ranchers in the field. The climate in Ñacuñán is dry and temperate, with cold winters. Around 75% of the annual rainfall occurs in the warmer months from October to March. Rainfall in the growing season is 273 ± 95 mm (mean ± SD; $n = 47$ year). Most grass seeds disperse and enter the soil in summer and early autumn (February-May; Marone et al. 2000). Plant species nomenclature follows Kiesling (2009).

Abundance and composition of the grass SSB

We studied the composition and size of the grass SSB in ungrazed areas of the reserve in the spring (October or November) in 1988, 1993–1998, 2009–2014 and 2016–2019, and in the same months in the grazed fields in 2009–2014 and 2016–2019. We sampled SSB before the beginning of the plant growth season to estimate the size and composition of seed reserves before rains trigger germination and establishment of new plants. We selected two 400-ha plots within the reserve and one 400-ha plot on every grazed ranch (i.e. two plots in grazed as well as ungrazed areas). Each spring, half sampling of both grazing conditions was allocated to every plot. Within each plot, we arranged two transects 400 to 700-m long and randomly allocated sampling points for soil core samples along both transects according to the cover of the main microhabitats in the landscape: beneath the tree canopy (15% cover and replicates in both grazing conditions) and the tall shrub canopy (35% in both grazing conditions), under low shrubs (13% in both grazing conditions) and grass (17% and 7% in ungrazed and grazed sites, respectively), and on bare soil (20% and 30% in ungrazed and grazed sites, respectively). We collected soil samples using a cylindrical sampler, 3.2 cm in diameter and 2.0 cm deep (80% of seeds are found in the upper 2 cm of soil). In the laboratory, soil samples were sifted through a 0.27-mm mesh sieve (the smallest seeds recorded from each microhabitat did not pass through the sieve), washed under water pressure in the same sieve and air-dried. We searched for sound seeds under a stereoscopic microscope and identified them to species or genus level using a reference collection. In the reserve, the total sampling effort in 1988 and 1993–1998 was $n = 73$ replicates, in 2009 $n = 60$, and from 2010 onwards it was $n = 120$. In the grazed plots, the sampling effort in 2009–2014 and 2016–2019 was always $n = 120$.

Rainfall and grass SSB size

We carried out principal component analysis (PCA) for synthesising inter-sampling variability of the most abundant seeds of palatable (*Trichloris crinita*, *Pappophorum* spp., *Setaria leucopila*, *Digitaria californica*, *Diplachne dubia*), and less palatable (*Sporobolus cryptandrus, Aristida mendocina*, *Neobouteloua lophostachya*, *Jarava ichu, Bouteloua barbata*, *Schismus barbatus*) grass species. The analysis allowed to assess whether different rainfall and grazing conditions affected SSB composition along the years.

Using Pearson correlations, we associated the mean number of grass seeds in ungrazed (17 year) and grazed fields (10 year) with two proxies of effective rainfall: total precipitation and the number of effective rain pulses (Pol et al. 2010; Schwinning and Sala 2004) in the growing seasons (October–March). Pol et al. (2010) showed that seed production of perennial C_4 grasses is not triggered by precipitation events $<$ 10 mm in spring–summer and so we used the number of pulses $>$ 10 mm in each growing season as an indicator of effective rainfall. We correlated total grass SSB size with the precipitation of the previous growing season (current year rainfall) and with the precipitation accumulated during the two previous growing seasons. We also correlated the proportion of seeds of palatable grasses in the SSB of grazed and ungrazed fields with the precipitation in the two previous growing seasons to find out whether rainfall has a resilient effect on the grass SSB (i.e. rainfall increases the proportion of seeds of palatable grasses) in both habitats. Based on historical records (1973–2020; $n = 47$) of precipitation accumulated during the two previous growing seasons (544 ± 140 mm; mean ± SD), sampling periods were classified as dry (mean − 1 SD, < 404 mm), mesic (404–684 mm), and rainy (mean + 1 SD, > 684 mm) (Fig. 1).

Grass SSB and aboveground vegetation

The average SSB size of different grass species in 1988, 1996–1997 and 2010–2011 was compared with the aboveground cover of the same species measured in the ungrazed fields in 1986–1987, 1996–1997 and 2010–2011, respectively. The cover of standing grasses was measured in 40 parallel transects (25-m long, > 20-m apart) interspersed over two 20-ha areas. Within each transect, we recorded all the grasses touching a stick at 25 random sampling points in March–May of every year and identified them to species level. The percentage cover of grass species was calculated for each transect and averaged to obtain a mean cover for the ungrazed habitat on every sampling occasion. In the grazed areas in 2010–2011 an identical protocol was employed to measure grass cover, which was Pearson correlated with the abundance of grass species in the SSB.

Grass plant regrowth and seed set

Aiming at estimating the number of perennial C_4 grasses that tillered from the bud bank and set seed during the 2019–2020 growing season, we installed 9 plots of 400 m^2, > 300 m separated from each other along a 3-km transect, on August 3, 2019. The plots were in the same general area of the reserve where the SSB sampling was carried out. In every plot, we randomly selected 12 focal C_4 perennial grass plants ($n = 109$ plants). We only chose adult plants, as those that had or showed signs of having produced reproductive tillers during some previous seasons (e.g. the presence of old spikes), or plants with a base

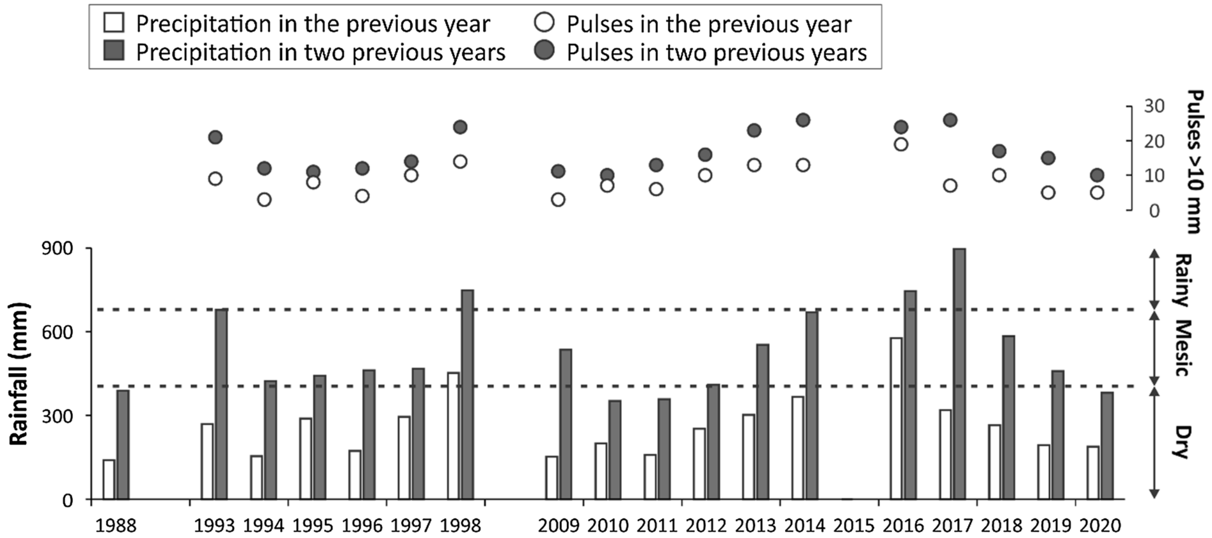

Fig. 1 Precipitation and number of effective rain pulses (> 10 mm) during the previous growing season (October–March) and the two previous growing seasons in the Biosphere Reserve of Ñacuñán, central Monte desert, Argentina. The year indicated (e.g. 1988) corresponds to the second year of the biennial period (e.g. 1987–1988). Based on historical records (1973–2020; $n = 47$) of precipitation accumulated during the two previous growing seasons (544 ± 140 mm; mean ± SD), sampling periods were classified as dry (mean − 1 SD, < 404 mm), mesic (404–684 mm), and rainy (mean + 1 SD, > 684 mm)

exceeding 5 cm in diameter (Pol et al. 2010). We monitored vegetative and reproductive tillers on the focal plant on October 31, December 3 and 17, 2019, January 13, February 14 and 20 and March 18, 2020. We followed all the regrown plants until reproduction and seed set over the grass growing season (September-March; Pol et al. 2010).

Results

Abundance and composition of the grass SSB

Despite important variations in the rainfall (Fig. 1), the overall SSB species composition remained widely similar in the ungrazed areas during the 17 years assessed (Table 1) where, almost every year, the most abundant species were: *S. cryptandrus*, *Pappophorum* spp., *D. californica*, *T. crinita*, and *S. leucopila*. Common species of grasses in the SSB of the grazed habitats showed more variability, although *S. cryptandrus*, *S. leucopila* and, to a lesser extent, *S. barbatus* were often among the most abundant (Table 1). Despite the qualitative stability, the grass SSB suffered important numerical fluctuations over the study period in the ungrazed (range 539–5334 seeds m^{-2}) and grazed habitats (301–5266 seeds m^{-2}) (Table 1). In some cases, species-specific variation was of several orders of magnitude. For example, in cattle-free habitats the less palatable perennial grass with shorter-lived tufts, *S. cryptandrus,* ranged from 83 seeds m^{-2} (2013) to 3297 seeds m^{-2} (2017), and the palatable perennial grass, *T. crinita,* ranged from no seeds m^{-2} (1997, 2009, 2018) to 1192 seeds m^{-2} (2014) (Table 1). Only one grass species appeared to be able to develop an abundant SSB in a relatively sudden fashion: *S. barbatus* (annual grass) in the ungrazed and especially in the grazed habitats ($>$ 1000 seeds m^{-2} in 2016, 2017, and 2019, Table 1). *S. cryptandrus* also increased suddenly in 2016 and 2017 in the grazed habitats, but this species had reached a high abundance in the ungrazed sites over several years (Table 1).

The first two axes of PCA accounted for 53% of the variance among samples (Table 2). The first principal component was associated positively with several palatable grass species (*Pappophorum* spp, *D. californica*, *D. dubia*, *T. crinita*), and *S. cryptandrus*. The second principal component was positively related to *S. leucopila* together with four less palatable grasses (*N. lophostachia*, *S. barbatus*, *B. barbata*, and *A. mendocina*; Table 2). Samplings on grazed sites located mostly on the upper-left side of the multivariate space, characterised by less palatable grasses, whereas samplings on the ungrazed sites distributed more heterogeneously on the right side of the figure, characterised by seeds of palatable species (Fig. 2). Notably, the samplings carried out during the rainiest period in this study (2016–2018), both in grazed and ungrazed sites, located close in the multivariate space reflecting a mixed composition of seeds from palatable and less palatable grasses after heavy rains despite grazing level (Fig. 2).

Rainfall and grass SSB size

In the reserve of Ñacuñán, the total grass SSB size correlated positively with the accumulated precipitation of the two previous growing seasons ($r = 0.55$, $P = 0.02$, $n = 17$) (Figs. 1, 3a), but not with the precipitation of the current growing season ($r = 0.31$, $P = 0.23$, $n = 17$). In a similar way, the total grass SSB size correlated with the number of effective pulses of rain (Fig. 1) in the two previous growing seasons ($r = 0.57$, $P = 0.02$, $n = 16$), but not in the current season ($r = 0.22$, $P = 0.40$, $n = 16$). The proportion of seeds from palatable perennial grasses was not correlated with the accumulated precipitation ($r = 0.10$, $P = 0.71$, $n = 17$) (Fig. 3b), although if the extremely rainy 2016–2017 period is eliminated from the analysis, a positive correlation is obtained ($r = 0.49$, $P = 0.05$, $n = 16$) (Fig. 3b). The 2016–2017 period was exceptional because it was the wettest period in 48 years of records in the Ñacuñán region (1972–2020). If we had only considered the ten years in which the SSB was assessed in the grazed habitats (2009–2014, 2016–2019), our results and their major implications would remain unchanged.

In the grazed habitats, the correlation between total grass SSB size and the precipitations of the two previous growing seasons was positive and strong ($r = 0.88$, $P < 0.001$, $n = 10$) (Figs. 1, 3c), but it was weaker with the current year rainfall ($r = 0.58$, $P = 0.08$, $n = 10$). The number of effective rain pulses (Fig. 1) of the two previous growing seasons ($r = 0.65$, $P = 0.04$, $n = 10$), but not of the current year ($r = 0.25$, $P = 0.49$, $n = 10$), correlated positively with the total grass SSB. The proportion of seeds

Table 1 Mean soil seed bank density (seeds m^{-2}) of palatable and less palatable grass species in ungrazed habitats in the Biosphere Reserve of Ñacuñán (17 years) and in adjacent fields subject to continuous cattle grazing (10 years) in the central Monte desert, Argentina

Species	Ungrazed																
	1988	1993	1994	1995	1996	1997	1998	2009	2010	2011	2012	2013	2014	2016	2017	2018	2019
Palatable grasses																	
Pappophorum spp.	323	1568	630	562	239	68	869	373	52	62	104	404	404	62	73	238	62
Digitaria californica	87	631	307	187	68	119	494	352	10	73	342	352	114	684	187	10	104
Trichloris crinita	336	682	85	34	34	0	153	0	290	197	62	736	1192	83	31	0	31
Setaria leucopila	211	324	85	68	17	34	204	0	166	301	498	363	207	871	363	93	41
Diplachne dubia	50	272	68	34	34	17	17	0	10	10	0	0	83	10	83	0	21
Chloris castilloana	0	0	0	0	17	0	0	0	0	21	31	0	0	0	31	0	0
Cottea pappophoroides	0	0	0	0	0	0	51	0	0	0	0	21	0	0	0	0	0
Bromus spp.	0	0	0	0	0	0	0	0	0	21	0	0	10	0	0	0	0
Total palatable grasses	1007	3477	1175	885	409	238	1788	725	528	685	1037	1876	2010	1710	768	341	259
Less palatable grasses																	
Sporobolus cryptandrus	2028	1806	2368	1823	562	596	1636	352	270	477	2146	83	850	943	3297	187	425
Aristida mendocina	87	51	17	51	0	0	17	41	52	73	41	73	10	73	0	0	0
Jarava ichu	25	0	17	0	0	0	0	249	10	10	0	10	21	0	0	10	0
Neobouteloua lophostachya	37	0	85	17	0	0	0	0	0	21	0	41	166	10	21	0	10
Schismus barbatus	0	0	0	0	0	0	0	0	0	0	0	0	0	145	788	0	0
Bouteloua aristidoides	0	0	0	0	51	17	0	0	0	0	0	0	0	21	0	0	0
Bouteloua barbata	0	0	0	0	0	0	0	0	0	10	0	0	0	10	21	0	0
Eragrostis spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	10	21	0	0
Total less palatable grasses	2177	1857	2487	1891	613	613	1653	642	332	591	2187	207	1047	1212	4137	197	435
Total grasses	3184	5334	3662	2776	1022	851	3441	1367	860	1276	3224	2083	3057	2922	4905	539	694

	Grazed									
	2009	2010	2011	2012	2013	2014	2016	2017	2018	2019
Palatable grasses										
Pappophorum spp.	41	31	31	10	83	62	73	124	0	0
Digitaria californica	21	41	0	21	31	10	93	73	52	0
Trichloris crinita	0	10	31	31	10	259	0	52	0	0
Setaria leucopila	31	73	83	145	52	124	404	156	228	218
Diplachne dubia	0	0	0	0	10	0	0	21	0	0
Chloris castilloana	0	0	0	0	10	0	0	0	0	0
Cottea pappophoroides	0	0	10	0	0	0	0	0	10	0
Bromus spp.	0	0	0	0	0	0	10	0	0	0
Total palatable grasses	93	156	156	207	197	456	581	404	290	218

Table 1 continued

	Grazed									
	2009	2010	2011	2012	2013	2014	2016	2017	2018	2019
Less palatable grasses										
Sporobolus cryptandrus	62	73	10	41	207	187	1379	2768	860	41
Aristida mendocina	0	10	31	31	10	259	52	31	10	0
Jarava ichu	301	62	10	10	0	10	0	10	62	10
Neobouteloua lophostachya	21	0	31	467	52	10	73	21	114	31
Schismus barbatus	197	0	21	10	0	394	1420	2022	52	1358
Bouteloua aristidoides	0	0	0	21	21	0	0	0	0	0
Bouteloua barbata	0	10	41	0	0	0	0	10	197	0
Eragrostis spp.	0	0	0	0	0	0	0	0	0	0
Total less palatable grasses	581	156	145	601	290	860	2924	4862	1296	1441
Total grasses	674	311	301	809	487	1317	3505	5266	1586	1659

Note that information from the reserve comes from three discontinuous periods (1988, 1993–1998, 2009–2019)

Table 2 Factor loadings for the two first principal components after a principal component analysis on a data matrix with the 11 most abundant seeds of palatable and less palatable grass species in ungrazed and grazed habitats of the central Monte desert

Species	Components	
	I	II
Palatable grasses		
Pappophorum spp.	**0.44**	− 0.19
Digitaria californica	**0.41**	0.02
Trichloris crinita	**0.34**	0.26
Setaria leucopila	0.08	**0.57**
Diplachne dubia	**0.40**	0.07
Less palatable grasses		
Sporobolus cryptandrus	**0.38**	0.16
Aristida mendocina	0.15	**0.30**
Jarava ichu	− 0.27	− 0.13
Neobouteloua lophostachya	− 0.15	**0.42**
Schismus barbatus	− 0.26	**0.37**
Bouteloua barbata	− 0.19	**0.35**
Eigenvalue	3.72	2.11
% variance	33.9	19.2
% cumulative variance	33.9	53.1

Loadings > 0.30 are indicated in bold

of palatable perennial grasses was negatively correlated with the precipitation of the two previous growing seasons ($r = -0.64$, $P = 0.05$, $n = 10$) (Fig. 3d). When the extremely rainy 2016–2017 period is eliminated from the analysis, the association remained negative ($r = -0.53$, $P = 0.14$, $n = 9$) (Fig. 3d).

Grass SSB and aboveground vegetation

The aerial cover of grass species was positively, but only weakly, correlated with the abundance of the same grass species in the SSB of the ungrazed habitat in 1988 ($r = 0.51$, $P = 0.11$, $n = 11$), and 2010–2011 ($r = 0.31$, $P = 0.35$, $n = 11$) and it was not correlated at all in 1996–97 ($r = -0.06$, $P = 0.86$, $n = 11$). Grass species cover was not correlated with their abundance in the SSB of grazed areas ($r = 0.22$, $P = 0.51$, $n = 11$). If *S. cryptandrus* is eliminated from the analyses (see Discussion for the justification), however, all correlations for the ungrazed habitat were

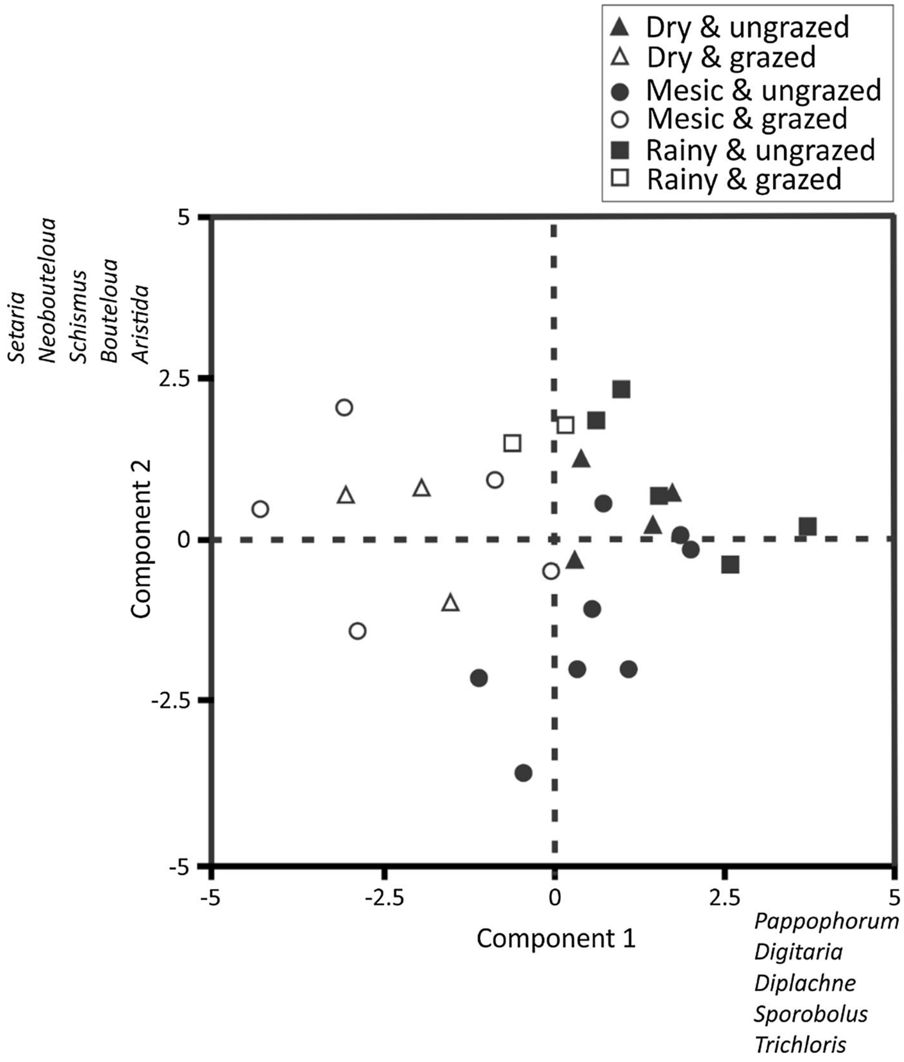

Fig. 2 Position of samplings carried out in different years and grazing conditions on the two first principal components after a principal component analysis on a data matrix with the 11 most abundant seeds from palatable and less palatable grass species in the central Monte desert. Based on precipitation accumulated during the two previous growing seasons (October–March), sampling periods were classified as dry (triangles), mesic (circles), and rainy (squares). Grazed (in white) and ungrazed (in black) samplings are noted. Names along each axis correspond to the more important variables loading on it (see Table 2)

significant at least at $P < 0.06$ ($n = 10$; Fig. 4a–c), but not for the grazed areas (Fig. 4d).

Grass plant regrowth and seed set

Total precipitation in the 2019–2020 growing season was 188 mm, a value that is below the year-to-year average (273 mm). We recorded tiller production in only three of the 109 focal plants, all of them at the beginning of the growing season (October 31). These plants remained unchanged from then until the end of the season and none of the monitored plants grew reproductive tillers or set seed during the entire 2019–2020 growing season.

Discussion

Hopfensperger (2007) emphasised the high similarity between standing vegetation and SSB in grasslands worldwide, but this did not seem to be true in the central Monte. However, Ericksson and Ericksson

(2008) noted that SSB and vegetation may differ in desert grasslands if the abundant species in the SSB are species that produce the largest number and smallest seeds because such seeds will be over-represented in the SSB. *S. cryptandrus* behaved this way in our study. It produces a lot of tiny seeds (Pol et al. 2010) and it was often the most abundant grass species in the SSB (Table 1). If *S. cryptandrus* is eliminated from the correlations, they were all positive in cattle-free habitats (Fig. 4a–c) suggesting that plant richness in the absence of domestic herbivores may be causally related to SSB richness, driving a virtuous circle of plant recovery.

The most common species in the SSB of the ungrazed areas persisted over the years, although they showed notable numerical fluctuations in the long term (Table 1) as reported for other South American deserts (Meserve et al. 2003). The lack of long-term persistence of grasses in the SSB may be caused by the dispersal of seeds that are ready to germinate despite a minor portion becoming dormant in the soil, or seeds having short-term dormancy and/or suffering heavy loss due to seed predation or pathogen attack (Bertiller and Aloia 1997; Marone et al. 2000; Thompson et al. 2003). In the Monte desert, several grass species disperse seeds with short-term or low dormancy (Sartor and Marone 2010) and autumn–winter seed predation notably reduces the number of grass seeds in the SSB ($> 50\%$ of seeds from palatable grasses, Marone et al. 2008). Notwithstanding, the presence of a stand of plants of perennial grasses, that can produce lot of seeds even under moderately dry conditions (Marone et al. 1998; Pol et al. 2010), would allow the persistence of a palatable grass SSB in the cattle-free habitats in most years.

As previously reported in other arid zones (Dudney et al. 2017; LaForgia et al. 2018), the effect of the annual amount of rainfall on grass SSB size was less notable than the effect of the sequential rainfall pattern over the years in cattle-free and grazed areas. Perennial grass mortality may occur in some dry years in the Monte, as seemed to be the case in 2018 and 2019 (Fig. 1), but more often the basal area and tuft size of grasses decrease substantially without complete mortality (O'Connor 1994). Later, and given effective rainfall, the tufts can recover from the activation of axillary buds. Therefore, accumulated rainfall may better explain the amount of seed produced because it accounts for plant regrowth as well as seed production per plant. This idea is reinforced because, in contrast to the behaviour of the grass SSB, the SSB of annual forbs showed a stronger positive correlation with the current year than with the accumulated precipitation in Ñacuñán, which is in accordance with the life history of annual plants, but not the perennials (see Table 1 in Marone et al. 2000).

Finally, floristic stability in the ungrazed habitat was not seriously disrupted by rainfall level. Total grass seeds in the SSB responded positively, and in a continuous fashion, to precipitation (Fig. 3a). Further, the proportion of seeds of palatable and preferred grasses remained usually unchanged (or increased) with rainfall (Fig. 3b). A call for attention, however, is that during the extremely 2016–2017 rainy period, the proportion of seeds from palatable grasses decreased even in the ungrazed areas (Figs. 2, 3b), suggesting that heavy rainfall may not always act as a restoration force there. Despite this, the positive responses of SSB composition to precipitation in most years (dry, mesic, and rainy) imply that important mechanisms of SSB resilience exist in cattle-free habitats of the central Monte (Fig. 2).

What patterns arose in the grazed habitats? The species composition of the grass SSB differed from the standing vegetation, a result that does not change if *S. cryptandrus* is removed from the analyses (Fig. 4d). Year-to-year fluctuations in the grass seeds were also the norm in the SSB (Table 1). Drought combined with grazing (e.g. 2011, 2018, 2019) resulted in a SSB with < 50 seeds m^{-2} for several palatable grasses (e.g. *Pappophorum* spp., *D. californica*, *T. crinita*), a low number since O'Connor and Pickett (1992) suggested that palatable grasses in African savanna grasslands with SSB size of < 100 seeds m^{-2} might become locally extinct. The SSB of the grazed habitats suffered the irruption of *S. barbatus*, an annual exotic grass that had already shown its high invasive ability in the Monte desert (Pucheta et al. 2011), and an increase in the mean proportion of less palatable grasses (73% against 52% in the cattle-free areas, $n = 10$ year and 17 year, respectively, Table 1). The invasion of opportunistic annual species or the replacement of palatable by less palatable grasses in the SSB have also been found in other grazed semiarid grasslands (O'Connor and Pickett 1992; Bertiller and Aloia 1997; Distel 2016; Tessema et al. 2016).

In grazed habitats, the positive association between rainfall and total grass SSB (Fig. 3c) seems to be good

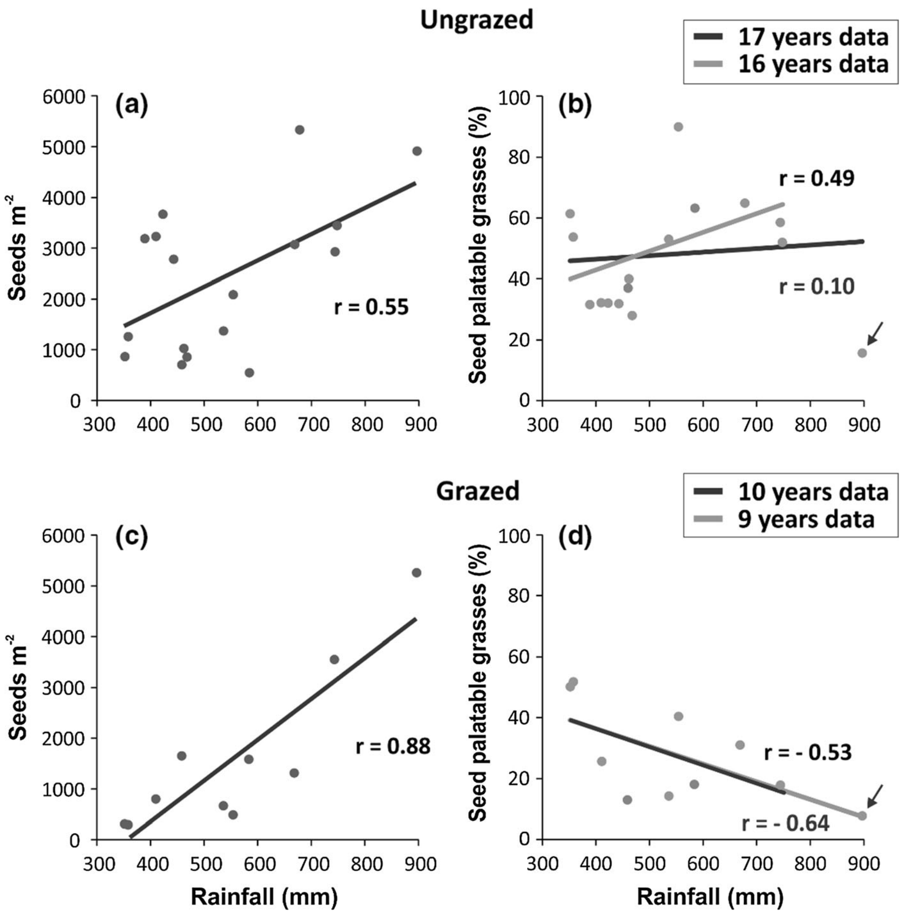

Fig. 3 Correlation between the precipitation accumulated during the two previous growing seasons (October–March) and the mean number of total grass seeds in the soil seed bank (**a**, $n = 17$ year), and the mean percentage of palatable grass seeds in the soil seed bank (**b**, $n = 17$ year) in cattle-free habitats of the Reserve of Ñacuñán, and between the same variables measured in grazed habitats near the reserve (**c** and **d**, $n = 10$ year). In figures b and d, the correlations for 17 year and 10 year data and for 16 year and 9 year data are shown. In the latter cases, the extremely rainy 2016–2017 period, indicated with arrows, was removed from the analysis (see Results)

news for a likely effect of the SSB on plant community resilience. Westoby et al. (1989) suggested that the environmental circumstances (e.g. rainfall windows) that lead to rangeland recovery (e.g. from rangelands with low palatable perennial grass density to a state with higher density of these plants) provide not only spontaneous opportunities but also management opportunities for community recovery (i.e. opportunistic management). However, the effectiveness of rainfall windows as spontaneous opportunities for grass recovery in the central Monte is not clear. Our study showed at least two reasons for the disruptive effect of grazing despite favourable climatic conditions. First, years with low and moderate precipitation (350–600 mm accumulated over two years) in the undisturbed sites were related to low, as well as high, grass SSB size (Fig. 3a), whereas in the grazed habitats low and moderate rains were always associated with low SSB size (< 2000 seeds m^{-2}; Fig. 3c). The implication is that the replenishment of the grass SSB in grazed habitats would depend on extraordinarily heavy rains. Second, whereas the proportion of palatable grasses in the SSB of the ungrazed habitat rarely changed with the rainfall level (Fig. 3b), that proportion diminished as the precipitation increased in the grazed habitats (Fig. 3d). This phenomenon was affected by the very rainy 2016–2017 period but it did not depend exclusively on it as the proportion of seeds of palatable grasses was scarce in other rainy years (Figs. 2, 3d). The main implication is that rainfall

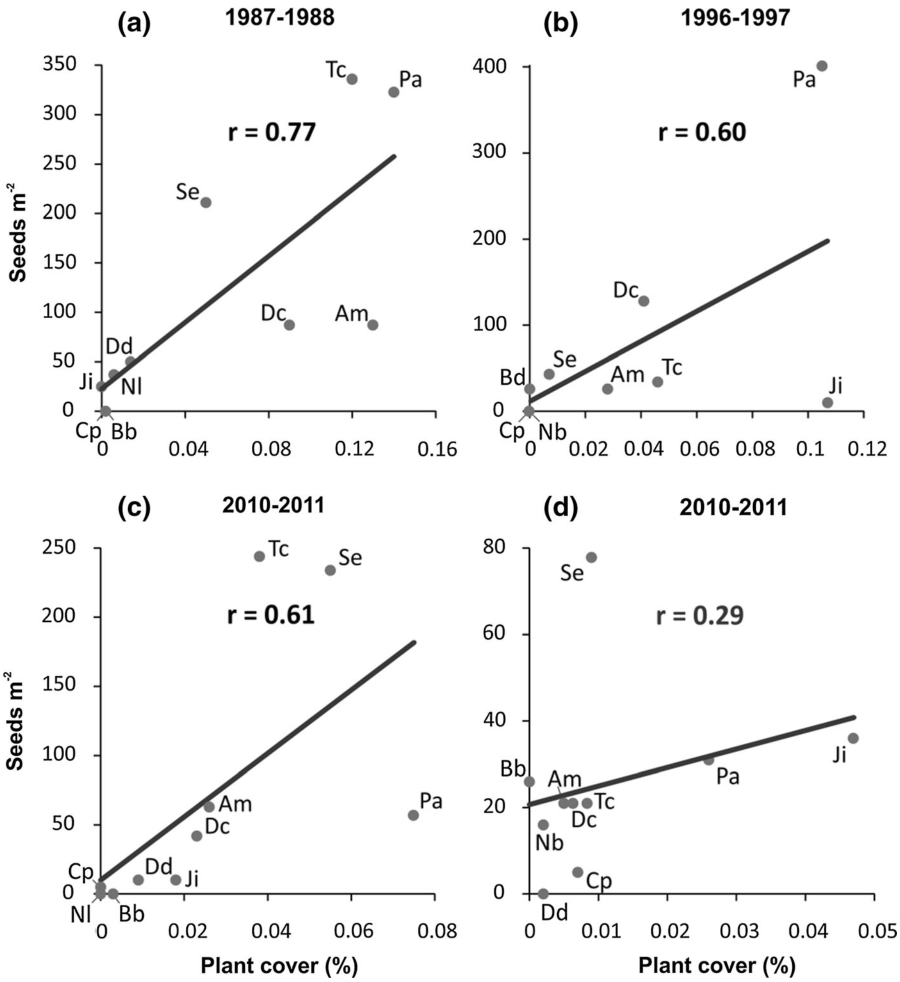

Fig. 4 Correlation between the mean size of the soil seed bank and the aboveground cover of 10 abundant grass species (Pa, *Pappophorum* spp.; Dc, *Digitaria californica*; Tc, *Trichloris crinita*; Se, *Setaria leucopila*; Dd, *Diplachne dubia;* Cp, *Cottea pappophoroides*; Am, *Aristida mendocina*; Ji, *Jarava ichu*; Nl, *Neobouteloua lophostachya*; Bb, *Bouteloua barbata*) in cattle-free habitats of the Biosphere Reserve of Ñacuñán in three periods: 1987–1988 (**a**), 1996–1997 (**b**), 2010–2011 (**c**), and in one period in grazed habitats (2010–2011, **d**). Note that the scales on both axes differ in each case. The species *Sporobolus cryptandrus* was not included in these analyses (see Discussion)

increases the proportion of less palatable and opportunistic grass species in the SSB under continuous grazing, hampering the long-term recovery of the palatable grasses. Even when empirical or physiological models are used to give foundation to opportunistic management by predicting the occurrence of favourable climatic conditions that drive field emergence events of grasses (Westoby et al. 1989; Bisigato and Bertiller 2004; Rotundo et al. 2015), the success of such a practice could be limited by the disruptive effects of grazing history promoting the replacement of the palatable by less palatable grass species in the SSB of disturbed habitats of the Monte desert (Bertiller et al. 2009).

In cattle-free habitats, rainfall is a bottom-up force capable of increasing the size of the grass SSB, maintaining (or increasing) the proportion of palatable grasses in most years. Grass seed production would occur even under low rainfall (Pol et al. 2010) since SSB size responds in a continuous and positive fashion to precipitation. Consequently, in most years the rainfall could buffer the seed decline caused by natural herbivores, seed-eating animals or pathogens. By contrast, in the grazed areas, rainfall increases the size of the total grass SSB, but reduces the proportion of seeds of palatable grasses. The SSB incorporates a high proportion of seeds from less palatable shorter-lived annual as well as perennial grasses. Rainfall cannot buffer the effect of grazing. Further, the composition of grass SSB was similar to the composition of extant grasses in the cattle-free areas but not in the grazed areas, which would promote community resilience only in the former. Finally, we tested whether a potential bank of plants of perennial grasses recovered quickly enough after a severe drought to produce seeds during the following growing season. If the plants recovered, they could act as a buffer for SSB size and composition after extremely dry periods. However, we found no grasses reproducing or setting seed during the entire growing season evaluated, which also was a dry season. This fact limited our universe of inference, but it suggests that the replenishment of the SSB from a potential bank of plants could only occur during moderately dry or mesic growing seasons following drought periods.

If the SSB has a role in the recovery of palatable grass plants in grazed areas of the central Monte, continuous grazing seems to be reducing rangeland resilience by depleting the SSB of palatable grass species even during rainy periods. There is also evidence of a negative effect of grazing on the behaviour (Marone et al. 2017; Pol et al. 2017) as well as on the abundance of seed-eating animals (Pol et al. 2017; Sagario et al. 2020) due to an abrupt reduction in their preferred seeds. In a context of an increased frequency of extreme climatic events (e.g. heavy rains and droughts) grazing management should be urged to include long periods of rest from cattle grazing on a rotational basis, lightening the effect of overgrazing, a key component of global change.

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Data availability Not applicable because all raw data are included in Table 1.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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