Grass seed production in the central Monte desert during successive wet and dry years

Rodrigo G. Pol · Gabriela I. Pirk · Luis Marone

Abstract In desert regions, water availability triggers primary production, which determines seed production, the composition and size of soil seed reserves and the abundance and behaviour of seed-eating animals. In the central Monte desert, large precipitation events (≥ 10 mm) account for a high proportion of growing season's rainfall. Our first objective here was to assess whether and how timing and amount of seed production of C_3 and C_4 perennial grasses are linked to spring and summer precipitation pulses and to estimate the seasonal and year-to-year variability in seed production. Our second aim was to calculate grass seed production and compare it with seed requirements by granivorous animals to infer whether the animals can exert top-down effects on plant populations. Seed production of C_3 and C_4 species was triggered by significant spring and summer rainfall, respectively. Such distinct response may be associated with the effect of precipitation during flower development and seed set in both functional groups. In all species, seed production varied among years. Rainfall pulses in the summer triggered and positively affected the magnitude of seed production in most C_4 grasses. However, all perennial grasses were able to produce high amount of seeds even during a year subjected to extreme drought, suggesting that perenniality would allow these species to make large reproductive investment despite harsh environmental conditions. The comparative assessment of seed production and consumer demands suggests that it is unlikely that granivory exerts a top—down control on grasses in the Monte desert.

Keywords Drought · Granivory · Masting · Perennial grasses · Rainfall pulses · Seed production

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Introduction

Water availability governs primary production in deserts (Noy-Meir 1973), affecting seed production processes (Kemp 1989; Ernest et al. 2000) and, at least partially, the composition and size of soil seed

reserves (Marone et al. 2000). By cascading key mechanisms related to plant growth, the size and amount of rainfall pulses may affect both the timing and the amount of seed production and, consequently, the population dynamics of plants and seed-eating animals (Chambers and MacMahon 1994).

When water enters a dry soil, it triggers a cascade of biogeochemical transformations that eventually elevate rates of carbon assimilation by plants, which can be translated into growth (Schwinning and Sala 2004). Not all episodes of water input, however, increase carbon gain rates and trigger new growth. Plants from different functional groups (Jackson et al. 1996; Golluscio et al. 1998; Schenk and Jackson 2002) or species (Sala and Lauenroth 1982) are functionally prepared to use different water sources and to react to particular precipitation thresholds. For example, shallow-rooted grasses seem to be structurally better adapted to take advantage of small pulses than desert shrubs (Schwinning et al. 2003), although it is not clear whether such pulses are big enough to induce grass flowering and seed production. Schwinning and Sala (2004) put forward a hierarchical-response model of desert plants to rainfall in which small pulses trigger only minor biological events (e.g. increase of leaf water potential and conductance, carbon fixation or new vegetative growth), whereas larger pulses trigger a more inclusive set of larger biological events (e.g. flowering and seed production). Pulses as little as 5 mm size affected leaf water potential and leaf conductance in *Bouteloua gracilis* (C_4) (Sala and Lauenroth 1982), but pulses of 2–6 mm had no significant effect on the water status or photosynthetic rate of *Hillaria jamesii* (C_4) and *Oryzopsis hymenoides* (C_3) (Schwinning et al. 2003). Using information from Beatley (1974) and Bowers (1996), Schwinning and Sala (2004) showed that rainfall pulses up to 25 mm may be needed in some cases to trigger major biological events like germination, flower and seed production in grasses.

Perennial grasses are the most widespread species of herbs (McNaughton 1991). In undisturbed habitats of the central Monte Desert, Argentina, they usually cover 25–50% of the soil. Most of these grasses are perennial C_4 Poaceae species, except for *Stipa ichu* (C_3) (Marone et al. 2000). Given sufficient water, theoretical expectations suggest that C_3 species should be more active and productive in cool spring and fall periods, whereas C_4 species should be more productive in midsummer (Ode et al. 1980; Seligman

et al. 1992; Tieszen et al. 1997; Gardener et al. 2003). The test of such expectations in the central Monte desert would allow to increase the knowledge of temporal and spatial patterns of seed production, a key input to research programs dealing with grassland dynamics (Aguiar and Sala 1994) as well as granivory interactions (Marone et al. 2000).

Our first aim was to estimate seed production of seven abundant perennial grass species (six C_4 and one C_3) during three growing seasons subjected to different amount of rainfall to verify whether and how timing and amount of water input trigger seed production. We specifically test the hypotheses that (i) precipitation during flower development and seed set is a major factor governing grass seed production (if this is true, precipitation in spring and summer will be positively associated to seed production of C_3 and C_4 species, respectively) and (ii) year-to-year variability in seed production is positively related to differences in summer rainfall (in particular, to differences in the number of big pulses) in C_4 species, and positively related to differences in spring rainfall in C_3 species.

Seed reserves in different habitats depend on both total seed production and the fate of seeds after primary dispersal. In arid regions, seed consumption usually constitutes an important environmental sieve, and some authors have suggested that animal predation may limit seed numbers and plant recruitment (Chambers and MacMahon 1994). The estimates of seed production referred in the previous paragraph widely correspond to the same plant species consumed by seed-eating animals in the central Monte desert (Marone et al. 2008, Pirk and Lopez de Casenave 2006). Further, Lopez de Casenave (2001), Marone et al. (2008) and Pirk and Lopez de Casenave (2006) calculated seed consumption by ants, birds and rodents for the same area. Our second aim was to combine both kind of information to infer whether granivory can exert some kind of top-down control on grass seeds and—ultimately—grass populations in years subjected to different rainfall regimes.

Materials and methods

Study area

We carried out our studies in the most widespread habitat of the Biosphere Reserve of Ñacuñán

(34°03′S, 67°55′W), the open woodland of *Prosopis flexuosa* and *Geoffroea decorticans*. This habitat consists of individuals of these tree species scattered within a dense matrix of tall shrubs (>1 m height), mostly *Larrea divaricata*, *Atriplex lampa*, *Capparis atamisquea* and *Condalia microphylla*, and low shrubs (<1 m height) including the genera *Lycium*, *Junellia* and *Acantholippia*. There is also an important grass layer where C_4 perennial species predominate (e.g. *Pappophorum* spp., *Digitaria californica*, *Sporobolus cryptandrus*, *Aristida mendocina*, *Trichloris crinita*, *Setaria leucopila*). Most forbs (e.g. *Chenopodium papulosum*, *Phacelia artemisioides*, *Glandularia mendocina*, *Parthenium hysterophorus*) are annual, and their cover is usually lower than grass cover, but highly variable from year to year (Marone 1991). The seeds of C_4 grasses form mostly transient soil seed banks owed to post-dispersal losses in autumn and winter (Marone et al. 1998b; Marone et al. 2004).

The climate in the reserve is dry and temperate with cold winters. Mean annual precipitation is 342 mm (1972–2004, $n = 33$). More than 75% of annual rainfall occurs during warmer months (262 mm, range: 104–453 mm, $n = 33$), which coincides with the growing season (October–March). On average, there are 41 small pulses ≤5 mm per year in Ñacuñán, which account for only 18% (55 mm) of annual precipitation. In contrast, an average of 11 big pulses ≥10 mm accounts for 66% (225 mm) of annual precipitation. The amount of water received in pulses ≥10 mm is positively correlated with annual precipitation ($r = 0.96$, $P < 0.01$, $n = 33$), but water received in pulses ≤5 mm is not ($r = 0.42$, $P = 0.07$, $n = 33$; Fig. 1a). These data indicate that year-to-year differences in total rainfall are widely associated to the amount of water received in big pulses in Ñacuñán, as has also been shown in other studies in arid and semiarid areas (Sala and Lauenroth 1982; Golluscio et al. 1998).
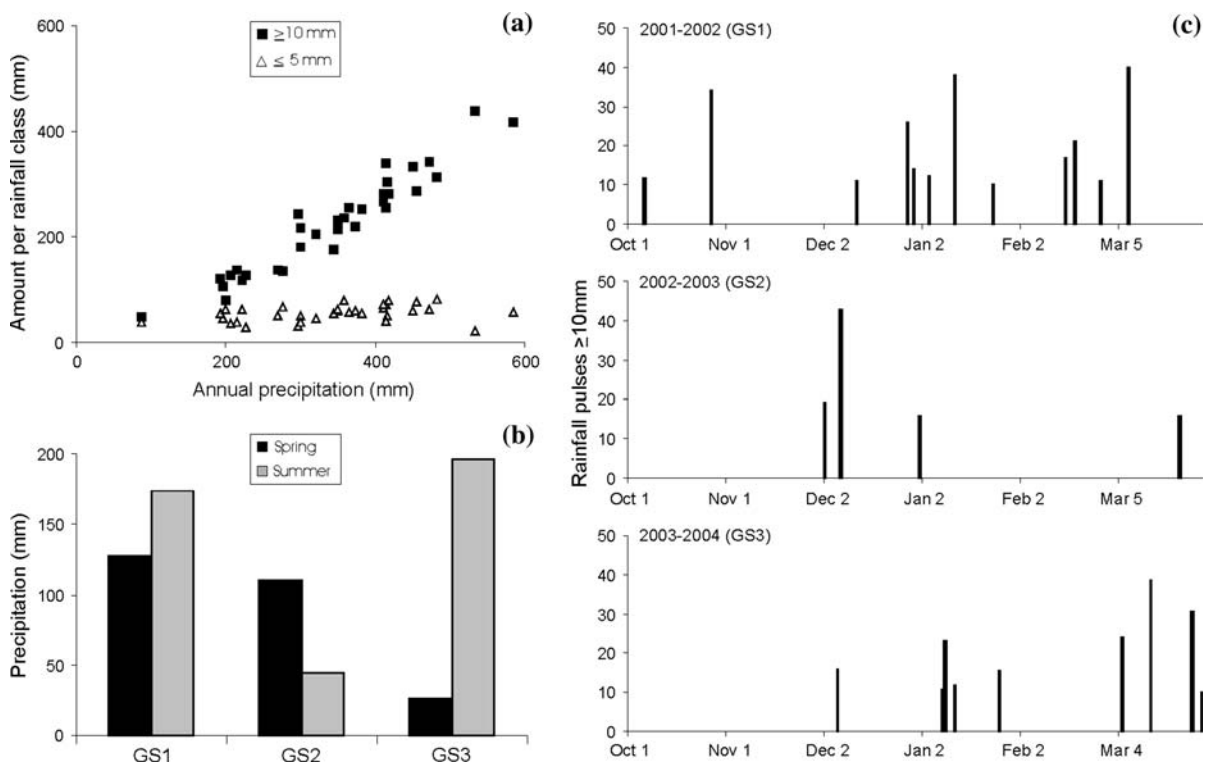

Fig. 1 Precipitation regime in the open woodland of the Biosphere Reserve of Ñacuñán, central Monte Desert, Argentina. **a** Amount of water received in small (≤5 mm) and large events (≥10 mm) as a function of annual precipitation recorded during 33 years. **b** Spring (October–December) and summer (January–March) precipitation during the growing seasons studied here: 2001–2002 (GS1), 2002–2003 (GS2) and 2003–2004 (GS3). **c** Magnitude and dates of rainfall events ≥10 mm throughout GS1, GS2 and GS3

Total precipitation at the Biosphere Reserve of Ñacuñán during the growing seasons (October through March) included in this study was 302 (GS1: 2001–2002), 154 (GS2: 2002–2003) and 222 mm (GS3: 2003–2004) (Fig. 1b). Spring (October through December) and summer (January through March) rainfall were highly variable during the study period. GS1 and GS2 springs were both relatively wet, but GS3 spring was extremely dry (the second driest record in 33 years, Fig. 1b). GS1 as well as GS3 summers were relatively wet, whereas GS2 summer was very dry (the driest record in 33 years, Fig. 1b). Mean temperature was very similar between those growing season: 21.5 ± 0.22 (SE) in GS1, 23.1 ± 0.18 in GS2 and 23.8 ± 0.16 in GS3.

Grass seed production per plant

Average seed production of the C_3 grass *S. ichu* and of six C_4 species (*A. mendocina*, *T. crinita*, *S. leucopila*, *D. californica*, *S. cryptandrus* and *Pappophorum* spp.) was estimated for the three growing seasons. On every season, we harvested all spikes from 10 adult individuals (i.e. individuals producing new seeds or that had previously produced seeds) of each species on four sampling occasions (spring: October and December; summer: February and April). For this purpose, 10 parallel transects (70 m long and 40 m apart) were set in an area of about 3 ha in the open woodland. Sampling stations were established 10 m apart on every transect, and all spikes from the closest adult individual belonging to a randomly determined species were collected, avoiding already harvested plants. Spikes and seeds of each plant were stored in paper bags. In the laboratory, fully formed seeds of each individual were removed from spikes and counted under a stereoscopic microscope. Only newly produced seeds, which did not crumble when probed with forceps (Mull and MacMahon 1996) and lacked signs of fungal attack or other kind of damage, were considered for analyses. These seeds, which were less than 1 year old, were easily recognized because they are yellowish (Aguiar and Sala 1994) and transparent, whereas the older ones are brownish and opaque.

In order to test the crucial assumption of our analysis that samplings performed two months apart were mostly independent, we sampled seed production also in January 2003 and 2004. Consecutive samplings in January and February each year would allow us to estimate the magnitude of grass seed dispersal (i.e. the percentage of seeds lost between both sampling occasions) within a month. If seed dispersal was high, we considered that the assumption was mostly met.

In order to compare spring versus summer seed production, we calculated the mean number of seeds per individual of every grass species for spring and summer months: October and December samples were pooled to obtain an estimation of spring seed production, whereas February and April samples were pooled to estimate summer seed production ($n = 20$ in both cases). Mann–Whitney tests were used to appraise differences between seasons (Zar 1996). Two-tailed Kruskal–Wallis tests, and a posteriori non-parametric multiple trials (Dunn's tests), were employed for assessing year-to-year comparisons of seed production in C_4 and C_3 species (Zar 1996).

Grass seed production and consumption by granivores

In order to assess the overall meaning of grass seed production to granivorous animals, we also estimated seed production per area. For that purpose, we surveyed grass species density in the open woodland in December 2003. Individuals of the seven grass species were counted in 400 1 × 1 m quadrats located every 10 m on 40 100-m long transects laid 10 m apart. When several individuals occurred very close to each other, soil surface was dug around them to establish if they were sharing the same root system (i.e. if they were the same individual). We only considered adult plants, those that were already producing seeds, or had at least one new spike, or were not producing seeds yet but showed signs of having produced them during the previous season, like the presence of old spikes (*D. californica*, *S. leucopila*, *A. mendocina*, *Pappophorum* spp., *T. crinita* and *S. cryptandrus*). Adult *S. ichu* individuals were those that we consider were big enough to produce seeds (i.e. plants whose base exceeded 5 cm diameter).

Adult individuals of each species per area were multiplied by mean number of seeds per plant to obtain the amount of seeds produced. Here we assumed that overall plant density varied very little throughout our study (3 years), given that all species are perennial grasses.

We compared the amount of seeds produced with consumer demands, which have been assessed previously by using three different approaches: (a) according to seed removal information on bait experiments (Lopez de Casenave et al. 1998) and bioenergetic models (Nagy 1987), Lopez de Casenave (2001) estimated maximal seed consumption during autumn and winter for ants, birds and rodents in Ñacuñán. (b) Marone et al. (2008) used enclosure field experiments to assess seed consumption by autumn–winter granivores in two different years. (c) Summer seed consumption by the harvester ants *Pogonomyrmex rastratus* was estimated from information on diet composition, colony-foraging activity and colony density (Pirk et al. 2004; Pirk and Lopez de Casenave

2006). We weighed every estimator of seed consumption per unit area against our calculations of grass seed production to assess the general idea that granivory may limit grass recruitment.

Results

Timing of seed production differed clearly between C_4 and C_3 species. In the former, it was widely restricted to summer months (Fig. 2), whereas in *S. ichu* seed production began earlier in the growing season. However, it was not restricted to spring months but continued during the summer (Fig. 2). As a consequence, our year-to-year comparisons of seed

Fig. 2 Seed production (mean + SE) of seven grass species in the central Monte desert in spring and summer of growing seasons 2001–2002 (GS1), 2002–2003 (GS2) and 2003–2004 (GS3). Seed production is measured as the mean number of seeds per plant ($n = 20$) of each grass species during spring (October–December) and summer (January–April). *Asterisks* indicate significant differences between spring and summer seed production within each growing season (* $P < 0.05$; *ns* not significant; Mann–Whitney tests)
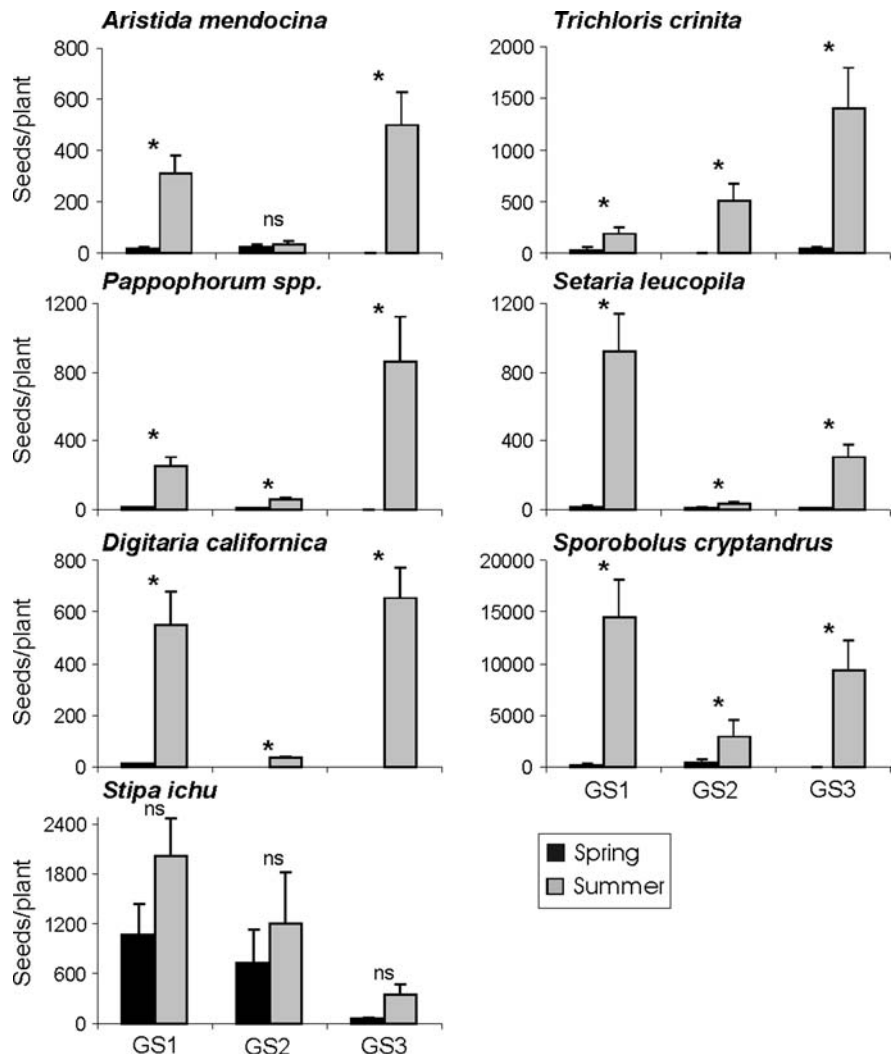
production in C_4 species were based only on summer month samplings (February and April), whereas differences in *S. ichu* were calculated for every sampling occasion during the whole growing season (October, December, February and April).

Seed production of C_4 species varied greatly among years and was usually lower during the driest GS2 summer (in February as well as in April; Fig. 3). This was very clear for *S. leucopila*, *D. californica* and *A. mendocina*, and to a lesser extent for *Pappophorum* spp. and *S. cryptandrus*. Only *T. crinita* did not follow the general pattern (Fig. 3). Seed production of *S. leucopila*, *D. californica*, *A. mendocina*, *S. cryptandrus* (April data only) and *Pappophorum* spp. was, on average, more than an order of magnitude higher in GS1 (range 3.4–39.7) and GS3 (range 4.5–29) than in GS2. In contrast, the pattern of year-to-year variation in seed production of *S. ichu* was more difficult to establish given certain variability within every growing season (Fig. 4). However, the GS3 spring—subjected to severe drought—was followed by low seed production of this species despite heavy summer rains (Fig. 4).

Based on grass species density (Table 1) and number of seeds per plant (Fig. 2), we estimated seed production per unit area for C_4 species (Table 2). Total seeds produced in February and April constitute a conservative estimator of annual seed production, given that some seeds could be produced in January and March too. A range of $16–55 \times 10^6$ (or 3–10 kg) C_4-grass seeds per ha was our estimation for the 3-year study period.

Three important rainfall pulses interrupted a drought at the end of the spring 2002 (Fig. 1c). Such pulses were followed by major seed production in most grass species by January 2003, about 3–6 weeks after rainfall (Table 3). On the contrary, after the dry spring of 2003 (with just an isolated pulse of 16 mm on December 6; Fig. 1c) grasses did not produce seeds by January (Table 3). Only after heavy rains in January 2004 (Fig. 1c), the majority of C_4 grasses produced abundant seeds by February (Fig. 3). Seed dispersal between January and February was high and occurred quickly in several species in 2003. Conversely, we could not assess seed dispersal in the summer of 2004 owing to the low seed production observed in January, following a very dry spring (Table 3). The number of seeds on plant stalks in February 2003 allowed us to conclude that

S. leucopila (92%), *Pappophorum* spp. (84%), *D. californica* (77%), *S. ichu* (77%) and *A. mendocina* (65%) had all dispersed most of the seeds produced in January 2003 (Table 3; Figs. 3, 4). Only *T. crinita* dispersed a low amount of seeds (26%). *S. cryptandrus* dispersal could not be assessed because this species had not produced seeds neither by January 2003 or 2004 (Table 3). This information suggests that our sampling assumption of independence was mostly correct.

It is important to note that if seed production of C_4 grasses in GS2 (Table 2) had been calculated by using January (Table 3) instead of February data, total numbers would have risen to $20–25 \times 10^6$ seeds per ha. Such value is still lower than those in GS1 and GS2 (Table 2), but it shows that C_4 perennial grasses can produce a high number of seeds even during summers subjected to extreme dry conditions given significant rainfall pulses in due time, especially during flower development and seed set.

Lopez de Casenave (2001) estimated that 1.5 kg of seed per ha is required by all seed-eating animals during autumn–winter in the Monte desert. Marone et al. (2008) reported that seed predation by autumn–winter granivores could reduce grass seed reserves by 50–60%. Finally, seed removal by the harvester ant *P. rastratus* during spring–summer is about 8.3×10^5 grass seeds per ha (Pirk and Lopez de Casenave 2006), and the other two sympatric congeners, *P. inermis* and *P. pronotalis*, could likely achieve similar seed removal as their diet, level of activity and colony density are similar to those of *P. rastratus* (Pol and Lopez de Casenave 2004; Pirk et al. 2004; Pirk and Lopez de Casenave 2006). In perspective, seed consumption demands by granivorous animals, calculated through any of the three approaches, were all substantially lower than seed production estimates.

Discussion

The way water is incorporated in relation to temperature shapes the reproductive developmental patterns of desert plants (Reynolds et al. 2000; Huenneke et al. 2002; Schwinning et al. 2002). Our results suggest that there are marked differences between C_3 and C_4 grass species in the timing of seed production and seed setting in the central Monte desert. Reproductive growth in *S. ichu* started in the cooler spring

Fig. 3 Seed production (mean + SE) of C_4 grass species in the central Monte desert during growing seasons 2001–2002 (GS1), 2002–2003 (GS2) and 2003–2004 (GS3). Seed production is measured as the mean number of seeds per plant ($n = 10$) for the summer months February and April. *Different letters* indicate significant differences between growing seasons' seed production (Kruskal–Wallis tests and a posteriori Dunn's tests)
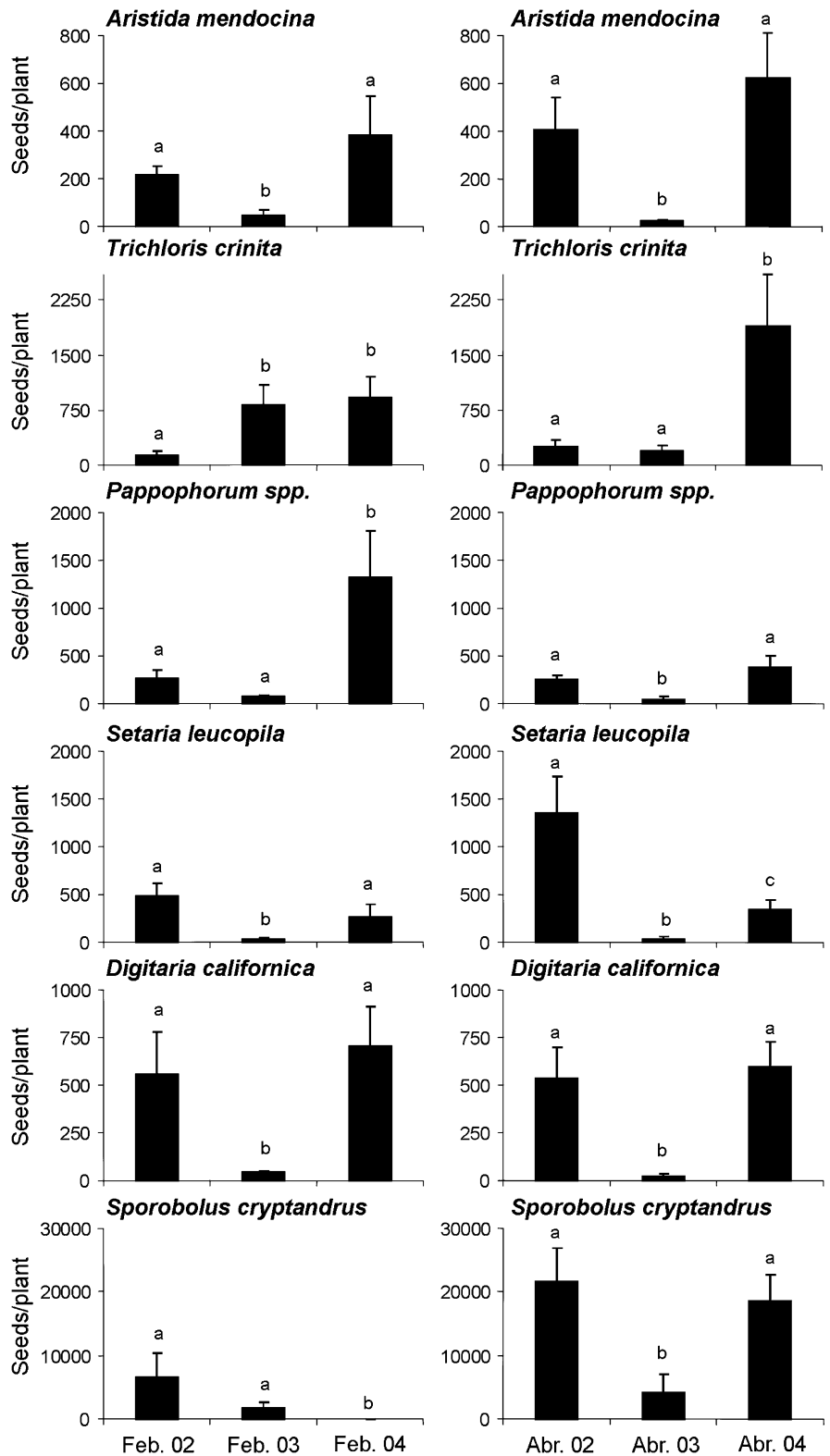
Fig. 4 Seed production (mean + SE) of the C_3 grass *Stipa ichu* in the central Monte desert during growing seasons 2001–2002 (GS1), 2002–2003 (GS2) and 2003–2004 (GS3). Seed production is measured as the mean number of seeds per plant ($n = 10$) for October, December, February and April. *Different letters* indicate significant differences between growing seasons' seed production (Kruskal–Wallis tests and a posteriori Dunn's tests)
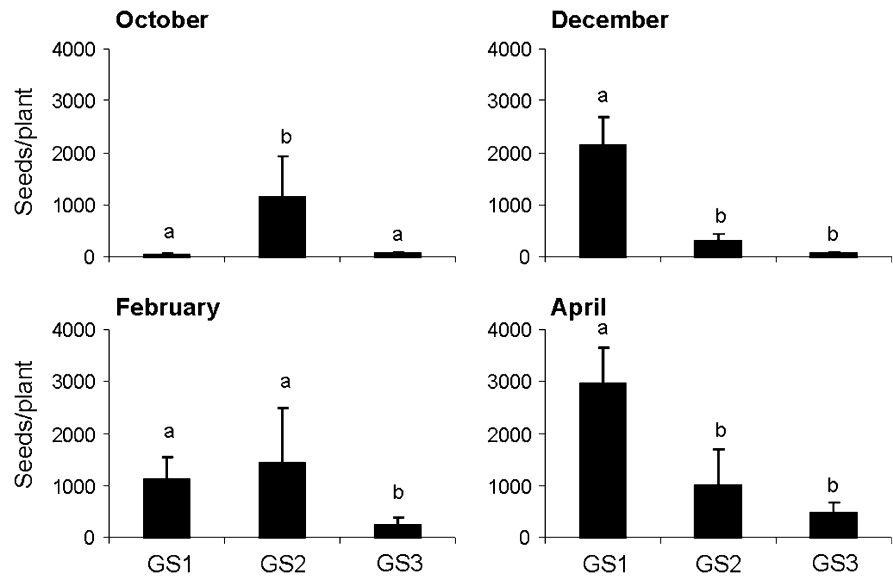

Table 1 Density of adult plants of grass species in the open woodland of the Biosphere Reserve of Ñacuñán, central Monte Desert, Argentina

	Adult plants density
Aristida mendocina	3800 (509)
Trichloris crinita	10950 (1067)
Pappophorum spp.	3075 (392)
Setaria leucopila	2125 (351)
Digitaria californica	1600 (253)
Sporobolus cryptandrus	675 (157)
Stipa ichu	2380 (361)

Values are expressed as the average plant abundance per hectare (SE)

period and seed production occurred earlier in the growing season than in C_4 grasses. The latter species began to produce significant amount of seeds almost simultaneously in the summer and reached maximum seed load per plant at the end of that

season. Synchronization of flowering and seed production of C_4 grass species under favourable temperature conditions may be a consequence of a coincident response of those species to biologically significant precipitation (e.g. Beatley 1974; Turner and Randall 1987; Ghazanfar 1997; Gardener 2003; Schwinning et al. 2003). We found that an isolated rainfall pulse of 16 mm in December 2003 was insufficient to trigger seed production in January 2004, but that a combination of several pulses—one of them surpassing 40 mm—in December 2002 triggered seed production by January 2003 (Figs. 1c, 3, 4; Table 3). This evidence appears to be mostly in accordance with inferences of Schwinning and Sala (2004) that major biological events like germination, flower and seed production in grasses need significant water inputs, at least in warm deserts. On average, 60% of pulses >20 mm occurs in the summer in Ñacuñán (R. Pol unpublished), and C_4 perennial grasses—that are better adapted to take advantage of

Table 2 Seed production per hectare of C_4 grasses during growing seasons 2001–2002 (GS1), 2002–2003 (GS2) and 2003–2004 (GS3)

Values are expressed as seeds produced from adult plants per hectare

	GS1	GS2	GS3
Aristida mendocina	2.37×10^6	2.61×10^4	3.82×10^6
Trichloris crinita	4.13×10^6	11.26×10^6	30.77×10^6
Pappophorum spp.	1.55×10^6	36.35×10^4	5.25×10^6
Setaria leucopila	3.90×10^6	14.41×10^4	1.29×10^6
Digitaria californica	1.76×10^6	10.80×10^4	2.09×10^6
Sporobolus cryptandrus	19.06×10^6	4.00×10^6	12.53×10^6
Total	32.78×10^6	16.14×10^6	55.75×10^6

Table 3 Grass seed production during January of growing seasons 2002–2003 (GS2) and 2003–2004 (GS3)

	January 2003	January 2004
Aristida mendocina	133 (52)	0
Trichloris crinita	1113 (252)	6 (5)
Pappophorum spp.	476 (104)	0
Setaria leucopila	398 (165)	0
Digitaria californica	186 (27)	0
Sporobolus cryptandrus	0	0
Total C_4	2306	6
Stipa ichu	6301 (2108)	73 (53)
Total	8607	79

Values are expressed as the mean number of seeds per plant ($n = 10$) of each grass species (SE)

such summer water input—appear to have been favoured becoming dominant in the herbaceous stratum in the central Monte (Marone et al. 2000).

The level of spring rainfall affected seed production of *S. ichu*—but not of C_4 grasses. Wet conditions during the springs of GS1 and GS2 induced one or two peaks of high seed production, whereas the dry spring of GS3 was related to low seed set. Although *S. ichu*'s seed production continued in the summer, there was no clear association between summer rainfall and seed production (it was, for example, high during the extremely dry GS2 summer and low in the wet GS3 summer; Figs. 1b, 4). C_4 grasses set seeds always in summer, although the specific date varied notably among years. First seeds of *A. mendocina*, *T. crinita*, *S. leucopila*, *D. californica* and *Pappophorum* spp. were produced all in late December in GS1, in January in GS2 and in February in GS3. Year-to-year differences were always associated with the first significant precipitation events (Figs. 1c, 3; Table 3). In contrast, *S. cryptandrus* never responded to the synchronized pattern and as has been previously reported (Marone et al. 1998a), started to set seeds later every summer.

Total amount of seeds produced by C_4 grasses every year responded partially to differences in total summer rainfall, with maximum production in GS3 (196 mm), minimum in GS2 (44 mm) and intermediate-high in GS1 (174 mm). The general tendency was followed by five out of the six species assessed, with *T. crinita* as the exception since it produced more seeds in the dry GS2 than in the wet GS1. There are many cases in which plants may not clearly

respond to rainfall in arid zones, and the causes are multiple (Yahdjian and Sala 2006; Fernandez 2007). For *T. crinita*, Greco and Cavagnaro (2002) showed that the biomass of reproductive structures as panicles, culms and sheaths of plants harvested in Pichi Ciego, located 20 km away from Ñacuñán, remained similar under drought—applied experimentally during flowering and seed maturation stages—and control conditions. These authors found that biomass partitioning towards roots was low under control as well as under experimental conditions due to strong sinks in the reproductive organs, a mechanism that could account for the high number of seeds produced by *T. crinita* even in the very dry GS2. Such mechanism does not explain, however, why this grass species produced a lower number of seeds in the wet GS1.

Some characteristics of seed production by C_4 grasses, like the high degree of variation among years and synchronization of seed setting in most of them, may be viewed as typical elements of masting (Kelly 1994). This reproductive strategy is usually associated with plants whose seeds are highly consumed by animals since it allegedly confers selective advantages to avoid the effect of post-dispersal seed predation on the probability of seed germination and seedling recruitment (Ims 1990). If the masting hypothesis were correct, grass seeds should be an attractive food resource for granivorous animals in the central Monte desert and, as has been mentioned above, current evidence appears to corroborate this assertion. The most abundant sparrow species in the central Monte select, consume and prefer seeds of the C_4 grasses studied here (Lopez de Casenave 2001; Cueto et al. 2001, 2006; Marone et al. 2008). Further, 90% of the seeds harvested by ants in the genus *Pogonomyrmex* are from *Aristida*, *Trichloris*, *Pappophorum* and *Digitaria* (Pirk et al. 2004; Pirk and Lopez de Casenave 2006; Pirk et al. 2009).

Regarding the question about whether seed consumption can exert a top-down control on grass recruitment, the most abundant C_4 grasses were able to produce 16–55×10^6 seeds (or 3–10 kg) per ha per year, whereas the calculations of animal seed consumption were always well below these figures. The comparison entails that even during years of low production thousands of grass seeds would escape animal predation, leaving behind sufficient grass seeds in the general habitat at the beginning of every

growing season every year as to produce—given sufficient rainfall—thousands of new plants in the central Monte desert. This supports the idea that a top-down effect of granivores on grass populations is unlikely. However, we should note that selective seed consumption and selection of foraging sites were observed in birds (Cueto et al. 2006; Milesi et al. 2008) as well as in ants (Pirk 2007; Pol 2008), suggesting that at least some grass species, in particular microhabitats, may be subjected to a top-down control. Moreover, seed limitation could still be expected very infrequently during multiannual dry cycles in which the number of reproductive plants, not only the production of seeds per plant, may be severely reduced.

In summary, seed production of C_3 and C_4 species was triggered by significant spring and summer rainfall, respectively, probably conditioned—in both cases—by precipitation during flower development and seed set. Further, seed production varied among years, partly associated to the level of significant precipitation, although several perennial grasses were able to produce huge amounts of seeds even in years subjected to intense drought. These features of grass natural history may have important implications for the ecology of arid and semiarid zones.

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