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El Niño effects on soil seed bank dynamics in north-central Chile

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Abstract The soil seed bank was monitored in four 75×75 m plots over 6 years (1990–1995) in an arid thorn scrub community in north-central Chile. Sixty-six species were identified. Total seed densities ranged from 2,000 to 42,000/m^2. Average mass of shrub seeds was significantly greater than that of other growth-forms. Between 70 and 90% of the seeds were less than 1 mg, with those in the 0.51–1.00 mg size class being most numerous. Seed densities were highly variable between years as well as within years, but were also closely associated with plant cover patterns and rainfall regime. Higher seed densities were found in wet years, and in samples taken in early summer and early autumn (i.e., after seed set); the lowest seed densities were in late winter (i.e., after annual plant germination). The annual plant species with the highest cover were also the most abundant in the soil seed bank and exhibited the largest seed density fluctuations. In general, seed densities were 5- to 10-fold higher during the 1991–1992 El Niño/southern oscillation (ENSO) years than non-ENSO years, showing the importance of this phenomenon for seed bank replenishment in the arid region of Chile.

Keywords Annual plants · Chile · Coastal desert · Arid environment · ENSO

Introduction

Recently, much attention has been directed towards the dramatic impact of El Niño/southern oscillation (ENSO) events on community dynamics in terrestrial ecosystems (Ostfeld and Keesing 2000; Holmgren et al. 2001; Jaksic 2001). In western South America, ENSO events are associated with unusually high rainfall (Aceituno and Montecinos 1992), which in turn affects vegetation (Gutiérrez et al. 1993, 1997, 2000). In Parque Nacional Fray Jorge (hereafter Fray Jorge) in north-central Chile, Gutiérrez et al. (1997) showed that shrub species richness and shrub cover remained relatively constant from 1989 to 1994 (~60%), but that herb cover changed dramatically from 1989–1990 (a pre-ENSO period; 15–28%), to 1991–1992 (an ENSO period; 54–80%) and 1993–1994 (a post ENSO period; 26–37%).

Several studies on desert ecosystems have shown that seed reserves in the soil are highly variable over time. Kemp (1989) reported between-year differences of up to 20-fold in soil seed densities for the Sonoran desert. Nelson and Chew (1977) reported a 10-fold annual change in the seed bank under shrubs and a 23-fold change in open areas at a Mojave desert site. Seed rain, granivores, seed senescence and death, and seed germination account for temporal variation of the soil seed bank (Harper 1977; Fenner 1985). Much of the temporal variation in seed banks is associated with the variability of primary production of annual species (Nelson and Chew 1977).

Despite the importance of seeds to the structure and function of desert plant communities, surprisingly little is known about desert seed banks and their relationship to plant population dynamics (Kemp 1989). This lack of information is even more obvious for South American deserts (but see Marone and Horno 1997; Marone et al. 1998, 2000).

Since 1989, we have been studying the role of abiotic and biotic factors in an arid thorn scrub community of north-central Chile using large (0.56 ha) replicated experimental plots. We have analyzed the effect of vertebrate predators on small mammals (Meserve et al. 1996, 1999; Jaksic et al. 1997) and the effects of predators and small mammals on plants (Gutiérrez et al. 1997; Gutiérrez and Meserve 2000). We have monitored cover

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and soil seed densities of shrubs, perennial and annual herbs at regular intervals. This has also allowed us to follow plant responses to abiotic effects such as annual rainfall. Here, we examine the data from control plots for the period 1990–1995 to determine: (1) species composition (and seed sizes) of the soil seed bank; (2) variation in soil seed densities over time; and (3) the relationship between seed densities (after seed set) and both annual precipitation and plant biomass of annuals (measured as plant cover).

Materials and methods

Study site

The study site is located in an interior valley ("Quebrada de Las Vacas", 230 m elevation) in Fray Jorge in north-central Chile (30°38'S, 71°40'W). The climate is arid Mediterranean, with 90% of the 85 mm annual precipitation falling in the winter months (May–September). The mean maximum temperature in the warmest month (January) is 24°C, and the mean minimum temperature in the coolest month (July) is 4°C. Precipitation patterns in the region currently show a periodicity of approximately 3–4 years; a high rainfall year is typically followed by an intervening 2–3 year period of low or average rainfall. High rainfall events along the Pacific coast have been associated with the ENSO phenomenon (Dillon and Rundel 1990), i.e., infrequent but recurrent perturbations of normal marine and meteorological currents of the tropical Pacific basin (Graham and White 1988). When these conditions occur, coastal waters warm up considerably during the winter months, thereby breaking down the thermal inversion and allowing the intrusion of moist Pacific air masses (Rundel et al. 1991). In Fray Jorge, after a normal year in 1989 (89 mm) and a dry one in 1990 (32 mm), ENSO in 1991–1992 resulted in 233 mm and 229 mm rainfall, respectively. The years 1993–1995 were normal to below normal (77, 35, and 54 mm, respectively).

The plant community of the study area is characterized by spiny drought-deciduous and evergreen shrubs 2–3 m in height, with an herbaceous understory. This community has been termed the *Porlieria chilensis-Adesmia bedwellii-Proustia pungens* association (Muñoz and Pisano 1947). A complete account of plant species composition and abundance at the site is provided in Gutiérrez et al. (1993).

Plant and seed sampling

We determined shrub and perennial herbaceous cover in four randomly located 75×75 m plots (0.56 ha) within the valley. In each plot, four permanent parallel lines (75 m long each), located 15 m apart, were sampled every 3 months from 1990 on, using the point intercept technique (Mueller-Dombois and Ellenberg 1974). To measure the cover of annuals and geophytes, the point intercept technique was applied to ten randomly located 1.5-m long segments along the permanent lines every month during the growing season (winter–spring). Twenty soil samples per plot were randomly collected every 4 months (in April, August, and December) beginning in April 1990 using a 35.4-cm^2 collecting tube (3 cm diameter ×5 cm depth). Previous sampling to 6 cm demonstrated that less than 10% of the seeds are found in the 4–6 cm interval (Meserve 1981). April samples contain the seeds present in the soil after seed set but before germination of annuals, August samples contain the seeds remaining after germination of annuals, and December samples contain the seeds 1–2 months after seed set of annuals. Samples were taken to the laboratory, initially separated by mechanical sieving (mesh sizes 0.5–3.35 mm) and the smallest seeds were then extracted by flotation. Seeds were oven-dried and identified to species under a stereoscopic microscope (NIKON SMZ-10) using verified seeds collected from plants in the field. To measure mean seed mass (hereafter seed size), seeds were collected from naturally occurring specimens at Fray Jorge, weighed with a Sartorius balance in lots of 10–100 seeds, and the mean weight seed^{-1} determined by dividing by seed number.

Statistical analyses

Double within-subject repeated measures analysis of variance (rmANOVA, PROC ANOVA, SAS 1988) was used to analyze total soil seed numbers over time. For statistical analyses, all samples taken in a plot were pooled. Within-subject factors were year and month. Soil seed density data was transformed [ln(x+1)] prior to statistical analysis because of the large variances. All *P* values were Huynh-Feldt-adjusted, a procedure that corrects for deviations in the sphericity assumption of the variance co-variance matrix (von Ende 1993). To determine time effects at the species level, rmANOVAs were run on plant species. Because of the large number of rare species in the soil seed bank, only those with seed densities over 100 seeds m^{-2} during any one sampling period were included in the analyses. We applied the sequential Bonferroni adjustment to maintain a table-wide significance level of 0.05 (Rice 1989). Seed sizes for growth-forms were compared by one-way ANOVA. Relationships between soil seed densities and precipitation, and soil seed densities and plant cover were analyzed by linear or quadratic regressions.

Results

Species composition and seed sizes of the soil seed bank

During ENSO years 1991–1992, seeds of annuals made up over 50% of total seeds in the soil, sharing dominance with *Chenopodium petiolare* seeds (a suffruticose shrub), which is by far the most abundant seed species in the soil (Table 1). Seeds of perennial grasses and geophytes had very low numbers in the soil. Sixty-six seed species (15 shrubs, 6 geophytes, 3 perennial grasses, and 42 annuals) were found in the soil samples. Only 19 species had enough seeds to perform statistical analyses (Table 1). Seeds of shrubs (other than *Ch. petiolare*) were poorly represented in the soil seed bank. Perennial grasses were represented mainly by two species: *Nasella pubiflora* and *Stipa plumosa*, and the geophytes by *Leucocoryne purpurea*. Among annual seeds, the more abundant species were *Oxalis micrantha* and *Plantago hispidula* with 4,000–10,000 seeds m^{-2} during the 1991–1992 ENSO years (Table 1).

Average seed sizes of shrubs were significantly higher than the seed sizes of the other growth-forms ($F_{(3,46)}=2.97$; $P=0.0415$; Table 1). Seed sizes of annuals, perennial grasses and geophytes did not differ from each other (Tukey a posteriori test, Table 1). Of the four growth-forms, species showing the most abundant seed production were also the ones with the smallest seed sizes. Over time, between 70 and 90% of the seeds in the soil had sizes lower than 1 mg (Fig. 1), the 0.51–1.00 mg size class being the most numerous. However, the frequency distribution of seed sizes among years differed significantly (Pearson $\chi^2=159.29$, $df=20$, $P<0.0001$). The 2.01–2.5 mg size class changed the most between years, largely in response to *P. hispidula*, the most frequent annual in that

Table 1 Weight and density of the 19 most abundant seed species in the soil at Parque Nacional Fray Jorge, north-central Chile. Density values x ± 1 SE correspond to samples collected in December of each year

Species	Density (seeds m^{-2})						
	Weight (mg)	1990	1991	1992	1993	1994	1995
Shrubs							
Bahia ambrosioides	0.61	0.0	17.7	123.8	0	17.7	53.1
	0.01	0.0	17.7	123.8	0	17.7	53.1
Chenopodium petiolare	0.77	15,402.8	15,526.6	9,514.0	4,491.8	5,110.7	990.3
	0.05	6,848.2	6,295.4	4,328.8	2,303.5	2,470.1	338.0
Total for shrubs	61.82	15,438.2	15,597.4	9,867.7	4,509.4	5,234.5	1,061.1
	30.61	6,267.9	6,274.3	4,446.7	2,304.7	2,570.5	364.1
Perennial grasses							
Nassella pubiflora	0.56	0.0	282.9	141.5	123.8	70.7	17.7
	0.03	0.0	259.9	141.5	123.8	70.7	17.7
Stipa plumosa	2.26	265.3	17.7	353.7	17.7	0.0	0.0
	0.12	242.3	17.7	104.1	17.7	0.0	0.0
Total for perennial grasses	1.41	265.3	300.6	495.2	141.5	70.7	17.7
	0.85	242.3	254.0	225.5	141.5	70.7	17.7
Geophytes							
Leucocoryne purpurea	0.80	194.5	106.1	176.8	70.7	35.4	0.0
	0.01	120.4	84.2	89.0	70.7	35.4	0.0
Total for geophytes	3.62	194.5	141.5	194.5	70.7	53.1	35.4
	1.15	120.4	119.1	78.4	70.7	53.1	20.4
Annuals							
Adesmia tenella	0.93	106.1	229.9	406.7	70.7	0.0	0.0
	0.06	67.7	67.0	196.7	70.7	0.0	0.0
Apium laciniatum	0.47	247.6	176.8	1,308.6	70.7	159.2	17.7
	0.01	130.8	35.4	784.8	50.0	136.6	17.7
Calandrinia sp.	0.19	760.4	1,803.8	672.0	990.3	1,096.4	282.9
	0.01	760.4	1,803.8	625.7	920.0	1,026.1	282.9
Erodium cicutarium	1.12	106.1	53.1	141.5	35.4	53.1	0.0
	0.12	61.3	17.7	64.6	35.4	33.9	0.0
Eryngium coquimbanum		141.5	70.7	70.7	0.0	17.7	35.4
		57.8	70.7	70.7	0.0	17.7	35.4
Helenium aromaticum	0.29	0	229.9	159.2	159.2	88.4	106.1
	0.02	0	166.8	113.2	93.0	88.4	67.7
Malva nicaensis	0.75	159.2	601.3	300.6	53.1	0.0	0.0
	0.05	159.2	601.3	300.6	53.1	0.0	0.0
Moscharia pinnatifida	0.30	123.8	1,644.6	1,237.9	176.8	424.4	35.4
	0.04	60.4	616.9	383.7	106.1	175.7	35.4
Oxalis micrantha	0.09	725.0	9,301.8	4,509.4	1,043.4	1,326.3	866.5
	0.00	415.9	6,592.6	1,722.2	358.8	514.5	120.4
Parietaria debilis		17.7	229.9	1,520.8	35.4	0	0
		17.7	229.9	1,497.4	20.4	0	0
Plantago hispidula	2.17	4,085.0	5,022.3	8,329.2	1,750.7	901.9	654.3
	0.08	1,515.9	1,757.8	3,593.1	1,119.3	258.9	209.0
Schismus arabicus	0.07	0	318.3	265.3	70.7	0	88.4
	0.00	0	295.2	123.8	28.9	0	17.7
Schizanthus litoralis	0.25	424.4	2,794.1	1,733.0	760.4	442.1	194.5
	0.01	214.2	1,397.4	1,054.2	425.8	169.3	133.5
Viola pusilla	0.41	742.7	1,591.6	848.8	229.9	159.2	88.4
	0.03	502.3	663.9	335.5	78.4	113.2	33.9
Total for annuals	4.02	8,081.6	25,323.6	22,335.0	6,136.4	4,916.2	2,528.8
	2.38	2,793.0	9,563.1	7,219.9	1,998.5	1,158.9	344.6
Undetermined		1,715.4	477.5	336.0	0.0	2,917.9	371.4
		1,300.9	171.8	151.1	0.0	2,658.7	53.1
Total seeds		25,695.0	41,840.6	33,228.4	10,858.0	13,192.3	4,014.3
		8,560.6	8,299.3	5,027.5	3,210.1	4,151.9	302.0

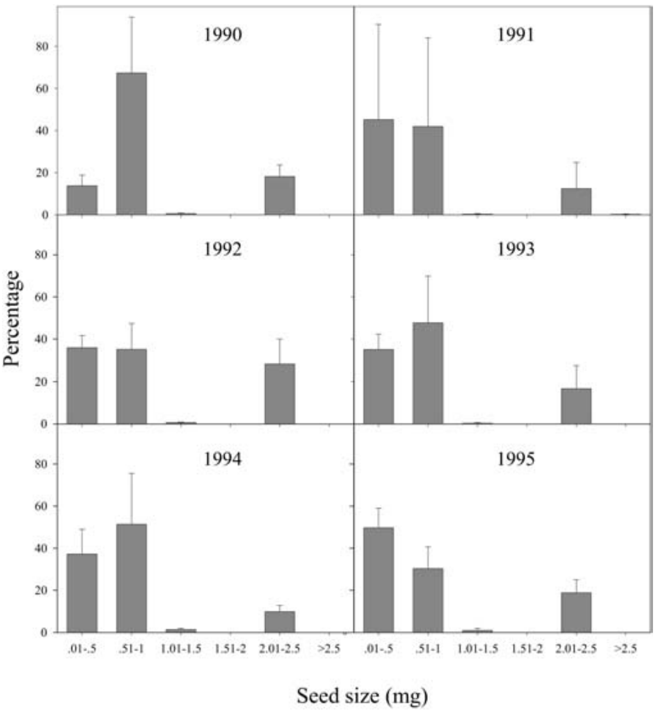

Fig. 1 Proportion of seed-size classes (all the species pooled) in Parque Nacional Fray Jorge, north-central Chile, for 1990–1995. *Error bars* 1SE

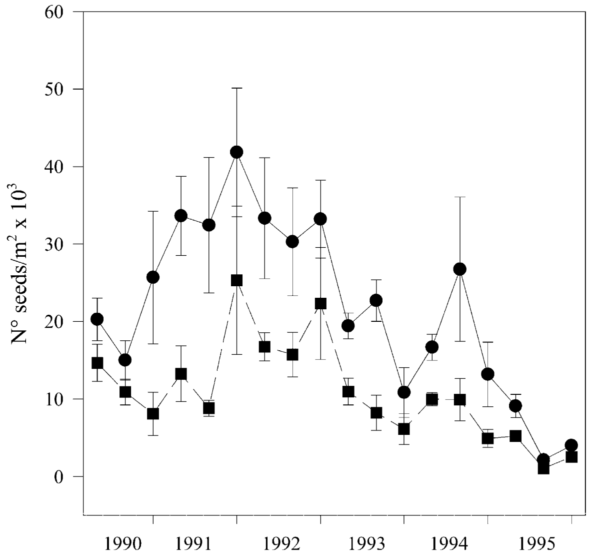

Fig. 2 Total seed densities of all species (*circles*) and annual plant species (*squares*) in Parque Nacional Fray Jorge, north-central Chile, for 1990–1995

category. The 1.51–2.00 mg size class was not represented in the soil seed bank. Seed sizes over 2.5 mg were either absent or poorly represented in the soil (Fig. 1).

Variation in soil seed densities with time

Total seed numbers (all the species pooled) showed significant differences between years ($F_{(5,15)}$=19.07; P<0.0001), a marginally significant seasonal difference ($F_{(2,6)}$=4.17; P=0.073), and a significant year × season interaction ($F_{(10,30)}$=4.06; P=0.0014). The higher seed densities (30,000–40,000 seeds m^{-2}) were found during 1991–1992 ENSO years and the lowest in 1995 (Fig. 2), after three consecutive below-average rainfall years. During non-ENSO years, seed densities varied between 2,000 and 25,000 seeds m^{-2} (Fig. 2). Greater between-year variation in seed density was found in annuals ($F_{(5,15)}$=18.30; P<0.0001; Fig. 2), followed by perennial grasses ($F_{(5,15)}$=8,46; P=0.007) and differences were marginally significant for shrub seeds ($F_{(5,15)}$=4.58; P=0.0538). Seed densities of geophytes did not differ between years ($F_{(5,15)}$=3.02; P=0.1074). Only in the case of annuals did seed densities change significantly within years ($F_{(2,6)}$=8.41; P=0.0401; Fig. 2).

Of 19 species analyzed, only 8 (~40%) showed significant time effects. All probabilities (after Bonferroni adjustment) equal to or lower than 0.0026 were considered significant. The annuals *Adesmia tenella* ($F_{(5,15)}$=7.25; P=0.0012), *Moscharia pinnatifida* ($F_{(5,15)}$=11.44; P<0.0001), *O. micrantha* ($F_{(5,15)}$=12.51; P<0.0001), *P. hispidula* ($F_{(5,15)}$=14.52; P<0.0001), and *Schizanthus litoralis* ($F_{(5,15)}$=6.98; P=0.0015) showed significant differences between years, whereas differences were marginally significant for *Ch. petiolare* ($F_{(5,15)}$=8,76; P=0.0073), *Eryngium coquimbanun* ($F_{(5,15)}$=7.09; P=0.0036) and *Erodium cicutarium* ($F_{(5,15)}$=14.37; P=0.0040). In general, seed densities by species were 5- to 10-fold higher in the 1991–1992 ENSO years (Table 1). None of the species showed significant within-year variations.

Relationship between seed density, annual precipitation, and plant biomass

Total seed densities in the soil (in December) were significantly correlated with the annual precipitation (r^2=0.64, P<0.05), and this correlation increased when only annual plant species were included in the analysis (r^2=0.92, P<0.01, Fig. 3). This high correlation is due largely to the large increases in soil seed densities in 1991–1992. However, if only those years with rainfall below 100 mm are considered (i.e., the majority of the years at the study site) no correlation with soil seed densities was found. Very low precipitation results in no predictable relationship with seed density.

Seed densities of the subshrub *Ch. petiolare* were not correlated with plant cover (r^2=0.007, P>0.05); however, seed densities of annuals (all species pooled) showed a positive significant correlation with plant cover (r^2=0.70, P<0.05). At the annual species level, *O. micrantha* showed a dramatic increase in soil seed density at high cover values. *P. hispidula*, a species restricted to the open spaces, showed a weak correlation between soil seed density and plant cover (Fig. 4).

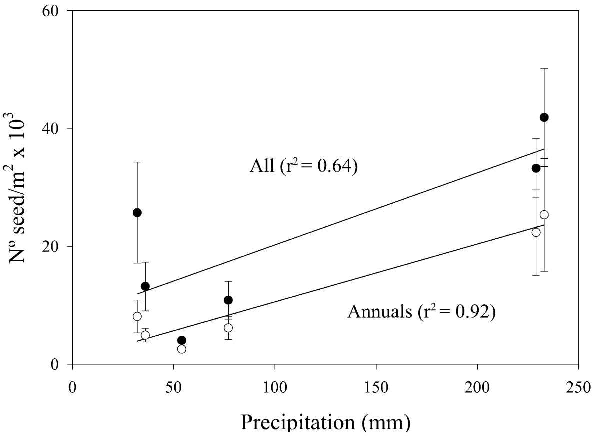

Fig. 3 Relationships between precipitation and total seed densities (all the species pooled) and seed densities of annual species in Parque Nacional Fray Jorge, north-central Chile, for 1990–1995. *Error bars* 1SE

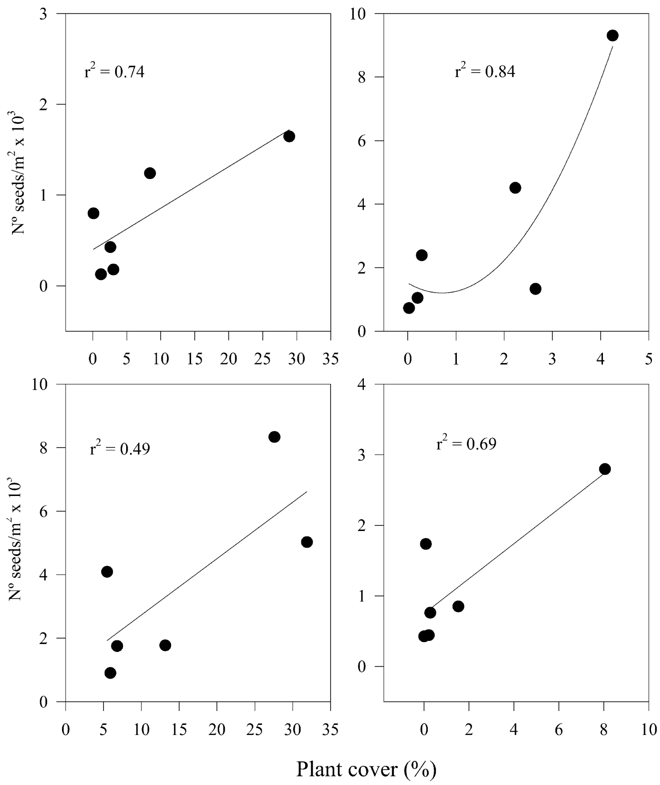

Fig. 4 Relationships between plant cover (%) and seed densities of annual species in Parque Nacional Fray Jorge, north-central Chile, for 1990–1995

Discussion

At our site, annual plant species comprised 64% of the total seed species in the soil, dominated by the seeds of the forbs *O. micrantha* and *P. hispidula*. *P. hispidula* also has the highest cover among annual species at the site, whereas *O. micrantha* is abundant (cover >5%) in wet years only (Gutiérrez et al. 1993). A similar situation has been described for Aucó, a site 200 km south of Fray Jorge (Gutiérrez et al. 2000). It was hypothesized that annual plant species respond to infrequent water pulses associated with ENSO by producing large seed crops that allow them to persist in the system during intervening dry years.

Unlike the neighboring central Monte Desert of Argentina or the northern Chihuahuan Desert, where grasses are well represented in the seed bank (Marone and Horno 1997; Pulliam and Dunning 1987), only three species were present in Fray Jorge and none of them reached 500 seeds m^{-2}.

Seeds of shrub species were either absent or scarcely represented in the soil, except for the suffruticose shrub *Ch. petiolare*, which had a soil seed bank unexpectedly large and variable for a perennial species (1,000–15,000 seeds m^{-2}). A comparable pattern has been described for the subshrub *Artemisia frigida* in the Great Basin cold desert in North America (Kemp 1989).

As in North American deserts (Guo et al. 1999), shrub species had larger seed sizes than herbaceous species. The difference in seed weight appears to be a trade-off between larger food reserves in heavier seeds and increased seed dispersal and reproductive output when smaller seeds are produced in larger numbers (Baker 1972). At our site the most numerous seed species are smaller (<1 mg) than the average for their respective growth-form. Depending on the year, the proportion of seeds weighing <1 mg varied between 70 and 90%, with the 0.51–1.00 mg size class being most numerous. Between 15 and 50% of the seeds had weights lower than 0.5 mg; however, these proportions were lower than those reported for the central Monte desert and the Sonoran desert where seeds weighing <0.25 mg constituted ~80% of total seed number (Price and Reichman 1987; Marone and Horno 1997). The differences between Fray Jorge and the other two deserts could be explained by the large amount of seeds of *Ch. petiolare*, which have an average seed weight of 0.77 mg. Another alternative, but not mutually exclusive, explanation is reduced granivory pressure as compared to northern hemisphere deserts (Kelt et al. 1996). Seed sizes of some cosmopolitan species such as *Erodium cicutarium* (1.12 mg) and *Schismus arabicus* (0.07) are remarkably similar to seed sizes of these species in North American deserts (Inouye 1991), and the Negev and Judean deserts of Israel (Gutterman 1994), respectively, suggesting that seed size is likely to be a very conservative character and relatively insensitive to environmental changes.

The tremendous increase in precipitation associated with the 1991–1992 ENSO profoundly affected the seed bank in Fray Jorge. As expected, seeds of annual plant species exhibited the largest temporal variation, followed by seeds of perennial grasses, whereas seeds of shrubs showed a low temporal variation. The massive germination of annuals during the wet years was followed by a sharp increase in seed production. In general, seed densities of annual plant species were 5- to 10-fold higher in the 1991–1992 ENSO years. A similar result was obtained by Gutiérrez et al. (2000) at Aucó, where densities of seeds increased 4- to 5-fold in 1997 associated with an ENSO event. Thus, the responses of soil seed banks in northern Chile are broadly similar, even for ENSO in different years. The annual species showing the more dramatic response to ENSO years were those restricted to sites under bushes. Some of these species are very scarce or absent above ground during dry years. The strong responses of annuals and the seed bank to the ENSO-driven wet years of 1991–1992 demonstrate the importance of this phenomenon in replenishing, recovering and probably maintaining ephemeral vegetation in the arid region of Chile.

Mares and Rosenzweig (1978) stated that low granivory by small mammals in the Monte Desert (generalized for arid South America) was due to the low seed availability in these ecosysterms. However, seed reserves in the Monte Desert (Marone and Horno 1997), central Chile (López-Calleja 1995) and north-central Chile (Meserve 1981; Gutiérrez et al. 2000; this study) do not appear to be smaller than those in several North American deserts. Kemp (1989) has reported that all warm deserts have maximum seed bank sizes of 8,000–30,000 seeds·m^{-2} at the habitat scale, this also includes South American deserts.

Seed bank structure, to a large extent, reflected the above ground plant community. Several species of annual plants were absent above ground during dry years, but were well represented in the soil seed bank. Seeds that remain dormant in the soil for at least 1 year form a persistent seed bank (Thompson and Grime 1979). This persistent seed bank would enable sudden increases of annuals in wet years.

In the arid ecosystem studied, the ENSO episodes translate into increased rainfalls, enhancing plant production, and this causes an increase in seed abundance. The response of vegetation, mainly of annuals species, to increased pulses of water via rainfall is very fast (usually within a year). The delayed response of small mammals (Meserve et al. 1995, 1999) and predators (Jaksic et al. 1997) to these pulses of primary production at the site have been already published.

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