

Effects of low water supplementation and nutrient addition on the aboveground biomass production of annual plants in a Chilean coastal desert site*

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Summary. The effects of low water supplementation and nutrients on the aboveground biomass production of annual plants was tested in the field by mimicking small rainfall events of 5 mm per month and by adding fertilizers to experimental quadrats. Field measurements were made during an extremely dry year, so the potential additional effects of rainfall probably had no important effect on plant responses. Biomass of non-native species was higher in irrigated than in non-irrigated quadrats. No significant responses to irrigation treatments were detected in native species. This lack of response may be due to higher thresholds of watering being required for either germination and/or growth. Because of the low water inputs, fertilizer additions did not promote any biomass response in either native or non-native species. Responses of non-native species to low and frequent pulses of water, which is characteristic of this arid system, may be important for the persistence of these species in this environment.

Key words: Ephemeral plants – Chilean Desert – Weeds – Water effects – Nutrient effects

In most deserts precipitation is low and unpredictable in time and space (Noy-Meir 1973). However, total annual rainfall can vary greatly among them. For instance, North American deserts, such as the Chihuahuan and Sonoran Deserts, often have more than 100 mm of annual precipitation (Ludwig and Whitford 1981), while in the Chilean Desert several years of drought with less than 100 mm of annual precipitation are common (Di Castri and Hajek 1976). Water is generally considered to be the main limiting factor for germination, growth and productivity of herbaceous plants and shrubs in desert

ecosystems (Went 1948, 1949; Went and Westergaard 1949; Juhren et al. 1956; Tevis 1958a, b; Beatley 1967, 1974; Noy-Meir 1973). Few experiments have been conducted to test the effect of water on plant performance in the Chilean arid region (Santibañez et al. 1976; Vidiella and Armesto 1989). Vidiella and Armesto (1989) studied the effect of different amounts of irrigation on emergence of annuals and geophytes in outdoor experiments and in growth chambers, and showed that emergence of weeds occurred at lower levels of irrigation relative to native ephemerals, and geophytes exhibited higher water requirements for germination than annuals. These authors concluded that higher water requirements for germination appear to correlate positively with increasing aridity.

Another distinctive feature of ephemeral plant communities in the Chilean arid region is the high species richness observed in small areas. These species form a mosaic of patches dominated by different species. Chemical analyses of surface soil samples taken from patches of different species at the Lagunillas Experimental Station (30° S, Coquimbo, Chile) showed significant differences in nitrogen and phosphorus availability (unpublished data). Therefore, it can be hypothesized that the structure of the Chilean ephemeral plant communities may be related to differences in available soil nutrients.

At Lagunillas, a relatively wet year (1987; 170 mm), was followed by three consecutive dry years (15.7 mm in 1988, 22.1 mm in 1989, and 19.6 mm in 1990). This situation provides an opportunity to test the predictions of Vidiella and Armesto (1989) in the field, by mimicking small rainfall events through artificial irrigation. I hypothesize that: (a) low but frequent (monthly events rather than sporadic) amounts of watering will promote an increment in biomass of introduced but not native annual plants; and (b) because of low water provided by irrigation I would not expect species to respond to fertilizers. Here I report the results of a field experiment designed to test these hypotheses in a Chilean coastal desert site.

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Methods

Study site

The study area is located on an old (Miocene-Pleistocene) coastal marine terrace with soils derived from fossil dunes and/or colluvial deposits on top of a calcareous hardpan ("tertel" hereafter) formed by deposits of shells of molluscs (Paskoff 1970). Experimental plots were set up at Lagunillas (30° 06' S, 70° 21' W; 30 m elevation), 15 km south of Coquimbo and about 2 km from the coast, in a wheat field abandoned about 30 years ago. At present the area is subject to moderate seasonal grazing by livestock (mainly goats and sheep). The climate is arid mediterranean with a high maritime influence. Records from Punta Tortuga Lighthouse (29° 55' S, 71° 22' W), ca. 15 km north of the experimental plots, indicate an average annual precipitation of 80.9 mm with a CV of 68% (range=4.3–188 mm) for the last 18 years. Temperature and relative humidity are much less variable. Mean average temperature ranges from 12 to 18° C (range=6–22° C). Mean relative humidity is about 80–85% (range=60–100%).

Experimental design

In 1987 two 1-ha experimental areas differing in soil parent material and in depth of the tertel layer were established. Plot 1 (shallow tertel) is characterized by a soil derived from fossil dunes and tertel less than 30 cm below surface, outcropping in some places. Plot 2 (deep tertel) is located on an alluvial fan or bajada. The soil is formed by colluvial deposits resulting from erosion of a nearby watershed and by air-borne particles. Tertel is deeper than 1.2 m below the surface. In Plot 1, the dominant shrub species is *Encelia canescens* var. *tomentosa* (Walp.) Back (0.3 plants/m², 7.3% cover), while in Plot 2, *Haplopappus cerberanus* (Remy) Reiche is the dominant shrub (2.7 plants/m², 24.3% cover).

Both plots were wire-fenced to exclude livestock and hares. Within each plot, 42 quadrats (3 × 3 m) were arranged in six blocks of seven quadrats each. Blocks were 10 m apart from each other and the distance between quadrats was 6 m. Each quadrat was bordered by a line of house bricks wrapped in polyethylene bags, buried 8 cm deep in the soil and forming a boundary 7 cm high. The brick lines prevented any possible contamination from neighboring quadrats due to water runoff. Treatments were: nitrogen (10 g/m²), phosphorus (5 g/m²), potassium (30 g/m²), calcium (5 g/m²), magnesium (8 g/m²), and ground tertel (50 g/m²) addition, plus a control (no fertilizer addition). N was added as (NH₄)₃ CO, P as CaHPO₄, K as KHSO₄, Mg as Mg₂SO₄, and Ca as Ca₂CO₃. The six treatments and control were randomly assigned to the seven quadrats within each block. Fertilizers were hand-broadcast once just before the onset of winter rains for four consecutive years from 1987 onwards. Three of the six blocks of quadrats were irrigated monthly starting in May 1987. The irrigated blocks received a volume of well water equivalent to 5 mm of rain each month and the other three received only natural rainfall. Sprinkler heads were located 1.5 m above the ground surface to mimic natural rainfall. There were a total of 7 nutrient by 2 water treatments. Each combination was replicated 3 times in each plot.

Vegetation sampling

At the end of the growing season for annuals (October 1990) we harvested all species present at ground level in two randomly located 30 × 30 cm quadrats in each experimental quadrat in both plots. Harvested plants were oven-dried at 70° C for 48 h and weighed to the nearest mg. This allowed us to determine the dry aboveground biomass ("biomass" hereafter) for each species for each treatment.

The data were analyzed by a factorial ANOVA and the corresponding error terms were used to reflect the split-plot design.

Table 1. Average aboveground dry biomass (g/m²) of annual plant species in irrigated (IQ) and non-irrigated (NIQ) quadrats pooled over nutrient treatments in Plot 1 (shallow tertel) and Plot 2 (deep tertel)

Species	Plot 1		Plot 2	
	IQ	NIQ	IQ	NIQ
<i>Adesmia tenella</i>	0.019 (0.019)	0.019 (0.019)	0.088 (0.047)	0.016 (0.012)
<i>Amblyopappus pusillus</i>	0.344 (0.264)	– –	0.048 (0.037)	– –
<i>Camissonia dentata</i>	– –	– –	0.098 (0.088)	– –
<i>Calandrinia coquimbensis</i>	0.544 (0.534)	– –	– –	– –
<i>Cryptantha glomerata</i>	– –	0.002 (0.002)	0.699 (0.510)	0.111 (0.051)
<i>Erodium cicutarium</i> *	0.736 (0.307)	0.762 (0.308)	0.952 (0.537)	0.228 (0.158)
<i>Erodium malacoides</i> *	0.034 (0.030)	0.508 (0.266)	0.016 (0.016)	– –
<i>Eryngium coquimbantum</i> *	– –	– –	0.494 (0.492)	– –
<i>Medicago polymorpha</i> *	0.106 (0.053)	0.006 (0.006)	0.061 (0.046)	– –
<i>Mesembryanthemum* crystallinum</i>	0.011 (0.011)	– –	0.276 (0.218)	– –
<i>Nolana paradoxa</i>	0.084 (0.084)	0.021 (0.021)	1.289 (1.289)	– –
<i>Oxalis micrantha</i>	– –	– –	0.119 (0.061)	– –
<i>Pectocarya</i> sp.	0.006 (0.006)	– –	– –	– –
<i>Plantago hispidula</i>	0.460 (0.339)	4.500 (1.138)	7.847 (1.398)	11.270 (1.064)
<i>Schismus arabicus</i> *	1.211 (0.478)	0.056 (0.026)	37.299 (12.54)	0.178 (0.090)
Native species	0.972 (0.525)	3.028 (0.978)	7.120 (2.392)	7.548 (0.180)
Non-native species	1.398 (0.395)	0.877 (0.185)	25.735 (5.948)	0.178 (0.073)
Total biomass	2.370 (0.759)	3.915 (1.049)	32.856 (6.319)	7.776 (0.167)

Standard errors are in parenthesis. *: non-native species

Fertilizer comparisons to the control were done by the Dunnett procedure (Steel and Torrie 1980). Plots 1 and 2 were analyzed separately because of the lack of replicates.

Results

Biomass responses to nutrients

Total biomass did not respond to nutrient addition in either Plot 1 ($F=0.95$, $df=6,24$, $P>0.05$) or in Plot 2 ($F=0.62$, $df=6,24$, $P>0.05$). The biomass of individual species was not significantly different between nutrient treatments either.

Biomass responses to irrigation

Because there were no significant differences in plant responses to nutrient additions, data from irrigated and non-irrigated quadrats were lumped for statistical analysis.

A total of 12 and 13 annual species were found in Plot 1 and Plot 2, respectively (Table 1). In Plot 1 total biomass in irrigated and non-irrigated quadrats was not significantly different ($F=1.89$, $df=1,4$, $P>0.05$). In Plot 2 biomass was almost five times higher in the irrigated quadrats than in the non-irrigated ones (Table 1) ($F=15.41$, $df=1,4$, $P<0.05$). ANOVAs run on individual species revealed few significant differences. In Plot 1, only two species responded to the water treatment, one of them increasing its biomass (*Medicago polymorpha*) ($F=13.50$, $df=1,4$, $P<0.05$) and the another decreasing its biomass (*Erodium malacoides*) ($F=14.37$, $df=1,4$, $P<0.05$). In Plot 2, only the introduced grass *Schismus arabicus* increased its biomass significantly in the irrigated quadrats and was by far the most abundant species. When the data for total biomass of native and non-native species were analyzed separately, we detected no water treatment effect on either native or non-native species in Plot 1. In Plot 2 the total biomass of non-native species in the irrigated quadrats was two orders of magnitude higher than in the non-irrigated quadrats (Table 1). Despite several species being present only in the irrigated quadrats, the biomass differences compared to the non-irrigated quadrats were not statistically significant. For instance, in Plot 2, 13 species were present in irrigated plots, and only 5 species were present in non-irrigated ones.

Discussion

These results support the hypothesis that annual weeds respond to lower thresholds of soil moisture than native annual species (Vidiella and Armesto 1989). As expected 5 mm per month of irrigation had little effect on the biomass of most of the annual plants in the system analyzed. Two species, *Medicago polymorpha* and *Schismus arabicus*, both of which are weeds, responded positively to watering. These species are characteristic of mediterranean climates (Hunter et al. 1987) and the area studied apparently represents the septentrional (and drier) limit of their distributions in Chile. The presence of these species in Lagunillas is due mainly to anthropic activities such as dry farming and livestock raising (Solbrig 1984). These species come from more temperate environments where the first rain indicates the onset of the rainy season and is a cue triggering germination and growth processes. Since in xeric environments small pulses of water are often followed by long periods of drought, annual species are expected to show high water requirements for germination. Their propagules remain dormant as seeds waiting for higher pulses of water, thus ensuring that the life-cycle will be completed (Noy-Meir 1973). Vidiella and Armesto (1989) argued that the rapid germination responses of plants to small rainfall events may have evolved in an environment where competition,

rather than soil moisture predictability was the main problem for survival. If there are no additional rains, or if rains are spread out in the season, survival and reproduction of these species may be severely reduced. In fact, several weeds emerging in the plots after a small natural rainfall died before being able to flower or produce fruits, a phenomenon also reflected in the soil seed bank (unpublished data). Differences in total biomass response to irrigation between Plots 1 and 2 are probably related to differences in the substrate and the depth of terrel. Plot 2 had a sandier substrate and a deeper terrel. Therefore, water infiltration into the soil may be deeper in Plot 2 and less exposed to evaporation as compared to Plot 1.

The lack of response of the species to fertilizer additions was expected because of the low water input provided by both irrigation and natural rainfall. It has been demonstrated in the Chihuahuan Desert that nitrogen addition under conditions of average to above-average rainfall greatly increased plant production and changed species composition (Ettershank et al. 1978; Gutiérrez and Whitford 1987; Gutiérrez et al. 1988; Ludwig et al. 1989). However, this did not occur under below-average rainfall conditions. Apparently, the low inputs of water used were insufficient to move the added fertilizers down into the soil to make them available to plant roots. However, the added water could have been enough to alter the osmotic concentration of the germinating environment. In fact, germination of weedy species have been noted to be stimulated by nitrate (Mayer and Poljakoff-Mayber 1989). If so, this would explain in part the results obtained.

Although small rainfall events are frequent in arid regions, their ecological importance has not been assessed (Sala and Lauenroth 1982). This work suggests that for certain species small frequent pulses are sufficient to trigger germination and growth. Although a major fraction of the seed bank is probably lost because seedlings die before reproducing, those plants surviving to maturity could make a significant contribution to the seed bank allowing adequate renewal. If viability of weed seeds in the soil is lower than that of native species, low, frequent pulses of rain would favor the persistence of weeds in this ecosystem. This also has interesting implications for patterns of community change in areas where accelerated desertification has been accompanied by increasingly erratic and sparser rainfall events. However, further research is needed to verify this hypothesis.

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