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The effect of water, nitrogen, and human-induced desertification on the structure of ephemeral plant communities in the Chilean coastal desert

El efecto del agua, el nitrógeno y la desertificación inducida por el hombre en la estructura de comunidades de plantas efímeras en el desierto costero chileno

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ABSTRACT

The generality of the water-limited-nitrogen-regulated plant growth hypothesis for desert ecosystems was tested by applying water and nitrogen to experimental plots set up in a marine terrace at Lagunillas, Coquimbo (30° S). Biomass response of ephemeral plants to increased water and nitrogen fertilization were species and site specific. Depth of a calcium carbonate hardpan present in the terrace modulated plant responses to water. Germination and growth of introduced species was triggered at lower water levels than native plants. This characteristic could be important for the persistance of these weeds in this ecosystem, since low precipitation is common for this region. This has interesting implications for patterns of community change in areas where accelerated desertification has been accompanied by increasingly erratic and sparser rainfall events. Human impact has differently affected plant communities in Chilean coastal desert and North American deserts. In North American deserts overgrazing seems to be the main factor changing the previously grass-dominated communities to an unpalatable shrub-dominated system. Dry farming (wheat crop) in foothills, overgrazing, and intense use of woody plants as fuel for home and mining activities during the last two centuries have all greatly contributed to the desertification process in north-central Chile. Herbs in chronic disturbed areas do not seem to be more abundant under bushes, forming the "fertility islands" which are typical of North American deserts. However, in protected areas some herb species are restricted to areas under bushes, while others are present only in open areas. Chemical analysis of soil samples taken under and between bushes show large differences in nutrients. North of La Serena, where rainfall becomes extremely low, annual herbs appear (in years with rains) only under bushes. I propose that man, by removing trees and shrubs previously present in the Chile coastal desert, has allowed the invasion of introduced annual species and the reduction of species associated with bushes. Additionally, native species inhabiting open areas would have increased their presence in this system.

Key words: Chilean desert, ephemeral plants, water, nitrogen, desertification.

RESUMEN

La generalidad de la hipótesis de que el crecimiento de plantas está limitado por el agua y regulado por el nitrógeno en ecosistemas desérticos fue evaluado aplicando agua y nitrógeno a parcelas experimentales en una terraza marina en Lagunillas, Coquimbo (30° S). La respuesta de la biomasa de plantas efímeras a la adición de agua y nitrógeno fue especie y sitio específico. La profundidad de una capa dura de carbonato de calcio presente en la terraza afectó la respuesta de las plantas al agua. La germinación y crecimiento de especies introducidas fue gatillada a niveles de agua más bajos que las especies nativas. Esta característica podría ser importante para la persistencia de estas malezas en este ecosistema, ya que las bajas precipitaciones son comunes para esta región. Esto tiene implicaciones interesantes para patrones de cambio comunitario en áreas donde la desertificación acelerada ha sido acompañada por eventos de lluvia cada vez más erráticos. El impacto humano ha afectado en forma distinta las comunidades del desierto costero chileno y los desiertos norteamericanos. En los desiertos norteamericanos el sobrepastoreo parece ser el principal factor cambiando comunidades previamente dominadas por pastizales a sistemas arbustivos no palatables. La agricultura de secano (cultivo de trigo) en laderas de cerros, el sobrepastoreo y el uso intenso de plantas leñosas como combustible hogareño y en actividades mineras durante los últimos dos siglos han contribuido fuertemente al proceso de desertificación en el Norte Chico de Chile. Las hierbas en áreas crónicamente alteradas no parecen ser más abundantes bajo arbustos, formando las "islas de fertilidad" que son típicas en los desiertos de Norteamérica. Sin embargo, en áreas protegidas algunas especies herbáceas están restringidas a áreas bajo arbustos, mientras otras están presentes sólo en áreas abiertas. Análisis químico de muestras de suelo tomadas bajo y entre arbustos muestran grandes diferencias en nutrientes. Al norte de La Serena, donde las lluvias son extremadamente bajas, las plantas herbáceas anuales aparecen (en años con lluvia) sólo bajo arbustos. Propongo que el hombre, al remover árboles y arbustos previamente presentes en el desierto costero chileno, ha permitido la invasión de especies anuales introducidas y la reducción de especies asociadas con arbustos. Adicionalmente, las especies nativas habitando áreas abiertas han aumentado su presencia en este sistema.

Palabras claves: Desierto chileno, plantas efímeras, agua, nitrógeno, desertificación.

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INTRODUCTION

The arid environment of north-central Chile (between 18 and 32° S) is caused by a climatic regime influenced by the cool, north-flowing Humboldt Current and the high pressure cell of the central western Pacific, which prevents the northward movement of storm tracks except in some winters. Atmospheric conditions, influenced by a stable subtropical anticyclone, result in a mild, uniform coastal climate with scarce rainfall. The presence of a thick cover of stratus clouds below 1,000 m appears to be common during the winter months. Where steep coastal slopes intercept the clouds, a fog-zone develops. In some localities, this moisture maybe sufficient to allow the development of forest communities (Arroyo *et al.* 1988). The geomorphology of the coastal area is dominated by the Cordillera de la Costa, a line of faulted cliff which rise abruptly from a narrow coastal plain a few kilometers wide (Rundel *et al.* 1991).

Despite water has been generally considered the main limiting factor for germination, growth and productivity of herbaceous plants and shrubs in desert ecosystems (Went 1948, 1949, Went & Westergaard 1949, Juhren *et al.* 1956, Tevis 1958a, b, Beatley 1967, 1974, Noy-Meir 1973, Gutiérrez & Whitford 1987a), few experiments have been conducted to evaluate the effect of water addition on plant performance in the Chilean arid region (Santibáñez *et al.* 1976, Vidiella & Armesto 1989, Gutiérrez 1992). Less attention has been paid to the effect of nitrogen, another factor often considered limiting for plant growth in desert ecosystems (West & Skujins 1978, Gutiérrez & Whitford 1987a). Recent studies to test the effect of water and nutrients on ephemeral plant growth have been conducted in two sites of the IV Region of Chile: Lagunillas and Parque Nacional Fray Jorge (both at 30° S). I will comment on the results of these studies and compare them with similar studies made in other deserts. In the second part of this paper, I will advance some hypotheses on the effect of human-induced desertification on the structure of ephemeral plant communities in the Chilean coastal desert.

STUDY SITES

Parque Nacional Fray Jorge

The park (30° 38' S, 71° 40' W) lies on the northern fringe of the Chilean mediterranean zone and on the sourthern edge of the Pacific Coastal Desert. The climate is arid mediterranean, with 90% of the 85 mm annual precipitation falling in winter months (May-September). Summer months are warm and dry, but fog contributes with significant additional moisture during many months (Kummerow 1966). Mean maximum temperature in the warmest month (January) is 24° C (all weather data are from the park headquarters, collected and analyzed by the Oficina Meteorológica de Chile, Santiago).

The study site is located in an interior valley ("Quebrada de Las Vacas", 230 m elevation) in the park, about 5 km east of the Pacific coast, on the eastern side of the coastal range, which reaches about 600 m elevation there. The general plant community is characterized by spiny drought-deciduous and evergreen shrubs, with an herbaceous understory, and generally unvegetated sandy areas between shrubs. The specific community of the study site has been termed the *Porlieria chilensis-Adesmia bedwellii-Proustia pungens* association for its most characteristic shrubs (Muñoz & Pisano 1947). The flora of this region combines elements of the dry western Andean slopes with a few species from the Monte desert on the opposite side of the Andes (Sarmiento 1975).

Lagunillas

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 formed by deposits of shells of mollucs (Paskoff 1970). Two 1-ha experimental plots were set up at Lagunillas (30° 06' S, 71° 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. Presently, the area is subject to moderate seasonal grazing by livestock (mainly goats and sheep). Climate is arid mediterranean with high maritime influence. Records from Punta Tortuga

Lighthouse (20° 55' S, 71° 22' W), ca. 15 km north of 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 12-18° C (range = 6-22° C). Mean relative humidity is about 80-85% (range = 60-100%).

In Lagunillas, from a total of 191 vascular plant species collected within an area of 1 km^2, annual plants represented the highest proportion of the total flora (41%), and annuals and geophytes combined (*i.e.*, all ephemeral plants) comprised 51% of the total flora. Fifteen percent of the species collected were introduced and 86% of them annuals (Armesto & Vidiella, 1993).

Effect of water

As in other world deserts, precipitation in the Chilean coastal desert is low and highly variable in time and space (Armesto *et al.* 1993). Rainfall occurs mainly between May and August (winter season). Annual average precipitation ranges from 250 mm in the southern border of the Chilean coastal desert (31° S) to practically 0 mm north of Chañaral (26° S) in the Atacama Desert, one of the driest desert in the world. In this latitudinal gradient, ephemeral plant species (annuals and geophytes) increase in importance from south to north reaching their maximum richness at 28° S (Armesto *et al.* 1993). Along the coast at lower latitudes, plant species richness decreases, disappearing entirely north of 26° S. Patches of plants are found in oases, along water courses (riparian plants), and in places influenced by coastal fog (Rundel & Mahu 1976, Rundel *et al.* 1991).

Germination and growth of ephemeral native plants occur in response to pulses of rainfall of about 20 mm (Vidiella & Armesto 1989). Lower rain pulses promote the germination and growth only of weeds (mostly mediterranean plants) but not of native plants (Gutiérrez 1992). The higher water thereshold showed by native plants compared to weeds in deserts has been considered as a cautionary strategy of plants by Noy-Meir (1973). Since a rain event in deserts is often followed for a long period of drought, seeds germinate only when the amount of water fallen is sufficient for the plants to complete their life cicle. Plant responses to water in one year are apparently related to the rainfall regime of the previous year. It has been observed that a wet year following several years of drought produces larger ephemeral plants biomass than the second of two consecutive wet years, suggesting that other factors (*e.g.*, nutrients) become limiting for plant growth in the second year. Similar findings have been reported for Australian (West & Skujins 1978) and Chihuahuan deserts (Gutiérrez & Whitford 1987b).

Plant response is not only associated to the amount of rainfall accumulated in a given year but also to the timing, frequency and time interval among rain pulses (Ludwig & Whitford 1981). The same amount of water but differently distributed through time can have different effects on plants. Small and frequent pulses of rain can be more effective on annual plants having shallow root systems. On the contrary, large and infrequent pulses of rain can be more important for deep-rooted plants (Gutiérrez & Whitford 1987b, Ludwig *et al.* 1988) and geophytes. The latter stores part of their photosynthate in bulbs which remain belowground (between 10 and 30 cm deep) during dry years.

In the Chilean coastal desert, all annual plants may be classified as winter annuals because they germinate in the fall or in the winter season, depending on the time of the first rain, and last until spring. Only a few are present in summer (*e.g.*, *Chaetanthera*, Compositae). Absence of summer annuals seems to be due to the lack of significant rains during summer. In North American deserts summer annuals increase from west to east and they are directly related to the occurrence of summer rains (Ludwig *et al.* 1988). In Chile, temperatures along the coast are mild (freezing and hot temperatures are practically absent) and fairly constant throughout the year and among sites (Armesto *et al.* 1993). Consequently, tem-perature may not be a limiting factor for seed germination year-round. In this sense, water appears as the main driving force of the phenomenon known as the "blooming of the desert".

Biomass response of ephemeral plants to experimental irrigation in the field have been reported elsewhere (Gutiérrez 1992, Gutiérrez *et al.* 1992). In brief, results showed that water limits growth of several species, but the degree of plant biomass response was related to the underlying soil substrate. Plant biomass response to additional water was higher in soils where the calcareous hardpan layer was deeper.

As mentioned above, low pulses of water (< 10 mm) at a time promoted the germination and growth of Eurasian weeds but not of native species. Gutiérrez (1992) suggested that small pulses of water in disturbed areas of the Chilean coastal desert would allow the renewal of the seed bank of weeds favoring their persistance in the system. In the relatively undisturbed Parque Nacional Fray Jorge weeds decreased in a wet year (1991, 230 mm) (Gutiérrez *et al.*, 1993a). This suggests that these species, which were found in low numbers at the site, may be outcompeted by native species during wet years, and that their persistence in this system depends on the occurrence of years with low precipitation (Gutiérrez 1992).

Effect of nitrogen

After water, nitrogen appears as the major limiting nutrient in several deserts (West & Skujins 1978). Low nitrogen availability is related to the low soil organic matter in deserts. Vertical and horizontal distribution of soil nitrogen is strongly linked to vegetation distribution, composition and biomass (West & Klemmendson 1978). This spatial pattern is mainly the result of plants absorbing nitrogen through their root system and redepositing it on the soil as mulch.

Soil samples taken under the canopy of *Porlieria chilensis* (Zygophyllaceae) shrubs at Parque Nacional Fray Jorge had higher organic matter (2.57 vs 0.76%), available nitrogen (41.5 vs 6.5 ppm), and phosphorus (32.5 vs 20.0 ppm) compared to intershrub spaces. Values found in the intershrub spaces are similar to those found in soil samples collected in a disturbed site in Lagunillas (Gutiérrez *et al.* 1992). In this latter place, 42 soil samples were collected in each of two 1-ha plots (Table 1). Although, distance between samples was less than 10 m, a high variability was observes in the organic matter contents (CVs: 41.7 and 23.3% plots 1 and 2 respectively), nitrogen (CVs: 27.1 and 32.2%), and phosphorus (CVs: 23.1 and 11.7%). This suggests that annual plants living relatively close to each other may be exposed to significantly different rates of nutrient supply. Tilman (1980, 1982) postulates that when there is a high heterogeneity in resource distribution, potential competitors in a more homogeneous environment may coexist through small-scale spatial segregation.

TABLE 1

Physical and chemical characteristics of soil samples taken in Plot 1 (surface hardpan layer) and Plot 2 (deep hardpan layer) in Lagunillas. Each value corresponds to the mean ($\bar{x}$), one standard deviation (SD), and the coefficient of variation (CV) of 42 samples. * : $p < 0.01$.

Características fisicoquímicas de muestras de suelo tomadas en el Plot 1 (tertel superficial) y Plot 2 (tertel profundo) en Lagunillas. Cada valor corresponde al promedio ($\bar{x}$), una desviación estándar (SD) y el coeficiente de variación (CV) de 42 muestras. * : $p < 0.01$.

		pH	E.C. (mmhos/cm)	O.M. (%)	N (ppm)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)
Plot 1	$\bar{x}$	6.78	0.74	0.96	14.0	19.5	213.5	791.8	86.0
	SD	0.23	0.28	0.41	3.8	4.5	77.5	103.3	11.2
	CV	3.39	37.84	41.72	27.1	23.1	36.3	13.1	13.0
Plot 2	$\bar{x}$	6.81	0.31	0.60	11.5	22.2	364.5	455.3	85.4
	SD	0.20	0.14	0.14	3.7	2.6	73.6	102.1	10.2
	CV	2.94	45.16	23.33	32.2	11.7	20.2	22.4	11.9
t values		0.64	8.90*	5.39*	3.01*	3.30*	9.15*	15.01*	0.26

In Parque Nacional Fray Jorge there were large differences in floristic composition, density and biomass of ephemeral plant species between areas underneath and outside *Porlieria chilensis* canopies. There were almost four times as many individuals outside than under shrubs, but no significant differences in total biomass (Table 2). Several herb species had higher density and/or biomass outside than under shrubs, whereas other showed the opposite trend. Species richness was lower underneath *P. chilensis* canopy. Gutiérrez *et al.* (1993b) suggested that the spatial microdistribution of herbaceous species would be associated to their differential nutrient requirements. Another evidence for this is the analysis of soil samples taken from monospecific patches of five annual plant species in Lagunillas (Table 3). Patches differed significantly with respect to nitrogen, potassium and magnesium.

TABLE 2

Mean and standard error (in parentheses) of density (number of plants/m^2) and aboveground-dry biomass (g/m^2) of ephemeral plants outside (0) and underneath (U) the canopy of *Porlieria chilensis*. Number of replicates was ten.

Promedio y error estándar (en paréntesis) de densidad (número de plantas/m^2) y biomasa seca sobre el suelo (g/m^2) de plantas efímeras fuera (0) y bajo (U) el follaje de *Porlieria chilensis*. El número de réplicas fue diez.

	Density			Biomass		
Type	0	U	F	0	U	F
Native plants	3,674.44 (1,078.89)	983.33 (183.89)	8.06*	89.97 (11.02)	115.63 (15.02)	1.27
Exotic plants	103.33 (59.00)	80.00 (57.56)	0.53	5.59 (4.74)	2.66 (1.84)	0.13
Total	3,867.78 (1,052.89)	1,063.33 (194.11)	10.05**	95.57 (13.32)	118.29 (15.28)	0.98

* $p < 0.05$; ** $p < 0.01$.

TABLE 3

Chemical characteristics of surface soil samples collected in patches of five annual plant species. Values are the mean of 4 replicates ± 1 SD.

Características químicas de muestras de suelo superficial en parches de cinco especies de plantas anuales. Los valores son el promedio de 4 réplicas ± 1 DE.

Dominant species in patch	pH	O.M. (%)	E.C. (mmhos/cm)	N (ppm)	P (ppm)	K (ppm)	Ca (meq/100)	Mg meq/100)
Bromus berterianus	7.78 0.45	0.60 0.11	0.07 0.04	17.75 2.22	13.75 3.59	300.50 60.25	3.38 0.45	1.15 0.17
Eryngium coquimbanum	7.71 0.61	0.88 0.78	0.14 0.08	28.25 5.44	16.75 5.62	503.00 129.49	2.35 0.19	1.15 0.13
Helenium aromaticum	7.67 0.69	0.87 0.42	0.08 0.07	22.00 6.48	13.00 6.48	488.25 311.02	2.85 0.33	1.30 0.36
Mesembryanthemum cristallinum	8.25 0.29	1.20 0.73	0.23 0.18	37.25 19.10	35.50 45.99	537.25 117.14	5.63 5.81	1.88 0.73
Plantago hispidula	7.10 0.15	0.39 0.16	0.06 0.06	17.00 5.16	13.75 1.89	195.75 38.83	2.70 0.24	0.90 0.08
$F_{(4, 15)}$	3.01*	1.37	1.68	3.04*	0.83	3.35*	1.00	3.75*

* $p < 0.05$.

Biomass of ephemeral plants did not show significant responses to the addition of nutrients other than nitrogen in experimental plots at Lagunillas. Several weeds showed an increase in biomass in response to nitrogen fertilization. This fact has also been reported for the northern Chihuahuan Desert (Gutiérrez *et al.* 1988). The lack of plant response to K, Ca, and Mg would be associated to the high levels of these elements in the soils of the Chilean arid zone (Carrasco *et al.* 1978). The lack of plant response to P addition would be the result of the immobilization of phosphorus by calcium carbonate or precipitated carbonates (Dregne 1976, Schlesinger 1982). Plant response to nitrogen was more pronounced in a wet (Gutiérrez *et al.* 1992) than in a dry year (Gutiérrez 1992). Hence, nitrogen may become limiting when moisture is available.

Causes of desertification and its effect on ephemeral plants in north-central Chile

The original vegetation of north-central Chile has been removed to a large extent by human activities (Bahre 1979). Woody plants have been a source of fuel for homes, and for mining activities during the past two centuries (Solbrig 1984). Dry farming on foothills and overgrazing by goats and sheep have also contributed to the strong desertification process (Fuentes & Hajek 1978, 1979, Mabbutt & Floret 1983, Solbrig 1984). The effect of rainfall variability during the last 50 years seems minor in comparison to human-related disturbances (Fuentes & Hajek 1978, Gutiérrez *et al.* in press a). Thus desertification may be viewed largely as a human-driven process, and not necessarily a consequence of recent climatic changes. Several shrub species which are frequent only in undisturbed sites are currently endangered species (Benoit 1989) due to the intense explotation that they have borne. Clearing of land has provoked the erosion and dispersal of nutrients stored under shrubs, thus affecting the survival of the emphemeral plants which are restricted to these nutrient-rich microsites. The same disturbance, on the other hand, may have favored those species which are now abundant in the intershrub spaces (*e.g.*, exotics and weedy native annuals).

Human disturbance appears to have affected differently the desert plant communities in the Chilean coast and in North America. In North America, overgrazing by cattle appears to be a major factor changing the previously grass-dominated herbaceous communities to shrub-dominated communities (Schlesinger *et al.* 1990). Hence, disturbance in North America deserts has altered a previous, relatively uniform distribution of water and nitrogen by increasing their spatial and temporal heterogeneity, thus leading to changes in community composition and biogeochemical processes (Schlesinger *et al.* 1990). By symmetry I propose that man, by removing shrubs and tress previously present in the Chilean coastal desert may have changed a formerly heterogenous spatial distribution of nutrients and water to the more homogenous one observed today (Gutiérrez *et al.* 1992). The clearing of large areas also reduces the moisture holding capacity of soils and increases the evaporation rate (Keeley & Johnson 1977, Jaksic & Montenegro 1979), thus allowing the invasion of introduced annual species which prosper in low moisture conditions and prompting the reduction of native ephemeral species associated with shrubs and trees. As a consequence, restoration of disturbed lands in the Chilean coastal desert should not only consider soil fertilization schemes but also a revegetation with native shrubs and trees in order to reconstruct the formerly heterogenous pattern of fertility islands.

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