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Emergence of ephemeral plant species from soil samples of the Chilean coastal desert in response to experimental irrigation

Emergencia de plantas efímeras en muestras de suelo del desierto costero del Norte Chico de Chile en respuesta a riego experimental

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ABSTRACT

The structure of ephemeral plant communities, dominated by annuals and geophytes, in the Chilean coastal desert may be regulated by the quantity and the distribution of winter rains. We designed field and laboratory experiments to study the effects of different quantities of artificial precipitation on seedling emergence from surface and deep soil samples of the Chilean coastal desert.

A total of 15 ephemeral species were identified in our samples. No differences in species composition were detected between soil depths, but seedling density was greater in surface soil samples. For both soil types, seedling density and species richness increased proportionally with increasing irrigation between 10 and 180 mm. For some species, emergence was "all or none" above a certain minimum quantity of irrigation, which was defined as the "response threshold". For other species, emergence increased gradually with increasing irrigation above the threshold. According to their response thresholds, we recognized two major groups of ephemerals: The first consisted mainly of cosmopolitan weeds that responded to low amounts of rainfall (≈10 mm). The second group included most species endemic to the Chilean-Peruvian coastal desert which emerged in response to a greater accumulation of rainfall (≥40 mm).

We propose that interspecific differences in response thresholds to rainfall may account for much of the temporal and spatial variability in the structure of ephemeral vegetation in the Chilean coastal desert.

Key words: Seedlings, rainfall, aridlands, annuals, geophytes.

RESUMEN

Las comunidades de plantas efímeras del desierto chileno, anuales y geófitas, estarían reguladas por la cantidad y distribución de la precipitación invernal. En terreno y en laboratorio se realizaron experimentos para estudiar los efectos de distintas cantidades de precipitación artificial en la emergencia de plántulas a partir de muestras de suelo superficial y profundo del desierto costero de Chile.

Un total de quince especies herbáceas aparecieron en las muestras. No hubo diferencias en la composición de especies entre los dos tipos de suelo, pero el número de plántulas que emergieron fue mayor en las muestras de suelo superficial. Para ambos tipos de suelo, la densidad de plántulas y la riqueza de especies aumentaron proporcionalmente con la precipitación entre los 10 y los 180 mm de riego. La emergencia de algunas especies herbáceas fue del tipo "todo o nada" por sobre una cantidad mínima de riego que fue definida como "umbral de respuesta". Para otras especies la cantidad de plántulas aumentó con la cantidad de precipitación sobre el umbral. De acuerdo a sus umbrales de respuesta pudimos distinguir dos grupos de plantas efímeras: uno constituido principalmente por malezas cosmopolitas, que responden a cantidades bajas de precipitación (≈10 mm), y otro constituido por muchas de las especies endémicas del desierto costero chileno-peruano, que requieren una mayor acumulación de precipitación (≥40 mm) para emerger. Entre estas especies se encuentran las que caracterizan al llamado "desierto florido".

Proponemos que las diferencias interespecíficas en los umbrales de respuesta a la precipitación podrían dar cuenta de una gran parte de la variabilidad temporal y espacial en la estructura de las comunidades herbáceas del desierto chileno.

Palabras clave: Plántulas, precipitación, zonas áridas, anuales, geófitas.

INTRODUCTION

In a year of above average rainfall, the barren aspect of the coastal desert of north-central Chile (26°-32°S) changes due to the synchronous growth and mass flowering of many ephemeral species, predominantly annual and geophytes. These epi-

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sodic events are known locally as the "blooming of the desert" (Muñoz 1965, Solbrig 1976, Raugh 1983, Muñoz 1985). Massive blooming events are also common in other arid regions of the world, such as the Mojave (Went & Westergaard 1949, Went 1955), Sonoran (Shreve 1951, Jaeger 1957) and Chihuahuan deserts (Solbrig & Orians 1977) in North America, the deserts of Australia (Mott 1972), the Namib in South Africa (Walter 1986), and the deserts of North Africa (Le Houérou 1986), Afghanistan (Breckle 1983) and southern Peru (Raugh 1983).

In arid regions of North America (Went 1948, 1949, Went & Westergaard 1949, Juhren *et al.* 1956, Tevis 1958a, 1958b) and Australia (Mott 1972), there are often two growing seasons, characterized by a different ephemeral flora. Ephemeral plants respond to the bimodal distribution of rainfall as well as to the large seasonal differences in temperature. For instance, in the Mojave, Sonoran and Chihuahuan deserts, monthly mean minimum temperatures during winter are below 5°C, with nightly frost common, whereas during summer monthly mean maximum temperatures are above 35°C (Tevis 1958a, MacMahon & Wagner 1985). Likewise, absolute difference between minimum winter and maximum summer temperatures in the arid region of Murchinson, Australia, reach 50°C (Mott 1972). Two groups of annual plants have evolved under this climatic regime: summer annuals, which germinate in response to rainfall during the warm season, and winter annuals, which respond to rainfall during the cold season (Mulroy & Rundel 1977). The existence of different germination strategies may be considered a mechanism that allows the maintenance of high regional species richness (Grubb 1977, Angevine & Chabot 1979), because more species can coexist in the same area growing at different times.

In contrast, in the coastal desert of north-central Chile rain is concentrated within a few months (May to August) and thermal fluctuation during the year is only 6.7°C (Fuenzalida 1965). Because in the Chilean coastal desert there is only one rainy season and because seasonal differences in temperature are much lower than those recorded in the deserts of North America and Australia, all ephemeral plants must grow and flower in response to the same environmental cues.

We suggest that the quantity and distribution of rainfall during the wet season regulate the emergence of ephemeral plant species in the desert, thereby influencing local species richness, composition, and plant density. To investigate this hipothesis, we conducted experiments applying artificial rainfall to samples of coastal desert soils maintained both outdoors and in growth chambers. Our specific goals were:

1. To compare seedling emergence from the seed bank of surface (0-3 cm depth) and deep (3-6 cm depth) soil, in order to detect differences in species composition and stored viable seed in relation to depth.
2. To determine the minimum amounts of rainfall required by different ephemeral species for seedling emergence ("response thresholds").
3. To assess the effects of artificial rainfall on species richness and seedling density.

STUDY AREA AND METHODS

The desert plant community from which soil samples were collected was located at the experimental station of the Universidad de La Serena, about 15 km south of Coquimbo (30°06'S, 71°21'W, 50 m elevation). Soils were sandy-clay with a high drainage, derived from fossil dunes overlaying an impermeable calcium carbonate layer located at depths varying between 0 and 30 cm. The study area was formerly a crop field, abandoned in 1962. After abandonment it was intermittently grazed by cattle and sheep until it was fenced one year before this study. Dominant shrub species are *Encelia canescens* and *Haplopappus cerberoanus* (J. Gutiérrez, unpublished data). Although the area has been disturbed, its ephemeral flora is representative of that of other areas in the coastal desert, except for the higher abundances of some ephemeral weeds associated with range lands (e.g. *Erodium* spp.).

In March 1987, we collected soil samples from 0-3 cm and 3-6 cm depth within an area of c. 1 ha. The soil samples from each depth (surface and deep soil) were mixed separately within plastic bags in order to homogenize the distribution of seeds and nutrients in the samples. The homogenized soil samples were distributed (c. 1000 cm^3) in 160 plastic pots (216 cm^2 of surface area), 80 for surface soil and 80 for deep soil. There were 8 irrigation treatments: 0 (unwatered control), 5, 10, 20, 40, 80, 160 and 320 mm, and each treatment was replicated 10 times for both soil depths. Pots were watered twice a week, with a maximum of 7 mm of precipitation each time, until the corresponding total amount of artificial precipitation for each treatment was accumulated. All the pots were arranged in a randomized complete block design and left outdoors at the experimental station. The spatial arrangement consisted of 10 rows with every watering treatment for each soil depth represented once in each row. The number of seedlings of each species appearing in the pots was recorded two days after the final irrigation of each treatment. Previous observations indicated that seedling emergence did not continue after that time. It took 109 days to complete the 320 mm treatment. The pots receiving 160 and 320 mm of artificial precipitation, received an additional 20 mm of natural rain during the course of the experiment. Thus, the last two treatments were 180 and 340 mm. The highest temperature recorded during the period of study was 22°C (March) and the lowest was 6.2°C (June).

In order to eliminate photoperiod and temperature variation in testing germination responses of seeds to rainfall, and to determine more precisely the responses to low quantities of rainfall, we conducted a parallel experiment in a growth chamber with a photoperiod of 8 hrs and a constant temperature of 25°C. Six groups of two pots containing surface soil (0-3 cm) were watered daily with a maximum of 2.5 mm of precipitation each time until the following totals were accumulated: 3, 5, 10, 40, 80 and 100 mm. Two control pots were left unwatered. Seedlings were counted and identified daily, until two days after the final irrigation.

Statistical analyses of the data from both experiments were carried out by a two-way analysis of variance, with soil depth and irrigation as the main effects. Data were square-root transformed previous to the analysis, as adviced by Steel & Torrey (1980).

RESULTS

Outdoor experiments

Seedlings emerged from pots receiving 10 or more mm of artificial precipitation. More seedlings emerged from surface soil than from deep soil for all watering regimes (Two-way ANOVA, $F_{1,108} = 40.1$; $P < 0.001$; Fig. 1). For surface soil, the number of seedlings per pot increased proportionally with the increase in irrigation from 10 to 180 mm. A similar pattern was observed for deep soils (Fig. 1).

A majority of ephemeral species emerged from both surface and deep soil samples, with the exception of *Plantago hispidula* which was only present in surface soils (Table 1). On the average, however, species richness (the mean number of species per pot) was higher in surface than in deep soil for all watering regimes ($F_{1,108} = 31.9$; $P < 0.001$; Fig. 2). Maximum species

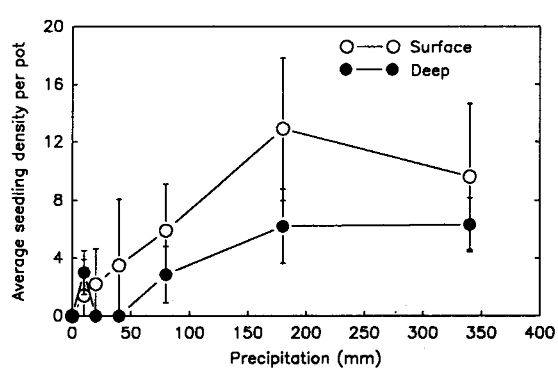

Fig. 1: Average number of seedlings emerged from surface and deep soil in pots subjected to different irrigation treatments in the outdoor experiment. Bars represent ±1 SD.

Número promedio de plántulas registradas en macetas, conteniendo suelo superficial y profundo, sometidas a distintos tratamientos de riego en experimentos de terreno. Las barras representan ±1 DE

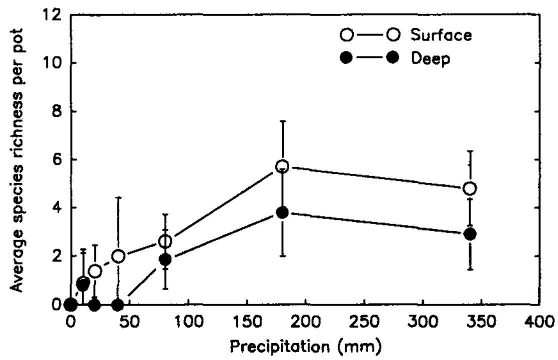

Fig. 2: Average number of species emerged from surface and deep soil in pots subjected to different irrigation treatments in the outdoor experiment. Bars represent ±1 SD.

Número promedio de especies registradas en macetas, conteniendo suelo superficial y profundo, sometidas a distintos tratamientos de riego en experimentos de terreno. Las barras representan ±1 DE

richness was observed in pots that received 180 mm (Fig. 2).

Pots receiving different irrigation treatments differed in species composition and in the relative abundances of seedlings of each species (Table 1). Eight species were recorded in pots receiving between 10 and 40 mm. The dominant species in these pots were: *Erodium* spp. (12-58%), *Chenopodium* sp. (23-40%), and grasses (mainly *Schismus arabicus,* 15-36%). Seedlings of species which characterize the events known as "blooming of the desert" emerged from pots receiving 40 mm or more (Table 1). These species were: *Leucocoryne coquimbensis, Oxalis micrantha, Calandrinia* sp. and *Nolana paradoxa.* Because of this, species richness was higher in pots which were irrigated with 80 or more mm. For a majority of the species, seedling density was greater in surface than in deep soil samples (Fig. 3). However, *Oxalis micrantha* and *Leucocoryne coquimbensis,* the latter a geophyte which emerged from bulbs, were more frequent in deep soil.

Growth chamber experiments

No seedlings emerged from controls and from pots that received the equivalent of 3 mm of precipitation. Only *Erodium* spp. emerged from pots that received a total of 5 mm (Table 2). As in the outdoor experiments, the number of emerging seedlings per pot increased with increasing irrigation although we did not test rainfall values over 100 mm (Fig. 4). The explanation for the higher density of seedlings in the growth chamber (Fig. 4) compared to the outdoor (Fig. 1) experiments is that densities in the

TABLA 1

Relative proportion (%) of all seedlings of different ephemeral species emerged from surface (S) and deep (D) soils in pots subjected to different irrigation treatments.

Porcentajes relativos de plántulas por especie en cada tratamiento de riego, en suelo superficial (S) y profundo (D).

	Irrigation treatment											
	10 mm		20 mm		40 mm		80 mm		180 mm*		340 mm*	
Species	S	D	S	D	S	D	S	D	S	D	S	D
Erodium spp. **39	39	58	15	–	12	–	12	21	18	5	15	10
Chenopodium sp.	23	32	40	–	27	–	19	5	5	7	10	9
Malva nicaensis	8	10	5	–	15	–	2	–	3	–	4	–
Grasses***	15	–	35	–	36	–	58	31	33	10	32	21
Plantago hispidula	15	–	5	–	6	–	2	–	2	–	7	–
Medicago polymorpha	–	–	–	–	3	–	5	10	4	7	3	4
Leucocoryne coquimbensis	–	–	–	–	1	–	–	21	1	14	–	5
Mesembryanthemum cristallinum	–	–	–	–	–	–	2	–	1	3	2	2
Oxalis micrantha	–	–	–	–	–	–	–	12	4	15	–	9
Calandrinia sp.	–	–	–	–	–	–	–	–	6	2	2	–
Crassula closiana	–	–	–	–	–	–	–	–	23	37	23	38
Nolana paradoxa	–	–	–	–	–	–	–	–	–	–	1	–
Adesmia tenella	–	–	–	–	–	–	–	–	–	–	1	2

* Total includes 20 mm of natural rain.

** Includes three species which were indistinguishable as seedlings *Erodium cicutarium, E. moschatum,* and *E. malacoides.*

*** Mainly *Schismus arabicus.*

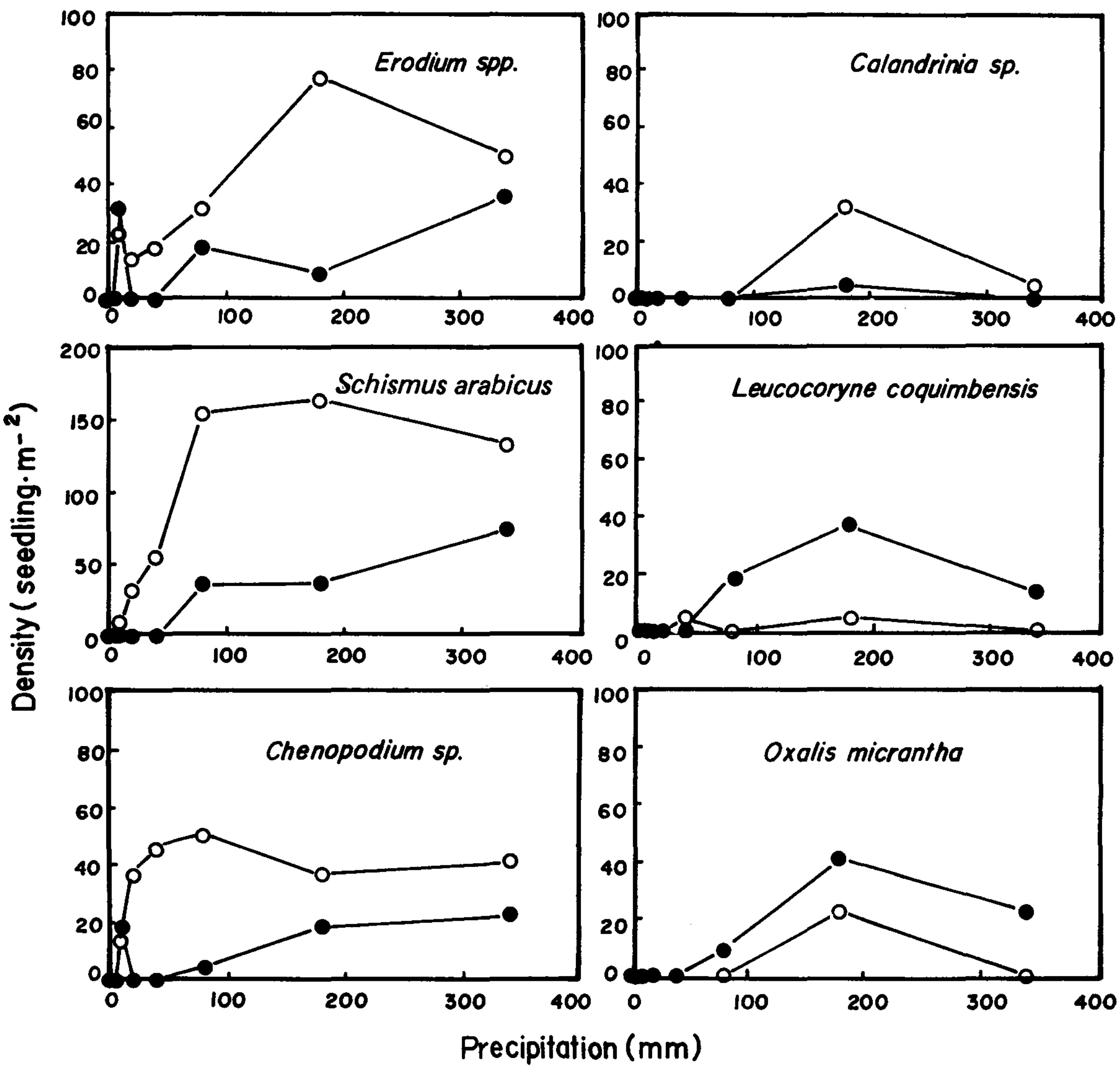

Fig. 3: Emergence of selected species from surface (empty circles) and deep (filled circles) soil, in response to different irrigation treatments in the outdoor experiment.

Respuesta de algunas especies herbáceas, en macetas conteniendo suelo superficial (círculos blancos) y profundo (círculos negros), a distintos tratamientos de riego en experimentos de terreno.

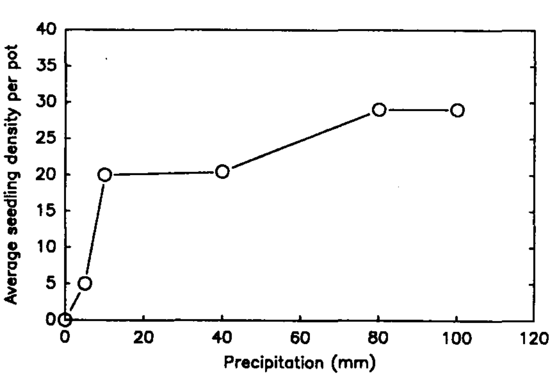

Fig. 4: Average number of seedlings emerged from surface soil in pots subjected to different irrigation treatments in the growth chamber experiment. These averages represent the total number of seedlings emerged throughout the course of the experiment.

Número promedio de plántulas por maceta registradas en macetas conteniendo suelo superficial, durante el transcurso de cada uno de los diferentes tratamientos en condiciones de laboratorio.

TABLA 2

Minimum quantities of irrigation (mm) causing emergence of seedlings in the outdoor and in the growth chamber, and species responses to seasonal rainfall at the field site.
Cantidades mínimas de riego (en mm) que produjeron una respuesta de las especies en los experimentos de terreno y en cámara de crecimiento, y umbrales de respuesta de las especies a la lluvia estacional en el sitio de estudio.

Species	Outdoor Surface soil	Outdoor Deep soil	Growth chamber Surface soil	Seasonal rain***
Group A				
* *Erodium* spp.	10	10	5	18
Chenopodium sp.	10	10	10	18
* *Malva nicaensis*	10	10	10	18
* Grasses #	10	80	10	18
Plantago hispidula	10	**	10	18
Group B				
* *Medicago polymorpha*	40	80	**	18
Leucocoryne coquimbensis	40	80	40	38
Mesembryanthemum crystallinum	80	180	**	38
Oxalis micrantha	180	180	**	18
Calandrinia sp.	180	180	**	38
Nolana paradoxa	340	**	40	**
Group C				
Crassula closiana	180	180	10	**
Adesmia tenella	340	340	10	38

* Introduced species (Marticorena & Quezada 1985).
** Species not recorded.
*** Observations of response threshold for species in the field during the 1987 growing season (J. Gutiérrez, personal communication).
\# Mainly *Schismus arabicus.*

growth chamber experiment represent the cumulative number of seedlings emerged throughout the course of the experiment (mortality was not discounted), whereas in the outdoor experiments we only counted those seedlings present two days after the end of a watering treatment.

In the growth chamber essays most species had "all-or-none" responses to artificial rainfall up to 80 mm, that is, no seedlings emerged until a threshold quantity of precipitation was reached, and no further emergence occurred for quantities of precipitation above the threshold level (Fig. 5). However, in the field experiments we detected a germination response which increased gradually with precipitation over a similar range of watering treatments (Fig. 3).

Response thresholds to rainfall

The minimum amount of irrigation inducing seedling emergence was defined as the "response threshold" for a species. Ephemeral species were grouped (Table 2) according to their response thresholds (Fig. 5) in the outdoor experiments (surface and deep soil) and in the growth chamber experiments (only surface soil):

(1) Species which emerged in response to 5 or 10 mm of irrigation in both sets of experiments (Group A).

(2) Species which emerged in response to irrigation levels of 40 mm and above in both sets of experiments (Groups B).

(3) Species wich had markedly lower thresholds in the growth chamber as compared to outdoor experiments (Group C).

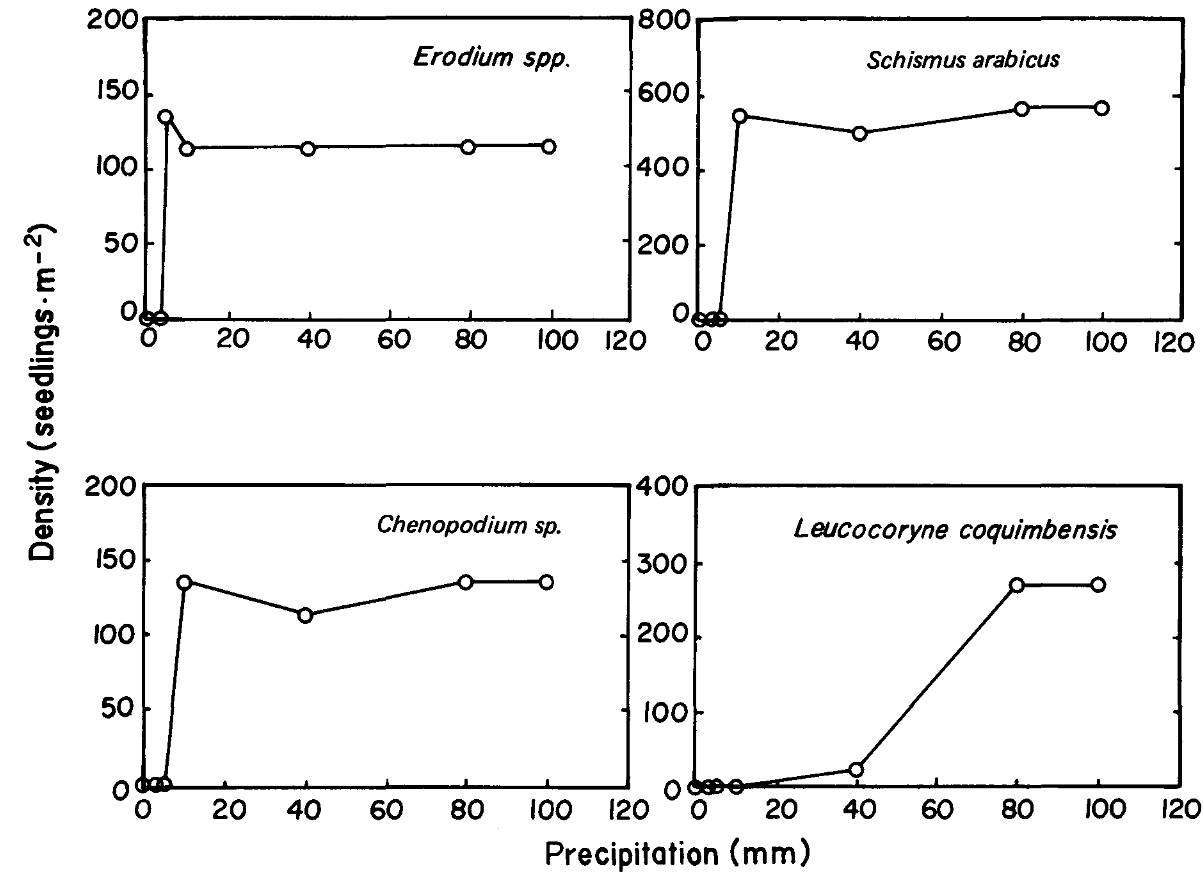

Fig. 5: Emergence of selected species to different irrigation treatments in the growth chamber experiment. Notice the "all or none" responses to low levels of irrigation.

Respuesta de algunas especies herbáceas a los distintos tratamientos de riego en condiciones de laboratorio. Se puede apreciar respuestas del tipo "todo o nada" a cantidades bajas de precipitación.

No differences in response thresholds were observed between surface and deep soil, except for the grasses, where more than one species may be involved (Table 2).

We compared these results with records of seedling emergence in response to seasonal rains in the study area during the 1987 growing season (J. Gutiérrez, personal communitation). Responses of species to natural rainfall were qualitatively consistent with our experimental observations. Species of Group A (Table 2) emerged in response to the first rainfall event (c. 18 mm), and most species of Group B (Table 2) emerged after the cumulative total of rainfall was ≥ 38 mm.

DISCUSSION

This study provides the first empirical basis for understanding the periodic events known as the "blooming of the desert" in the Chilean arid zone. This information is important to understand how plant populations respond to uncertain rainfall regimes in desert environments, and is critical for the management and conservation of natural resources in this arid region.

From the 15 ephemeral species found in the irrigated soil samples, six species are cosmopolitan weeds (Table 2). Their presence is probably associated with the history of cultivation and grazing of the study area. The remaining nine species have a geographic distribution restricted mainly to the Pacific coastal desert of South America. Two species, *Leucocoryne coquimbensis* and *Nolana paradoxa* (Muñoz 1985) are endemic to the Chilean coastal desert. We found that cosmopolitan species generally have lower response thresholds than desert endemics (Table 2). The latter did not emerge with rains of less than 40 mm. This pattern was consistent with the records of emergence of these species in response to seasonal rains in the same study site (Table 2).

According to these results, cosmopolitan weeds appear to be "opportunistic", emerging in response to small (c. 10 mm) rainfall events. This rapid germination response may have evolved in an environment where competition, and not soil moisture uncertainty, was the main problem for survival. However, if there are no additional rains, or if the following rain occurs much later in the season, survival and reproduction of these weed species may be severely reduced. In contrast, desert ephemerals, particularly those characteristic of the "blooming of the desert" in north-central Chile (e.g. *Leucocoryne coquimbensis, Nolana paradoxa* and *Calandrinia* sp.), respond to greater accumulated rainfall which would enhance seedling survival. These ephemeral species have evolved in desert environments where they must recognize environmental cues which indicate periods in which there is a higher probability of survival and reproduction (Cohen 1967, Venable & Lawlor 1980). This type of response, which precludes germination when environmental conditions are unsuitable for successful maturation, has been called "predictive dormancy" (Venable & Lawlor 1980).

More seedlings emerged from surface than from deep soil samples. This difference may be related to a greater accumulation of seeds on or near the soil surface. In general, the number of seeds in the soil decreases with depth (Fenner 1985); however, induced secondary dormancy (Bazzaz 1979), or loss of viability in deeply buried seeds, may also account for the reduction in seedling emergence.

Even though the mean number of seedlings and the mean number of species per pot was higher in surface soil, there was no major difference in the flora of the two depths. The only species which was absent from deep soil was *Plantago hispidula.* Its seeds lack mechanisms for self-burial, such as those present in the seeds of *Erodium* (Stamp 1984). On the other hand, the geophyte *Leucocoryne coquimbensis* was found predominantly in deep soil samples.

Differences in emergence patterns between growth chamber and outdoor experiments ("all-or-none" vs. gradual response to increasing irrigation) may be partly related to the contrasting watering frequencies. Pots left outdoors were subjected to some desiccation between consecutive irrigations thus altering species responses. Desiccation of pots left outdoors may also explain the discrepant reponse thresholds of the species in group C (Table 2), and account for the higher thresholds in outdoor essays compared to natural rainfall (Table 2). Another possible factor contributing to the discrepancy between the results of outdoor and growth chamber experiments is the variation in photoperiod under field conditions. There is a need for further experiments to assess the role of actual soil moisture and photoperiod on the emergence of desert ephemerals.

We propose that, within an interval from 10 to 180 mm of rain, density and richness of ephemeral plants in the Chilean coastal desert depends largely on the amount of accumulated rainfall. Response thresholds may be characteristic for each species. Based on the response thresholds of the two major groups of ephemeral plants we can make some specific predictions. Ephemeral species which characterize the "blooming of the desert" would emerge only in response to rainfall events ≥ 40 mm. If precipitation is < 40 mm, ephemeral communities would be poor in species, and dominated by cosmopolitan weeds. To test these predictions we need data on the frequency of rainfall episodes ≥ 40 mm in the Chilean desert and the years of "blooming of the desert". This information is currently been analyzed, and tends to support the above predictions (P. Vidiella, unpublished data).

We conclude that temporal and spatial variation in the structure of herbaceous communities in the Chilean desert may be related in part to interspecific differences in response thresholds to precipitation.

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