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Plant communities of the fog-free coastal desert of Chile: plant strategies in a fluctuating environment

Comunidades vegetales del desierto costero de Chile: estrategias de plantas en un ambiente fluctuante

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ABSTRACT

Plant communities of the fog-free coastal desert of northern Chile depend on highly variable rainfall inputs. Precipitation is concentrated in the winter, but it varies in quantity and frequency among and within years. We discuss the importance of this variability in the structure of the plant communities along a latitudinal gradient encompassing the entire range of the coastal desert (27-30°S). We present the results of three years of records of plant cover, species richness and phenology in permanent plots, and laboratory assays to determine the moisture thresholds for seedling emergence from soil samples. The communities comprise a high proportion (30-60%) of annuals. Northwards, shrubs increase in relative importance. Geophytes are more abundant in the center of the gradient. In a wet year, absolute plant cover varied between 10 and 60% among sites, more than one half of which was contributed by ephemeral plants. In a dry year (< 20 mm of rain) the ephemeral plant cover did not develop. This minimum amount of rain required for ephemeral plant growth coincides with the threshold for seedling emergence determined in laboratory experiments. Flowering showed a pronounced peak two months after the rain, and in some species it may continue during part of the dry period. Maximum richness of native plant species and high endemism occur in the central part of the gradient studied, where areas protected from human activities are lacking.

Key words: Arid zones, dormancy, seed germination, species richness, endemism, life forms.

RESUMEN

Las comunidades de plantas del desierto costero sin influencia de neblina del norte de Chile dependen de episodios de lluvia que son altamente variables. La precipitación se concentra en el invierno, pero varía en cantidad y frecuencia entre y dentro de los distintos años. En este trabajo discutimos la importancia de esta variabilidad en la estructura de las comunidades de plantas a lo largo de una gradiente latitudinal que abarca el área de distribución del desierto costero sin influencia de neblina (27-30°S). Presentamos resultados de tres años de registros de cobertura de vegetación, riqueza de especies y fenología realizados en parcelas permanentes, y de ensayos de laboratorio para determinar los umbrales de humedad de emergencia de las plántulas a partir de muestras de suelo. Encontramos que las comunidades poseen una alta proporción (30-60%) de especies anuales. Los arbustos aumentaron en importancia relativa hacia el norte. Las geófitas fueron más abundantes en el centro del gradiente latitudinal. En un año lluvioso, la cobertura absoluta de la vegetación de los sitios varió entre 10 y 60%, contribuyendo las plantas efímeras con más de la mitad de la cobertura. En un año seco (< 20 mm de lluvia), en cambio, la cobertura de plantas efímeras no se desarrolló. Esta cantidad mínima de agua requerida para el crecimiento de las plantas efímeras en condiciones de terreno coincidió con el umbral de emergencia de plántulas determinado en los experimentos de laboratorio. La floración mostró un máximo pronunciado dos meses después de la lluvia, continuando durante parte del período seco en el caso de algunas especies. La máxima riqueza de especies de plantas nativas y el mayor grado de endemismo se registró en la parte central del gradiente estudiado, donde no existen áreas silvestres protegidas.

Palabras claves: Zonas áridas, latencia, germinación, riqueza de especies, endemismo, formas de vida.

INTRODUCTION

Two major types of plant communities can be recognized along the coastal desert of northern Chile (18-30°S) based on their dependence on different sources of moisture. North of 26°S, in the Atacama Desert of Chile, the contribution of rainfall to soil moisture becomes negligible in most years. In the coastal Atacama desert, no significant rainfall has been recorded over periods of 20 years or more (Di Castri & Hajek 1976, Rauh 1985, Rundel *et al.* 1991). In this area, the vegetation, known as "lomas", is restricted to a narrow fog zone

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above 600 m on the coastal mountains (Rundel & Mahu 1976, Rundel *et al.* 1991). The activity of plants is entirely dependent on the constancy and frequency of fogs. In contrast, from 26 to 30°S, seasonal rain becomes the most significant source of moisture for plant growth on the coastal plains and canyons where fog is absent. After the rains, a rich plant cover develops over extensive gently-sloping terraces formed by fossil dunes, often overlying a calcareous hardpan substrate of marine origin (Contreras & Gutiérrez 1991).

General descriptions of vegetation and plant adaptations are available for the fog-dependent communities, which extend discontinuously from northern Chile to subtropical latitudes in Peru (e.g., Rauh 1985, Rundel & Mahu 1976, Péfaur 1982, Rundel *et al.* 1991). Much less is known, however, about the plant communities in the fog-free areas of the coastal desert. In this study we are concerned primarily with the structure and dynamics of vegetation in these areas (Fig. 1). Our goals are: (1) to describe the environmental setting for these coastal desert communities, (2) to analyze the vegetation, in terms of species richness and life-form composition, along the latitudinal range of the fog-free coastal desert, and (3) to examine the changes in the plant communities over a three-year period in relation to rainfall. We discuss the results in the framework of the question of how communities are assembled in an extremely variable environment.

RAINFALL REGIME OF THE FOG-FREE COASTAL DESERT

As are other deserts of the world, the Chilean coastal desert is characterized by variable rainfall. For a given locality in the coastal desert, the variability of rainfall has two components: (1) the total amount of rainfall varies between years, and (2) precipitation varies in distribution over the year. These two sources of variability need to be analyzed to characterize rainfall regimes.

Although the analysis of rainfall variability is hindered by the lack of reliable long-term climatic records, especially for lowland coastal sites, information available for some of the major cities within the area of the fog-free coastal desert (Almeyda 1950, Di Castri & Hajek 1976) illustrate the two components of variation. The annual averages of rainfall for Copiapó (26°S) and Vallenar (28°s) are 40 and 63 mm respectively (Almeyda 1950), however few years if any will receive the average rainfall. The lowest and highest extremes of rainfall in 27 years of records in these two cities (Fig. 2A, B) are zero (no rain recorded) and more than 120 mm, respectively. Severe droughts may last longer than one year. Thus, very little rain was recorded in Vallenar or Copiapó in 1978 and 1979 (Fig. 2), and in Copiapó between 1974 and 1976. An important limitation of the analysis of interannual variability in precipitation is that long-term trends are difficult to ascertain from the observation of limited data sets. For instance, in Fig. 2 we have compared two periods,1930-1948 and 1970-1983. In the first period (Fig. 2A), there seems to be a decreasing trend towards the present; however, in the second period (Fig. 2B) annual rainfall appears to be increasing since 1970. It is possible that the analysis of longer time series, as they become available, may allow the detection of trends or oscillations which remain hidden by the high variability between years. The trends for the two localities are weakly correlated. During most years, annual rainfall in Copiapó seems to be less than one half of that recorded in Vallenar, located only 2° of latitude (140 km) to the south (see Fig. 1).

The basis for this interannual variability in precipitation is not well understood, but recent work by P. Aceituno (personal communication) suggests that years of copious annual rainfall are associated with strong "El Niño" events in the subtropical Pacific Ocean. The periodicity of wet and dry years in the desert may thus be related to global climatic anomalies, such as the Southern oscillation. Understanding these global climatic events will help us identify the sources of environmental uncertainty in the coastal desert.

The distribution of daily rain events, or individual rainstorms, over time may be an important parameter to characterize the coastal desert environment, yet climatic data are hardly available in this form. In the Chilean coastal desert, there is a strong tendency for rainstorms to occur in the cool season, between April and September (Fig. 3). In the area of Lagunillas, near the southern end of the coastal desert, we

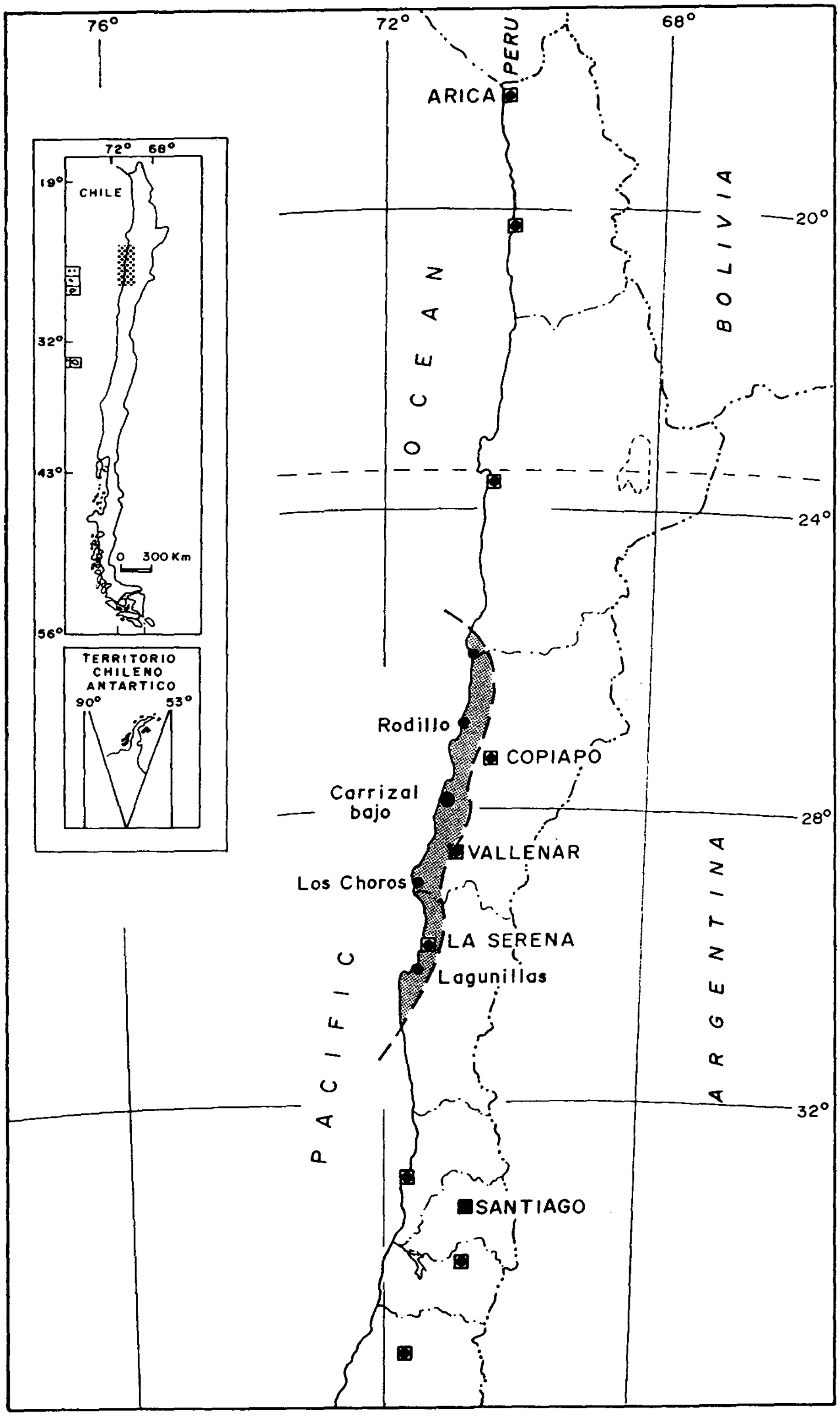

Fig. 1: Geographic location of the four study sites (Lagunillas, Los Choros, Carrizal Bajo, and Rodillo) in area of the fog-free Chilean coastal desert (shaded).

Localización geográfica de los cuatro sitios de estudio (Lagunillas, Los Choros, Carrizal Bajo y Rodillo) en el área del desierto costero chileno sin influencia de neblina (área sombreada).

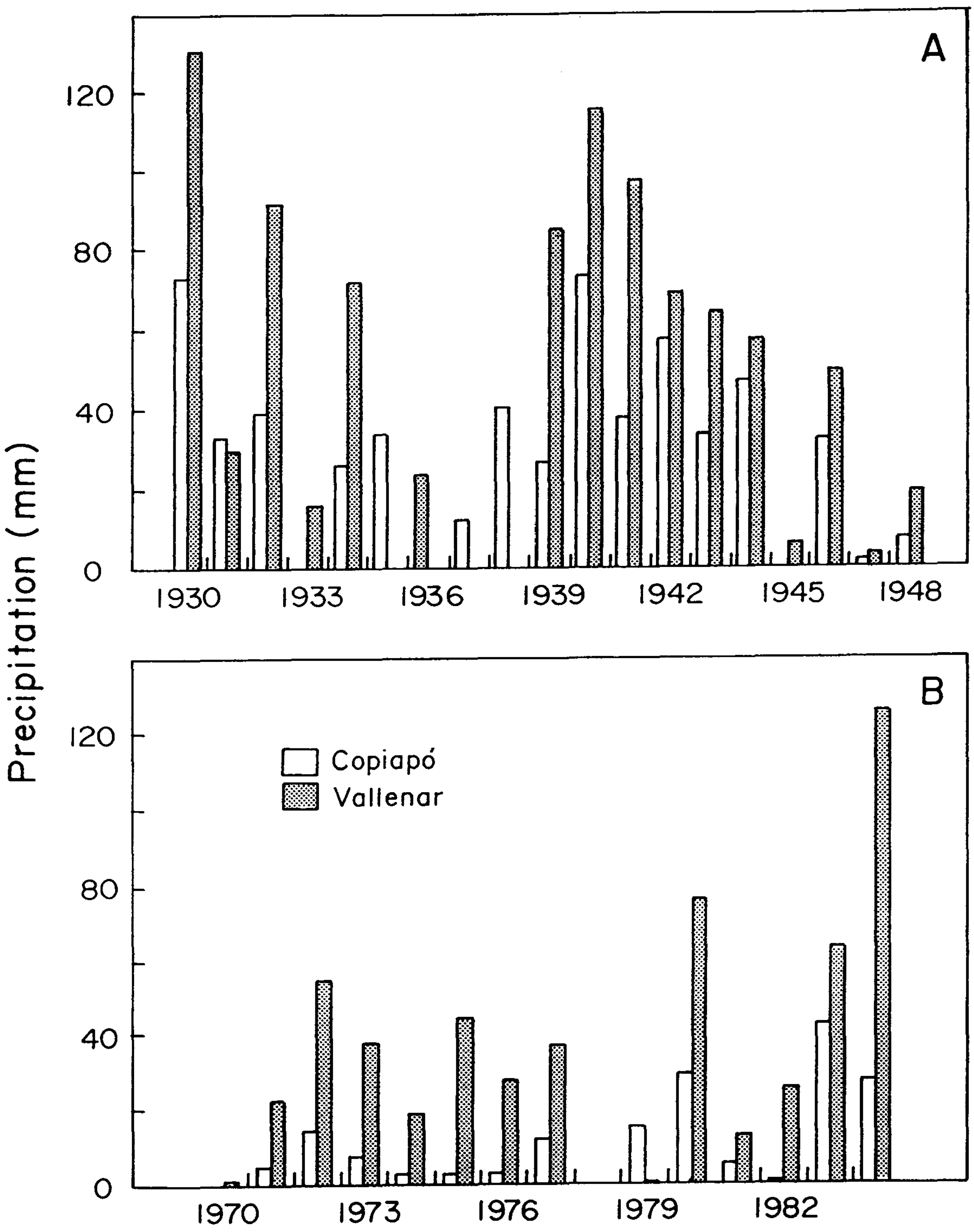

Fig. 2: Variation in annual rainfall for two major cities, Copiapó (27°21'S) and Vallenar (28°35'S), located in the range of the Chilean coastal desert. A) Period 1930-1948 (data from Almeyda 1950). B) Period 1970-1984 (data from Muñoz 1985).

Variación de la lluvia anual de dos ciudades situadas en el área del desierto costero chileno, Copiapó (27°21'S) y Vallenar (28°35'S). A) Período 1930-1948 (datos de Almeyda 1950). B) Período 1970-1984 (datos de Muñoz 1985).

can see examples of years with high rainfall spread over several months of the year, or concentrated in one or two large storms, as well as years of low rainfall where each rain event is also low (Fig. 3). Annual rainfall regimes may vary in total amount of rain per event, in the frequency of events, and in the length of the interval between events. In some years, several rains may occur within one month, in other years, rain pulses may be separated by one or two months of drought (Fig. 3). The dry period between wet seasons may last longer than 10 months.

PLANT RESPONSE THRESHOLDS

Variation in rainfall may be important for plant responses in aridlands because a single rain pulse may elicit plant growth. Plants actually respond to individual rains rather than to the accumulated rainfal in one year. The amount of rain in one pulse may or may not elicit germination or plant growth depending on the thresholds for physiological activity.

We investigated the thresholds for germination of ephemeral plant species in Lagunillas (30°S), in the southern border of the fog-free coastal desert (Fig. 1), by applying different amounts of water to soil samples (Vidiella & Armesto 1989). We identified and counted all the plant seedlings that appeared in the samples. Two groups of plants were apparent: low-threshold, non-native weeds that germinated in response to low water inputs (10 mm or less), and native ephemerals that had higher thresholds (more than 20 mm). Additional growth-chamber experiments conducted with soil samples from four sites along the latitudinal range of the fog-free coastal desert (Fig. 1) revealed that most native species appeared after 15 mm or more of rain were applied, regardless of the position of the sample in the gradient (Table 1). Thus, plants native to the coastal desert seem to require bigger rain pulses to emerge than exotic weeds. The higher thresholds shown by native desert ephemerals may prevent false starts, that is, emergence in response to a rain pulse which does not provide enough moisture to comple-

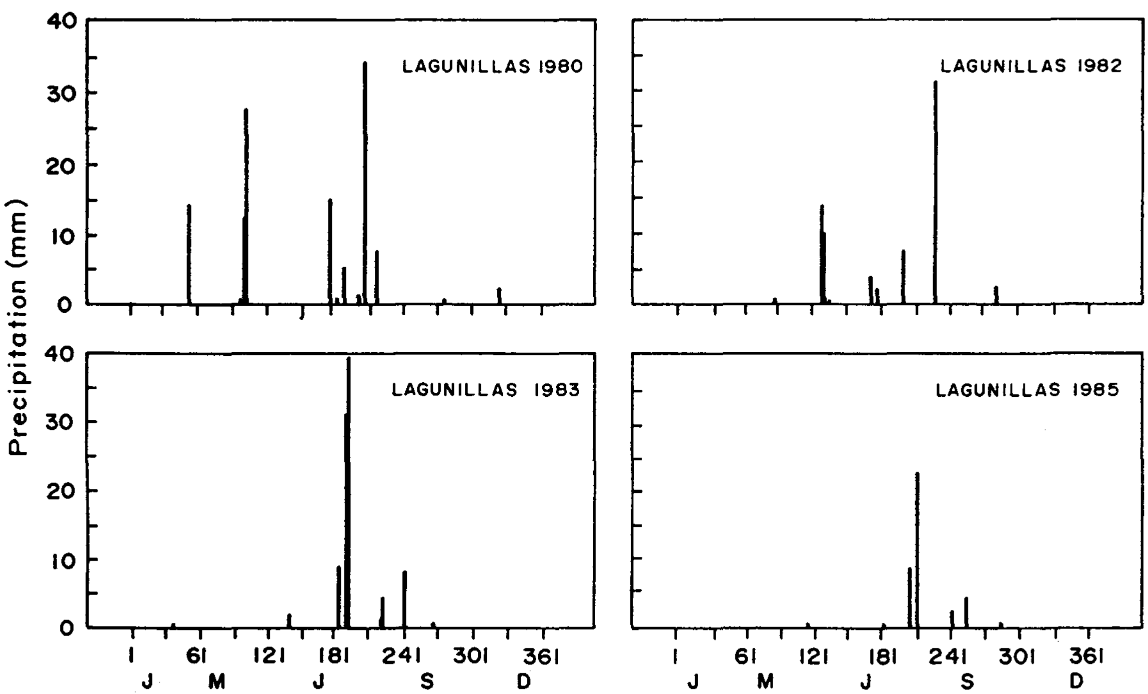

Fig. 3: Daily record of precipitation in Lagunillas (30°06'S) in the Chilean coastal desert for selected years. Horizontal axis labels are the day of the year starting on January 1st.

Registros diarios de precipitación en Lagunillas (30°06'S) en el desierto costero chileno durante años seleccionados. El eje horizontal indica los días del año, comenzando el primero de enero.

te the plant's life cycle. Failure to reproduce following germination in a desert ephemeral could, theoretically, lead to rapid local extinction (Cohen 1966). The threshold does not seem to change with latitude despite the fact that average annual rainfall decreases sharply northwards along the coastal desert. This result indicates that the response threshold may have evolved as a safety mechanism, independently of the total amount of rainfall accumulated over the year. Hence, the response threshold can be interpreted as the minimum amount of moisture provided by a single rainstorm which allows a plant to complete its life cycle, without additional inputs of moisture. Because air temperature shows very little latitudinal change within the coastal desert, it seems likely that the same moisture threshold evolved in plants irrespective of the site of origin.

TEMPORAL CHANGES IN THE PLANT COMMUNITY

Plant responses to temporal changes in soil moisture availability have not been documented for the Chilean coastal desert. However, anecdotal information indicates that the growth and flowering of desert ephemerals does not occur every year. The "blooming of the desert" in north-central Chile is a well known phenomenon which attracts increasing numbers of photographers and tourists to the coastal desert in wet years (Muñoz 1985).

For the first time, we are maintaining a continuous quantitative record of plant abundances within permanently marked plots at four sites separated by about 1° of latitude (Fig. 1), covering nearly the entire extent of the coastal desert receiving significant rainfall inputs in Chile. All the sites are located on coastal terraces, 1-2 km from the ocean, with a predominantly sandy soil derived from ancient dunes. Mean temperature varies little latitudinally (1-2°C), but mean annual precipitation decreases northwards from 130 mm (Lagunillas) to 24 mm (Copiapó). At each site, three 50 x 20 m plots were permanently marked with stakes. Vegetation was sampled in fourteen 1x1 m quadrats randomly located within each of the three plots, four of which were permanently marked. Only data from permanently marked quadrats at each site were considered in the present analysis.

Total cover

Records for the past three years (1989-1991) indicate that total plant cover varies tremendously depending on the amount of rain. Annual rainfall recorded in Lagunillas was 60 mm for 1989, 18 mm for 1990, and more than 100 mm for 1991. The temporal patterns of change in relation to rainfall are similar for the four localities studied, but the absolute cover values decrease from Lagunillas, in the south, to Rodillo, in the north (Fig. 4A-D). In 1989, Maximum plant cover occurred in late September and was over 60% in Lagunillas, 20% in Los Choros, near 30% in Carrizal Bajo, and less than 10% in Rodillo, the northernmost site. The increase in plant cover was less pronounced in Rodillo, as less rain reached the northernmost site. Total cover measured at the peak of the growing season was 3-5 times higher than that present during the dry season. Records from 1991 (Fig. 4) suggest that this difference may be even larger during wetter years.

In contrast, the increase in plant cover in the growing season of 1990 was reduced in Lagunillas (Fig. 4D) and Los Choros (Fig. 4C) and did not occur at all in Carrizal Bajo and Rodillo (Fig. 4A, B). At the two northernmost sites, rainfall in 1990 was less than 3 mm, that is, insufficient rain to stimulate plant growth. Thus, these results seem to agree with the conclusions from lab assays that more than 15 mm of rain (response threshold) are necessary to elicit seed germination and growth of coastal desert plants.

Life forms

Desert plants have developed strategies to cope with the uncertain moisture availability. Shrubs and Cactaceae represent a drought-tolerant strategy, while herbs, including both annuals and geophytes, may represent a drought-evader strategy. Drought-tolerant plants rely heavily on the survival of above ground parts and their resprouting ability to respond to moisture inputs, whereas drought-evaders depend entirely on underground dormant propagules. In this section we analyze the behavior of these two groups of plants in response to moisture variation in the Chilean coastal desert.

TABLE 1

Percent of the total number of seedlings

Porcentaje del número total de plántulas

STUDY SITES

Precipitation (mm)	Lagunillas		Los Choros		Carrizal Bajo		Rodillo	
	Natives	Weeds	Natives	Weeds	Natives	Weeds	Natives	Weeds
5	0.2	0.1	6.5	0	0	0	0	0
10	7.6	22.9	16.1	22.5	15.0	20.0	6.9	0
15	20.6	29.9	33.3	25.0	29.9	20.0	15.5	0
20	37.0	25.5	24.7	25.0	30.6	20.0	26.7	0
30	34.6	21.6	19.4	27.5	24.5	40.0	50.9	0
n =	422	2,957	93	40	147	5	116	0

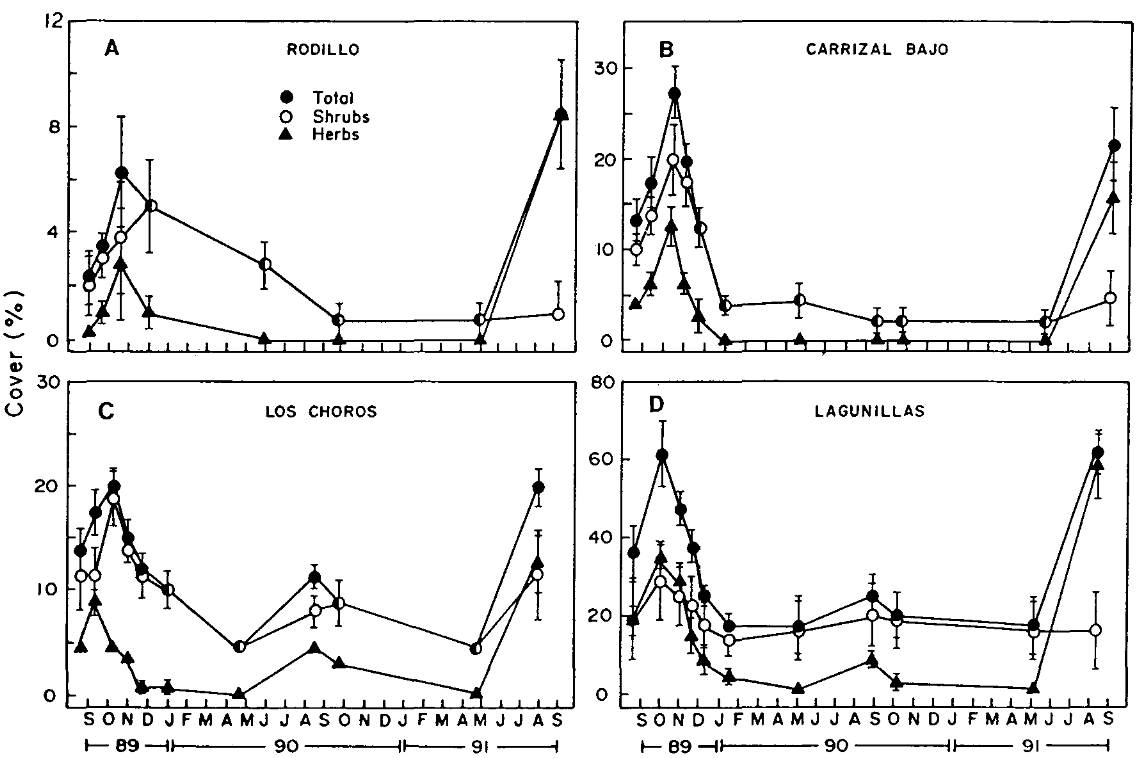

Fig. 4: Absolute cover (%) of vegetation in four sites of the Chilean coastal desert on three consecutive growing seasons. Cover was estimated visually in 12 permanently marked 1x1 m quadrats. Bars are ± 1 SE. Sites, from north to south, are (A) Rodillo, (B) Carrizal Bajo, (C) Los Choros y (D) Lagunillas. Notice the change of scale of the vertical axes.

Cobertura absoluta (%) de la vegetación en cuatro sitios del desierto costero chileno en tres estaciones de crecimiento consecutivas. La cobertura fue estimada visualmente en 12 cuadrantes de 1x1 m marcados en forma permanente. Las barras indican ± 1 EE. Los sitios, de norte a sur, son: (A) Rodillo, (B) Carrizal Bajo, (C) Los Choros y (D) Lagunillas. Note que las escalas del eje vertical varían entre los sitios.

Cover of drought-deciduous or tolerant shrubs increased almost synchronously with herb cover in 1989 at all sites (Fig. 4). Shrub cover decreased from south to north (30% in Lagunillas, 20% in Los Choros and Carrizal, and 5% in Rodillo). Peak cover for shrubs was higher than for herbs, except in Lagunillas, the southernmost locality, where herb and shrub cover were the same at the peak of the growing season (Fig. 4D). Herb cover decreases to near zero at all sites within four months after the wet season. In 1990, shrub and herb cover remained low in the two northernmost sites (Fig. 4A, B). This result indicates that, in some years, winter rains are insufficient to induce germination of

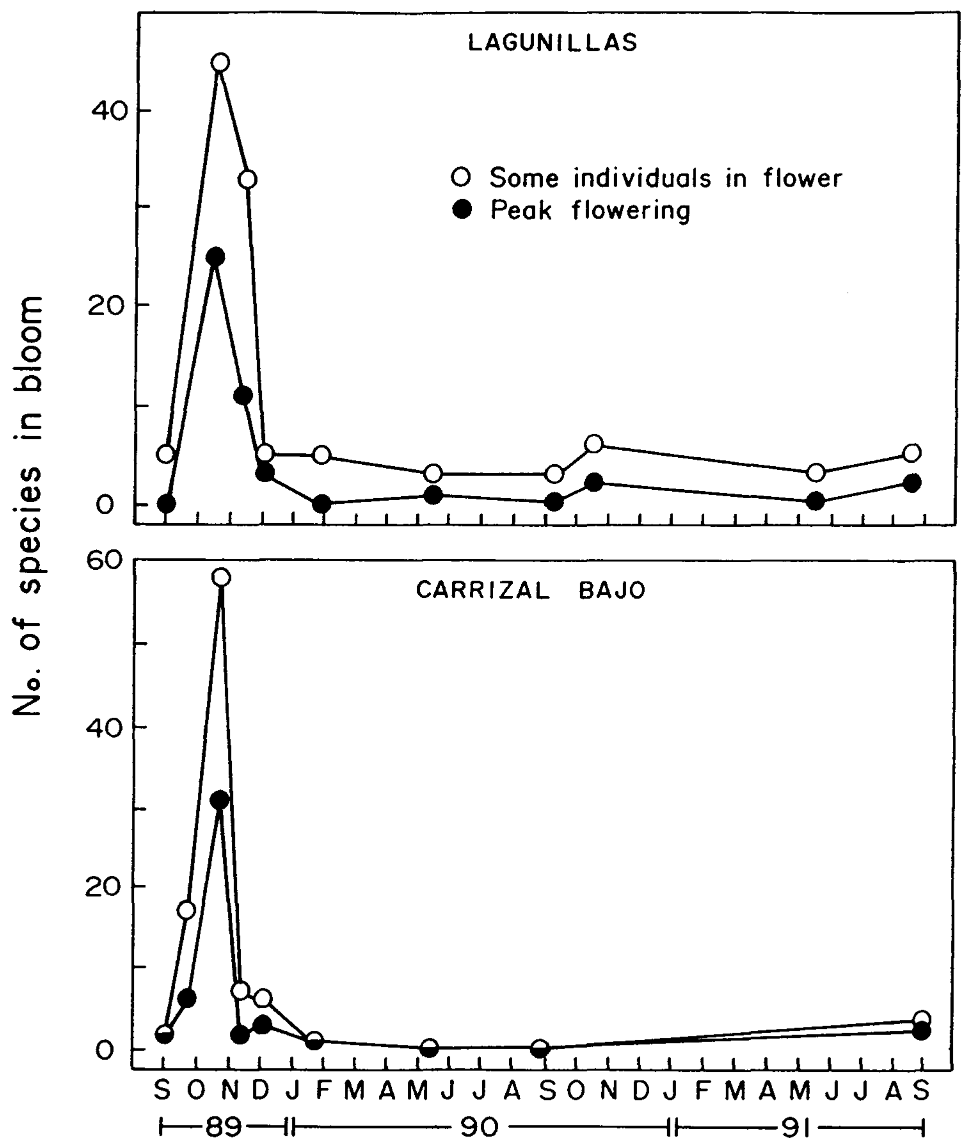

Fig. 5: Flowering patterns of the coastal desert plant community in Lagunillas and Carrizal Bajo on three consecutive years. Data shown are the number of species in bloom on each date, and the number of species which had their maximum number of individuals flowering on a particular date. Notice that none of the species flowered in Carrizal in 1990. Flowering was highly synchronous both among and within species.

Patrones de floración de las comunidades de plantas del desierto costero de Lagunillas y Carrizal Bajo en tres años consecutivos. Se muestra el número de especies en flor en cada fecha, y el número de especies con el máximo número de individuos en flor en una fecha en particular. Nótese que ninguna especie floreció en Carrizal en 1990. La floración fue sincrónica tanto entre las especies como en una misma especie.

ephemerals or growth of perennials in the northernmost sites in the coastal desert.

In 1991, after a one-year long drought, shrub cover did not increase as rapidly as herb cover (Fig. 4), except at Los Choros. These results and field observations indicate that a wet season following a long drought may favor the response of herbs, especially annuals and geophytes (drought-evaders), over shrubs (drought-tolerators). We have observed that long droughts may reduce the ability of shrubs to grow back from above-ground or near ground tissues after the rain. Some species (e.g., *Encelia tomentosa, Cristaria* spp.) may shed most or all of their foliage and stems over the dry period. In some cases, the entire shrub appears to die leaving a "ghost" of dry branches. At all sites, but especially in the northern localities, we observed the establishment of herbs around these ghosts of shrubs. It is possible that organic matter deposited under shrubs may favor the growth (and germination?) of herbaceous plants after the rains (e.g., Gutiérrez 1993). This effect can be more important in the northern range of the coastal desert, where droughts are longer and more severe.

Phenology

We compared the flowering patterns of species at the two sites showing the highest species richness in the coastal desert, Lagunillas and Carrizal (see below). Flowering occurs very rapidly following the establishment of annual species. Between 40 and 60 species are found in bloom within one month after the rain (Fig. 5). The peak is very pronounced indicating that most ephemeral plants start flowering shortly after emergence. Maximum flowering (the "blooming of the desert") occurs in early October at both sites, regardless of the difference in latitude. This is due to the similar timing of rainfall at all latitudes in the coastal desert. Flowering seems to be highly synchronous within species as shown by the coincidence between the maximum number of species in flower and the number of species in peak flowering, The flowering period seems to be more extended in Lagunillas, as species were found in flower throughout the year (Fig. 5). Few species were able to flower in Lagunillas in 1990, and no flowering was recorded in Carrizal (Fig. 5).

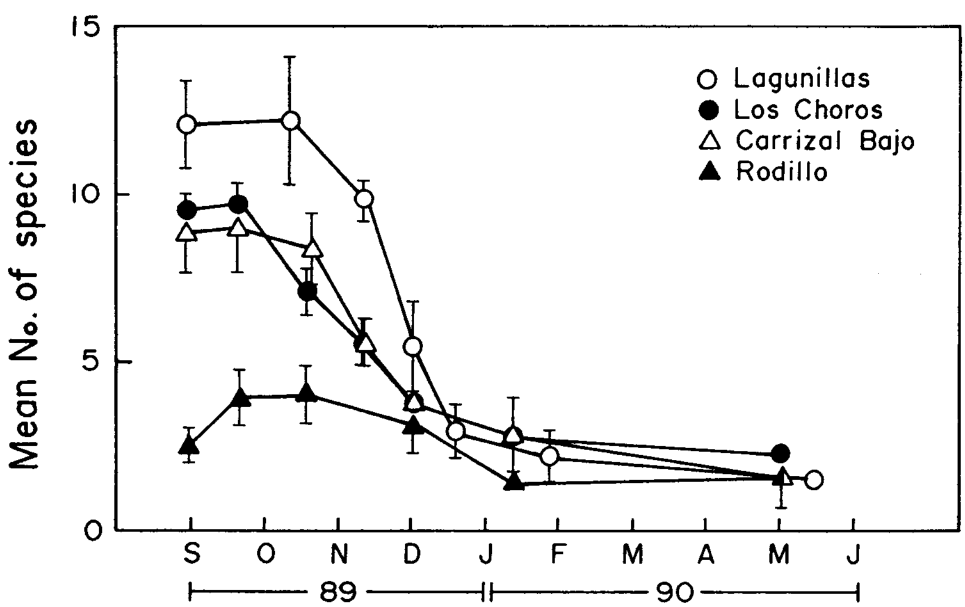

Fig. 6: Changes in the mean number of species per plot during the growing season of 1989-90 in four sites of the fog-free Chilean coastal desert. Bars are ± 1 SD.

Variaciones en el número promedio de especies por parcela durante la estación de crecimiento de 1989-90 en cuatro sitios del desierto costero chileno sin influencia de neblina. Las barras representan ± 1 DE.

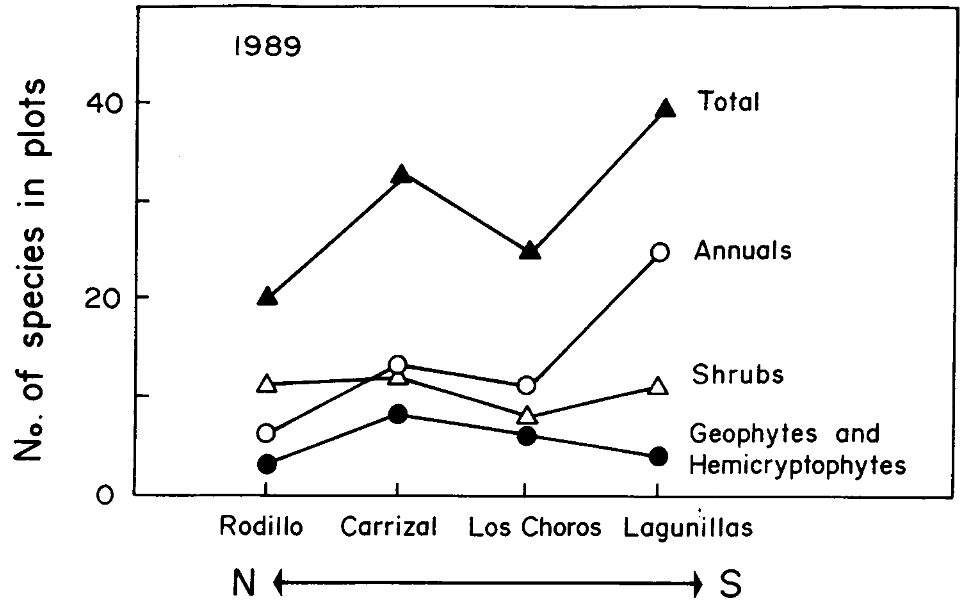

Fig. 7: Latitudinal changes in species richness in the fog-free Chilean coastal desert, and number of species of different life forms.

Cambios latitudinales en la riqueza de especies en el desierto costero chileno sin influencia de neblina y número de especies de las diferentes formas de vida.

COMMUNITY ASSEMBLAGE AND FLORISTICS

The assemblage of desert communities following the rain can be analogous to the successional recovery of a community after a disturbance, from a propagule and bud bank (Pickett & White 1985). In the coastal desert all ephemeral species appear soon after the rains (Fig. 6). Maximum species richness is reached within one month and decreases rapidly afterwards. This model of community development resembles the "initial floristics" model of successional change (Burrows 1990), where temporal differences in community structure are related to differences among the species in the time required to complete their life cycles rather than to delayed establishment. Thus, selection for an early start may have prevailed among coastal desert ephemerals, since site preemption can be as important as in early succession in determining species composition.

Annual plants are more important components of the community in the southern border of the coastal desert (Fig. 7), where they may represent more than 60% of all the species present. They decrease in importance northwards, at the same time that the relative importance of shrubs increases.

In terms of the total number of species, the latitudinal gradient studied shows two peaks, one in Lagunillas, and one in Carrizal Bajo (Fig. 7). Shrubs do not show any significant latitudinal trend, but the number of species of annuals decreases to less than 1/3 from Lagunillas to Rodillo. The maximum species richness of geophytes (8 species) is found in the plots of Carrizal Bajo (Fig. 7), in the central portion of the gradient.

The high number of species in Lagunillas may be inflated because of the abundance of exotic weeds, mostly of a mediterranean origin, which are associated with the longer history of dry farming and livestock raising at the southern range of the coastal desert (Armesto & Vidiella 1993). About 25% of the species in Lagunillas are alien (Fig. 8), but the number of weeds falls abruptly northwards as the human impact becomes less significant. No alien weeds were present in the study plots in Rodillo.

The coastal desert flora is high in endemism: between 40 and 60% of the genera appearing in the plots are endemic to Chile (P. E. Vidiella,

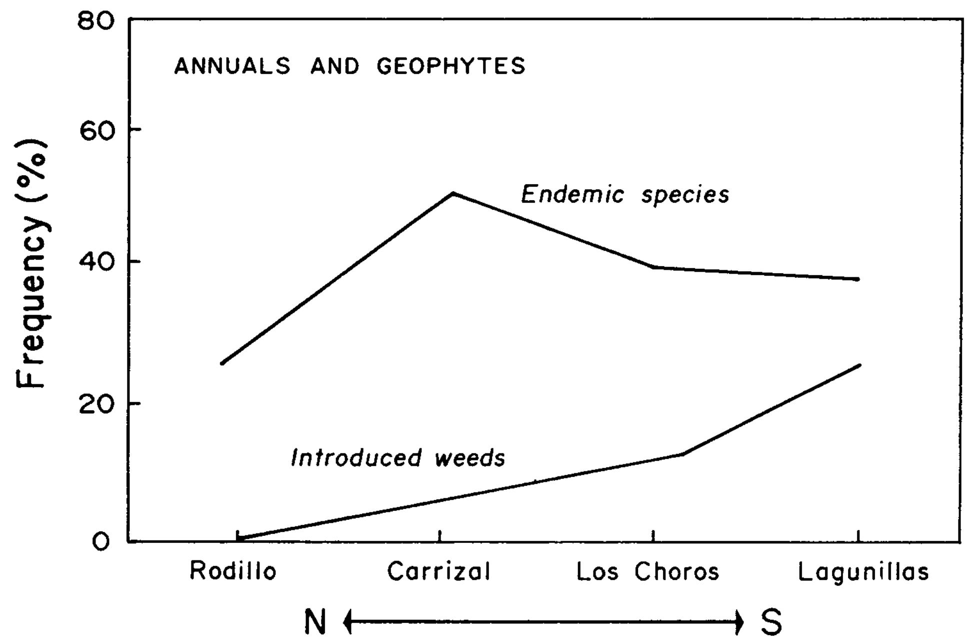

Fig. 8: Relative importance of endemic species and introduced weeds in four sites of the Chilean coastal desert. Endemic species are a conservative estimate based on endemic genera listed in Marticorena (1990).

Importancia relativa de las especies endémicas y malezas introducidas en cuatro sitios del desierto costero chileno. Las especies endémicas representan una estimación conservadora basada en los géneros endémicos listados por Marticorena (1990).

unpublished). The number of species belonging to endemic genera shows a peak in Carrizal Bajo (Fig. 8). Thus, the coastal desert plant communities seem to have their maximum richness in Carrizal. Further south, in Lagunillas, plant communities are strongly influenced by human impact, whereas in the northern range of the coastal desert species richness becomes reduced because of the low rainfall and extremely uncertain environment.

CONCLUSIONS

The study shows that drought-evader plant species (annuals and geophytes) are very important components of the plant communities in the Chilean coastal desert, comprising more than 60% of all the species, and one half of the plant cover at its peak following rainfall. Drought-tolerants are represented mainly by drought-deciduous shrubs, which tend to be more important towards the drier, northern end of the grandient. A comparison of shrub and herb responses to rainfall in the three years of study indicate a possible relationship between these two groups of plants. In dry years, as in 1990, no growth occurs, and shrubs tend to discard their above-ground tissues. Organic material accumulated under shrubs during dry periods appears to enhance herb responses in subsequent wet years. In this light, extraction of dry shrub material for use as fuel, as it has occurred in many areas, particularly in the south of the coastal desert (e.g., Bahre 1979), may have negative effects on the development of ephemeral communities in rainy years. It is possible that the resprouting ability of many shrubs may also require the presence of organic debris from previous growth.

Because of the pattern of atmospheric circulation, northern localities tend to receive less quantity and frequency of rains. Thus, in some years plant communities may only develop in the southern range of the coastal desert. As a consequence, we can postulate that soil seed banks in the northern range of the desert may be older than in the south.

Plants native to the desert will only respond to rains higher than a minimum threshold for physiological activity. This threshold seems to be 15 mm, according to lab assays (Vidiella 1992). In the field, however, due to the increased evaporation this threshold may be somewhat higher. Records of plant responses to rainfall over the three years of study indicate that the field threshold may be around 20 mm of rain. Records for 1990 show limited plant growth and almost no flowering with less than 20 mm of rain.

The only two protected areas (Fray Jorge and Pan de Azúcar National Parks) in the coast of the semiarid region of Chile today are located in the southern and northern extremes (31° and 26°S). The high species richness and the concentration of endemic taxa found in Carrizal Bajo (Fig. 1) calls for the creation of a protected area in the central part of the coastal desert. Such a protected area should be suited for the long-term monitoring of climatic variables and community response to the fluctuating desert environment.

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