Journal of Arid Environments (1999) 43: 449–458
Article No. jare.1999.0565
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Vegetation changes and sequential flowering after rain in the southern Atacama Desert

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(Received 4 January 1999, accepted 1 July 1999)

We describe the changes in plant cover, species richness, and flowering after rainfall over an entire growing season (September 1989–January 1990) in a southern Atacama Desert site in Chile. One month after the rain, vegetation was dominated by annuals and geophytes which dried out after 19 weeks. Among all species, including shrubs, we found differences of 4–10 weeks in the length and peak of the flowering period. The flowering sequence of the species belonging to the families Brassicaceae, Liliaceae, Onagraceae, and Asteraceae matched closely the sequences described for temperate plant communities, suggesting that this phenological character is phylogenetically determined.

Keywords: coastal desert; Chile; annuals; geophytes; precipitation; vegetation dynamics; flowering periods; phylogenetic constraints

Introduction

In desert ecosystems, short and infrequent pulses of rainfall result in increased soil moisture levels that regulate the pattern of productivity of desert biota (Noy-Meir, 1973). After rainfall, productivity may be extremely high, supporting a rich but short-lived biotic assemblage (Went, 1955; Beatley, 1969; Raugh, 1985; Shmida, 1985). A major proportion of the biota remains dormant during the intervening periods between rain pulses. The coast of the southern Atacama Desert (26–32°S) is characterized by 2 to 5 years of drought (Vidiella, 1992) followed by marked increases in plant cover after winter precipitation events of at least 15 mm (Vidiella & Armesto, 1989; Vidiella, 1992). The responsive plant species are primarily short-lived annuals, bulbous geophytes, and summer dormant shrubs (Armesto *et al.*, 1993). Their fast growth and abundant flowering after rainfall is a phenomenon locally known as the 'blooming of the desert' (Muñoz, 1965; Solbrig, 1976; Raugh, 1985; Muñoz, 1991), which has important ecological and economic implications for the region. It represents a sharp increase in the resources available to the local trophic web (e.g. herbivores, frugivores, pollinators, detritivores) as well as to domestic livestock, all of which may depend on this short period of high plant productivity. Despite the ecological importance of this phenomenon for the coastal desert of Chile, we know of no published information regarding the patterns and mechanisms of plant response to rain. Data on the sequence of species emergence, and the magnitude and length of a given blooming event in relation to the timing and amount of rainfall pulse are completely lacking. Botanists have noticed that, even though the growing season is short, not all species flower at the same time (Muñoz, 1991). This observation has been based on few species and, usually, on one short visit to different sites. No study has been conducted in this area to determine the flowering patterns of a plant community during an entire growing season in one site.

In this study, we report on vegetation surveys conducted in a coastal site during one growing season produced by a late winter rain pulse (early August 1989). We chose the locality of Carrizal Bajo as our study site because it shows the highest species diversity along the coast of the southern Atacama Desert (Armesto *et al.*, 1993). We designed the survey to answer the following questions: (1) what is the length of the growing season for the plant community? (2) what is the sequence of establishment of the different species? (3) how do plant cover and species richness change during the growing season? and (4) are the flowering patterns different among species?

Methods

Study area

The study was conducted at Carrizal Bajo (28° S) (Fig. 1), a coastal site in the southern part of the Atacama Desert, between the cities of Vallenar (28°35′ S) and Copiapó (27°21′S). The study site is located on a flat marine terrace, covered by fossil dunes over a bed of marine sediments (Paskoff, 1970), a geologic formation characteristic of this area. The general climate of the southern coast of the Atacama Desert (26–32° S) is arid with a Mediterranean influence, characterized by long dry periods and irregular and short rainfall events concentrated during the winter months (May–August) (Fuenzalida, 1965; Schneider, 1969; di Castri & Hajek, 1976). There is no rain during most of the year due to the overriding influence of a subtropical, high pressure cell located over the South Pacific (Trewartha, 1961; Fuenzalida, 1965; Schneider, 1969). Between the southern-most (30° S) and the northern-most (26° S) coastal localities, mean annual precipitation ranges from 131 to 23 mm (Almeyda, 1950). The amount and distribution of precipitation are also highly variable between and within years (Vidiella, 1992; Armesto *et al.*, 1993). Relative humidity and temperature are less variable than rainfall; mean annual relative humidity is about 70–80%, and mean annual temperature ranges from 14·7 to 16·1°C (Fuenzalida, 1965; di Castri & Hajek, 1976). Temperature fluctuations are low, both daily and yearly, due to the stabilizing effect of the cold Humboldt Current which runs parallel to the Chilean coast (Almeyda & Saenz, 1958; Fuenzalida, 1965; Schneider, 1969). Because there are no rainfall records for the area of Carrizal Bajo, we used long-term records available for the nearest cities of Vallenar and Copiapó located 112 km south-east and 158 km north-east of the study site, respectively. Mean annual precipitation ranges from 55 mm (CV = 73%, 26 years) in Vallenar to 25 mm (CV = 94%, 74 years) in Copiapó (Almeyda, 1950; Vidiella, 1992). For 1989, recorded rainfall was 29·2 and 16·5 mm in Vallenar and Copiapó, respectively (Muñoz, 1991). Most of the rain occurred in a single event (within 24 hours) in early August (Vallenar received 20·5 mm, Copiapó received 16·4 mm). We assume that plant responses are a direct consequence of this late winter rainfall event. Although the annual precipitation in 1989 was lower than the average for both cities, these values are above the suggested threshold level of 15 mm required to trigger emergence of ephemeral plant species in the Chilean coastal desert (Vidiella, 1992).

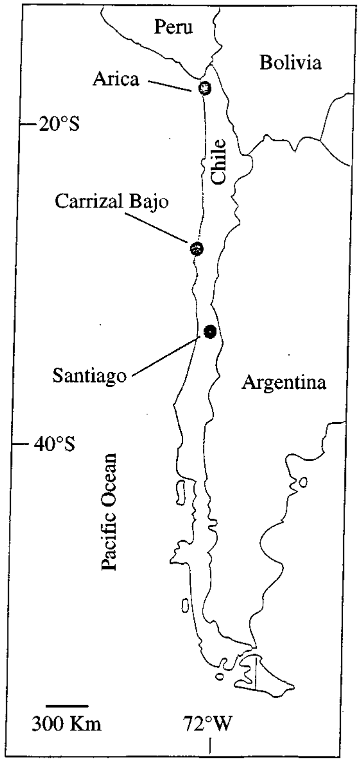

Figure 1. Location of Carrizal Bajo in the coast of the southern Atacama Desert.

Vegetation sampling

During the growing season (September 1989–January 1990) the vegetation was sampled six times (on 8 and 29 September, 29 October, 19 November, 9 December, and 17 January) over a period of *ca.* 19 weeks, and once again on 7 May 1990, before the start of the rainy season. On each sampling date, plant cover (%) and species composition were recorded in 14 quadrats (1 m^2) randomly located in each of three permanent plots (50×20 m each). Plant cover was estimated according to Braun-Blanquet's cover abundance scale (Mueller-Dombois & Ellenberg, 1974). The nomenclature for species names followed Marticorena & Quezada (1985), except for *Nolanaceae,* which followed Mesa (1981). Flowering periods and dates of flowering peak were recorded for each species present in the plots. At least 20 individuals per species were observed on each sampling date. For each species, the flowering period was defined as the time when $\geq 5\%$ of the individuals were in flower, and peak flowering as the time when $\geq 50\%$ of the individuals were in flower.

Results

Plant cover and species richness

After the rain, the growing season lasted for *ca.* 19 weeks. At first there was a rapid increase in mean plant cover in all plots, reaching a peak of 23·6% by late October (Fig. 2),

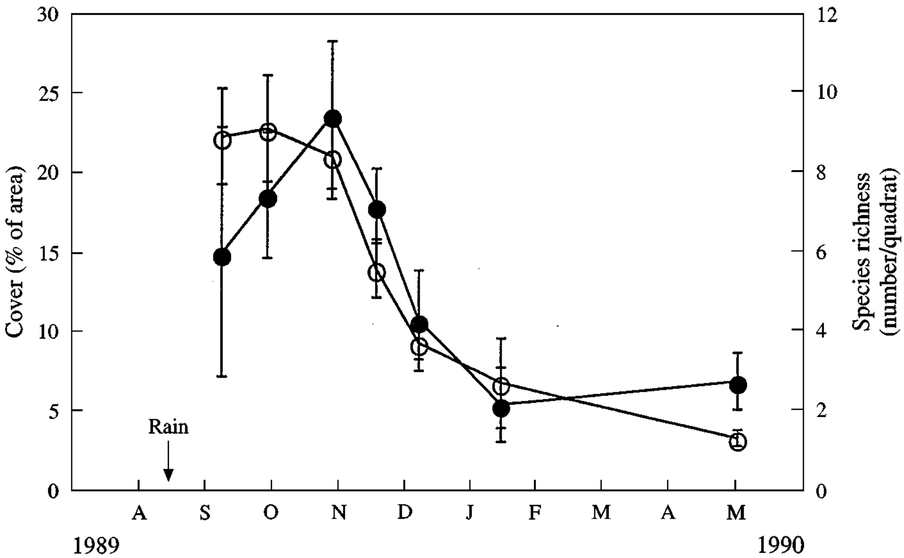

Figure 2. Mean plant cover (●) and mean species richness (○) per quadrat (1 × 1 m) during the growing season in the study site. Vertical lines are ± 1 S.D. The *x*-axis corresponds to the months elapsed since the first sampling date on 8 September 1989 (1 month after the rain).

i.e. 2 months after the triggering rainfall event. From November to January, total plant cover decreased rapidly to its lowest value of 5·4%. All the plant species recorded in the plots were present from the first date of sampling (Fig. 2), approximately 1 month after the rain. There was a rapid decline in the mean number of species per quadrat, from 9 species in September to 3 species in January, and to only 1 species in May (Fig. 2).

A total of 36 plant species were recorded within the three permanent plots: 15 annuals, 12 shrubs, 8 geophytes, and 1 parasite. The number of shrub species remained constant during the sampling period, while the number of annuals and geophytes declined abruptly after mid-November (Fig. 3).

Flowering periods

There were species in flower during the entire sampling period, from September 1989 to May 1990 (Fig. 4). About one half of the species began to flower in late September. The flowering peak (≥ 50% of the individuals in bloom) of the whole community occurred about 2 months after the onset of the growing period, and coincided with the time of the maximum number of species in flower in the community (Fig. 4).

In Fig. 5 we show the 25 most abundant species in the plots classified according to their flowering patterns (length and date of peak), into three different groups or 'blooming guilds'. Group 1 shows the species with a flowering peak in late September (i.e. *Schizopetalon gayanum* and *Hippeastrum bagnoldii*); group 2 shows the species with a peak in late October (i.e. *Zephyra elegans*, *Cristaria glaucophylla*, and *Encelia canescens*); and group 3 shows the species with a flowering peak near the end of the growing season, that is, between mid-November and early December (i.e. *Chaetanthera limbata*, and *Frankenia chilensis*). All individuals of the earliest flowering species (not shown in Fig. 5), the geophyte *Oxalis maritima*, were in bloom on 8 September 1989, and again on 7 May 1990, but no individuals were found in flower between these two sampling dates.

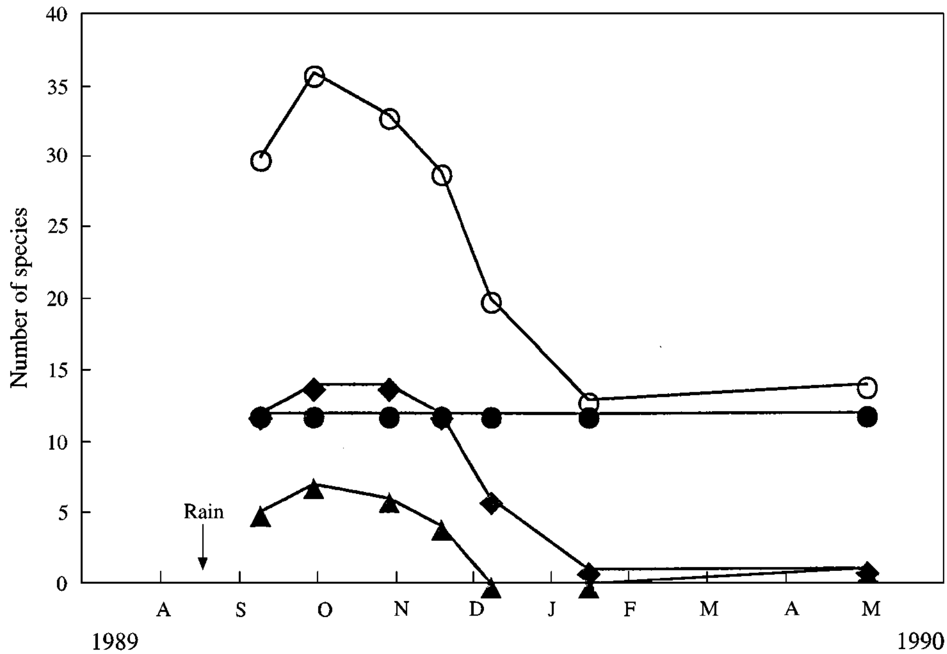

Figure 3. Total number of species (○), shrubs (●), geophytes (▲), and annuals (■) recorded in all the plots sampled during the growing season 1989–1990 in Carrizal Bajo.

Discussion

Our data show that a late winter rain event of *ca.* 20 mm triggered the emergence, growth, and flowering of plant species in a coastal site of the Atacama Desert. Laboratory assays, conducted with soil samples containing the seed bank from the study site, indicated abundant emergence of seedlings as a consequence of simulated rainfall pulses of 15 mm (Vidiella, 1992). This threshold of 15 mm is lower than the 25 mm reported for desert plant communities of India (Gupta, 1979) and North America (Went, 1949; Tevis, 1958; Beatley, 1974; Gutiérrez & Whitford, 1987). The discrepancy could be related to differences in the germination requirements of plant species, or to differences in evapotranspiration levels between deserts. For instance, lower temperature and higher cloudiness in the coastal Chilean Desert than the Mojave or Chihuahuan Desert could translate to lower evapotranspiration and consequently more available water from a given rainfall for seed germination and plant establishment (Vidiella, 1992).

Plant species richness and cover changed markedly throughout the growing season, due mainly to the emergence and growth of annuals and geophytes (Fig. 3). During the dry period these species remain dormant in the soil as seeds and bulbs, respectively, and therefore are undetectable until their emergence after the rain. Since all species became established during the first month of sampling, the increase in plant cover observed in the first 8 weeks of the study was a consequence of further growth and recruitment of species of annuals and geophytes already established, rather than the addition of new species to the plots (Fig. 2). If we make an analogy between the pattern of vegetation change in the southern Atacama Desert and the changes in plant community during succession, the pattern of species establishment fits with the Initial Floristic Composition model (Connell & Slatyer, 1977; Egler, 1954), which states that all species become

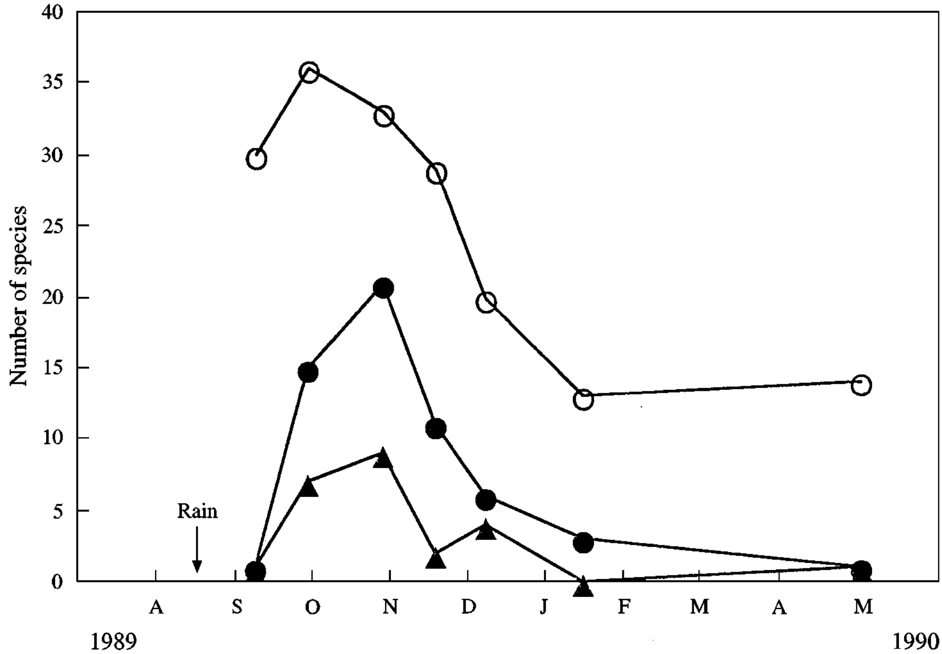

Figure 4. Total number of species (○), species flowering (●, ≥ 5% of individuals in flower), and species in flowering peak (▲, ≥ 50% of individuals in flower) within the plots sampled at the study site.

established early in the growing season, although they differ in their time of flowering, subsequent recruitment, and growth. These differences result in separate peaks of activity and cover during the growing season.

Comparable plant dynamics have been described in the winter-rainfall zone of the Succulent Karoo of South Africa. Like in our study site, the growing season in this area is triggered by winter rains and most species reach their flowering peak in the spring (van Rooyen *et al.*, 1979; Le Roux *et al.*, 1989; Milton *et al.*, 1997). In terms of life forms, the plant communities at the Succulent Karoo and Carrizal Bajo have similar composition and relative proportions, but they exhibit slight differences in their phenological sequences. In both areas, annuals were the most abundant species followed by shrubs and geophytes: 39·4%, 39·2%, and 21·4% respectively, for the Succulent Karoo (van Rooyen *et al.*, 1979) and 41·7%, 33·3%, and 22·2% for Carrizal Bajo. However, in the Succulent Karoo, annual species were the first group to complete their growing cycle, followed by geophytes and shrubs (van Rooyen *et al.*, 1979). In Carrizal Bajo, geophytes were first to become dormant, followed by annuals, and lastly by most shrubs (data not shown).

Although species were flowering throughout the entire period of our study in Carrizal Bajo, the peaks and lengths of their blooming times varied among the different species. The sequence of flowering does not seem to be related to differences in growth form, since annuals, geophytes, and shrubs are found in all three blooming guilds, except for geophytes which are absent from the group that flower later in the growing season. Moreover, most shrub species began flowering early in the season, but their peaks occurred at various times throughout the study period. The same pattern has been observed for shrubs in the Succulent Karoo, however most annuals were found in full bloom in early spring, and geophytes reached their flowering peak during late spring

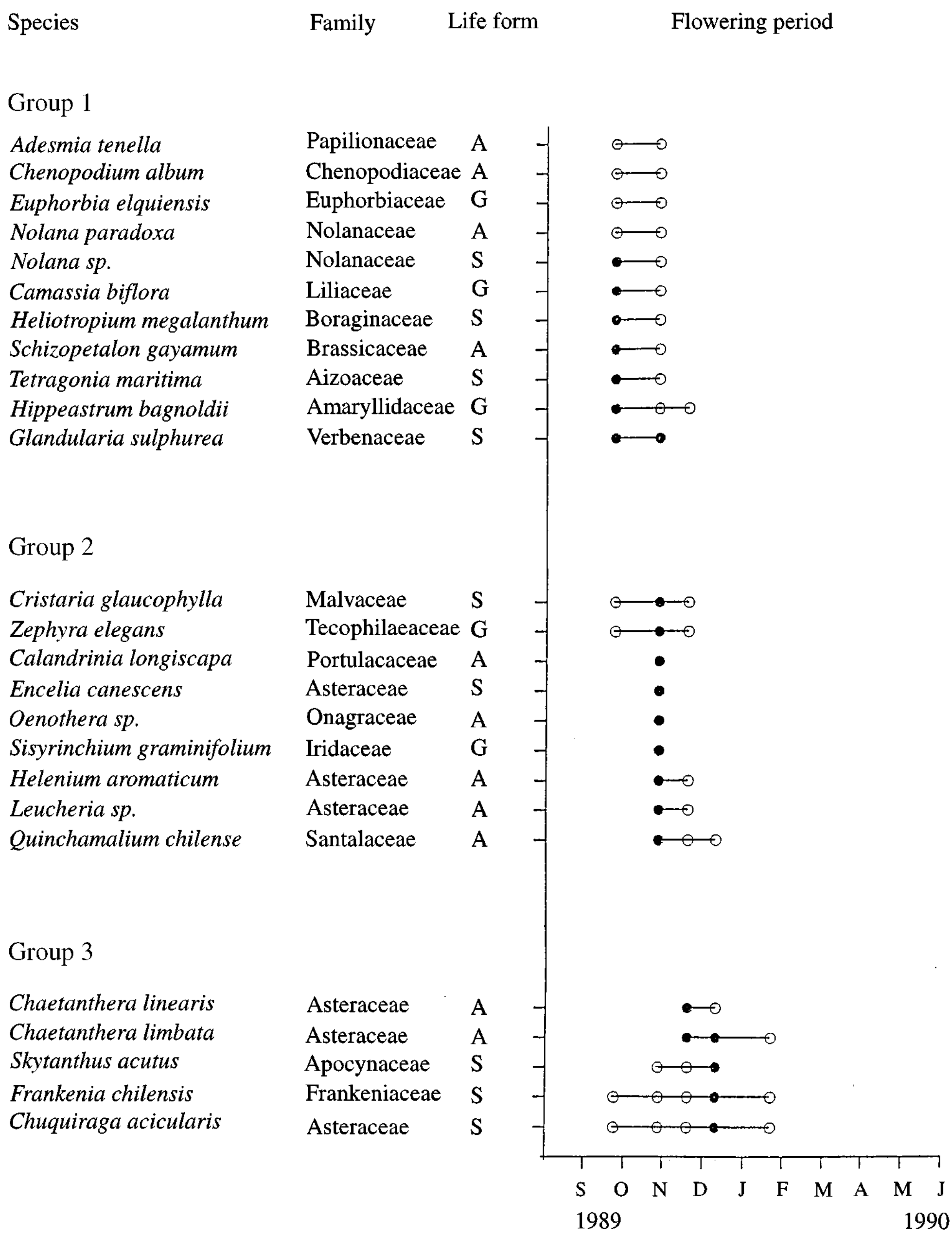

Figure 5. Flowering patterns for the most abundant plant species growing in the study site. The flowering periods ($\geq$ 5% of individuals in flower) are shown with open circles, and the date when the species were found in flowering peak ($\geq$ 50% of individuals in flower) are shown with filled circles. Life forms: A = annual, G = geophyte, and S = shrub.

(van Rooyen *et al.*, 1979). We suggest that the difference in the phenological patterns found between both areas could be related to differences in the length of their growing seasons, which are closely related to their rainfall regimes. The precipitation pattern in the winter-rainfall zone of the Succulent Karoo is comparable to the one at our study site, with the exception that the amount of annual rainfall is higher and more reliable, and that rain is concentrated, but not restricted, to the winter months (van Rooyen *et al.*, 1979; Le Roux *et al.*, 1989; Vidiella, 1992; Milton *et al.*, 1997). In fact, substantial rain promoting the growth of all life forms could occur as early as the end of the summer and as late as the end of the spring, producing a considerable extension of the growing season in the Succulent Karoo (van Rooyen *et al.*, 1979). An extended growing season with more reliable precipitation could result in less overlapping of the phenological patterns of the different species compared to a shorter growing season with reliable precipitation, where all species would have a small window to complete the growing cycle before the onset of the dry season.

The sequence of flowering peaks of the species recorded in Carrizal Bajo agrees with the sequence observed in animal-pollinated angiosperm floras of North and South Carolina (U.S.A.) and temperate Japan (Kochmer & Handel, 1986). Despite the obvious differences in species composition and life forms between the communities studied by Kochmer & Handel (1986) and the plant community in Carrizal Bajo, the flowering sequence of species ordered by families in the coastal desert closely matches that of North American and Japanese temperate plant communities. Brassicaceae and Liliaceae are the earliest flowering species, whereas Onagraceae and Asteraceae flowered late in the growing season. Phenological studies of perennial species from the Mediterranean vegetation of southern France (Floret *et al.*, 1989), Israel (Orshan, 1989), Cape Province of South Africa (Le Roux *et al.*, 1989), and central Chile (Montenegro *et al.*, 1989) also show analogies in their flowering pattern with species from the same families occurring in our study site. Similar to our results in Carrizal Bajo, the families that concentrated their flowering period early in the growing season were Euphorbiaceae (represented in France, South Africa, and central Chile), Boraginaceae and Liliaceae (both in France), Aizoaceae (in South Africa), and Amaryllidaceae (in central Chile), while most of the species of Asteraceae described in all four regions flowered later in the growing season. In the winter-rainfall zone of the Succulent Karoo, species from Brassicaceae and Euphorbiaceae also flower earlier in the season, however, the flowering times of species in the families Asteraceae and Liliaceae do not seem to be restricted to a specific period within the growing season (van Rooyen *et al.*, 1979). Our results suggest that flowering times in the southern Atacama desert might be subject to strong phylogenetic constraints, but long-term data would be needed to determine if the flowering patterns are consistent with this hypothesis or if the patterns are dependent upon rainfall regimes.

This research was funded by The National Geographic Society, U.S.A. Final writing was supported by FONDECYT 197-0576 to JRG. We appreciate the assistance of H. Vásquez in the field, and G. Arancio in the identification of plant species. We are deeply grateful to S. Dhillion, S.T.A. Pickett, T. Dawson, E. Grote, and S. Milton for their constructive criticism and contributions to earlier versions of the manuscript.

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