Factors affecting establishment of a gypsophyte: the case of *Lepidium subulatum* (Brassicaceae)[1]

Adrián Escudero,[2,5] José M. Iriondo,[2] José M. Olano,[3] Agustín Rubio,[4] and Roberto C. Somolinos[2]

[2]Departamento de Biología Vegetal, Escuela Universitaria de Ingeniería Técnica Agrícola, Universidad Politécnica de Madrid, Madrid, E-28040, Spain;
[3]Departamento de Biología Vegetal y Ecología, Universidad del País Vasco, Apdo. 644, Bilbao, E-48080, Spain; and
[4]Departamento de Silvopascicultura, Laboratorio de Edafología, Escuela Técnica Superior de Ingenieros de Montes, Universidad Politécnica de Madrid, Madrid, E-28040, Spain

The restriction of vascular plants to gypsum-rich soils under arid or semiarid climates has been reported by many authors in different parts of the world. However, factors controlling the presence of gypsophytes on these soils are far from understood. We investigated the establishment of *Lepidium subulatum*, a gypsophyte, in a nondisturbed semiarid gypsum-soil landscape in central Spain, both from spatial and temporal perspectives. Over 1400 seedlings were tagged, and their growth and survival were monitored for a 2-yr period. Several biotic and abiotic variables were measured to determine the factors controlling the emergence and early survival. These variables included the cover of annual plants, bryophytes, lichens, litter, gypsum crystals, bare fraction and cover of each perennial plant, and several soil properties (gravel, fine gravel, and fine-earth fraction, conductivity, pH, gypsum content, organic matter and penetrometer soil resistance). Our results support the linkage of gypsophily with some physical properties of the surface crust. Seedlings tended to establish on the gypsum surface crust, and their survival was size dependent, probably as a consequence of the necessity of rooting below the surface crust before summer drought arrives. However, once seedlings emerged, a higher survival rate occurred on the alluvial soils of the piedmont-slope boundary where soil crusts are absent or thinner. We conclude that *Lepidium subulatum* may be considered a refuge model endemic with a distribution range that occupies a reduced fraction of a wider habitat from which it is probably excluded by competition.

Key words: Brassicaceae; gypsophily; gypsum-rich soils; *Lepidium*; penetrometer soil resistance; seedling growth; seedling survival; structural equation modeling.

Soil endemics of arid systems have received remarkably little study (Meyer, 1986; Meyer and García-Moya, 1989; Meyer, García-Moya, and Lagunes, 1992), in spite of their abundance in local floras (Meyer, 1989). Furthermore, studies on the critical early stages of these plants are almost absent (Escudero, Pérez-García, and Carnes, 1997; Escudero et al., 1999). For the last two decades, a model describing the establishment of desert plants has been developed. This involves some biotic interactions such as competition (Fowler, 1986; Kadmon and Shmida, 1990; Paruelo and Sala, 1995; Goldberg and Novoplansky, 1997), and facilitation (Franco and Nobel, 1989; Callaway and D'Antonio, 1991; Valiente-Banuet et al., 1991; Puignaire, Haase, and Puigdefábregas, 1996). The relative importance of competition vs. facilitation is a key factor in explaining the establishment of these plants, because individuals may either compete for resources with new seedlings or facilitate establishment (Aguiar and Sala, 1994, 1997; Callaway et al., 1996; Callaway, and Walker, 1997). On the other hand, from a temporal perspective, the establishment of plants requires not only the availability of propagules, but the occurrence of favorable climatic events, such as unusually heavy rains during certain seasons (Jordan and Nobel, 1979, 1981; Goldberg and Turner, 1986). As a consequence, populations of desert perennial plants may be composed of cohorts established in successful years, with wide temporal gaps between events. This widely accepted model has not been tested in soil endemic plants of arid systems (Escudero et al., 1999). Thus, two questions that arise are whether the establishment of soil endemics follows this model and what the factors determining the restriction of these soils are.

Gypsophytes represent one of the most conspicuous sets of arid soil endemic plants (Jonhston, 1941; Parsons, 1976; Powell and Turner, 1977; Meyer, 1986; Meyer and García-Moya, 1989). These plants are confined to gypsum soils or gypsosols, which extend over 100 million ha in the world (Verheye and Boyadgiev, 1997) and are mainly composed of narrowly distributed and threatened species (Meyer, 1986). Gypsosols are characterized by a gypsum (hydrous calcium sulfate) content over 5%. Several authors (Meyer, 1986; Verheye and Boyadgiev, 1997) have suggested that the existence of a hard surface gypsum crust may inhibit seed germination of nongypsophytes, whereas gypsophytes may be able to could surpass

the soil crust. Anyhow, direct evidence of the relationship between gypsum crust strength and emergence and survival of gypsophytes has rarely been reported (Escudero et al., 1999). The ability of adult gypsophytes to persist under certain chemical restrictions of gypsum soils has also been stressed (Duvigneaud and Denaeyer-De Smet, 1966, 1968; Boukhris and Loissant, 1970; Cannon, 1971). However, recent field studies show little evidence of this type of soil restriction (Meyer, 1986; Meyer, García-Moya, and Lagunes, 1992; Verheye and Boyadgiev, 1997). The effect of soil properties and microhabitat features (litter, lichens, bryophytes, bare fraction, and gypsum crystals cover) on earlier life stages of gypsophytes needs to be tested.

Thus, in the present study, several specific questions about the establishment pattern, both from spatial and temporal perspectives, of a widely distributed and non-threatened gypsophyte, *Lepidium subulatum* L. were posed. The main hypotheses were evaluated in this study using structural equation modeling (SEM), taking into account a priori knowledge based on other studies of gypsophytes (Jonhston, 1941; Parsons, 1976; Powell and Turner, 1977; Meyer, 1986; Meyer and García-Moya, 1989) and our experience with these plants (Escudero, Pérez-García, and Carnes, 1997; Escudero et al., 1999). We hypothesized that since gypsum soils are characterized by the presence of a gypsum crust, soil strength is a primary factor affecting emergence. Furthermore, we hypothesized that soil resource availability and microhabitat affect emergence and survival. From the perspective of biotic interactions, competition by annuals has been shown to be an active factor limiting emergence of other Iberian gypsophytes (Escudero et al., 1999), so the cover of annuals was included in the model. We also expected that the presence of mature perennial plants could result in a positive interference (facilitation) at the emergence stage; although later, this could pose a negative effect due to competition. Furthermore, we considered that the presence of adult plants of *Lepidium subulatum* could increase the emergence of new seedlings due to the short-range dispersion of mucilaginous seeds (Gutterman, 1993). The effect of germination date on seedling growth and survival, the response of seedling emergence to interannual climatic variation, and the relationships between seedling size and probability of survival were also evaluated. Finally, the effect of herbivory on the early survival of seedlings was studied.

MATERIALS AND METHODS

Study site—This study was carried out in El Espartal, a site close to Ciempozuelos, 30 km south of Madrid, in Central Spain (40°11′ N, 3°36′ W, 570 m altitude). The bioclimate is upper semiarid mesomediterranean, with an annual average rainfall for the last 30 yr of 415 mm, but with almost no rainfall in the summer. Mean daily maximum and minimum temperatures in January are 9.6°C and 0.6°C, respectively, and 32.7°C and 15.4°C in July. The soils are classified as Calcic Gypsisols, developed over gypsum parental rocks (Monturiol and Alcalá del Olmo, 1990). Soil texture is normally fine (clay content between 45 and 60%), and texture class is clay loam (Monturiol and Alcalá del Olmo, 1990).

The study site was located on a southern slope (average 30–40%) on gypsum sediments that includes the alluvial gypsum soils of the piedmont and bottom flats. It was covered with very sparse perennial com-

munities on slope and piedmont, and dense grass tussocks in the bottom flat (Rivas-Martínez and Costa, 1970; Izco, 1984). This community pattern was studied in detail by Rivas-Martínez and Costa (1970) and three main community bands were identified: *Centaurea hyssopifolia* Vahl–*Gypsophila struthium* L. community on gypsum slopes, *Artemisia herba-alba* Asso–*Frankenia thymifolia* Desf. community in the piedmont, and *Lygeum spartum* L. tussocks on the bottom flats.

Lepidium subulatum L. is a small shrub that grows in dwarf scrubs ("tomillares" in Spanish) at low elevations (100–1000 m) on gypsum soils in the western half of the Mediterranean Basin (Hernández-Bermejo and Clemente, 1993). The species can grow in the three community bands, although it is most frequent in the gypsum slope community. The fruits are very numerous small capsules (silicules) 2.5 × 1.5 mm ($N = 120$). Seeds are also very small (0.9 × 0.7 mm, $N = 90$), with no structures to assist dispersion, except for a mucilage that favors seed adhesion to soil. Certain morphological traits have been reported by Gómez et al. (1996), such as a mean number >1000 flowers per plant, two ovules, 4.12 mm mean flower size, and a 40–60 cm height.

Sampling design—A rectangular surface (30 × 110 m, x and y components, respectively) was selected according to the maximum slope, with a maximal altitudinal range of 15 m. A 10 × 10 m grid was laid on this surface resulting in 4 × 12 lines and 48 grid nodes. Each horizontal line was considered as an altitudinal level. The three first levels (1–3) comprised the *Lygeum spartum* band; levels 4 and 5, the *Artemisia herba-alba* band and the rest, the *Centaurea hyssopifolia* band (6–12).

In late spring of 1996, the cover (percentage) of several variables, perennial plants, annual plants, bryophytes, lichens, litter, gypsum crystals, and bare fraction, was estimated in 1 × 1 m quadrats centered at each grid node. The percentage of ground cover of the 30 perennial plant species identified at the study site, including *Lepidium subulatum*, was also recorded. Three soil cores (5 cm deep and 5 cm in diameter) were randomly collected in each quadrat and mixed before analyses to reduce soil heterogeneity within each quadrat (Palmer, and Dixon, 1990). All soil samples were dried in laboratory conditions and sieved; different fractions were separated and their percentages calculated: gravel (particles >6 mm in diameter), fine gravel (6–2 mm) and fine-earth (<2 mm). Electrical conductivity of the saturated extract, organic matter (Walkley, 1946) and pH value in H_2O (1:2.5) were determined in the last fraction. Gypsum content was estimated by a thermogravimetric method based on mass loss due to gypsum dehydration when a sample containing gypsum is heated. The total conversion of gypsum to anhydrite is attained at 200°C (Eswaran and Zi-Tong, 1991; Porta, 1996). Gypsum soil crust strength was measured by a portable penetrometer (RIMIK CP-20, Toowoomba, Australia) with a conical probe 5 mm long and with a 30° apex (Borselli et al., 1996). Values were obtained at 15, 30, 45, and 60 mm in water-saturated conditions (January 1998). Three punctures were randomly carried out in each seedling plot. A hand clinometer (Meridian) was used to measure the slope at the center of each 100-m² cell (macroslope) and also of each seedling plot (microslope).

Seedlings of *Lepidium* were identified and tagged in 48 plots (35 × 50 cm) centered in each of the 48 quadrats. Growth measured as maximum height was recorded regularly every 2–4 wk (for a total of 23 censuses) from February 1996 to October 1997. No recent seedlings or remains of *Lepidium* were recorded at the beginning of the study. This suggests that no new establishments had taken place for at least 2 yr prior to the study, because dead seedlings remain identifiable for at least 2 yr (Somolinos, 1997). Mortality causes were grouped into three categories: (1) drought, (2) physical damage, and (3) herbivory. Seedlings that died with exposed roots were classified as physical damage. Seedlings that died after hypocotyls had been partially eaten or cut or over half of the total leaves had been eaten since the previous census were placed in the herbivory category, as well as those that had disappeared.

No evidence of any disease was found in remaining dead seedlings, which were placed in the drought category.

In order to estimate the influence of mature *Lepidium* plants as seed sources, we measured maximum width, height, distance to the center of the quadrat, and orientation (in relation to the maximum slope axis) of every *Lepidium* individual located within a circle of 2 m radius. As the correlation ($r^2 = 0.83$) between width and height was highly significant ($P < 0.001$), only height was considered in further analyses. Seed sources (SS) for each quadrat were estimated as:

$$SS = \sum [(\cos \alpha_i + 1)/2]H_i/d_i \qquad (\text{slope} > 15°) \qquad (1)$$

or

$$SS = \sum 0.5H_i/d_i \qquad (\text{slope} \leq 15°) \qquad (2)$$

where H is the height of each mature plant, d is the distance to the center of every seedling plot, and "α" is the angle between the direction of the maximum slope and the line linking the plant to the centre. These equations assume that seed production is a function of plant size and that dispersion, which is not very efficient as suggested by the presence of mucilaginous seeds (Gutterman, 1993), depends on distance and slope.

Equation 1 evaluates the seed-supplying efficiency of mature plants as a function of location (the coefficient multiplying the height ranges from 0, when the mature plant is located below the seedling plot ($\alpha = 180°$) to 1 when it is directly above ($\alpha = 0°$ or $\alpha = 360°$). On steep slopes, mature plants located above plots are more efficient seed sources than those located below them (gravity and run-off effects) but, when the slope is shallower, the effect of each plant as seed source is not affected by its position, but only by its distance and size. The accuracy of both equations has been previously studied in *Lepidium subulatum* and *Helianthemum squamatum* (Cistaceae), other Iberian gypsophyte (Somolinos, 1997).

Numerical analyses—All data variables were assessed for normality prior to statistical analyses. Appropriate transformations were performed when necessary to improve normality according to Zar (1984). In order to avoid multicollinearity problems, the variance inflation factor (VIF) for each variable was carried out (Philippi, 1993). Following Chatterjee and Price (1991), only gravel fraction surpassed the criterion rule for deletion of values higher than 10.

The effect of the two main Cartesian spatial components x and y (not the altitudinal or z axis), on the survivorship matrix was evaluated in order to obtain the spatially structured variation (for details, see Borcard, Legendre, and Drapeau, 1992; Legendre, 1993). For this purpose a partial canonical correspondence analysis (ter Braak and Prentice, 1988) and a permutational test of significance of the extracted axes (ter Braak, 1990) were carried out. Matrix vectors were the number of seedling emergences and deaths by censuses (46 vectors), emergences in February, March, April, and May (four vectors), deaths by drought and herbivory (two vectors) and seed source value (one vector).

Variation explained by the x and y spatial components on the survivorship matrix was very low and the extracted constrained axes were not significant ($P = 0.45$ for the x component and $P = 0.52$ for the y component after 1000 randomizations). Consequently, the four seedling plots located at similar altitudinal levels were assumed to not be autocorrelated, and thereby considered to be real replicates.

Survival functions were estimated by the Kaplan-Meier method for each altitudinal level (1–12). Shape differences were tested by the log-rank test (Pyke and Thompson, 1986).

Seedling size at different landform levels was compared using a Kruskal-Wallis nonparametrical test as a consequence of the low number of replicates and the difficulties found in normalizing the variable.

The relationship between seedling size and probability of survival at the end of July (date of maximum mortality rate in both 1996 and 1997) was established with logistic models. Coefficients were estimated by maximization of the likelihood function (L). Differences among fitted curves for each altitudinal level (with surviving seedlings at this census) can be tested by calculating the $\ln(L_{\max})$ for pooled and separate groups with the statistic Λ, which compares the goodness of fit for the pooled data with that of each separate altitudinal level. Λ follows approximately a χ^2 with $2k$-2 degrees of freedom, with k as the number of compared groups. This method is described in detail by Wesselingh et al. (1993, 1997).

Finally, we used structural equation modeling (SEM) to test the relevance of several factors to emergence and survival (Browne, 1982; Hayduk, 1987; Loehlin, 1987). The advantages of SEM in path analysis are related to the possibility of testing the overall agreement between the path model and the data, the use of latent variables, and the evaluation of nested models (Cloninger et al., 1983; Breckler, 1990). As the sample size is relatively small (48 seedling plots), we followed the recommendations of Tanaka (1987) when designing the model to test (see Geweke and Singleton, 1980). Thus, the number of variables used in the model was limited to seven. The number of survivors at the end of the first year, January 1997, was used and the number of survivors in September 1997 was omitted since they were rather similar. A "habitat" variable was built using the first extracted axis of a principal components analysis from soil variables and the cover of several elements (cover of gypsum crystals, bare fraction, bryophytes, lichens, and litter). The effect of the presence of mature plants was evaluated by another first principal component synthesizing the cover value of the six most frequent mature plants. The relationships included in our model come from a priori knowledge, based on other studies on gypsophytes (Jonhston, 1941; Parsons, 1976; Powell and Turner, 1977; Meyer, 1986; Meyer and García-Moya, 1989), and field experience with these plants (Escudero, Pérez-García, and Carnes, 1997; Escudero et al., 1999).

The maximum likelihood method was used to estimate standardized path coefficients, which are equivalent to standardized partial regression coefficients. The degree of fit between the observed and expected covariance structures was first examined by a goodness-of-fit χ^2. A significant χ^2 indicates that the model does not fit the data. As this test may present inadequate statistical power because valid models can be rejected (Mitchell, 1993; Bishop and Schemske, 1998) and because unsatisfactory models can be retained (Tanaka, 1984), other fit indices were also considered. The Bentler-Bonnet Normed Fit Index (NFI) was used as it gives a measure of the practical fit of the model ignoring the number of subjects "sample size free" (Bentler and Bonnet, 1980; Mitchell, 1992). Tanaka (1987) also recommended the simultaneous use of the Goodness-of-Fit index (GFI) (Tanaka and Huba, 1985) because it is not affected by the methods of estimation. NFI and GFI range between 0 and 1, with values above 0.90 indicating a good fit (Tanaka, 1987; Mulaik et al., 1989; Mitchell, 1993). The multivariate significance of each individual path coefficient was assessed through the stepwise multivariate Wald test, which detects those paths whose absence implies a nonsignificant increase of the χ^2 ($P > 0.05$) (Buse, 1982). Analyses were conducted by the CALIS procedure of SAS.

RESULTS

Germination—Emergences occurred in 1996, but not in 1997, even though rainfall in 1997 was also above average (Fig. 1). No seedlings from previous years (1994–1995) were found. The total number of *Lepidium* seedlings was 1416, with 1109 seedlings (78.3%) emerging in February and fewer in March (115, 8.1%), April (143, 10.1%), and in May/June (49, 3.5%). Emergences were unevenly distributed in space (Fig. 2), were absent in the lowest zone, the *Lygeum spartum* community (altitudinal levels 1–3), and very scarce in the lower portion of the *Artemisia-Frankenia* community (level 4). Germination was very high at level 5, with an average of 222 seedlings/m^2 and a maximum of 468 seedlings/m^2 (Fig. 2) This level corresponds to the contact between
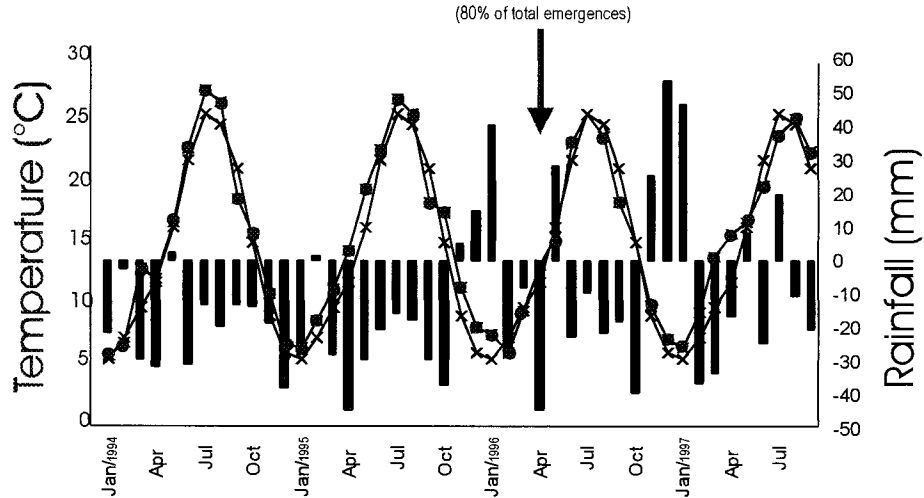
(80% of total emergences)

Fig. 1. Monthly mean temperature over the course of the study (dotted line) and averaged over the period 1960–1990 (x line). Histogram bars indicated monthly rainfall departure from the averaged value over the period 1960–1990. Arrow indicates the time of maximum seedling emergence (February cohort comprised >80% of emergences) although emergences extended until June. Monthly averaged rainfall for the last 30 yr are as follows: January, 40.2 mm; February, 37.8 mm; March, 33.3 mm; April, 53.6 mm; May, 42.7 mm; June, 26.7 mm; July, 11.0 mm; August, 17.5 mm; September, 43.27 mm; October, 45.61 mm; November, 49.7 mm, and December, 52.59 mm.

alluvial soils of the piedmont and the gypsum slope. The number of emergences in the steeper gypsum slope (level 7) reached similar values than in level 5. The highest densities were at the summit zone (level 10), where inclination decreases, with an average of 467 seedlings/m² and a maximum of 988 seedlings/m². Germination extended to June in almost all the levels (Fig. 2).

Survival and growth—In the 21-mo study period the total number of seedlings that died was 1333. Drought was the main cause of mortality of seedlings (98.72%), with a very low incidence of herbivory (0.05%). The highest rate of mortality coincided with the beginning of the first summer, June/July 1996 (census 9 in the levels, 5 and 6, and census 8 for the rest).
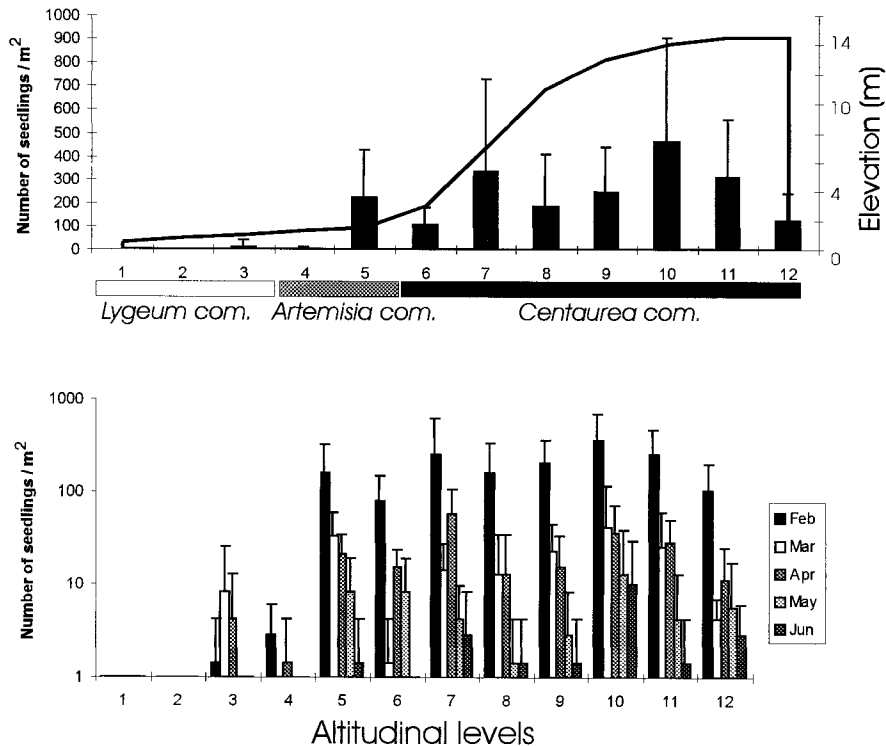

Fig. 2. Seedling density at each of the 12 altitudinal levels: (a) all the cohorts pooled and (b) considering each monthly cohort independently (shown on log scale). Error bars represent standard deviations. In (a) the outline of the sampling site slope is represented in the background.
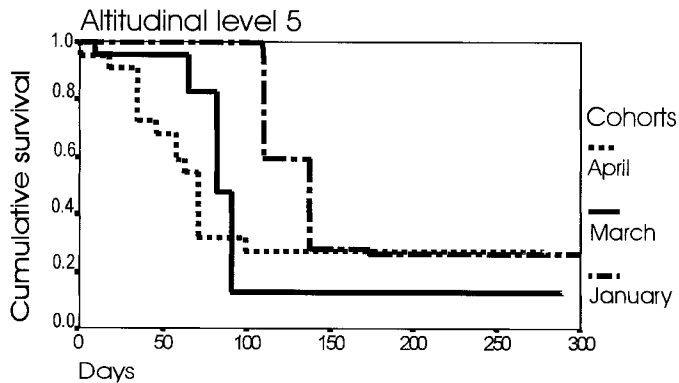
Fig. 3. Survival curves of the cohorts considered in the altitudinal level 5 (contact between piedmont and slope) during the first year. The April class comprises cohorts of April, May, and June. The log rank statistic was 57.18 between February and March cohorts ($P < 0.0001$), 15.41 between February and April ($P = 0.0001$) and 0.64 between March and April ($P = 0.433$).

TABLE 1. Comparison between size of surviving seedlings vs. dead seedlings of *Lepidium subulatum* in Ciempozuelos (Spain) during the census previous to that when maximum mortality rate was reached (Kruskal-Wallis test). Survivors and Total indicate, respectively, the number of survivings at the end of the period and the number of seedlings at the beginning of the period. Boldface type denotes $P < 0.01$.

Altitudinal level	Period	χ^2	Significance	Survivors	Total	Survival (%)
Pooled	1 Jun/18 Jun	83.24	**0.0000**	546	1153	47.3
5	18 Jun/1 Jul	14.46	**0.0001**	72	150	48.0
6	18 Jun/1 Jul	9.17	**0.0025**	27	65	41.5
11	1 Jun/18 Jun	5.66	0.0173	99	297	33.3
12	1 Jun/18 Jun	0.04	0.831	26	99	26.2

Eighty-three seedlings survived to January 97 and this number was only slightly lower by September 1997 (79 survivors). Final survivors were primarily restricted to the piedmont (levels 5 and 6, with 48 and 18% of the surviving seedlings, respectively, and a mean of 54 seedlings/m² at level 5) and to the summit area (levels 11 and 12, with 10 and 9.6%, respectively). Hereafter only these four levels were considered because the number of survivors in the rest was extremely low. Significant differences in the final percentage of surviving seedlings between these four levels ($G = 41.44$, df = 3, $P < 0.0001$) were found, with 24% of the total number of emerged seedlings at level 5 and 19% at level 6 ($G = 0.86$, df = 1, $P = 0.351$) and only 4 and 8% at levels 11 and 12 ($G = 2.26$, df = 1, $P = 0.132$).

Survival curves of seedlings growing at these four levels were compared. The shape of these curves showed significant differences (log rank statistic 71.36, df = 3, $P < 0.0001$). These curves were similar for seedlings emerged on levels 5 and 6 (log rank statistic 1.17, df = 1, $P = 0.27$), but the rest of pairwise comparisons were significantly different ($P < 0.01$), with delayed mortality in lower levels.

Only seedlings of the February cohort survived in the slope and summit area levels (6–12). Germination cohorts (seedlings of February, March, and the rest) did not differ in their survival rate in the piedmont-slope contact, level 5 ($G = 0.86$, df = 2, $P = 0.351$), although the shape of the survival curve for the first cohort was significantly different from those of the other two cohorts, with delayed mortality for the former seedlings (Fig. 3).

Seedling size at the end of the first year, January 1997, was similar in the four levels ($\chi^2 = 6.81$, df = 3, $P = 0.08$). However, this trend was not maintained in September 1997 when significant differences ($\chi^2 = 14.25$, df = 3, $P = 0.002$) were found, the largest seedlings being found at level 5.

In order to assess whether seedling survival was size dependent, we compared the size shown in the preceding census, for seedlings that either appeared dead or survived at census when maximum mortality was recorded. Survivors were significantly larger than those that died

for pooled data and within each level, except in level 11 (Table 1).

To determine the threshold size for survival at the date when maximum mortality rate is reached, an independent logistic model for each level with size as predictor was developed and tested. These logistic models were highly significant for pooled data and for the considered levels (improvement of the model $\chi^2 = 32.83$, $P < 0.0001$ for pooled data; $\chi^2 = 13.19$, $P = 0.0001$ for level 5; $\chi^2 = 11.93$, $P = 0.005$ for level 6; and $\chi^2 = 5.25$, $P = 0.0218$ for level 12) predicting correctly for over 60% of the cases. Furthermore, logistic curves for the probability of survival did not differ significantly by pairs between levels 5 and 6 ($\Lambda = 0.758$, df = 2, $P > 0.1$), levels 5 and 12 ($\Lambda = 0.507$, $P > 0.1$) and levels 6 and 12 ($\Lambda = 1.752$, df = 2, $P > 0.1$). Threshold size for survival during the first summer was ~3 cm height (Fig. 4).

The model—Our path model (Fig. 5) provided a good overall fit to the data set because it had a nonsignificant χ^2 ($\chi^2 = 2.31$, df = 2, $P = 0.31$), indicating that the covariance matrices of the experimental data and those specified by the model were not different. Furthermore, NFI and GFI values over 0.90 were obtained (NFI =
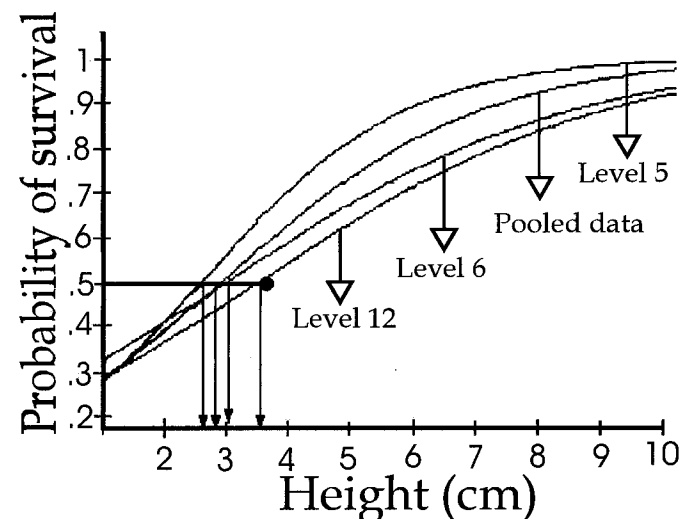

Fig. 4. Comparison of threshold sizes for surviving in different altitudinal levels. The lines are the fitted logistic curves. Arrows indicate the estimated size at which 50% of the plants survive.
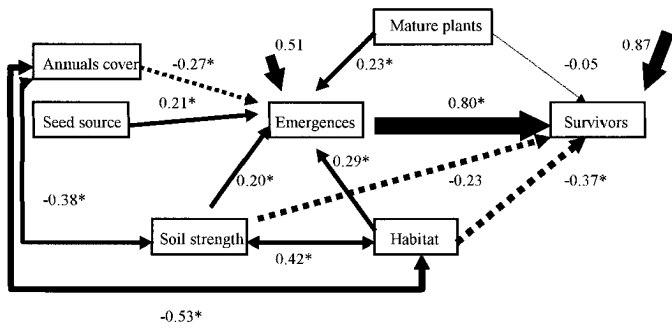
Fig. 5. Path model for the establishment of *Lepidium subulatum* in which "emergences" and "survivors after one year" are the dependent variables. Width of each arrow is proportional to the standardized path coefficient, and dashed lines denote negative paths. Coefficients indicate the expected change in the dependent variable if the predictor variable is changed one unit. Arrows not originating from a variable show the effect of unexplained causes. Asterisks indicate values significantly different from zero ($P < 0.05$). Goodness-of-fit statistics for the model are: $\chi^2 = 2.3$, df $= 2$, $P = 0.31$; Normed Fit Index (NFI) $= 0.98$; and Goodness-of-Fit Index (GFI) $= 0.99$. NFI and GFI values above 0.90 together with a nonsignificant χ^2 indicate a good model fit. The variables "seed source," "soil strength," "emergences," and "survivors" were log transformed and "annual cover" was arcsine transformed.

0.983, GFI $= 0.986$), indicating that the experimental data fit our model better than a null model where variables are assumed to be uncorrelated. The excellent fit of the path model was largely due to the strong relationship between "emergences" and "survivors" (Fig. 5). "Emergences" were greatly and almost equally affected (standardized coefficient over 0.21) by "seed source," "soil strength," "habitat," and "mature plants." The variable "habitat" was positively correlated to "lichen cover" (0.69), "bare fraction" (0.59), "gypsum crystals" (0.63), and negatively correlated to "fine earth fraction" (−0.69), "organic matter" (−0.66), and "litter cover" (−0.61). On the other hand, the variable "mature plants" was positively correlated with the presence of genuine shrubby gypsophytes, such as "*Helianthemum squamatum* (L.) Dum. Cours." (0.71), "*Thymus lacaitae* Pau" (0.63), and "*Centaurea hyssopifolia* Vahl." (0.58). Only "habitat" and mainly "emergences" showed a significant direct effect on "survivors." The negative direct effect of habitat on "survivors" (path coefficient: −0.37) was partially compensated by a positive indirect effect through "emergences" (partial correlation coefficient: 0.23), being the total effect only −0.14. On the other hand, "mature plants" had a nonsignificant negative effect on "survivors," but a positive indirect effect (0.19) through "emergences."

DISCUSSION

Timing of emergence—Winter germination is the prevailing trait in *Lepidium subulatum*. Approximately 80% of total seedlings emerged in February 1996. Germination at low temperatures has been reported to be a typical strategy of Mediterranean plants (Corral, Pita, and Pérez-García, 1990; Thanos et al., 1992; Bell, Plummer, and Taylor, 1993). Greenhouse experiments have also shown that germination of Iberian gypsophytes is higher and faster at low temperatures (optima temperatures ranging

between 5°C and 15°C) (Escudero, Pérez-García, and Carnes, 1997).

Germination occurred after a period of rainfall far above the average (autumn 1995 and early winter 1995/1996), following 4 yr of severe drought (1992–1995) (Fig. 1). It has been shown that the length of the drought period limits the establishment of many desert perennials to certain favorable years (Brum, 1973; Jordan and Nobel, 1981) and that in demographic terms it leads to sporadic recruitments (Boyd and Brun, 1982; Grice and Westoby, 1987; Milton, 1995).

According to this pattern, a high germination event would have also been expected in early 1997, because rainfall in the autumn of 1996 and in the winter of 1996/1997 was also very high (Fig. 1). However, no emergences were detected in that year. A similar response with a very high emergence in 1996 and a low one in 1997 was also found in *Helianthemum squamatum* in our experimental area (Somolinos, 1997; Escudero et al., 1999). This suggests an intense depletion of the local soil seed bank as a consequence of a long drought period (1992–1995) followed by a mass germination event (maximum of 988 seedlings/m^2) during a favorable period. The absence of new emergences in 1997 is also related to a significant scarce seed production during the spring and summer of 1996. According to Coffin and Lauenroth (1989) and Mott (1973) most perennials in arid environments have transient seed banks. Little work has been done in order to quantify the proportion of viable seeds that remain dormant in the soil after a pulse of germination event (Venable, 1989). In the case of *Lepidium subulatum* and also *Helianthemum squamatum* (Somolinos, 1997; Escudero et al., 1999) the depletion might be very important.

Factors controlling emergence—Meyer (1986) and Meyer, García-Moya, and Lagunes (1992) have proposed that the main limitation of gypsum soils takes place at the establishment stage, probably as a consequence of their unusual physical properties. Mineral nutrition restrictions are not likely to play an important role in the phenomenon of gypsophily (Meyer, García-Moya, and Lagunes, 1992; Verheye and Boyadgiev, 1997).

Soil strength—Surface soil layers with a gypsum content over 25%, as in our study site, show a tendency to slake and form gypsum surface crusts (Verheye and Boyadgiev, 1997), which are notoriously thicker than those found in typical desert soils. These crusts are of two types, physical soil crusts formed by gypsum crystals which are unable to support plant life, and cryptobiotic crusts that are of biological origin. In desert crust soils, it is known that the development of high crust strength is one of the most limiting factors for the emergence of new seedlings (Hanks and Thorp, 1956; Harper, Williams, and Sagar, 1965; Cary and Evans, 1974) and that there is a negative correlation between vascular plant distribution and cryptobiotic crust cover (West, 1990; Eldridge, 1993; Boeken and Shachak, 1994). Furthermore, Johansen (1993) has suggested that desert crusts may inhibit seed germination because they prevent the penetration of seeds into the soil below the crust layer. Our results support the hypothesis of Meyer (1986) linking gyp-

sophily to soil crust strength (see Verheye and Boyadgiev, 1997) because *Lepidium subulatum* emergence was mainly confined to the localities with higher soil strength. Although no significant gypsum content differences were found among the three community bands, mechanical strength was significantly higher (Kruskal-Wallis test) in the gypsum slope levels ($\chi^2 = 12.76$, df = 2, $P = 0.0017$; 466 kPa in the *Lygeum spartum* community, 647 kPa in the *Frankenia thymifolia* community, and 850 kPa in the *Centaurea hyssopifolia* community). Furthermore, in some seedlings plots of the gypsum slope, penetrometer soil strenght values over 1000 kPa were measured, which might pose severe problems in seedling recruitment (see Borselli et al., 1996). The ability of *Lepidium subulatum* to germinate on these hard soil crusts may be partially explained by the mucilaginous coats in its seeds. According to Zaady, Gutterman, and Boeken (1997) the production of mucilaginous seeds is one of the most efficient traits enabling plants to become established on crusted soils (see also Gutterman and Shem-Tov, 1996, 1997), because it minimizes the runoff depletion of the local seed bank and provides a humid environment during germination. Thus, this extended morphological trait of gypsophytes (Somolinos, 1997; Escudero et al., 1999) seems to link seedling emergence to crust strength.

The importance of the gypsum crust in the performance of gypsophytes may explain the fact that although gypsum outcrops also appear in mesic environments, gypsophily is consistently restricted to arid and semiarid zones (Rivas-Martínez and Costa, 1970; Meyer, 1986). Under more mesic climates, the gypsum crusts do not appear and the gypsum outcrops are covered with a calcicole vegetation (Rivas-Martínez and Costa, 1970).

Habitat—The relevant positive relationship found between "emergences" and "habitat" (Fig. 5) provides a clear description of additional differential habitat features found in the establishment of the gypsophytes, and also highlights the relevance of the gypsum crust. The "habitat" variable is positively correlated with "lichen cover," "bare fraction" and "gypsum crystal cover" and negatively correlated with "fine earth fraction," "organic matter content," and "litter cover." Gypsophyllous lichens, almost all narrow endemics, have been reported as dominant elements of semiarid gypsum landscapes (Crespo and Barreno, 1975), and they have been closely related to the presence of gypsum crust (Tarazona et al., 1980). On the other hand, bare cover and gypsum crust have also been related (Watson, 1979).

Annual plants cover—As hypothesized in our model (Fig. 5), annuals cover is a relevant factor during the emergence stage of *Lepidium subulatum*. Although competition by annuals was not studied directly, we think the influence of "annual plants cover" mainly underlines a competitive interaction. Competition by annuals with seedlings of perennial plants under arid conditions has been previously reported (van Epps and McKell, 1983). This is probably due to the fact that annuals are efficient water competitors, and seedlings have evolved to be able to use moisture quickly from the rapidly drying soil surface (Kadmon, 1997). Topographic gradients can create substantial spatial variation in the productivity and per-

formance of desert annuals (Pantastico-Caldas and Venable, 1993; Kadmon, 1997). These authors pointed out that competition tended to be weak on the slope and more intense in the two habitats below it because of higher water availability. We detected a similar geomorphological pattern in the performance of "annuals cover" ($\chi^2 = 25.62$, df = 2, P < 0.0001; 28.0% in the *Lygeum spartum* community, 23.6% in the *Frankenia thymifolia* community, and 5.0% in the *Centaurea hyssopifolia* community). Bottom levels had higher moisture availability than slope and summit levels due to higher percentages of fine soil texture ("fine earth," $\chi^2 = 18.16$ df = 2, $P < 0.0001$; 91% in the *Lygeum* community, 94.2% in the *Frankenia* community, and 66.9 in the *Centaurea* commmunity) and higher "organic matter content" ($\chi^2 = 24.60$, df = 2, $P < 0.0001$, 3.94% in the *Lygeum* community, 2.20% in the *Frankenia* community, and 1.11% in the *Centaurea* community).

Seed source—The inclusion of the "seed source" variable as one of the predictors of emergence in our model was related to the species dispersal strategy of this plant (Fig. 5). As pointed out by Gutterman (1993), anchoring by mucilages is a common dispersal mechanism of desert plants; thus, the seed bank is increased in the vicinity of mature plants. On the other hand, as suggested by Ellner and Shmida (1981, 1984), long-range dispersal may provide no benefit as an adaptive trait for desert plants because the most favorable environment is usually located in the vicinity of mother plants. In the case of gypsophytes, constraints to find new available gypsum outcrops might make the long-range dispersal even less desirable. This conclusion is also supported by Escudero et al. (1999) who found a similar dispersal pattern in *Helianthemum squamatum*, another widely distributed Iberian gypsophyte. This limited dispersal pattern may help explain why most gypsophytes are narrow endemics restricted to very local gypsum outcrops.

Mature plants—Although, no evidence of positive biotic interactions in gypsum environments has been reported, our results show that the emergence in our seedling plots is related to the presence of mature plants. This suggests that facilitation may be involved in the emergence of this gypsophyte, although our experimental approach cannot confirm that this interaction is the only process involved. In any case, this argument agrees with the extended idea that facilitation plays an important role in severe environments (Chapin et al., 1994; Escudero, 1997) including arid zones (Aguiar and Sala, 1994, 1997; Callaway et al., 1996; Callaway and Walker, 1997).

Factors limiting seedling survival and growth—Survival patterns varied significantly between cohorts and depended on the topography (see Fowler, 1988; Eldridge, Westoby, and Holbrook, 1991) (Fig. 4). Only seedlings of the first cohort had a chance of survival in the *Centaurea* community (levels 6–12), probably because it had more time to be established than subsequent ones before the arrival of the drought period in the summer. This observation agrees with the assertions that water is the limiting resource for seedlings in arid regions (Harrington, 1991) and that these seedlings are highly susceptible

to mortality from water stress (Chabot and Mooney, 1985). Thus, in *Lepidium subulatum,* deaths were primarily assigned to drought (>95%). The low final survival percentages observed were probably a consequence of the severe summer drought of 1996 (Fig. 1). Similar low survivals have also been reported in other desert perennials, such as *Artemisia tridentata* (Young and Evans, 1989) and Cactaceae species (Steenberg and Lowe, 1969).

Contrary to our results, Goldberg and Novoplansky (1997), under the scheme of their two-phase resource dynamics hypothesis, suggested that for low water availability scenarios, a negative correlation between survival and growth may happen. Some papers have reported earlier cohorts with lower survival rates, but a higher mean size (Gross, 1980, 1984; Klemow and Raynal, 1981; Marks and Prince, 1981; Mack and Pyke, 1983; Goldberg and Novoplansky, 1997). Two possible explanations for this behavior are: (1) smaller plants have lower water requirements and (2) water is much less easily accumulated in plants than other nutrients (Chapin, Schulze, and Mooney, 1990). However, our results clearly show that survival is size dependent in the opposite way. Therefore, larger seedlings are more likely to survive; similar behaviors have been reported in light-dependent communities (Kobe et al., 1995; Walters and Reich, 1996). The reason for this correlation may be related to the specific physical properties of gypsum soils such as high hydraulic conductivity, steep thermal gradients, and white color, which may result in a significant increase in water availability during summer drought (Meyer, 1986; Meyer and García-Moya, 1989). High water availability could also explain the summer flowering phenology and active summer growth of most gypsophytes (Meyer, 1986; Gómez et al., 1996; Somolinos, 1997). Only larger plants, over 3 cm height (Fig. 4), were able to surpass the gypsum crust and consequently benefit from the favorable hydraulic summer conditions of gypsum soils.

Although a relation between the "mature plants" and the "survivors" as a consequence of competition had been suggested (Fig. 5), the path coefficient obtained was not significantly different from zero. In addition to the obvious direct effect of "emergences" on "survivors," the only other significant direct path came from "habitat." Nevertheless, "mature plants" and "soil strength" presented a relevant indirect effect through "emergences" on "survivors." The negative effect of "habitat" on "survivors" suggests that conditions that are favorable for emergence are different from those for seedling survival. Thus, emergence occurred mainly on the crusted soils of the *Centaurea* community (levels 6–12) where competition with annuals is not relevant and *Lepidium subulatum* seedlings are able to surpass the surface crust. However, the low proportion of seedlings that emerged on the lower levels, had a better chance of survival after a 2-yr period. This suggests that *Lepidium subulatum* might conform to Gankin and Major's "refuge" model for soil endemics (Gankin and Major, 1964). Thus, *Lepidium subulatum* is confined to the crusted gypsum soils of slopes, which are relatively free from competition (Meyer, 1986), but grow and survive even better on alluvial gypsum soils. Somolinos (1997) previously reported a similar pattern in *H. squamatum* and also sug-

gested that there was an allelopathic boundary in the alluvial soils of the piedmont as a consequence of the high density of *Artemisia herba-alba* in this zone.

We conclude that emergence and recruitment of *Lepidium subulatum* seem to be controlled by a precise set of factors. Seedlings primarily emerge on the gypsum surface crust (Fig. 2), and their survival is size dependent (Fig. 4), probably as a consequence of the necessity of rooting below the surface crust before summer drought. However, once emerged, the chance of survival is positively related to the relatively alluvial soils of the piedmont-slope contact (level 5).

Although, our results link gypsophily to some properties of the surface crust, several other aspects need to be evaluated, such as the role of the physical properties of gypsum soils in the development of mature plants. Bridges and Burnham (1980) pointed out that roots of generalist plants cannot penetrate soils with gypsum contents over 25% since under these circumstances, soil material lacks plasticity, cohesion, and aggregation, and becomes completely mechanically unstable. On the other hand, the examination of soil chemical data has so far reported little evidence to explain this soil restriction behavior (Meyer, 1986; Meyer and García-Moya, 1989; Verheye and Boyadgiev, 1997). Further studies are needed to clarify the possible incidence of chemical soil properties on gypsophily.

The knowledge of the factors controlling seedling abundance and survival at spatial and temporal scales provide a basic tool for the management and conservation of this type of arid systems (Milton, 1995; Wiegand and Milton, 1996). In this sense, gypsum systems are considered one of the most threatened systems in the Mediterranean basin (Gómez-Campo, 1987) and have been included in the European Community Habitats and Species Directive (Comunidad Europea, 1992), which promotes the conservation of the most vulnerable ecosystems in Europe.

LITERATURE CITED

AGUIAR, M. R., AND O. E. SALA. 1994. Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. *Oikos* 70: 26–34.

———, AND ———. 1997. Seed distribution constrains the dynamics of the Patagonian steppe. *Ecology* 78: 93–100.

BELL, D. T, J. A. PLUMMER, AND S. K. TAYLOR. 1993. Seed germination ecology in southwestern Australia. *Botanical Reviews* 59: 24–73.

BENTLER, P. M., AND D. G. BONNET. 1980. Significance tests and goodness-of-fit in the analysis of covariance structures. *Psychological Bulletin* 88: 588–606.

BISHOP, J. G., AND D. W. SCHEMSKE. 1998. Variation in flowering phenology and its consequences for lupinus colonizing Mount St. Helens. *Ecology* 79: 534–547.

BOEKEN, B., AND M. SHACHAK. 1994. Changes in desert plant communities in human made patches and their implications for management of desertified landscapes. *Ecological Applications* 4: 702–716.

BORCARD, D., P. LEGENDRE, AND P. DRAPEAU. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045–1055.

BORSELLI, L, R. BIANCALANI, C. GIORDANI, S. CARNICELLI, AND G. A. FERRARI. 1996. Effect of gypsum on seedling emergence in a kaolinitic crusting soil. *Soil Technology* 9: 71–81.

BOUKHRIS, M., AND P. LOSSAINT. 1970. Sur la teneur en soufre de quelques plantes gypsophiles de Tunisie. *Acta Oecologica* 5: 345–354.

BOYD, R. S., AND G. D. BRUM. 1982. Postdispersal reproductive biology

of a Mojave Desert population of *Larrea tridentata* (*Zygophylla-ceae*). *American Midland Naturalist* 110: 25–36.

BRECKLER, S. J. 1990. Applications of covariance structure modeling in psychology: cause for concern? *Psychological Bulletin* 107: 260–273.

BRIDGES, E. M., AND C. P. BURNHAM. 1980. Soils of the state of Bahrain. *Journal of Soil Science* 31: 689–707.

BROWNE, M. W. 1982. Covariance structures. *In* D. M. Hawkins [ed.], Topics in applied multivariate analysis, 72–141. Cambridge University Press, Cambridge, UK.

BRUM, G. D. 1973. Ecology of Saguaro (*Carnegiea gigantea*): phenology and establishment in marginal populations. *Madroño* 22: 195–204.

BUSE, A. 1982. The likelihood ratio, Wald and Lagrange multiplier tests: an expository note. *American Statistician* 36: 153–157.

CALLAWAY, R. M., AND C. M. D'ANTONIO. 1991. Shrub facilitation of coast live oak establishment in Central California. *Madroño* 38: 158–169.

————, E. H. DELUCIA, D. MOORE, R. NOWAK, AND W. H. SCHLESINGER. 1996. Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. *Ecology* 77: 2130–2141.

————, AND L. WALKER. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78: 1958–1965.

CANNON, H. L. 1971. The use of plant indicators in ground water surveys, geologic mapping and mineral prospecting. *Taxon* 20: 227–256.

CARY, J. W., AND D. D. EVANS. 1974. Soil Crusts. Technical Bulletin, number 214. University of Arizona, Tucson, Arizona, USA.

CHABOT, B. F., AND M. A. MOONEY. 1985. Physiological ecology of North American Plant communities. Chapman and Hall, New York, New York, USA.

CHAPIN, F. S., III, E. D. SCHULZE, AND H. A. MOONEY. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* 21: 243–247.

CHATTERJEE, S., AND B. PRICE. 1991. Regression analysis by example, 2nd ed. John Wiley & Sons, New York, New York, USA.

CLONINGER, C. R., D. C. RAO, J. RICE, T. REICH, AND N. E. MORTON. 1983. A defense of path analysis in genetic epidemiology. *American Journal of Human Genetics* 35:733–765.

COFFIN, D. P., AND W. K. LAUENROTH. 1989. Spatial and temporal variation in the seed bank of a semiarid grassland. *American Journal of Botany* 76: 53–58.

COMUNIDAD EUROPEA. 1992. Directiva 92/43/CEE del Consejo del 21 de mayo de 1992 relativa a la conservación de los habitats naturales y de la fauna y flora silvestres. *Diario Oficial de las Comunidades Europeas* 206: 7–37.

CORRAL, R., J. M. PITA, AND F. PÉREZ-GARCÍA. 1990. Some aspects of seed germination in four species of *Cistus* L. *Seed Science and Technology* 18: 321–325.

CRESPO, A., AND E. BARRENO. 1975. Ensayo florístico y ecológico de los yesos del centro de España (*Fulgensietalia desertori*). *Anales del Instituto de Botánica A.J. Cavanilles, Madrid* 32: 873–908.

DUVIGNEAUD, P., AND S. DENAEYER-DE SMET. 1966. Accumulation du soufre dans quelques espèces gypsophiles d'Espagne. *Bulletin de la Societè Royal Botánique de Belgique* 99: 263–269.

————, AND ————. 1968. Essai de classification chimique (éléments minéraux) des plantes gypsicoles du bassin de l'Ebre. *Bulletin de la Societè Royal Botánique de Belgique* 101: 279–291.

ELDRIDGE, D. J. 1993. Cryptogams, vascular plants and soil hydrological relations: some preliminary results from the semiarid woodlans of eastern Australia. *Great Basin Naturalists* 53: 48–58.

————, M. WESTOBY, AND K. G. HOLBROOK. 1991. Soil surface characteristics, microtopography and proximity to mature shrubs: effects on survival of several cohorts of *Atriplex vesicaria* seedlings. *Journal of Ecology* 78: 357–364.

ELLNER, S., AND A. SHMIDA. 1981. Why are adaptations for long range seed dispersal rare in desert plants? *Oecologia* 51: 133–144.

————, AND ————. 1984. Seed dispersal in relation to habitat in the genus *Picris* (*Compositae*) in Mediterranean arid regions. *Israel Journal of Botany* 33: 25–39.

ESCUDERO, A., F. PÉREZ-GARCÍA, AND L. F. CARNES. 1997. Seed ger-

mination of gypsophites and gypsovags in semiarid Central Spain. *Journal of Arid Environment* 36: 487–497.

————, R. SOMOLINOS, J. M. OLANO, AND A. RUBIO. 1999. Factors controlling the establishment of *Helianthemum squamatum*, an endemic gypsophile of semi-arid Spain. *Journal of Ecology* 87: 290–302.

ESWARAN, H., AND G. ZI-TONG. 1991. Properties, genesis, classification and distribution of soils with gypsum. Special Publication number 26, 89–119. American Society of Soil Sciences, Madison, Wisconsin, USA.

FOWLER, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics* 17: 89–110.

————. 1988. What is a safe site?: Neighbor, litter, germination date and patch effects. *Ecology* 69: 947–961.

FRANCO, A. C., AND P. S. NOBEL. 1989. Effect of nurse plants on the microhabitats and growth of cacti. *Journal of Ecology* 77: 870–886.

GANKIN, R., AND J. MAJOR. 1964. *Arctostaphylos myrtifolia*, its biology and relationship to the problem of endemism. *Ecology* 45: 792–808.

GEWEKE, J. F., AND K. J. SINGLETON. 1980. Interpreting the likelihood ratio statistic in factor models when sample size is small. *Journal of the American Statistical Association* 75: 133–137.

GOLDBERG, D., AND A. NOVOPLANSKY. 1997. On the relative importance of competition in unproductive environments. *Journal of Ecology* 85: 409–418.

————, AND R. M. TURNER. 1986. Vegetation change and plant demography in permanent plots in the Sonoran desert. *Ecology* 67: 695–712.

GÓMEZ, J. M., R. ZAMORA, J. A. HÓDAR, AND D. GARCÍA. 1996. Experimental study of pollination by ants in Mediterreanean high mountain and arid habitats. *Oecologia* 106: 236–242.

GÓMEZ-CAMPO, C. 1987. Libro Rojo de las Plantas de la Península y Baleares. Instituto para la Conservación de la Naturaleza, Madrid, Spain.

GRICE, A. C., AND M. WESTOBY. 1987. Aspects of the dynamics of the seedbanks and seedling populations of *Acacia victoriae* and *Cassia* spp. in arid western New South Wales, Australia. *Australian Journal of Ecology* 12: 209–215.

GROSS, K. L. 1980. Colonization by *Verbascum thapsus* of an oldfield in Michigan: experiments on the effects of vegetation. *Journal of Ecology* 68: 919–927.

————. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology* 72: 369–387.

GUTTERMAN, Y. 1993. Seed germination in desert plants: adaptations of desert organisms. Springer, Berlin.

————, AND S. SHEM-TOV. 1996. Structure and function of the mucilaginous seed coat of *Plantago coronopus* inhabiting the Negev Desert of Israel. *Israel Journal of Plant Science* 44: 125–34.

————, AND ————. 1997. Mucilaginous seed coat structure of *Carrichtera annua* and *Anastatica hierochontica* from populations occurring in the Negev Desert highlands of Israel and adhesion of seeds to the desert soil crust. *Journal of Arid Environments* 35: 697–707.

HANKS, R. J., AND F. C. THORP. 1956. Seedling emergence of wheat as related to soil moisture content, bulk density, oxygen diffusion rate and crust strength. *Proceedings of the American Society of Soil Science* 20: 307–310.

HARPER, J. L., J. J. WILLIAMS, AND G. R. SAGAR. 1965. The behaviour of seeds in soil. I. The heterogeneity of the soil surface and its role in determining the establishment of plants from seed. *Journal of Ecology* 53: 273–286.

HARRINGTON, G. N. 1991. Effects of soil moisture on shrub seedling survival in a semiarid grassland. *Ecology* 72: 1138–1149.

HAYDUK, L. A. 1987. Structural equation modeling with LISREL: essential and advances. John Hopkins University Press, Baltimore, Maryland, USA.

HERNÁNDEZ-BERMEJO, J. E., AND M. CLEMENTE. 1993. *Lepidium. In* S. Castroviejo et al. [eds.], Flora Iberica, vol. IV, 311–327. Consejo Superior de Investigaciones Científicas, Madrid, Spain.

IZCO, J. 1984. Madrid Verde. Comunidad Autónoma de Madrid, Madrid, Spain.

JOHANSEN, J. R. 1993. Cryptogamic crusts of semiarid and arid lands of North America. *Journal of Phycology* 29: 140–147.

JONHSTON, I. M. 1941. Gypsophily among Mexican desert plants. *Journal of the Arnold Arboretum* 22: 145–170.

JORDAN, P. W., AND P. S. NOBEL. 1979. Infrequent establishment of seedlings of *Agave deserti* (*Agavaceae*) in the northwestern Sonoran desert. *American Journal of Botany* 66: 1079–1084.

———, AND ———. 1981. Seedling establishment of *Ferocactus acanthodes* in relation to drought. *Ecology* 62: 901–906.

KADMON, R. 1997. Neighbor competition modifies demographic responses of desert dune annuals to gradients in sand stability. *Journal of Arid Environments* 36: 557–564.

———, AND A. SHMIDA. 1990. Competition in a variable environment: a field experiment with the desert annual *Stipa capensis. Journal of Ecology* 83: 253–262.

KLEMOW, K. M., AND J. D. RAYNAL. 1981. Population ecology of *Melilotus alba* in a limestone querry. *Journal of Ecology* 69: 33–44.

KOBE, R. K., S. W. PACALA, J. A. SILANDER, AND C. D. CANHAM. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* 5: 517–532.

LEGENDRE, P. 1993. Spatial autocorrelation: trouble or new paradigm?. *Ecology* 74: 1659–1673.

LOEHLIN, J. C. 1987. Latent variable models. Lawrence Erlbaum, Hillsdale, Illinois, USA.

MACK, R. N., AND D. A. PYKE. 1983. The demography of *Bromus tectorum*: variation in time and space. *Journal of Ecology* 71: 69–93.

MARKS, M., AND S. PRINCE. 1981. Influences of germination date on survival and fecundity in wild lettuce *Lactuca serriola. Oikos* 36: 326–330.

MEYER, S. E. 1986. The ecology of gypsophile endemism in the Eastern Mojave desert. *Ecology* 67: 1303–1313.

———, AND E. GARCÍA-MOYA. 1989. Plant community patterns and soil moisture regime in gypsum grassland of north central Mexico. *Journal of Arid Environments* 16: 147–155.

———, ———, AND A. L. C. LAGUNES. 1992. Topographic and soil effects on gypsophile plant community patterns in Central Mexico. *Journal of Vegetation Science* 3: 429–429.

MILTON, S. J. 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *Journal of Applied Ecology* 32: 145–156.

MITCHELL. R. J. 1992. Testing evolutionary and ecological hypotheses using path analysis and structural equation modelling. *Functional Ecology* 6: 123–129.

———. 1993. Path analysis: Pollination. *In* S.M. Scheiner and J. Gurevitch [eds.], Design and analysis of ecological experiments, 211–231. Chapman and Hall, New York, New York, USA.

MONTURIOL, F., AND L. ALCALÁ DEL OLMO. 1990. Mapa de asociaciones de suelos de la Comunidad de Madrid. Escala 1:200.000. Consejo Superior de Investigaciones Científicas, Madrid, Spain.

MOTT, J. J. 1973. Temporal and spatial distribution of an annual flora in an arid region of western Australia. *Tropical Grasslands* 7: 89–97.

MULAIK, S. A., L. R. JAMES, J. VAN ALSTINE, N. BENNETT, S. LIND, AND C. D. STILWELL. 1989. Evaluation of goodnessoffit indices for structural equation models. *Psychological Bulletin* 105: 430–445.

PALMER, M. W., AND P. M. DIXON. 1990. Small scale environmental heterogeneity and the analysis of species distribution along gradients. *Journal of Vegetation Science* 1: 57–65.

PANTASTICO-CALDAS, M., AND D. L. VENABLE. 1993. Competition in two species of desert annuals along a topographic gradient. *Ecology* 74: 2192–2203.

PARSONS, P. F. 1976. Gypsophily in plants a review. *American Midland Naturalist* 96: 1–20.

PARUELO, J. M., AND O. E. SALA. 1995. Water losses in the Patagonian steppe: a modelling approach. *Ecology* 76: 510–520.

PHILIPPI, T. E. 1993. Multiple Regression Analysis: Herbivory. *In* S.M. Scheiner and J. Gurevitch [eds.], Design and analysis of ecological experiments, 183–210. Chapman and Hall, New York, New York, USA.

PORTA, J. 1996. Methodology and study techniques of gypsum in soils: a review. *In* R. M. Poch [eds.], International Symposium on soils with gypsum, 21–33. Universidad de Lleida, Lleida, Spain.

POWELL, A. M., AND B. L. TURNER. 1977. Aspects of the plant biology of the gypsum outcrops of the Chihuahuan desert. *In* R. H. Wauer and D. H. Riskind [eds.], Transactions of the Symposium of Biological Resources of the Chihuahuan desert region, United States and Mexico. U.S. National Park Service, Transactions and Proceedings Series 3, 315–325, Washington, D.C., USA.

PUIGNAIRE, F. I., P. HAASE, AND J. PUIGDEFÁBREGAS. 1996. Facilitation between higher plant species in a semiarid environment. *Ecology* 77: 1420–1426.

PYKE, D. A., AND J. N. THOMPSON. 1986. Statistical analysis of survival and removal rate experiments. *Ecology* 67: 240–245.

RIVAS-MARTÍNEZ, S., AND M. COSTA. 1970. Comunidades gipsícolas del centro de España. *Anales del Instituto Botánico A.J. Cavanilles* 27: 193–224.

SOMOLINOS, R. C. 1997. Factores que afectan al reclutamiento de *Helianthemum squamatum*, un endemismo gipsófilo de la Península Ibérica. Tesina de Lic. Fac. CC. Biológicas. Dept. Biología Vegetal I. Universidad Complutense, Madrid, Spain.

STEENBERG, W. F., AND C. H. LOWE. 1969. Critical factors during the first year of life of saguaro (*Cereus giganteus*) at Saguaro National Monument. *Ecology* 50: 825–834.

TANAKA, J. S. 1984. Some results on the estimation of covariance structure models. *Dissertation Abstracts International* 45: 924B.

———. 1987. How big is big enough?: sample size and goodness of fit in structural equation models with latent variables. *Child Development* 58: 134–146.

———, AND G. J. HUBA. 1985. A fit index for covariance structure models under arbitrary GLS stimation. *British Journal of Mathematical and Statistical Psychology* 38: 197–201.

TARAZONA, T., E. BARRENO, A. CRESPO, AND J. DÍAZ-LLANOS. 1980. Estudio estadístico de la vegetación liquénica de los yesos del centro de España. *Anales Instituto Nacional de Investigaciones Agrarias, Madrid* 4: 139–155.

TER BRAAK, C. J. F. 1990. Update notes: CANOCO version 3.10. Agricultural Mathematics Group, Wageningen, The Netherlands.

———, AND I. PRENTICE. 1988. A theory of gradient analysis. *Advances in Ecological Research* 18: 271–317.

THANOS, C. A., K. GEORGHIOU, C. KADIUS, AND C. PANTAZI. 1992. Cistaceae: a plant family with hard seeds. *Israel Journal of Botany* 41: 251–263.

VALIENTE-BANUET, A., A. BOLONGARO-CREVENNA, O. BRIONES, E. EZCURRA, M. ROSAS, H. NÚÑEZ, G. BARNARD, AND E. VÁZQUEZ. 1991. Spatial relationships between cacti and nurse shrubs in a semiarid environment in Central Mexico. *Journal of Vegetation Science* 2: 15–20.

VAN EPPS, G. A., AND C. M. MCKELL. 1983. Effect of weedy annual on the survival and growth of transplants under arid conditions. *Journal of Range Management* 36: 366–369.

VENABLE, D. L. 1989. Modelling the evolutionary ecology of seed banks. *In* M. A. Leck, V. T. Parker, and L. Simpson [eds.], Ecology of seed soil banks, 67–90. Academic Press. New York, New York, USA.

VERHEYE, W. H., AND T. G. BOYADGIEV. 1997. Evaluating the land use potential of gypsiferous soils from field pedogenic characteristics. *Soil Use Management* 13: 97–103.

WALKLEY, A. 1946. A critical examination of a rapid method of determinign organic carbon in soilseffect of variations in degestion conditions and of inorganic soil constituents. *Soil Science* 63: 25–263.

WALTERS, M. B., AND P. B. REICH. 1996. Are shade tolerance, survival and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology* 77: 841–853.

WATSON, A. 1979. Gypsum crusts in deserts. *Journal of Arid Environments* 2: 3–20.

WESSELINGH, R. A., T. J. DE JONG, P. G. L. KLINKHAMER, M. J. VAN DIJK, AND E. G. M. SCHLATMANN. 1993. Geographical variation in threshold size for flowering in *Cynoglossum officinale. Acta Botanica Neerlandica.* 42: 81–91.

———, P. G. L. KLINKHAMER, T. J. DE JONG, AND L. A. BOORMAN. 1997.

Threshold size for flowering in different habitats: effects of size-dependent growth and survival. *Ecology* 78: 2118–2132.

WEST, N. E. 1990. Structure and function of microphytic soil crusts in wild land ecosystems of arid and semiarid regions. *Advances in Ecological Research* 20: 179–223.

WIEGAND, T., AND S. J. MILTON. 1996. Vegetation change in semiarid communities. *Vegetatio* 125: 169–183.

YOUNG, J. A. AND R. A. EVANS. 1989. Dispersal and germination of big sagebrush (*Artemisia tridentata*) seeds. *Weed Science* 37: 201–206.

ZAADY, E., Y. GUTTERMAN, AND B. BOEKEN. 1997. The germination of mucilaginous seeds of *Plantago coronopus, Reboudia pinnata* and *Carrichtera annua* on cyanobacterial soil crust from the Negev Desert. *Plant and Soil* 190: 247–252.

ZAR, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, London, UK.