

CONFLICTING SELECTIVE FORCES UNDERLYING SEED DISPERSAL IN THE ENDANGERED PLANT *SILENE DICLINIS*

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Selective pressures underlying the distance of seed dispersal in *Silene diclinis* were evaluated in natural populations. We expected that high seed predation and high seedling density around mother plants would favor relatively long-distance dispersal and that microhabitat conditions might favor short-distance dispersal. We experimentally altered seed density and seed dispersal distance and found that seed predation by ants increased with density but not with distance. Observations of naturally occurring seedlings showed that their survival probability was higher at lower density and when closer to female plants. Overall, calculated cumulative survival probabilities (including both seed predation and seedling survival) favored limited dispersal. Observations of naturally occurring seedlings and adults showed a strongly clumped spatial population structure. Selection for reduced dispersal and the resulting reduction of colonization ability make *S. diclinis* populations extremely sensitive to environmental stochasticity, and in the long run, this could contribute to the extinction of this endangered species as a consequence of changing land-use patterns.

Keywords: Janzen-Connell model, seed predation, seedling survival, density- and distance-dependent survival.

Introduction

Dispersal of seeds away from parents is an important component of plant species biology (Primack and Miao 1991), and it has special importance for endangered species, given that dispersal can limit the negative consequences of local extinctions (Fischer and Matthies 1998; McKenna and Houle 2000; Quilichini and Debussche 2000). The principal selection pressures we may find acting on dispersal are avoidance of seed predators and pathogens, avoidance of inbreeding, reduced conspecific competition, and increased chance of finding new physically suitable sites (Willson and Traveset 2000). All of these processes are subject to selective forces that may act for or against dispersal and operate at different spatial and temporal scales as described below (Valverde and Silvertown 1997 and references therein; Ferriere et al. 2000).

Janzen (1970) and Connell (1971) suggested that the initial dispersal pattern might affect the intensity of seed predation and the survival of seedlings as a consequence of higher predation and pathogen attack near parents and reduced conspecific competition far from them. Seed predators usually do not act randomly but consume more at high seed densities (density-responsive predators) or on seeds near the seed source (distance-responsive predators). For instance, low seed density reduces the foraging efficiency of ants; hence, granivorous ants preferentially search near sites with high seed density (Bülow-Olsen 1984; Bullock 1989 and references

therein; Gorb and Gorb 2000). Seed predation may have a considerable impact on population dynamics because seed consumption may inhibit seedling recruitment (Maron and Simms 1997) and can be as high as 100% for some plant species in some years (Hulme 1998).

The perceived importance of both density and distance to seed parents in determining seed dispersal patterns (Janzen 1970; Connell 1971) has led to studies that examined how the rates of seed predation and seedling survival depend on both of these factors (Clark and Clark 1984; Hulme 1997; Fragoso et al. 2003; reviewed in Willson and Traveset 2000). Results are mixed, and a meta-analysis by Hyatt et al. (2003) investigating the distance-dependent component of the Janzen-Connell hypothesis failed to show support for this effect. Short-distance dispersal may be favored if the surrounding habitat is of lower quality or is not suitable (Van der Pijl 1972; Schnabel et al. 1998), such as in deserts (Ellner and Shmida 1981), islands (Cody and McOverton 1996), or closed-canopy habitats (Valverde and Silvertown 1997). In these environments, genotypes with more dispersal ability might be selected against.

Moreover, while competition may reduce the fitness of plants growing at high densities by decreasing the availability of resources, a number of investigations have shown that competition does not always negatively affect plant performance (Willson and Traveset 2000 and references therein). In fact, it has even been shown that aggregation can raise fitness by increasing pollination success or positively altering microhabitat quality (Howe and Smallwood 1982; Waddington 1983; Roll et al. 1997; Valverde and Silvertown 1997).

The intention of this study is to disentangle the selective pressures underlying seed dispersal in the endangered dioecious species *Silene diclinis*. Therefore, the effects of density

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and distance are studied separately, beyond the predictable correlation between these factors for a species with restricted dispersal. We determined experimentally how seed density and seed placement relative to female plants affected seed predation by ants for this species, which grows in semiarid areas of Spain where ants are significant seed predators (Hulme 1998). In addition, we surveyed naturally occurring seedlings to investigate how density and distance to a female plant affected seedling survival. Cumulative survival probabilities depending on density and distance were used as an estimate of fitness and the strength of selection. More specifically, we address the following questions: What is the intensity of seed predation by ants in *S. diclinis* populations? Is the probability of seed and seedling survival influenced by either seed or seedling density and/or distance from a female plant? Finally, what is the overall effect of density and distance-related selection pressures in *S. diclinis* population dynamics?

Material and Methods

Study Species

Silene diclinis (Lag.) Laínz (Caryophyllaceae) is a dioecious, hemicyptophytic, long-lived herb endemic to Southern València (Spain). The entire species consists of fewer than 2500 individuals found in the east of Spain in 17 locally dense populations located in an area smaller than 18 km × 9 km. The species is considered endangered by the International Union for Conservation of Nature and Natural Resources (<http://www.redlist.org/>). These populations are distributed in forest or shrub gaps and often in ancient agricultural terraces with low vegetation density. Allozyme diversity studies showed that most of the total diversity was explained by variation within subpopulations and that less common alleles were patchily distributed (Prentice 1984; Prentice and Andersson 1997). Species of the genus *Silene* are typically erect, and the fruits are pericidal capsules that open hygroscopically. Occasionally, seed ejection is facilitated by movement of the stems by wind or animals. In contrast, *S. diclinis* is a rosette-like plant with prostrate stems. Pedicels turn down when the capsules are mature, exposing the fruit pore to the soil immediately below the mother plant. This morphology corresponds with an atelechoric syndrome, i.e., total inability to disperse seeds. Seeds are 1–1.5 mm long by 1.2–1.5 mm wide (Castroviejo et al. 1990) and have an average mass of 1.26 ± 0.33 mg (mean \pm SD; $n = 1831$). Both the allozyme data and natural history observations strongly indicate restricted seed dispersal.

Study Sites

The eight experimental populations were distributed across the whole range of the species. Altitude ranged between 150 and 300 m, and the climate was typically Mediterranean, with maximum temperatures and minimum precipitation both occurring in summer. Average annual temperature in the middle of the distribution range of the species (at Xàtiva's climate station) is 17.8°C, and average precipitation is 729.9 mm/yr. Population nomenclature follows that in the *S. diclinis* recovery plan (Mateu and Nebot 1996). Table 1 has a list of populations and their characteristics.

Table 1

Population Name, Location, and Size (Mateu and Nebot 1996)		
Population	Location (universal transverse Mercator)	Population size (year)
1. Plà de Mora C	Quatretonda (30SYJ2719)	431 (2000)*
2. Plà de Mora E	Quatretonda (30SYJ2718)	5 (2002)*
3. Plà de Mora F	Quatretonda (30SYJ2720)	270 (1996)
4. Plà de Mora G	Quatretonda (30SYJ2720)	200 (1996)
5. Serra del Castell A	Xàtiva (30SYJ1518)	87 (1999)*
6. Clots d'Isidoro	Simat de la Vall digna (30SYJ2824)	118 (2001)*
7. Plà de Suro D	Barx (30SYJ3021)	57 (2000)*
8. Cerro Santa Ana	Llosa de Ranes (30SYJ1323)	54 (2000)*

Note. Asterisk indicates censused by D. Montesinos.

Seed Predators

Preliminary observations of predation of *S. diclinis* seeds showed that ants were the only significant seed predators. During the seed dispersal periods of the years 2000 and 2002, we collected ants preying on *S. diclinis* seeds directly from plants, from soil, or from the petri dishes of the experimental study. All the individuals observed belong to the species *Aphaenogaster iberica* and *Messor bowwieri* (D. Montesinos, personal observation; nomenclature follows Collingwood 1978).

Seed Predation

To examine the intensity of seed predation by ants, we performed an experimental seed removal study in three different populations. Petri dishes (5-cm diameter) with five seeds each were randomly distributed in spaces between plants along each population as follows: 10 dishes in populations 6 and 5 (years 2001 and 2002) and, because of its greater size, 20 dishes in population 1 (years 1997, 1998, 2001, and 2002). Each of the dishes had a 5-mm hole in the side that allowed the ants to enter and remove the seeds. The seeds used in this study were collected the previous year from the same study populations; seed viability is above 95% 1 yr after seed collection (D. Montesinos, personal observation). If there were not sufficient seeds from a single population, seeds from the nearest available population were pooled with them. The dishes remained in the field for 2 wk during the periods of natural dispersal: May 11–25, 1997; May 24–June 7, 1998; May 21–June 5, 2001; and June 7–21, 2002 (seed dispersal dates vary between years depending on weather conditions). A generalized linear model with binomial distribution was calculated with the R statistical package (Ihaka and Gentleman 1996) to test for differences in percentage of predation between years and populations.

To determine the effect of seed density on seed predation, we selected nine sites close to each experimental population. No *S. diclinis* plants were present in such locations, so natural population seed density did not affect our experimental design. In each of the nine locations, we set up two groups of seeds with different densities: the high-density group with 25 clumped seeds and the low-density group, where 25 seeds were separated by 1 m from each other in a 5 × 5-m grid. Each seed or group of seeds was protected from predators

other than ants and from raindrops inside a petri dish as described above. Seeds remained in the field from May 21 to June 6, 2001. A generalized linear mixed model with binomial distribution and population as a random factor was calculated with the R statistical package to test for the effect of seed density on seed predation.

To examine the effect of the distance of the seeds from female plants on seed predation, 10 sets of two petri dishes, each containing 25 seeds, were placed in each of the populations. One of the dishes was placed just next to a reproductive female and the other 1.5 m away from it. All the dishes were more than 2 m from any other dish or *S. diclinis* plant to avoid interference in seed predation. Dishes remained in the field from June 7 to June 21, 2002, and then the percentage of predation was calculated. A generalized linear mixed model with binomial distribution and population as a random factor was calculated with the R statistical package to test for the effect of seed distance to female plants on seed predation.

Seedling Survival and Spatial Population Structure

We analyzed the spatial pattern of seedling and adult distribution in the entire population to understand the long-term effect of dispersal. We conducted monthly seedling censuses in population 6 from November 2000 to November 2001 and adult censuses in March of 2001. This population was chosen because of its accessibility and flat terrain. Movement of seeds through slopes must be low in this site, and environmental noise caused by local topography is minimized, reflecting only the initial seed dispersal pattern. The locations of both adults and seedlings were recorded in a coordinate system. Each individual was permanently marked with an aluminum tag. In each census, we visually determined the sex of the adult plants and the emergence and fate of each seedling. We searched for seedlings up to 10 m away from the adults at the edge of the population. Predation of seedlings was not detected. Observed seedling mortality appeared to have been caused exclusively by desiccation.

We examined the population spatial structure with Ripley's *K* analysis (Ripley 1977). Analyses were done with the statistical environment R (Ihaka and Gentleman 1996) and the software package spatstat (Baddeley and Turner 2004). Ripley's *K(r)* analysis compares the observed number of plants within a distance *r* of an arbitrary plant with the expected number of plants within that distance in a random distribution. If values of the observed densities are above the critical interval for a random distribution, plants are significantly clumped; if observed densities are below the critical interval for a random

distribution, plants are significantly overdispersed. *K(r)* analysis was performed to test whether adults were significantly more aggregated than expected from a random spatial distribution. Bivariate Ripley's *K(r)* was calculated to determine whether seedlings were significantly aggregated near female plants before and after the dry season.

To obtain survival probabilities depending on distance and density from female plants, we performed logistic regression analysis using the SPSS statistical package (Norusis 2002). To test the survival probability of each seedling depending on the distance to the nearest female, the variable distance was logarithmically transformed. For the seedling density study, the test was applied to the survival probability of each seedling depending on the number of other seedlings growing less than 10 cm from it (hereafter seedling density is defined as the number of seedlings occurring at less than 10 cm from each seedling in the population).

Following the methodology described by Alcántara and Rey (2003) for multiplicative fitness analysis, we multiplied each seed survival probability (high or low density or distance) by each seedling survival probability along the observed range. Obtaining fitness estimates for each situation allowed us to compare the strength of the selection pressures through density and distance factors.

Results

Seed Predation

The mean seed predation was $81.3\% \pm 33.82\%$ (mean \pm SD), ranging from 54% to 100% (table 2). Neither population (estimate = -1323.02 ± 925.84 , $t = -1.43$, $P = 0.370$) nor year (estimate = -0.54 ± 0.50 , $t = -1.08$, $P = 0.210$) significantly affected seed predation, nor was the interaction significant (estimate = 0.66 ± 0.46 , $t = 1.43$, $P = 0.130$). Seeds in the high-density treatment were significantly more likely to be preyed on ($91.6\% \pm 20.04\%$) than seeds in the low-density treatment ($80.9\% \pm 19.06\%$) ($F = 10.43$, $df = 1$, 440 , $P = 0.001$). However, the effect of distance to a female plant was not significant, with seeds relatively close to a female plant being preyed on an average of $81.8\% \pm 30.31\%$ and seeds 1.5 m from a female plant averaging $76.7\% \pm 33.64\%$ ($F = 2.63$, $df = 1$, 2394 , $P = 0.105$).

Seedling Survival and Spatial Population Structure

Population 6 was composed of 131 adult plants. The average distance from an adult plant to the nearest adult

Table 2

Percentage of Seed Predation in Different Years and Populations

Population	1997	1998	2001	2002	Population average
Plà de Mora C	75.79 \pm 38.63	83.00 \pm 32.62	85.00 \pm 31.71	90.00 \pm 23.94	83.54 \pm 31.83
Clots d'Isidoro	92.00 \pm 19.32	62.00 \pm 43.67	77.00 \pm 36.29
Serra del Castell A	54.00 \pm 46.24	100.00 \pm 0.00	77.00 \pm 39.62
Year average	75.79 \pm 39.63	83.00 \pm 32.62	79.00 \pm 35.93	85.50 \pm 30.38	81.34 \pm 33.82

plant was 39.9 ± 61.64 cm, with a minimum of 0 cm and a maximum of 360 cm (fig. 1A). We found 155 seedlings emerging in the population. Assuming that the nearest female was the mother for each seedling, the average distance from a seedling to its mother was 47.9 ± 53.03 cm, ranging from 0 to 310 cm (fig. 1B). Only 20 seedlings (13%) survived the dry conditions of the first summer. Average distance from surviving seedlings to the nearest female was 29.5 ± 70.27 cm, ranging between 0 and 310 cm (fig. 1C).

Ripley's $K(r)$ spatial analysis showed that the studied distributions are significantly aggregated all along their distribution range for adults (fig. 2A), emerging seedlings (fig. 2B), and seedlings surviving the first summer (fig. 2C). Observed densities for each category are clearly above the critical interval for a random distribution.

Seedling densities, measured as the number of seedlings at less than 10 cm from each seedling in the population, ranged from 0 to 31. There was a significant negative correlation between seedling density and survival (intercept = -1.418 , $B = -0.077$, Wald = 6.301, $df = 1$, $P = 0.012$), indicating that the higher the seedling density, the lower the survival probability.

Seedling distance to the nearest female plant ranged from 0 to 301 cm. Logistic regression revealed a significant negative correlation between the logarithm of the distance to the nearest female plant and seedling survival (intercept = -0.8243 , $B = -1.034$, Wald = 10.489, $df = 1$, $P = 0.001$), indicating an increased probability of survival with increased proximity to the nearest female plant.

Multiplicative Fitness Analysis

Seeds survived with a probability of 8.44% at high density and 19.11% at low density. Seedling survival depending on density was modeled in the logistic regression analysis above. Hence, we can obtain regression lines for the accumulated probability of survival depending on seed and seedling density. By multiplying each of the two seed-density survival probabilities by each seedling-density survival probability in the regression equation (ranging from 0 to 31), we obtain cumulative survival probability lines depending on seed and seedling density (fig. 3).

Because seed distance to the nearest female plant did not have a significant effect on seed predation, the average probability of seed survival depending on distance (20.75%) can be multiplied by each seedling-distance survival probability in the regression equation (ranging from 0 to 310 cm) to obtain a cumulative survival probability line depending on seed and seedling distance to the nearest female (fig. 4).

The density-dependent cumulative survival probability ranges from 0.2% to 3.7%, and the distance-dependent cumulative survival probability ranges from 0.7% to 6.3% (figs. 3, 4). The difference between the minimum and the maximum survival probabilities indicates the maximum fitness gain achievable by reduction of seed and seedling density (3.5%) or by reduction of dispersal distance (5.6%), indicating that reduction of dispersal distance has a greater effect on survival than does density.

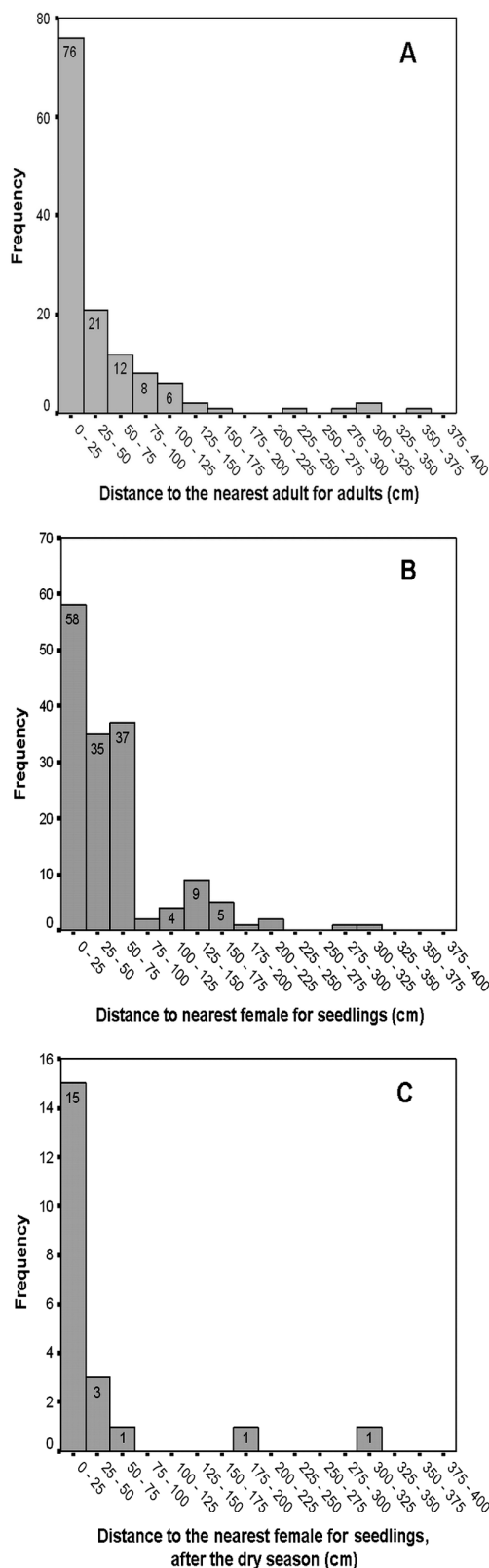


Fig. 1 Histograms of frequencies in relation to (A) distance to the nearest adult for adults, (B) distance to the nearest female for seedlings, and (C) distance to the nearest female for seedlings after the first summer.

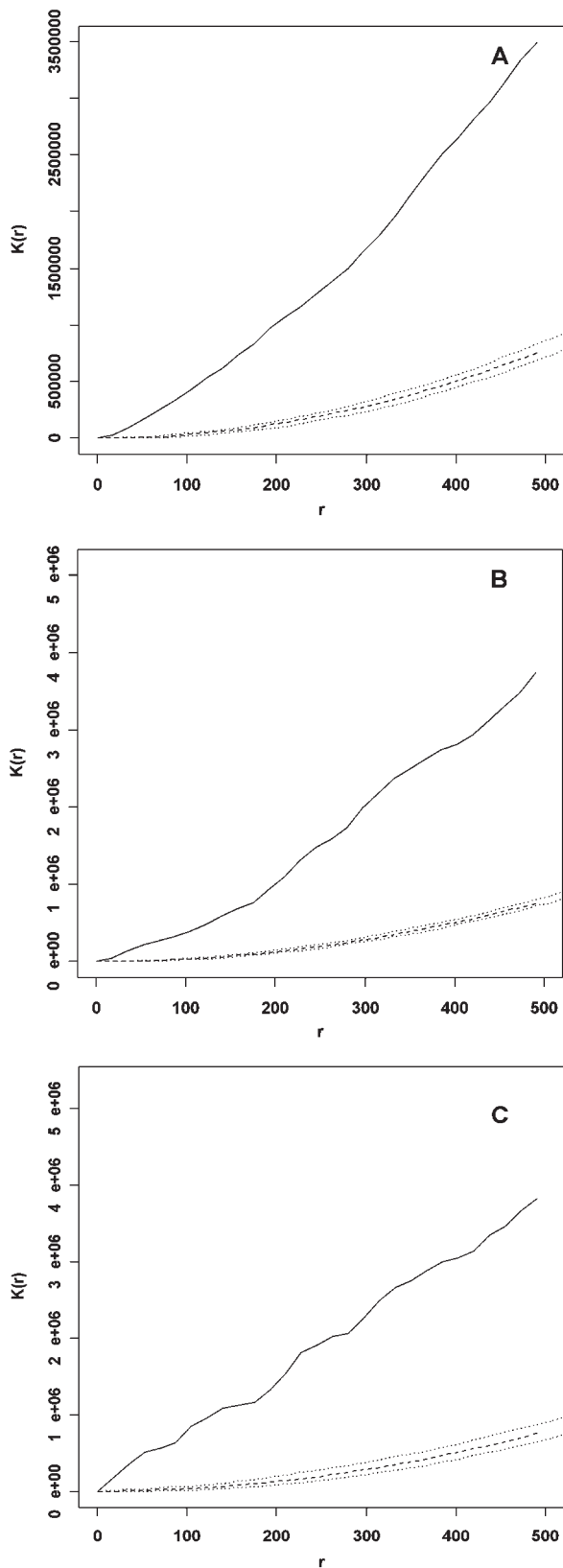


Fig. 2 Ripley's $K(r)$ compares the observed number of plants within a distance r of an arbitrary plant with the expected number of plants within that distance in a random distribution. Dashed line

Discussion

Seed Predation

High levels of seed predation in natural populations may be attributed in part to limited seed dispersal because restricted dispersal is associated with a clumped seed distribution, which improves the foraging efficiency of ants (Bulow-Olsen 1984; Bullock 1989; Gorb and Gorb 2000). We demonstrated experimentally that scattered seeds (i.e., dispersed away from maternal plants) have a lower predation risk than aggregated seeds. Seed predation by ants, however, was independent of the distance to a female plant, a result that was also reported in predation experiments with other Mediterranean species (López-Vila and García-Fayos, forthcoming). This indicates that ants did not search for seeds more intensely in the vicinity of adult female plants but that when they find a seed source, they consumed the majority of the seeds. Therefore, the ants in our study populations are not distance-dependent predators, but they are density-dependent predators (*sensu* Janzen 1970). These results are in agreement with those of Bullock (1989), who also found higher seed removal by ants if seeds are clumped. Given that scattered seeds have a higher probability of survival, this results in positive selection by ant seed predation toward increased dispersal.

Some studies have shown that occasional loss of seeds transported by granivorous ants can lead to seed dispersal rather than seed predation (Van der Pijl 1972). For example, in a study by Detrain and Tasse (2000), 0.1% of seeds removed by ants were not consumed. Despite such low effective dispersal by granivorous ants, rare long-distance dispersal events may play an important role in colonization and migration (Portnoy and Willson 1993; le Corre et al. 1997; Cain et al. 1998; Higgins and Richardson 1999; Nathan and Muller-Landau 2000). However, these events may be rarely effective in *Silene diclinis* because it is dioecious and at least one male and one female have to reach adulthood within a moderately short distance from each other in order for reproduction to occur. Giles and Goudet (1997) reported that a minimum of four to six colonizers are needed for effective reproduction in *Silene dioica*, which is closely related to *S. diclinis* and also dioecious. Combining the probable low percentage of seeds transported but not consumed with this requirement for multiple individuals to be dispersed to the same site, we conclude that the removal of seeds by granivorous ants should be interpreted as seed loss.

Population Structure and Seedling Survival

Adults and seedlings are significantly aggregated in space. This pattern is consistent with the presence of traits limiting seed dispersal in *S. diclinis*, e.g., the prostrate branches and

represents the expected density of plants for each distance r (cm) in a random spatial distribution. Dotted lines represent the critical interval for that random distribution. Continuous line represents the distribution of our studied population for the adult-to-adult distribution in the entire population (A), the seedling-to-female distribution in the entire population (B), and the seedling-to-female distribution in the entire population (C) after the first dry season.

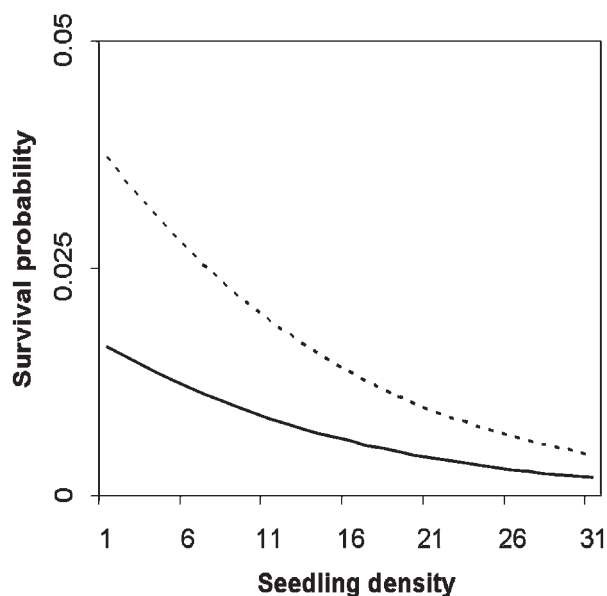


Fig. 3 Survival probability depending on density factors. Lines indicate survival probabilities for low seed density (dotted line) and high seed density (solid line) for each seedling density (number of seedlings at less than 10 cm of each seedling). No significant differences were found between years or between populations.

downward movement of the pedicel during fruit maturation, and with previous genetic studies (Prentice 1984; Prentice and Andersson 1997). In our spatial pattern analysis, we assumed that the nearest female was the mother plant. This assumption may lead to underestimation of dispersal distances, according to the model of Nathan and Muller-Landau (2000), in which at least some seedlings/seeds may originate from plants farther away than the nearest neighbor. Nevertheless, this assumption would work best when seed shadows overlap very little. Based on the morphology and dispersal syndrome of the plant, we have reason to believe that *S. diclinis* seed shadows are largely nonoverlapping.

Both the adult and seedling patterns show the leptokurtic relationship between number and distance (fig. 1) expected for a typical seed shadow (Willson and Traveset 2000). However, in *S. diclinis*, dispersal potential is extremely low, and the average distance between adult plants is lower than the average distance between seedlings. This pattern does not fit what would be expected according to the common hypothesis that survival probability should be higher the farther a seed or seedling is from its seed parent (Janzen 1970; Connell 1971; Platt 1976). This difference can be explained by our data that show higher probability of survival for seedlings occurring near female plants. Drought was the most likely cause of mortality, which indicates that suitable microhabitats are more likely to occur near female plants. Dispersal far from the mother plant therefore appears to be selected against because it is dispersal into sites unsuitable for survival. In contrast, selection for greater dispersal was found in our study via a negative effect of density on seedling survival (clumped seedlings survived less well than isolated seedlings). Clumped seedlings may have had reduced fitness

because of competition for the same resources—nutrients and water (Gorb and Gorb 1997; Augspurger 1984).

Multiplicative Fitness Analysis

To evaluate the tension between selective forces for and against dispersal, we compared the magnitude of the effects of density and distance, respectively. Overall, we found that fitness is maximized if dispersal is limited because the fitness gain achievable by reducing distance to a female plant was higher (5.6%) than the fitness gain associated with increasing dispersal so as to decrease seed and seedling density (3.5%).

Final Remarks

Once a selective force is detected, interpretation of its effect must be done carefully. Selective forces often act in opposite ways (Alcántara and Rey 2003), and other factors may be obscuring the effect of the detected selective process. Detection of a population-level pattern is needed to conclude the final consequence of the global selective process.

In *S. diclinis*, limited dispersal is globally favored, even though selective forces are opposite and partially counteracting. Restricted seed dispersal results in severe seed predation by ants, which prey more efficiently at high seed densities. However, seedlings occurring near female plants have a higher chance of survival. Higher seedling survival near adult plants seems to be the main factor shaping the population spatial pattern, surpassing the effect of other counteracting factors. This may explain the aggregated spatial population structure we found for both seedlings and adult plants. Selection pressures acting against dispersal are likely to lead to reduced colonization ability. In addition, landscape changes caused

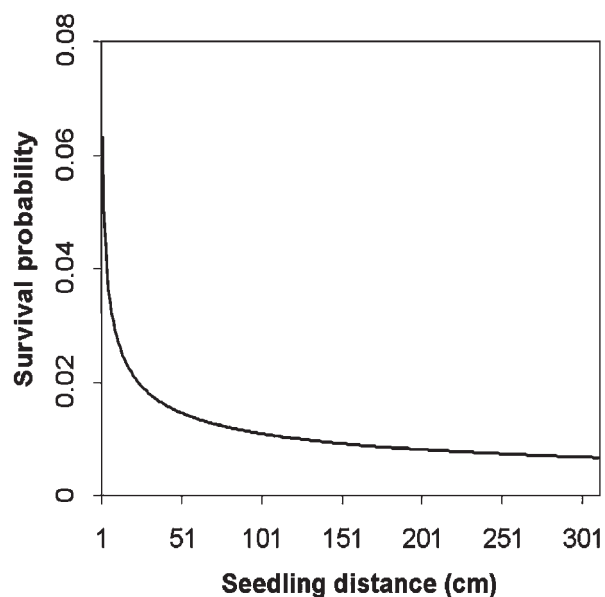


Fig. 4 Survival probability depending on distance factors. Line indicates cumulative seed and seedling survival probabilities for each distance from the mother plant (cm). Seed distance from the mother plant was not significant, so only one line for the average value is shown.

by intensive agriculture have been documented as a cause of extinction for some *S. diclinis* populations (I. Mateu, personal observation), and increased competition and shading from habitat change are negatively affecting some others (D. Montesinos, unpublished data). Inability to colonize new areas makes the remaining *S. diclinis* populations extremely sensitive to negative stochastic effects and is likely to increase the probability of extinction of this endangered species.

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