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Original article

Diplochory in *Ulex parviflorus* Pourr

J.R. López-Vila [a,*], P. García-Fayos [b]

[a] *I.E.S. Clara Campoamor, Alaquàs (Valencia), Spain*
[b] *Centro de Investigaciones sobre Desertificación–CIDE–(CSIC–UV–GV), Apartado Oficial 46 470, Albal (Valencia), Spain*

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Abstract

Ulex parviflorus (Fabaceae) is a fire-prone shrub of the western Mediterranean Basin that disperses their seeds both by the explosion of the legumes and the action of ants. Over 3 years we studied seed dispersal in a population from eastern Spain. We analysed the temporal and spatial patterns of primary seed dispersal and their consequences for the foraging behaviour of ants. We also studied the effect of seed manipulation by ants on germination success.

Primary seed dispersal correlated positively with air temperature. The curve of seed abundance as a function of distance of the plant displayed one peak under the plant and another peak at 130 cm. Ants of the species *Messor barbarus* were observed collecting seeds and they were attracted by the elaiosome. However, the spatial pattern of the seeds in the soil did not shape the foraging activity of the ants. Ants brought the seeds to their nest stores, removed the elaiosome and threw away the seeds in the refuse piles. By removing the elaiosome ants increased the germination rate in relation to intact seeds.

Results showed that diplochory operates on seeds of *U. parviflorus* allowing the species to exploit heterogeneous establishment conditions. Primary dispersal places seeds near the mother plant but at the expense of delayed germination. These seeds should be incorporated into the soil seed bank and then activated by forest-fires or canopy disturbance. Secondary seed dispersal by ants activates seed germination and allows the plant to establish immediately after seed dispersal.

Keywords: Fabaceae; Seed dispersal; Autochory; Myrmecochory; Diplochory; Elaiosome; Ants; *Messor barbarus*; *Camponotus cruentatus*; Forest fire; Mediterranean shrubland

1. Introduction

Some forms of seed dispersal involve more than one phase with distinctly different dispersal mechanisms. These complex dispersal systems are designated as diplochory or polychory in contrast to the more frequent cases that involve only one dispersal mechanism (Van der Pijl, 1982; Westoby and Rice, 1981; Clifford and Monteith, 1989; Stamp and Lucas, 1990; Vander Wall and Longland, 2004).

Single dispersal mechanisms seldom provide a plant with all the benefits of seed dispersal at the same time (Howe and Smallwood, 1982) but a combination of two or more mechanisms should improve this (Vander Wall and Longland, 2004). Accordingly, ballistic dispersal typically scatters seeds less than 5 m from the mother plant (Stamp and Lucas, 1990), leaving these seeds open to density-dependent causes of mortality (predation dependent on seed density and seedling competition). Ants can move seeds up to 77 m (Gómez and Espadaler, 1998) providing seeds with escape mechanisms from distance-dependent causes of mortality (predation dependent on distance to the seed source and parent competition). Ant nests have been considered as suitable sites for seedling establishment because of the soil enrichment in the refuse pile area (Dean and Yeaton, 1992,1993; MacMahon et al., 2000 but see Rice and Westoby, 1986) but at the same time the concentration of seeds in the refuse piles and ant nest stores may generate density-dependent mortality. Therefore, the combination of authochory and mirmechocory in the same species may result in more opportunities for plant establishment than if only one seed dispersal mechanisms is involved, allowing the plants to exploit temporally or spatially heterogeneous establishment conditions.

However, the relationships between the two dispersal modes are unknown and the hypothetic benefits for plant establishment deriving from the combination of both dispersal mechanisms untested. We do not know whether ant foraging behaviour is modified by the distribution of seeds

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* Corresponding author.
E-mail address: patricia.garcia-fayos@uv.es (P. García-Fayos).

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over time and space resulting from explosive dehiscence. Nor do we know whether the combination of both dispersal modes is more successful for plant establishment than only one of them would be.

Diplochory by explosive fruit dehiscence that scatters seeds that bear elaisomes that are sought by ants has been reported from many Fabaceae (Herrera, 1987a; Bossard, 1991; Moreno et al., 1992; López et al., 2000; Stokes et al., 2003), including some other species of the genus *Ulex*. Here we address the above questions by examining seed dispersal of *Ulex parviflorus* Pourr. (Fabaceae), a very common plant in fire-prone areas of western Mediterranean Basin, whose fruits have explosive dehiscence and the seeds bear elaisome.

2. Material and methods

2.1. Study species

U. parviflorus (Fabaceae) or Mediterranean gorse is a thorny bush measuring up to 150 cm in height, very common in the shrublands of the coastal Mediterranean areas of France and Spain (Baeza et al., 2003). The flowers are hermaphrodite and they bloom from October to March. Pollination takes place mainly by species of the genus *Apis* and only pollinated flowers yield pods with seeds (Herrera, 1987b). The fruits are dry legumes with explosive dehiscence and contain one to four seeds. As in other *Ulex* species, the seeds have a very hard coat and bear an elaiosome (Stokes et al., 2003). The great drought resistance of the plant, the high seed production, the ability of the seeds to form permanent soil seed banks and to resist the high temperatures of forest-fires account for its ability for colonisation of open spaces, such as old-fields and burnt areas (Ballini, 1992; Baeza et al., 2002). The extremely high population densities of Mediterranean gorse on abandoned farmlands and burned areas increases the susceptibility to fire (Baeza et al., 1998) and thus favours the long scale persistence of gorse populations in these areas. For these reasons much effort is expended on control measures (Baeza et al., 2003).

2.2. Study area

The study was carried out in the Desert de les Palmes (Castelló, Spain) (44°42′N and 2°48′E). The experimental site was located 3 km from the coastline at 550 m.a.s.l., with 15.2 °C average annual temperature and 540 mm annual precipitation (Quereda, 1985). The vegetation is a dense shrubland 0.5–1.5 m high dominated by *U. parviflorus, Rosmarinus officinalis* L. (Labiatae) and *Cistus albidus* L. (Cistaceae) and with a scattered tree layer of *Pinus halepensis* Mill. (Pinaceae).

2.3. Primary dispersal

To know the temporal dynamics of primary seed dispersal and what environmental factors affect the explosive opening of the fruits, we made weekly censuses of the number of open fruits on plants throughout the period of fructification and seed dispersal in 1997, 1998 and 1999. Since 98% of the fruits in our study area have only one seed (1.13 ± 0.39 seeds per fruit, J.R. López-Vila, personal observation from pod counts in 1997), the number of open fruits was considered a reliable measure of seeds dispersed. Over the same period, we measured air temperature and relative humidity as factors that can affect fruit opening, given the hygroscopic nature of the explosion of the legumes. We correlated the percentage of open fruits per week with average temperature and relative air moisture in the same period.

To study the spatial pattern of primary seed dispersal on the ground we selected three plants of *U. parviflorus* 5 m apart from each other to avoid interferences in seed arrival. These plants were representative in size of the species in the study area (h = 75.67 cm ± 24.44 and Ø = 78.03 cm ± 26.25). In April 1998, before any fruit in the experimental plants opened we covered the ground with a cloth in a 3 m × 3 m square around each plant to trap the dispersed seeds. We counted the seeds in the traps weekly during the seed dispersal period of 1998 and measured the distance of each seed to the main stem of the mother plant as well as its compass direction. To avoid modifications by ants of the spatial location of the seeds we applied an ant-repellent to the traps during the experiment.

2.4. Secondary dispersal

In May 1999 we estimated the ant density in a plot of 400 m^2 at the study area by the fall trap method (Lévieux, 1969). The fall traps consisted of recipients 9 cm in diameter and 1.5 cm in height buried up to the neck. The traps were filled with 60 ml of distilled water with some drops of detergent to eliminate surface tension and had a time of evaporation of 48 h. Ten fall traps were placed in two parallel lines three meters apart. After 24 h we visited the traps and counted the ants. The experiment was repeated weekly between the last week of May and the first week of July 1999. Only ants belonging to the species observed transporting the seeds of *U. parviflorus* were considered in the analysis. At the end of the experiment we counted all ant nests to estimate their density in the plot.

To check whether ants were attracted by the elaiosome, we offered seeds with and without elaisomes to ants. Under each of five individuals of *U. parviflorus* of the plot we placed two Petri-dishes with 1 cm diameter lateral holes to allow ant access and containing six seeds either with elaiosome in one dish or without elaiosome in the other. Both Petri-dishes were located at 60 or 150 cm from the mother plants and in different compass directions to avoid interferences. We counted the remaining seeds in the traps weekly from the last week of March to the first of May 1999. The dishes were rotated 45° clockwise with respect to the plant stem, to prevent the ants from learning their location. The variable used in the analysis was the number of surviving seeds per week and was analysed using the Kaplan–Meier test.

If ants actively look for the seeds of *U. parviflorus* it must be reflected in their spatial foraging patterns, and therefore, specialist ants should search for seeds more intensively in the areas with higher seed densities. Under this hypothesis, we would expect ants to remove more seeds from the traps in the peak zones of the primary seed dispersal curve than elsewhere. On the contrary, if the seeds of *U. parviflorus* are removed as the result of a generalist search by ants, then the removal pattern of seeds should be homogeneous through the landscape. To investigate this, we chose three individuals of *U. parviflorus* in the plot and placed 16 Petri-dishes per individual with 1 cm diameter lateral holes to allow ant access and containing five seeds with elaiosomes. The dishes were placed at 30, 90, 150 and 210 cm and along four orthogonal compass directions. Weekly counts were carried out of the seeds remaining in the dishes and these were refilled to reach five seeds at each visit. The dishes were rotated 45° clockwise with respect to the plant stem, to prevent the ants learning their location. The experiment lasted from March until June 1999. The variable analysed was the percentage of removed seeds and was analysed using a two-way ANOVA, the factors being the distance and the compass direction. Four levels for plant distance and four for compass direction were considered. This last factor was summarized as N, S, E and W by grouping the classes N and NE, S and SW, E and SE and W and NW.

To know the fate of the seeds removed by the ants and thus understand their role as potential seeds dispersers of *U. parviflorus*, we collected all the material accumulated in the refuse piles at the end of the seed dispersal season of 2000 from each of the six ant nests we found in the plot. Also we dug out one ant nest to determine the material stored by the ants. We checked for the presence of elaiosomes on all the seeds of *U. parviflorus* in the refuse piles and nest-store. To compare the representation of seeds with and without elaiosomes in the refused piles we used the *t*-test analysis for related samples.

To study the influence of the ants' manipulation on the germination of *U. parviflorus* seeds, we collected seeds with and without elaiosome from the ground as well as from the working ants in the study area. Four Petri-dishes per treatment with 25 seeds imbibed with 5 ml of distilled water were placed in a germination chamber with cycles of 12 h light/dark and 20°/10 °C respectively. The Petri-dishes were checked daily for seed germination for 90 days. We analyse the effect of the elaiosome on germination rate at day 90 and the T50%—the number of days needed until 50% germination in a Petri-dish with *t*-tests.

Previous to the all the statistical analysis we checked the data for the assumptions of parametric tests. The analyses were carried out with the statistical package SPSS v.12.0.

3. Results

3.1. Primary dispersal

Primary seed dispersal takes place from the end of March until June, with a maximum in May, and was consistent over the 3 years of study (Fig. 1).

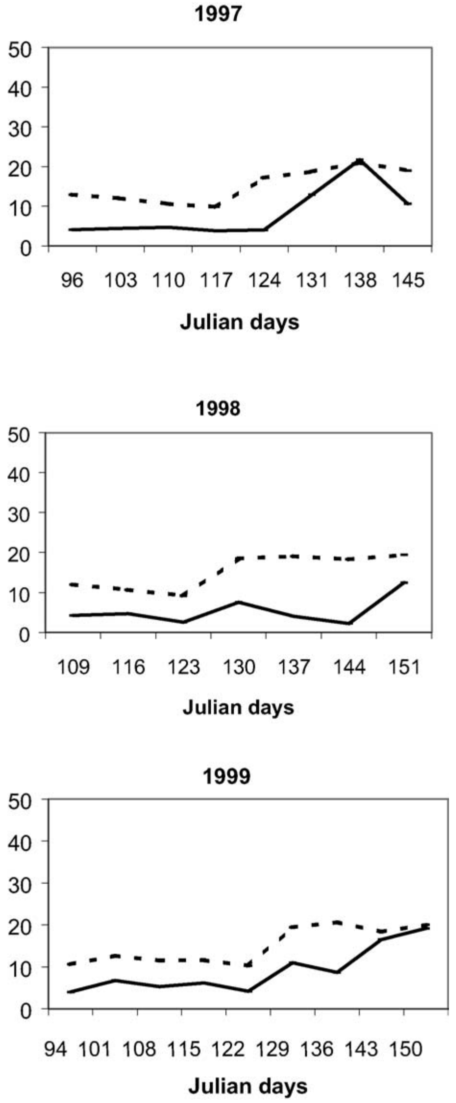

Fig. 1. Temporal pattern of seed dispersal (measured by fruit opening) in *U. parviflorus* in 1997, 1998 and 1999. Data are percentage of opened fruits per week (solid line) and weekly average of air temperature in Celsius degrees (dashed line). Time is expressed in Julian dates. Correlation indexes are $r_{1997} = 0.808, n = 8; P = 0.015; r_{1998} = 0.476, n = 7, P = 0.280; r_{1999} = 0.798, n = 9, P = 0.010$.

The correlation between the number of fruits that opened up weekly and the average temperature of the same period was significant and very high ($r \geq 0.8$) except for the year 1998 (Fig. 1). On the other hand the number of fruits opening did not vary with air moisture ($r < 1$; $P > 0.5$), which was high (> 40%) and invariant over the study period, possibly because of proximity to the sea.

The spatial pattern of primary dispersal of the seeds in terms of the distance and direction from the mother plant is represented in the Fig. 2. The seed dispersal curve displays two peaks, one under the plant, possibly as a result of the seeds dispersed from the most interior fruits crashing against the structures of the plant itself and another peak at 130 cm. Regarding direction, we found also two peaks, S and W, which coincided with the branches of the plants with highest production of flowers and fruits (López-Vila, 2003).

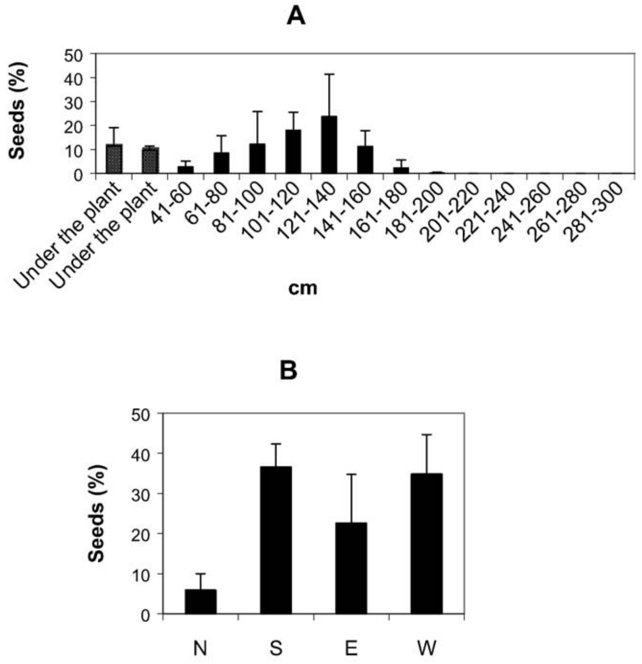

Fig. 2. Spatial pattern of seed dispersal in *U. parviflorus*. Data are percentage of seeds ($\overline{X}$ ± S.D.) falling at the different distances from the main stem of the mother plant (a) and in the compass directions (b).

3.2. Secondary dispersal

Camponotus cruentatus and *Messor barbarus* were the only ants caught in the pit-fall traps, but only *M. barbarus* was found collecting seeds of *U. parviflorus* in the study area. The density of *M. barbarus* individuals in the plot was more than five times that of *C. cruentatus* and strongly decreased in the study area as the number of available fruits in the plot decreased ($r = 0.968$; $n = 5$; $P = 0.007$) (Fig. 3). We found 1.5 *M. barbarus* nests per 100^2 in the study area was. *C. cruentatus* individuals were rare throughout the period of seed dispersal and no nest was found in the study plot, but ant density also highly correlates with the number of open fruits ($r = 0.891$; $n = 5$; $P = 0.043$). Ants collected most of the seeds in the predation experiments (68.7% ± 5.1; $n = 48$) but the removal of seeds by the ants did not vary with distance ($F_{3,48} = 1.456.$, $P = 0.245$) or compass direction from the plant ($F_{3,48} = 0.608$, $P = 0.217$) (Fig. 4).

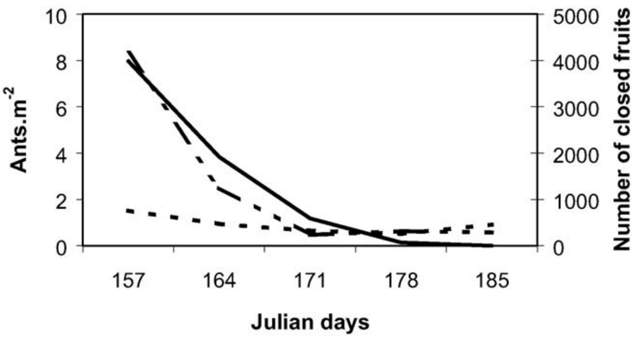

Fig. 3. Ant density of *M. barbarus* (dashed line) and *C. cruentatus* (dotted line) in the plot with respect to the number of closed fruits in the three studied plants of *U. parviflorus* (solid line) during the dispersal period of 1999 ($r_{Messor \times \mathrm{fruits}} = 0.968$, $n = 5$; $P = 0.007$ and $r_{Camponotus \times \mathrm{fruits}} = 0.891$, $n = 5$; $P = 0.043$).

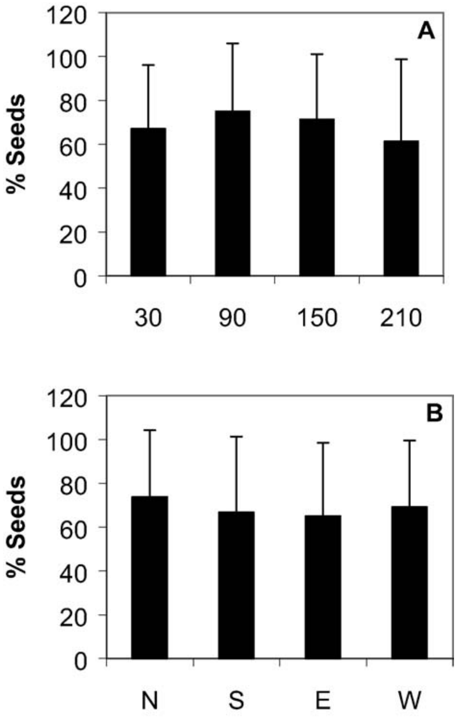

Fig. 4. Removal of *U. parviflorus* seeds by the ant *M. barbarus* in relation to the distance to the plant (a) and the compass direction (b). Neither, the distance nor the compass direction had effect on the removal rate (distance $F_{3,48} = 1.456.$, $P = 0.245$; compass direction $F_{3,48} = 0.608$, $P = 0.217$).

Ants preferentially removed seeds with elaiosomes. Seeds with elaiosomes remained in the Petri-dishes 9.80 ± 3.42 days ($\overline{X}$ ± S.D.; $n = 30$) but those without remained significant longer (25.20 ± 10.48 days; *Log-Rank* $\aleph^2 = 5.33$; $P = 0.021$). Refused piles and stores in the nests of *M. barbarus* contained seeds of *U. parviflorus*, both with and without elaiosomes in variable quantities among ant nests (Table 1). Seeds without elaiosomes were six times more common than those with in the refused piles ($t_r = -29.064$; df = 5; $P < 0.0001$). Stores in the one nest for which this was examined contained four times more seeds than did the refuse pile, and practically all of them still conserved the elaiosome.

Elaisome removal facilitated seed germination (Fig. 5). After 90 days about 15% more of the seeds without than with elaiosome had germinated ($t = 3.166$, df = 18, $P = 0.005$;

Table 1
Number of seeds of *U. parviflorus* found in the refused piles and stores of the ant nests of *M. barbarus* at the end of the seed dispersal season of 1999 in the study plot and percentage of seeds with and without an elaiosome

Ant nest	Source	Seeds examined	With (%)	Without (%)
1	Refuse pile	102	9	91
1	Nest store	398	93	7
2	Refuse pile	80	15	85
3	Refuse pile	69	16	84
4	Refuse pile	77	13	87
5	Refuse pile	50	8	92
6	Refuse pile	125	12	88

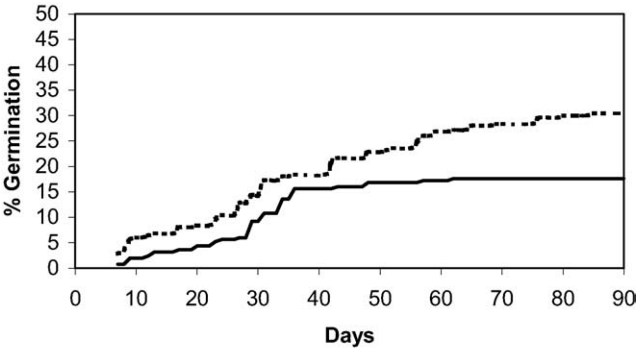

Fig. 5. Germination of *U. parviflorus* seeds with elaiosome (solid line) and without elaiosome (dashed line).

$n = 6$). However, the time that the seeds need to reach 50% of germination (T50) did not differ between treatments ($t = 1.674$, df = 18, $P = 0.110$; $n = 6$).

4. Discussion

U. parviflorus undergoes primary seed dispersal by explosive dehiscence of fruits at the end of spring. Dehiscence is positively related to average air temperature but not to relative air moisture and coincides with a considerable increase in the activity of the colonies of seed-harvesting ants. More than half of the seeds dispersed by a plant landed within 120 and 150 cm around the plant in a scattered pattern that paralleled the distribution of the fruits in the plant branches.

Ants of the species *M. barbarus* and *C. cruentatus* removed more than 60% of the seeds on the ground. The presence of these ant species in the study area seems to be linked to the availability of the seeds of *U. parviflorus*, the only plant that disperses seeds at that time, because the density of both ant species was correlated to the number of fruits opened. Despite this closed relationship, ants did not forage more intensively in areas that received most primary dispersed seeds around *U. parviflorus* plants as optimal foraging theory would predict (Stephens and Krebs, 1986). This result supports the hypothesis that seeds of *U. parviflorus* may be only one of several food sources for the ants, and therefore, the harvesting behaviour of the ants may be conditioned not only by their availability but by the presence of other food sources and the distance from the anthill (Willot et al., 2000).

The preference of ants for seeds with elaiosome and the differences in the proportion of seeds with and without elaiosome in the refuse piles of the nests of *M. barbarus* implies that these ants exploit the seeds of *U. parviflorus* for their elaiosome, as had been experimentally established by Martín-Azcárate et al. (1998). Although *M. barbarus* was the most important seed harvester ant in our study area other species of *Messor* that overlap in distribution with *U. parviflorus*, such as *M. capitatus* and *M. bouvieri*, may play the same role in other areas, given the non-specific nature of the foraging habits of all these ant species (Cerdá and Retana, 1994; Willot et al., 2000; Hensen, 2002; Picó et al., 2002). Nests of *M. barbarus* were not particular dense in our study area, higher densities being reported elsewhere in the Iberian Peninsula (Acosta et al., 1992; Gómez and Espadaler, 1994). *C. cruentatus* ants had a low but constant presence in the study area although we did not see them directly feeding on the seeds of *U. parviflorus*. This is an insectivore ant, mainly benefiting from the secretions of aphids (Alsina et al., 1988). However, we cannot rule out that they also consume *U. parviflorus* seeds because elaiosomes are know to attract insectivorous ants (Hughes et al., 1994).

U. parviflorus seeds, like those of many species belonging to the family Fabaceae, possess very hard testa or seed coverings impermeable to water and gases (Rolston, 1978; Cubas and Pardo, 1988; Serrato-Valenti et al., 1993). This makes immediate germination very difficult unless degradation of the testa occurs either through thermal shock from forest-fires or scarification by mechanical abrasion against the ground of wind- or water-borne seeds (Ballini, 1992; Baeza et al., 2002). Since the removal of the elaiosome also significantly increases germination probability, because it allows water and air to reach the embryo (Pacini, 1990), the elimination of the elaiosome by ants should then also be considered a way to break impermeability.

It has been suggested that the refuse piles of ant nests are safe sites for seeds with myrmecochorous dispersal, providing advantageous nutrient concentration and soil structure (Bennett and Krebs, 1987; Gómez and Espadaler, 1994). Indeed, a census of seedlings and young plants of *U. parviflorus* made during the spring of 2004 in the 400 m^2 experimental plot where secondary seed dispersal was studied in the year 2000 revealed 20 out of the 23 young individuals of *U. parviflorus* from 3 to 30 cm in height growing in anthills.

Our results confirm that Mediterranean gorse has two sequential seed dispersal mechanisms. This case of diplochory could contributed to maintain the populations of *U. parviflorus* under different circumstances by exploiting heterogeneous spatial or temporal conditions for seedling establishment, as has been described for some *Viola* species (Bülow-Olsen, 1984; Gorb and Gorb, 2000). Seeds that remain on the ground after primary seed dispersal and are not removed by ants incorporate into the soil seed bank where they may stay for a long time (Baeza et al., 2002). These soil seed banks represent a seed dispersal mechanism in time (Venable and Brow, 1988) since the seeds can germinate after forest-fires, when high temperatures break seed dormancy (Baeza et al., 2002) or after seed-coat degradation by weather (Baeza, pers. com.). This large and persistent seed bank has been documented by Baeza et al. (2002) in Mediterranean gorse shrublands from a very early age (3 years) and allows this species to persist in areas where fire is frequent, as also happens with *U. minor* and *U. gallii* (Stokes et al., 2004). On the other hand, the seeds removed from the ground by ants after primary seed dispersal are carried to ant nests where the elaiosome is regularly removed and the seeds placed in refuse piles where they germinate even in the absence of fire or scarification. In conclusion, diplochory allows *U. parviflorus* to exploit different establishment opportunities both after forest-fires and in absence of fire.

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