Seed production, predation and dispersal in the Mediterranean myrmecochore *Euphorbia characias* (Euphorbiaceae)

X. Espadaler and C. Gómez

Seed production of a population of 193 reproductive individuals of *Euphorbia characias* from the north-east Iberian peninsula was estimated at 155,000 seeds per year. The dehiscence period lasts for four weeks. The timing of ballistic dispersal is uniformly distributed throughout the day. Seeds remain on the surface a mean time (± SE) of 52.3 ± 6.7 min. Several ant species take the seeds in varying proportions: *Messor barbarus* (0.225), a granivorous ant which eats the seeds; *Aphaenogaster senilis* (0.313), *Formica pallida* (0.290) and *Tapinoma nigrum* (0.162) which take the seeds to their nests but do not eat them. Half a million ant foraging trips per day indicate a very strong short term influence of ants on fate of *Euphorbia* seeds. Ants as a group have a dual role of predation and dispersal of *Euphorbia characias* seeds. The characteristics of this *Euphorbia* (sclerophylly, diplochory, firmness of elaiosome, absence of subsidiary myrmecochorous features) better fit the syndrome described for Australian myrmecochores than the one proposed for European and North American myrmecochores.

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Recruitment patterns in vertebrate-dispersed seeds seem to have a strong haphazardous component (Howe 1989) since there are few, if any, predictable sites for escaping seed predators (Whelan et al. 1991). In contrast, ant-dispersed seeds have a precise point to reach: an ant’s nest. In an ant community there will be usually some “good” species and, so, there is a certain level of predictability from the plant’s point of view. Though sometimes the ant-plant interaction results in predation through granivory, active transport by ants often results in true myrmecochory in which seeds are directed to safe-sites (Beattie 1985). Ants, as a group, can act both as seed predators and as dispersal agents. Even granivorous ants can have a beneficial effect upon seeds they remove (Rissing 1986) but the significance of seed losses to population recruitment seems difficult to determine (Andersen 1989).

Competition for dispersal agents may affect plant population dynamics (Davidson and Morton 1981) and the timing of actual seed release may increase the probability of seeds being dispersed by ants (Turnbull and Culver 1983). Though all dispersal cases imply a physical transport, not all transport events end in effective dispersal. *Euphorbia characias* L. is a large Mediterranean perennial spurge measuring up to 1 m, found in sunny places. Capsules are three-seeded and, following explosive dispersal, the scattered seeds may be transported by ants (Sernander 1906, Baiges et al. 1991). The elaiosome is hard, non-collapsing, as is typical of myrmeco-
chores growing under xeric conditions (Berg 1975), and retains its attractiveness for a minimum of two years (preserved at room temperature; unpubl.). Flowering shoots get conspicuously dry one month after seed release. Most myrmecochores of xerophytic Mediterranean are ruderals or weeds and have woody characteristics.

Here we present the results of a study on the potential influence ants can have on recruitment in Euphorbia characias. We address the following questions: a) How large is the potential seed rain of Euphorbia? b) Which animals are seed predators? c) Is there any limit in the ant services to the plants? d) Can the ants be qualified as a postdispersal selective pressure for the plants?

Methods

Study site

The research was conducted at the Collserola Park, a protected area near Barcelona, NE Spain (41°25'N, 2°6'E; elevation 315 m) during the summers of 1991, 1993 and 1994, at the suburban site Can Llavallol. The site is located on an east-facing slope. The climate is Mediterranean, with 620 mm of annual rainfall. Mean monthly temperatures have a high in August with an average 22.6°C and a low of 7.1°C in January (data from 1914–1991). Soil is brown-red siliceous over schists (Xerocerpt Typp); the site is a clearing bordered by a mixed wood of Pinus pinea L., Pinus halepensis Mill and Quercus ilex L. with a developed underwood of Rhamnus alaternus L., Rosa spp., Pistacia lentiscus L., Hedera helix L., Ruscus aculeatus L. and Smilax aspera L. The clearing, a field abandoned 14 yr ago, comprises two distinct zones: a) a slope of 15° and 1788 m², and b) a flat surface of 638 m². Vegetation in the clearing is mainly an herbaceous community of Inulo-Oryzopsis-tem miliaceae (Bolós 1962) with Daucus carota L., Piptatherum milaceum (L.), Dittrichia viscosa (L.), Galactites tomentosa Moench., Rubus umbilfollia Schott., Foeniculum vulgare Mill., Anagallis arvensis L., Psoralea bituminosa L., Reichardia picroides (L.), Trifolium spp., Cymoglossum ceterifolium L., Medicago spp. and some bushes of Spartium junceum L. and Ulex parviflorus Pourr. All observations and measures were done at the clearing where individuals of E. characias (Euphorbia hereafter) were present. The site is grazed once a month. Rabbits and, occasionally, wild boars may frequent the site. Apodemus sylvaticus, Mus spretus and Microtus duodecimcostatus are known from other sites at the protected area.

Seed production, dehiscence and seed bank

Fruiting shoots per plant and number of capsules per shoot were estimated in 1993 and 1994, by counting a minimum of 100 plants and shoots. Total seed production of the Euphorbia population was estimated by using those estimates and counting the total number of mature plants. Seed set was estimated by counting seeds from 200 green capsules chosen randomly from twenty shoots of six mature plants. Abortion level was estimated by counting non dehiscent capsules; they have a whitish or brownish aspect, in contrast to greenish normal capsules. Timing of seed dispersal was checked by hourly counts of remaining capsules from an initial number on 20 marked fruiting shoots from different individuals from 9 h to 18 h during four days in June 1993. Air temperature was measured with a digital thermometer inside the uppermost flower umbrella of a mature shoot. The seed bank was evaluated in May 1994 by extracting 15 + 15 cylindrical soil cores (270 ml) at random points at 50 cm and 150 cm from mature plants and 30 additional cores at random points 5 m farther from any mature plant. Samples were water sieved and examined under a dissecting microscope.

Seed predation

Predator exclusion experiments were set up to investigate post-dispersal seed predators other than ants. Several treatments (25 isolated seeds/treatment; 2 m apart in line) precluded the access of different animals (ants, rodents, birds) to seeds. Experiments were set up for one day and one night in June 1994; they were repeated in June 1995 but with a random position of treatments.

1. Nocturnal ants exclusion. Single seeds were deposited inside a 8 cm plastic Petri dish and prevented from rolling by three small flat pebbles. A 4 cm nail was inserted through a 4 mm hole in the dish into the ground. The external border of the dish was coated with a fine thread of non drying glue. Birds and rodents had access to seeds. This was set at dawn and checked early in the morning the following day.

2. Nocturnal rodents + birds exclusion. A single seed was covered with a Petri dish slightly inclined with a small stone. The dish was attached to the soil with a nail as before. Ants could freely reach the seed. Set and checked as in nocturnal ants exclusion.

3. Nocturnal ants + rodents exclusion. As in #1 but with a coating of non drying glue both on external and internal borders. Birds had access to seeds. This was set at night.

4. Diurnal ants exclusion. A small plastic dish (1.5 cm Ø) with a shallow flat depression (1 mm) was inserted with a nail into the ground until it stood 3–4 cm in height. A fine thread of glue was applied to the nail. This treatment allowed birds and rodents to reach the seed. Set from 10 h to 19 h.

5. Diurnal ants + birds + rodents exclusion. The same setting as in #4 but with a card covering as a bridge
and impeding access to birds and rodents. Set from 10 h to 19 h.

6. Diurnal birds + rodents exclosure. Same setting as in #5 but without glue and with a cardboard bridge 1 cm over the whole set to exclude birds and rodents. Set from 10 h to 19 h.

7. Control. Same setting as #1, without glue. Ants, birds and rodents could reach the seeds. Set from 10 h to 19 h.

Level of seed predation by granivorous ants was assessed from 8.30 h to 19.30 h as follows. A single seed was put at each corner of a square of 7 cm side and the time elapsed since deposition and disappearance was recorded; the species initially finding the seed was noted. The widely used method of seed depots was not used because: 1) seeds are naturally scattered singly by ballistic dispersal and 2) a group of seeds could allow recruitment and this, in turn, lower the permanence time, biasing the estimates of removal rates of single seeds. Since prey robbing was not uncommon (Espadaler et al. in press), the species finally getting the seed to the nest was also recorded when possible. In addition, external middens from nests of several ant species were checked for seed remains under a dissecting microscope.

Behavioural interactions

Euphorbia seeds coming from this population and from a nearby (1 km) population and collected at the laboratory after dehiscence were offered to foraging ants; responses of ants were scored as in Culver and Beatle (1978) into five categories: Ignore, antennate, examine, pick-up attempt and removal. Seeds were kept refrigerated and used within 15 days of collection. A minimum of twenty seeds was presented to each ant species present in the site. Observations were performed during the dehiscence period of plants in May 1991, June 1993 and July 1994. Only those species showing an unambiguous transport (removal) response were subsequently investigated.

Ant activity

Nests of ant species involved in seed transport were observed to assess activity levels. Two nests each of Pheidole pallidula (Ny.), Aphaenogaster senilis Mayr, Tapinoma nigerimum (Ny.) and Messor barbarus (L.) were marked; activity was estimated by counting the number of ants leaving and entering the nest for five minutes; the mean of ongoing and outgoing ants was scored to avoid sudden bursts of activity (Rissing 1988, Simon and Hefetz 1992); hourly counts were made from 8.30 h to 19.30 h during two days (June 1994) of

the dehiscence period of Euphorbia. A global per day and per species activity level was estimated by using the sample of five minutes and the number of nests of each species. This global activity level per species is an underestimate since ants foraging before 8.30 h and after 19.30 h were not checked.

Nest density

Nest density was estimated by a direct count of all nests of A. senilis and Messor species; nests of A. senilis were detected by following returning workers or by offering spurge seeds to foraging ants; Messor nests were detected by foraging trails and/or outside middens; Pheidole and Tapinoma nests are much less conspicuous and were estimated by careful search of four random transects of 20 m length and 2 m width (160 m²) and 51 circles of 2 m diameter and centered on Euphorbia plants (160 m²). This was done to evaluate the possible different nest densities under and outside Euphorbia canopies; shade strongly influences the nest distribution of Pheidole and Tapinoma at a small scale (unpubl.).

Results

Seed production and dehiscence

The dehiscence period lasted for four weeks and, depending on the year, from mid May to the end of June. The whole mature population of Euphorbia consisted of 193 reproductive individuals (May 1994) with a wide variation in the number of shoots per individual. The number of capsules per shoot was smaller in 1993 (mean ± SE: 75.2 ± 4.5; n = 103) than in 1994 (88.1 ± 4.6; n = 150) (Kolmogorov-Smirnov test, D = 0.17; p < 0.05). Fruiting shoots per plant were not significantly different between years: 4.26 ± 0.3 in 1993; range 1–19 (n = 126) and 4.22 ± 0.3 in 1994; range 1–23 (n = 193) (KS test, D = 0.05; p > 0.05). Aborted capsules amounted to 14.5%. Counts from 150 shoots yielded 13 216 capsules. Seed set was 2.53 ± 0.04 seeds per capsule. A total of 815 shoots in 1994, without pre-dispersal seed predation and the abortion level of 14.5% and the seed set of 2.53 would produce up to 155 406 seeds.

Though temperature showed the usual rise at noon and fall at evening, timing of seed dispersal was smoothly continuous, without sharp explosive episodes (Fig. 1). Seeds of Euphorbia are ballistically dispersed throughout the day and not at specific times. No Euphorbia seeds were found in soil samples. There is no persistent seed bank outside the dispersal season.
Ants involved in seed transport

We did not find any evidence of olfactory cues on elaiosomes; ants not actually touching the seed ignored it even if passing a mm by. Vision may help but there are no data concerning detection of immobile objects in ants (Hölldobler and Wilson 1990). Seventeen ant species were present at Can Llavallol (Table 1). Seven species transported Euphorbia seeds: Aphaenogaster senilis, Messor barbarus, Messor bouvieri, Tetramorium semilaeue, Pheidole pallidula, Tapinoma nigrerrimum and Camponotus forel. Tetramorium semilaeue, a short-legged species, could transport the seeds with exceeding difficulty but also gnawed the elaiosome. Seed weight did not seem to be the problem (mean ± SE: 7.6 ± 0.3 mg (n = 20)). Nielsen et al. (1982) found that the carrying capacity is closely related to morphology, especially to leg length; in T. semilaeue mandibular opening is also much less wide than in Pheidole and offers less gap to manipulate Euphorbia seeds (unpubl.). For C. forel, a very nervous species, seeds were put at 2 cm from nest entrances to enhance probability of ant-seed contact; they sometimes ignored seeds (ten contacts) and sometimes transported them far from the nest; this global effect is only to move the seeds a mean distance of 39.8 cm (n = 10). Since seeds relocated by C. forel far from the nest are directly available to other ants, this last species, T. semilaeue and the other species from Table 1 were judged to have no relevance for the seed-ant interaction, except in that they may increase the distance that seeds are transported. Nearly all Messor nests belonged to M. barbarus and both Messor species will be treated together.

Table 1. Ant species from Can Llavallol (Barcelona, NE Spain). Reaction to Euphorbia characias seeds is indicated according to the following levels: 1: ignore; 2: antennate; 3: examine; 4: pick-up attempt and 5: removal (>10 cm). Levels 1 and 2 were combined since they could not always be distinguished with certainty. *: species too small in size to remove seeds; #: too few individuals, no nest located (no seeds offered). Feeding habits: O, omnivorous; G, granivorous; N, nectarivorous and/or aphid tending (data from various sources and unpubl.).

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Seed predation

Results show ants are the single group involved in seed disappearance (Table 2). Data from both years were not different (χ² = 5.2; d.f. = 5; p = 0.39) and were collapsed. Euphorbia seeds remain on the surface a short
time: $52.3 \pm 6.7$ min (mean ± SE; n = 256 obs.); the median is 7 min (Fig. 2). The probabilities for a seed being taken initially by each ant species are the following: *M. barbarus* (0.195), *Aphaenogaster* (0.227), *Pheidole* (0.313) and *Tapinoma* (0.263) (global data for 1993 + 1994; sample size: 285 seeds). Due to interspecific seed robbing, mainly of seeds initially taken by *Tapinoma*, these proportions change slightly; final probabilities are 0.225 (*Messor*), 0.313 (*Aphaenogaster*), 0.296 (*Pheidole*) and 0.162 (*Tapinoma*).

Some seeds were found without elaiosomes in nest external middens (data from two years). *Pheidole* (3 nests): one intact seed + no empty seeds; *A. senilis* (8 nests): 40 intact seeds + no empty seeds; *Messor* (9 nests): 2 intact seeds + 185 empty seeds. *Tapinoma* has no external debris but soil from galleries. Seeds in artificial nests remained uncleaned by *Tapinoma*, *Pheidole* or *Aphaenogaster* (unpubl.). Although we have no evidence that all seeds from middens of *Aphaenogaster* remain there without being subsequently removed by other ant species, we suspect this to be rare event. In any case, seeds would be removed by *Messor* (only this species accepts seeds deprived of elaiosomes; unpubl.). This would increase the proportion of seeds that are subjected to predation.

**Nest density**

A total of 485 nests of the five ant species involved in seed transport was found by both direct counts of *A. senilis* and *Messor* spp. nests and estimated values of *P. pallidula* and *T. nigerinimum* nests (Table 3). The density of nests for the five ant species in the 2426 m$^2$ is 0.2 m$^{-2}$.

**Ant activity**

The mean values for the five ant species set are shown in Table 4. Although it is difficult to precisely quantify the number of foraging ants at a given moment, an approximate value can be reached by assuming that the score for 5 min is a representative of the level of activity for a given hour; so, for each hour we multiplied by 12 the five minutes score. With this assumption in mind, and according to the number of nests (Table 3), *Messor* would provide 92,664 foraging trips 12 h$^{-1}$, *A. senilis* 145,975 foraging trips 12 h$^{-1}$, *T. nigerinimum* 254,398 trips 12 h$^{-1}$ and *P. pallidula* 84,182 foraging trips 12 h$^{-1}$. The five species interacting with *Euphorbia* seeds provide a minimum of 577,219 foraging trips during a single day at the 2426 m$^2$ studied.

**Discussion**

Total annual seed supply of the 193 mature individuals of *Euphorbia characias* was estimated as roughly 155,000 seeds; dehiscence period lasted for four weeks and timing of seed dispersal was uniformly distributed throughout the day. Seeds were actively collected by five ant species: *Aphaenogaster* (s. str.) *senilis*, *Pheidole pallidula*, *Tapinoma nigerinimum*, *Messor barbarus* and *Messor bousieri*. The first three species can be considered, at first, as good partners for the plant since they do not eat *Euphorbia* seeds. *Aphaenogaster senilis*, an omnivorous ant, is a species with a dubious reaction to seeds since some individuals were strongly positive and readily transported the seeds to the nest but others seemed to be absolutely unresponsive and others even showed an active refusal of seeds by transporting them far from the nest; this phenomenon is currently under investigation. Such variability in behaviour of individuals for a single colony was mentioned by Berg (1975) and has been observed also in some species of *Iridomyrmex* by L. Hughes (pers. comm.). *Messor* species (granivorous), *P. pallidula* (omnivorous) and *T. nigerinimum* (mainly nectarivorous) were active transporters of seeds to the nest; *Messor* species consume seeds; *M. structor* has been shown to collect seeds of *E. characias* and *E. cyparissias* in Italy (Pacini 1990), and Cerdan et al. (1986) found *Euphorbia* seeds from three species inside the granaries of *Messor* from southern France; they report that ants harvest 5–15% of total seed production. Ants are also assumed to be important seed predators in most plant communities in Australia (O'Dowd and Gill 1984, Andersen 1987) and dry regions of central Africa (Lévieux and Diamande 1978), South Africa (Kerley 1991), America (Mares and Rosenzweig 1978, Reichman 1979, Hobbs 1985) and in Costa Rica lowland rain forest (Levey and Byrne 1993). Seeds of *Euphorbia* are ballistically dispersed singly at low densities (2.3 seeds d$^{-1}$ m$^{-2}$) at Collserola. This scattering is regarded as an adaptation to reduce predation by granivores (Hughes and Westoby 1992). Due to the low permanence time on the soil surface it is highly improbable that any *Euphorbia* propagule can escape being found by ants. The absence of a seed bank also suggests that virtually all seeds are removed by ants. A similar conclusion was reached by Hughes and West-
Oby (1990) in southeast Australia. In summary, short-term fate of *Euphorbia* seeds is negatively influenced by *Messor*. Other species have a positive effect since they provide long (*Pheidole*, *Tapinoma*) or temporary (*Apheanogaster*) shelter to the seeds. This provides support for the suggestion of Hughes et al. (1994) for myrmecochory as a way to escape predation by granivorous ants.

The relative importance of these two opposite influences on seed survival on top of the soil will depend on the proportion of nests of different species, its foraging time and the level of soil surface scanning by the ants. The estimated 485 nests in the 2400 m² have similar densities to those in other published studies from Mediterranean habitats (Baroni Urbani and Pisanski 1978, Tinault 1981, Bernard 1983, Bigot et al. 1983, Restrepo et al. 1985, Sommer and Cagniant 1988). Although competing ant species do show temporal separation of foraging (Briese 1982, Gallé 1991), ants as a whole show considerable overlap of foraging time (Levings and Traniello 1981, Fellers 1989). During May–July, in western Mediterranean habitats there are foraging ants present throughout the day. Activity levels, as we measured them, are underestimated since it has been shown that *Pheidole* and *Messor* spp. have crepuscular and nocturnal activity in summer (Retana et al. 1992, Delalainde 1986) detected up to 20 000 passing ants per day on a single checking point in a nest of *Messor structor*. So, numbers from our site must be taken as conservative estimates: even with this restriction in mind, ants provide more than half a million foraging trips per day. According to the high number of foraging ants, there is apparently no limitation of ant services to the plant. Of course we do not suggest that each foraging ant removes a *Euphorbia* seed, but if we compare the mean *Euphorbia characias* seed dehiscence per day (5 550 seeds) to the estimated half million foraging trips, and that seeds remain on the soil surface an average time of less than an hour, we get an indication of the potentially very strong short term influence that ants have on *Euphorbia* seeds.

Several sources of evidence suggest that this influence may have a long term effect through opposing selective pressures. Seed predation is a major ecological and evolutionary force (Schupp 1988, Whelan et al. 1991). *Euphorbia* seed finding by *Messor* is a matter of chance and so, granivory may be important (Greenwood 1985). This particular group of ants is a guild found in dry Mediterranean open biotopes, where *E. characias* may also be present. The group of *Pheidole*, *Messor*, *Apheanogaster*, and *Tapinoma* are presented in Table 3. The number of ant nests found at Can Llava llo (Colbella, Barcelona, NE Spain). Values for *A. sentis* and *Messor* spp. are direct counts on the whole surface; values for *P. pallidula* and *T. nigerrimum* are estimated by four transects (20 x 2 m each; 160 m²) and 51 circles of 2 m diameter (160 m²), centered on *Euphorbia* plants.

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Fig. 2. Time (min; mean ± SE) elapsed from single seed deposition at random points in the soil to seed taking by ants. Seeds are rapidly retrieved early in the morning and late in the afternoon (mean: 15.7 ± 1.9 min; n = 173); from 10 h (a.m.) to 15 h (p.m.) seeds remain for much longer on the soil surface (mean: 128.3 ± 17.6; n = 83).
Table 4. Activity levels of ant species involved in Euphorbia seed transport at Can Llavallol (Collserola, Barcelona, NE Spain). Values are means for two nests per species and for two days (1 and 2 June, 1994). Activity was estimated by hourly counting the number of ants leaving and entering a nest for five minutes; the mean of ingoing and outgoing ants was scored.

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<td>8.5</td>
<td>8.7</td>
<td>0.7</td>
<td>6.2</td>
<td>0</td>
<td>–</td>
<td>20.5</td>
<td>17.7</td>
<td>22.3</td>
<td>11.7</td>
</tr>
<tr>
<td>Tapinoma</td>
<td>17.5</td>
<td>27.1</td>
<td>27.2</td>
<td>21.8</td>
<td>15.2</td>
<td>6.2</td>
<td>0</td>
<td>–</td>
<td>20.5</td>
<td>17.7</td>
<td>22.3</td>
<td>11.7</td>
</tr>
<tr>
<td>Soil temperature °C</td>
<td>21</td>
<td>23.8</td>
<td>27.7</td>
<td>34.4</td>
<td>34.7</td>
<td>35</td>
<td>35.6</td>
<td>–</td>
<td>33.6</td>
<td>30.5</td>
<td>25.1</td>
<td>22.8</td>
</tr>
</tbody>
</table>

*Tapinoma* and *Aphaenogaster* (s. str.) has been found elsewhere by Baroni Urbani 1968 (Malta); Ortiz 1985 (SE Spain); Rodriguez and Fernández 1983 (S Spain); Cagniant 1973 (Algeria) 1988 (Morocco); Casevitz-Weulerse 1989 (Corsica). Zorrilla et al. (1986) report this group of ants from therophytic pastures in central Spain with different degrees of disturbance: one, three, eight and forty years since last ploughing. Coexistence of three of the above genera is reported by Legakis (1983) in Greece, by Oler et al. (1978) from Israel and by Tohmé (1969) from Lebanon. From the plant's point of view the presence of the group *Pheidole*, *Tapinoma*, *Aphaenogaster* and *Messor* is fairly predictable. When considering the geographical distribution of *Euphorbia*, particular species of ants are not so important; what matters is the ecological interaction of ants as a group, with *Euphorbia* seeds. Since this interaction is consistent, dispersal agents are interchangeable (Hove 1989). Due to ant foraging habits, the global pattern of ant predation + myrmecochorous is in synchrony with *Euphorbia* ballistic dispersal. Ants as a group have a dual role of predation and dispersal thus fitting the concept of diffuse mutualism that has been suggested for the relationship between fruits and their dispersers (Herrera 1985).

The relation of *Euphorbia* seeds with ants offers a system in which to explore geographical differences of variation in conditional outcomes of the interaction (Bronstein 1994). The ant-*Euphorbia* seed interaction surely exists within changing and heterogeneous environments. This may provide a substrate for continued readjustment, with variation in the probability of seed escape through different degrees of dispersal and predation (Louda 1989). Seed predation would have significant effect in locations where, given the presence of *Messor* species, the dispersing non-granivorous ants were scarce. Hardness and persistence of elaiosome in *Euphorbia*, its shrubby habit, diplochory and late release of mature seeds, absence of rodent predation, presence of ant predation, and lack of secondary myrmecochorous features are all characteristics more like Australian myrmecochores as described by Berg (1975) than other European and North American myrmecochores. In fact, the image of scarcity of myrmecochorous species from the Mediterranean region, dating from Müller (1933), may be somewhat misleading: additions like those of Dietrich (1968, 1970), Speta (1972) and Danin and Yom-Tov (1990) indicate a potentially bigger number of myrmecochorous species for the Mediterranean region. The consideration of present day ecological conditions (mesophyllous vs xerophyllous vegetation) is probably far more important and promising than the phylogenetic or biogeographical history (viz. north vs south hemisphere comparisons) of the plants in shaping this dispersal system.

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