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Ant nests as primary habitats of *Silybum marianum* (*Compositae*)

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Abstract: The common Mediterranean ruderal thistle *Silybum marianum* is associated with nutrient-rich sites. Its wind-dispersed achenes possess an oily food body, that is attractive to harvester-ants. Following removal of the oily body, the achenes are deposited in the refuse zone together with rich organic material and soil removed from the nest; while in the nest the achenes are partly protected from fires. The thistle grows successfully in the nutrient-enriched refuse zone and thus dominates patches in the grassland. Preadaptations to live in association with harvester-ants enable *S. marianum* to occur also on marking stations of male gazelle, on cattle dung deposits, and in synanthropic ruderal habitats.

Silybum marianum (L.) GAERTNER is a common thistle of the Mediterranean and Irano-Turanian regions confined to "roadsides and waste places" (FEINBRUN-DOTHAN 1978). It is also regarded as synanthropic (growing in manmade habitats) in Turkey (KUPICHA 1975) and other countries in south eastern Europe (POLUNIN 1969, BOISSIER 1875, POST 1932–1933, QUEZEL & SANTA 1963, FRANCO 1976). Circles with 1–2 m in diameter of tall *S. marianum* plants in areas dominated by herbaceous annuals in the Mediterranean part of Israel attracted our attention. We found that these circles occur near nests of the harvesting ant *Messor semirufus* ANDRE (*Formicidae*), and near dung concentrations in marking stations of *Gazella gazella* L. (*Mammalia*: *Bovidae*). Harvester ants are often regarded as seed predators (PIJL 1972) and only rarely as agents in seed dispersal (O'DOWD & HAY 1980). Since *S. marianum* has not been regarded so far as a myrmecochorous plant, we studied some aspects of its life history and responses to the nest microenvironment. The influence of harvester-ants on soil properties and vegetation near their nests has been studied in many areas (COLE 1932, GOLLEY & GENTRY 1964, WIGHT & NICHOLS 1966, KOYUMDJISKY & al. 1967, KING 1977, OFFER 1980, BUCKLEY 1982, BEATTIE 1985, RISSING 1986). Most of these authors found increased soil fertility near the nests, better aeration, and increased production of phytomass by the natural vegetation.

Male gazelles mark their territory by excreting in piles, their activities resulting in dung concentrations 30–200 cm in diameter in the grassland area, thus introducing heterogeneity in nutrient concentration. These "marking stations" are usually found along the perimeter of the territories.

The aim of the present study is to examine the primary habitats of *S. marianum*; to point out some of its preadaptations for inhabiting sites disturbed by man; to examine the impact of harvester ants and gazelles on soil fertility; and to correlate species distribution, species diversity, and standing phytomass with animal-affected soil fertility.

Materials and methods

The study was conducted mainly near Kochav HaYarden, 9 km north of Bet Shean, Israel (35°31′50″E/32°34′30″N), altitude 200 m s.m. The climate is Mediterranean, and the annual precipitation is 370 mm (DORFMAN 1981), falling mainly between October and April. The study site was a flat natural terrace on a steep slope of the Lower Galilee facing the Jordan Rift Valley. The bedrock is basalt covered by basaltic protogrumusol (DAN & al. 1975). Six ant nests and five gazelle marking stations some 10 m apart, were selected and marked within an area of 0.5 ha, on December 9, 1986. In all the 11 sites there was animal activity when marked. Sampling of plants took place on April 12, 1987 when most species had ripe fruits. All above ground parts of the plants were harvested in squares of 50 × 50 cm, one square was harvested in each of the 11 sites. The nest plots were situated on the refuse zone while the entrance holes of the ant nests were at the edge of the plot. Similarly, the centre of the marking station was at the edge of the harvested plot. The 7 control plots of 50 × 50 cm were at least 5 m away from any obvious animal influence. Where a site of nest and a marking station were less than 10 m apart, only one control site without animal influence was selected and harvested.

The harvested plant material was separated into species, oven-dried for 48 h at 90 °C and weighed separately. SÖRENSEN's (1948) similarity coefficient (2 c × 100/a + b; a = number of species in the first list, b = number of species in the second list, c = number of species common in both lists) was calculated for individual plant lists on the ant nests or gazelle marking station and their closest control square. The coefficient was also calculated to compare the full lists of species in these three kinds of habitats. Dry weight of each species was used to calculate species diversity as e^H (HILL 1973). Those species that occurred in > 50% of their habitat samples (i.e., control, ant nest, and gazelle stations) were identified and the dry weight of each was calculated as a percentage of the total dry weight of each entire sample. Plant names after FEINBRUN-DOTHAN (1978, 1986) and ZOHARY (1966, 1972).

Soil was sampled at the date of harvesting, at the centre of each plot at depths of 0 – 5 cm and 5 – 10 cm in most sites. Soil content of NO_3^- was analyzed by the use of Szechrome NAS Reagent (SZEKELY & al. 1972). Phosphorus and potassium content were analyzed by the flame photometer methods (RICHARDS 1954). Analysis of nutrient content of gazelle dung was carried out as well.

Behaviour of *Messor semirufus* ants in gathering activities of *Silybum marianum* achenes was studied in Jerusalem. Some 250 achenes with their pappus were placed on an active ant path 1.5 m away from nest entrance. The position of mandibular holding of the achenes was recorded. All plant waste material deposited by the ants at the refuse zone was collected 4 – 30 d after the experiment and analyzed.

Environment and vegetation

The study site is in the Mediterranean plant geographical territory of Israel where biregional species, Mediterranean – Irano-Turanian, are the second most important chorotype (DANIN & PLITMANN 1987). A phytogeographical analysis of 130 species occurring in the study area showed Mediterranean = 62%, and biregional Mediterranean – Irano-Turanian = 25% of all chorotypes.

Savanna-like vegetation covers the study area: a few scattered trees of *Ziziphus spina-christi* (L.) DESF. and shrubs of *Z. lotus* (L.) LAM. contribute 5%. Most of the area is covered by dense herbaceous ephemeral vegetation with *Avena sterilis* L., *Hordeum bulbosum* L., *H. spontaneum* C. KOCH, and *Triticum dicoccoides* (ASCHERSON & GRAEBNER) ARONSOHN dominating. Accessory species mainly included seven *Trifolium* spp., other *Papilionaceae, Graminae*, and *Compositae.*

The tall thistles *Silybum marianum* and *Notobasis syriaca* (L.) CASS. occur in circles associated with harvester ants and gazelle marking stations. At the study site one of the largest populations of gazelles (*Gazella gazella*) in Israel exists, with densities of up to 30 gazelle per km^2. Male gazelles establish breeding territories on the terraces all year round, but mainly in October and November. The area is also grazed by cattle, and considerable numbers of *S. marianum* plants grow in the enriched soil in areas shaded by *Ziziphus spina-christi* trees, places where cattle herds rest in warm days.

Unpaved roads pass the margin of the study area and a path goes through it. The margins are managed by herbicides, and they are densely populated by the two thistles mentioned above.

Results

Soil fertility. In all the animal-affected sites the nitrate and phosphorus content was higher than in the control sites (Table 1). In 11 of the 16 samples which were compared, there were higher potassium values than in the control, and only 5 had low values. All nutrients had 2 – 5 times higher concentration on the top layer (0 – 5 cm) compared with a deeper layer of the soil.

Gazelle droppings collected in the area contained 0.04% NO_3^-, 0.3% potassium, 2.6% total nitrogen and 0.36% phosphorous.

Flora and phytomass. Values of standing phytomass (standing crop), number of species, and species diversity of each square are presented in Table 2. The mean values of phytomass production per 0.25 $m^2 \pm$ SE were 142.4 g ± 19.6 g for the control, 447.3 g ± 64.0 g for ant nests (3.14 times higher than the control), and 444.8 g ± 94.2 g (3.12 times higher than the control). Species number was the highest in the control (24.3 ± 2.9), lower in the ant nests (7.3 ± 2.0), and the lowest in the gazelle stations (6.4 ± 2.4). Species diversity was also highest in the control, lower in the gazelle stations and the lowest in the ant nests. A one sided t-test for equality of means has been used (assuming unequal variances) for all the values in Table 2. Those of the animal-influenced sites were found to differ significantly from their closest neighbouring control sites.

Table 1. Mean values of nutrient analysis of soils in the study area (ppm)

	Depth (cm)	Control			Ant nests			Gazelle stations		
		N	M ±	SE	N	M ±	SE	N	M ±	SE
NO_3^-	0 – 5	6	92.5	8.0	6	246.3	4.0	4	265.2	9.7
NO_3^-	5 – 10	5	18.8	2.9	5	54.3	3.2	4	93.7	5.4
P	0 – 5	6	12.0	1.4	6	54.2	3.6	4	69.7	4.2
P	5 – 10	5	4.6	1.4	5	32.2	3.8	4	18.0	3.5
K	0 – 5	6	12.3	2.3	6	15.0	1.9	4	35.7	3.5
K	5 – 10	5	4.8	0.8	5	8.2	1.6	4	11.2	1.5

Table 2. Standing phytomass, species number, and species diversity in various habitats. Results of one sided t-test for equality between means of animal-induced sites and their control. * Significant, $0.01 < p < 0.025$; ** very significant, $p < 0.0025$; *** highly significant, $p < 0.0005$

	Control (n=7)		Ant nests (n=6)		Gazelle stations (n=5)	
	M ±	SE	M ±	SE	M ±	SE
Phytomass $g/0.25\,m^2$	142.4	19.6	**447.3	64.0	*444.8	94.2
No. of species/$0.25\,m^2$	24.3	2.9	***7.3	2.0	***6.4	2.4
Species diversity (e^H)	9.9	1.4	***1.4	0.2	***2.0	0.8

Table 3. Percentage of presence (*P*) of the species which occurred in more than 50% of the squares in each habitat, and their average percentage of weight in each square where they were present (*W*)

Species	Control (7 squares)		Ant nests (6 squares)		Gazelle stations (5 squares)	
	P	W	P	W	P	W
Aegilops peregrina	85.4	2.6				
Avena sterilis	85.4	15.3	60.0	0.9	60.0	6.3
Bromus alopecuroides	57.1	2.6				
Carthamus glaucus	71.4	2.2				
Catapodium rigidum	57.1	0.1				
Hirschfeldia incana	57.1	0.2				
Hordeum bulbosum	85.4	10.2				
Hordeum spontaneum	85.4	13.4	80.0	3.2	60.0	2.0
Onobrychis crista-galli	71.0	2.7				
Silybum marianum			100.0	93.4	80.0	77.1
Sinapis arvensis			60.0	0.1		
Tetragonolobus palaestinus	57.0	1.3				
Trifolium alexandrinum	85.0	5.6				
T. campestre	57.0	1.3				
T. clypeatum	57.0	0.3				
T. pilulare	57.0	0.9				
T. purpureum	71.4	1.6				

Of the 77 plant species found in the harvested samples, 41 occurred only in the control plots, 3 occurred only on the ant nests, and 2 only on the gazelle marking stations. Those species that occurred in >50% of the plots are shown in Table 3. The importance of the oat and barley species in the control areas is clearly shown. The mean SÖRENSEN's coefficient of similarity ± SE for individual ant nests and their neighbouring control site was 28.5% ± 4.4% (n = 6); for gazelle stations and their controls 20.3% ± 3.8% (n = 5). The same coefficient calculated for the flora of gazelle stations and ant nests was 55.3% ± 3.5%.

Relationships of *Silybum marianum* to ant nests and gazelle stations. There were 24 ant nests and gazelle stations with tall plants of *S. marianum* in the 0.5 ha of the study area. The number of individual plants of *S. marianum* in the grassland, far from the impact of animals, was 14 per 0.5 ha. The characteristics of *S. marianum* plants near and far from ant and gazelle sites are presented in Table 4. The average weight of *S. marianum* in the animal-affected microhabitats is >9 times higher than in undisturbed grassland. The number of heads per plant is 3 – 4 times higher in the animal-affected sites. We did not measure growth rates but we can guess that growth rates are dramatically stimulated by animal activity; the fast growth of *S. marianum* soon after germination enabled us to detect easily the animal-affected sites throughout the growth season.

S. marianum has two modes of seed dispersal. Its achene has a pappus, falling off easily, and an elaiosome at the top (Fig. 1 a). This yellowish-white body leaves oily stain on paper and stains red by Sudan IV. The mean weight of a fresh achene from a populaton in Jerusalem was 28.3 ± 4.3 mg (n = 100) and that of an elaiosome was 0.71 ± 0.3 mg. The achene coat is shiny, mostly dark coloured, and hard. Ants in Jerusalem efficiently collected achenes of *S. marianum* that were placed on their path. Within 45 minutes, 232 of 250 achenes had been gathered into the nest: 64.2% were carried by ants grasping the elaiosome, 24.1% were held at the opposite side (base of achene), 6.5% were held at the lateral side. The pappus was still attached to the achene in the remaining 5.2% when brought towards the nest. The ants did not stop gathering achenes after the 45 min of our observation.

Table 4. Properties of *Silybum marianum* plants growing near and far from ant nests and gazelle marking stations; *n* number of specimens

Habitat	n	Average dry weight of plant (g)	Average no. of heads/plant
Near ant nests	41	81.7	5.6
On gazelle stations	22	84.4	7.4
In grassland (control)	14	8.7	1.7

Fig. 1. Achenes of *Silybum marianum*, *a* with an elaiosome at the achene's top. *b* As found in ant-nest refuse zone with a depression instead of the elaiosome. Bar: 5 mm

When our observation started (May 6, 1987) there were no achenes of *S. marianum* outside the nest. Within a month, the ants gradually removed all the achenes from the nest, all of which lacking the elaiosome. Of 155 random achenes that were found in the refuse zone, 40.6% were slightly bitten on one or two ends of the achene. In no case did the biting penetrate the hard achene coat.

Refuse material from an ant nest 7 km south of the study site, with *S. marianum* plants growing near the nest was also analyzed. Of 86 *S. marianum* achenes found, 90.7% had no elaiosome and were slightly bitten, 2% had an elaiosome with no signs of biting, and 6.9% were without an elaiosome and had no signs of biting. Refuse material from six nests in Jerusalem with *S. marianum* contained achenes with no elaiosomes.

Discussion

Our results show that the adaptations of *S. marianum* are principally directed towards interaction with harvester ants, e.g. the diplochorous seed dispersal by wind and by myrmecochory (sensu SERNANDER 1906). Diplochory (sensu BERG 1975) is a common strategy in herbaceous plants of the Middle East (PLITMANN 1986). In our manipulation of achene-gathering by the ants, we found that ants preferred holding *S. marianum* by the elaiosome. It acts as an ant-attractant (BEATTIE 1985) and was later removed from all the achenes inside the nest. Achenes without elaiosome are deposited by ants in the refuse zone, where the soil is enriched in nutrients. The successful vegetative growth and inflorescence development of *S. marianum* near the nests show that the directed diaspore dispersal by ants bring it to its preferred nutrient-enriched sites in the grassland. Once this species is established near a nest, harvester ants will continue to collect the achenes of *S. marianum* and replant them in the highly fertile refuse zone of the nest. RICE & WESTOBY (1986) found, in sclerophyllous vegetation in Australia, evidence against the nutrient-enrichment theory. Our data on microhabitat variation of soil fertility and on standing crop of phytomass and inflorescence production provide some support for the nutrient-enrichment hypothesis to account for the advantage of myrmecochory in Mediterranean grasslands. We did not identify which component of the ant-nest environment is important for *S. marianum* there; this question deserves further experimental work such as that of HORVITZ & SCHEMSKE (1986).

Achene gathering by the ants may increase the survival of the diaspores from possible fires, which are very common in the Mediterranean region (LE HOUEROU 1973, NAVEH 1973). The gradual disposing of achenes as observed by us, may protect, at least, some of the achenes for some time from being exposed at soil surface to fires. The refuse material contains soil particles and has lower flammability than dry material of annual plants in opened places. Hence, in the ant nests and its vicinity achenes have higher chances to survive fire catastrophes. This agrees with the fire-avoidance hypothesis, developed by BERG (1975) for fire-climax communities in Australia, and reviewed by BEATTIE (1985).

In conclusion, the relations seem to be a kind of protocooperation (sensu BARBOUR & al. 1987), or mutualism (BEATTIE 1985). The ants remove the elaiosome and feed with it their larvae (BEATTIE 1985) at the beginning of the summer; they do not consume the hard coated achenes and place them in the refuse zone. The thistle prospers on the nutrient-rich soil of the nest and produces much more diaspores than in the control sites. This is not an obligatory relationship, because ants use other food sources and thistles can develop in other nutrient-rich environments. However, it is a kind of mutualism that was not referred so far to *Messor* harvester-ants and to *S. marianum*. Recent reviews of myrmecochory (BUCKLEY 1982; BEATTIE 1983, 1985) do not mention (1) myrmecochorous plants from the Mediterranean grasslands, (2) *Messor* as a distributor of plants, and (3) grasslands as a classical myrmecochorous habitat.

Nests' vegetation. The number of species and species diversity are significantly lower near the animal-affected sites than in the control grassland sites. We suggest that the dominant plants near the nests and marking stations may be regarded as responsible for this decrease. Growing taller and having large leaves, and only little grazed by the cattle, the thistles overtop and ultimately deplete light and other resources from other species that may germinate in the animal-affected sites. Most plants that accompanied the thistles in the animal-affected plots were etiolants and failed to produce flowers and fruits. It is clear, from the difference in responses of the grassland species and the species dominating the animal-affected sites, that we do not deal here with relations of "trophically equivalent species" (sensu SHMIDA & ELLNER 1984).

Additional synanthropic habitats of *S. marianum*. Ant nests are not the only place where *S. marianum* succeeds more than other plants in the local flora of the Mediterranean grassland. Nutrient-enriched sites in the area reached by wind-dispersed diaspores of *S. marianum* may become long-term sites of the plant. Besides gazelle males, other organisms causing concentrations of highly fertile soil, such as herds of domestic animals in shade of trees, create additional sites for the plant. The gradual disintegration of organic material in the dung heaps leads to a constant supply of nutrients for the plants in these synanthropic sites. Large areas of disturbed habitats were created by man in the Mediterranean area in the last millennia (ZOHARY 1973; PIGNATTI 1978, 1983). During this relatively short evolutionary time human activity had probably led to only small changes in the life strategies of *Silybum marianum*.

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