Seed predation in a Mediterranean pasture: can ants modify the floristic composition of soil seed banks?

Depredación de semillas en un pastizal mediterráneo: ¿pueden las hormigas modificar la composición florística de los bancos de semillas?

TÍSCAR ESPIGARES[1]* & ANTONIO LÓPEZ-PINTOR[2]

[1]Departamento Interuniversitario de Ecología. Facultad de Ciencias, Universidad de Alcalá, Carretera Madrid-Barcelona, km 33'6, 28871 Alcalá de Henares, Madrid, Spain
[2]Departamento Interuniversitario de Ecología. Universidad Complutense de Madrid. Facultad de Biología, c/ José Antonio Novais s/n, 28040 Madrid, Spain;
*e-mail for correspondence: mtiscar.espigares@uah.es

ABSTRACT

Ants may play an important role on vegetation dynamics, especially in arid and semiarid environments, where they can consume a high proportion of the produced seeds. Although some works have analysed the influence of seed predation by ants on the density of vegetation in Mediterranean pastures, there are no studies on the influence of ant activity upon the floristic composition of the vegetation and the soil seed banks in this kind of ecosystem. We have studied the effect of ant exclusion on the floristic composition of the vegetation and the soil seed bank in a Mediterranean pasture of central Spain. We sampled the floristic composition of the pasture during 2002 and 2003 springs and also we collected soil seed bank samples in autumn 2002. Floristic composition of soil seed banks was estimated by means of greenhouse germination. *Cerastium semidecandrum* seeds were almost four times more abundant in the plots subjected to ant exclusion than in those with ant activity. Due to the high spatial heterogeneity shown by soil seed banks, we have corrected the differences found between the autumn soil seed banks subjected to different ant treatments by using the floristic composition of the pasture community in the previous spring, as it was the primary source of the seeds collected in autumn. We found significant differences between the floristic composition of the soil seed banks subjected to ant exclusion and control treatments. However, no effects where found when the same procedure was used to detect ant effects on the spring adult community, highlighting the necessity of longer time spans for these pastures to manifest changes taking place at the soil seed bank stage.

Key words: annual pasture, ant exclusion, predation, soil seed bank, spatial heterogeneity.

RESUMEN

La mirmecofauna juega un papel fundamental sobre la dinámica de la vegetación, especialmente en zonas de carácter árido o semiárido, donde puede llegar a consumir una elevada proporción de las semillas producidas, condicionando la composición florística de la vegetación. Aunque algunos trabajos han analizado la influencia de la depredación de semillas por hormigas sobre la densidad de la vegetación en ecosistemas de pastizal del centro peninsular, hasta el momento no hay estudios sobre cómo afecta este factor a la composición florística de los bancos de semillas. Se ha estudiado el efecto de la exclusión de hormigas sobre la composición florística del banco de semillas de un pastizal mediterráneo de la provincia de Madrid. En las parcelas sometidas a exclusión de hormigas, la densidad de semillas de *Cerastium semidecandrum* fue casi cuatro veces mayor que en las parcelas con actividad de la mirmecofauna. Dada la elevada heterogeneidad espacial, las diferencias en composición florística encontradas en el banco se han corregido utilizando la composición de la comunidad de primavera, fuente directa del banco de semillas recogido en otoño. Los resultados ponen de manifiesto un efecto significativo de la exclusión de hormigas sobre la composición florística del banco de semillas del pastizal.

Palabras clave: pastizal anual, exclusión de hormigas, depredación, bancos de semillas, heterogeneidad espacial.

INTRODUCTION

Ant activity constitutes a key factor in vegetation dynamics. Mechanisms by which ants influence vegetation are varied. One of the most known is myrmecochory, consisting in the dispersion of those seeds with elaiosomes that, rich in carbohydrates, attract ants that consume these tissues and afterwards leave the seeds with their intact germinability (Howe & Smallwood 1982, Handel & Beattie 1990, Gorb & Gorb 1995, Gómez & Espadaler 1998, Gorb et al. 2000). Seed predation is another mechanism by which ants affect vegetation dynamics, especially in deserts and arid ecosystems where seeds constitute one of the main food resources for the fauna (Brown et al. 1979). Many studies have pointed out that seed predation by ants can modify the density and spatial heterogeneity of seeds, as well as the floristic composition of the vegetation (Inouye et al. 1980, Andersen 1987, Mull & MacMahon 1996, Montiel & Montaña 2003). Besides, ant's nests are considered the most important small-scale disturbance affecting vegetation (Loucks et al. 1985, Woodell & King 1991, Farji-Brener & Ghermandi 2000). Finally, some authors have also described the role of ants in the pollination of some plant species (Gómez et al. 1996).

Mediterranean pastures are species rich plant communities that dominate wide areas of the centre and south of the Iberian Peninsula, which at present are expanding in abandoned fields. A high spatio-temporal heterogeneity has been found in this kind of pastures. This can be explained by factors of different nature: patch-like, vectorial or temporal (González-Bernáldez & Pineda 1980, Peco et. al. 1998a). Among the first factors, González-Bernáldez et al. (1969) described the changes imposed on pasture floristic composition by the presence of holm-oaks, due to modifications in the nutrients cycle. More recently, López-Pintor et al. (2003) have studied the spatial heterogeneity imposed on the soil seed bank of Mediterranean pastures by other woody plants. With regard to the vectorial factors, many papers have described the outstanding influence of topography on the changes in structure and floristic composition of herbaceous communities along slopes (Ruíz 1980, Ruíz et al. 1980, De Pablo et al. 1982). On a different scale, Sterling et al. (1984) have analysed the changes in floristic composition generated by the micro-topography of furrows after ploughing, which produces a fine-grain pattern in pasture community structure. Among the temporal factors, changes in species composition related to succession have been widely studied (Pineda et al. 1981a, 1981b, 1987, Peco et al. 1983a, 1983b, Peco 1989). At the same time, it has been demonstrated that interannual fluctuations in meteorological conditions also affect floristic composition of this type of pastures (Figueroa & Davy 1991, Espigares & Peco 1993, 1995). Annual species with transient seed banks are dominant in these communities, making their annual regeneration heavily dependent on the soil seed bank (Ortega et al. 1997, Peco et al. 1998b).

However, less attention has been paid to the influence of ant activity on the dynamics of annual Mediterranean pastures. Many authors state that harvester ants are the main seed predators in Mediterranean grasslands (Azcárate & Peco 2003, Cerdá & Retana 1994), being the granivore *Messor* species the most important (López et al. 1993a, Hensen 2002). Studies on floristic composition of *Messor* species diet show that they consume seeds from a wide variety of species, although it has been observed that their foraging strategy tends to reduce time costs by selecting preferably long propagules, which are more accessible and easily detectable (Reyes-López & Fernández-Haeger 2001, Hensen 2002, Azcárate et al. in press). This led some authors to the hypothesis that *Messor* ants could favour small-seeded species in plant communities (Detrain & Pasteels 2000, Willott et al. 2000). In fact, Azcárate et al. (2002) found that small-seeded species are overrepresented in Mediterranean grasslands.

In spite of the importance of seed predation by ants in Mediterranean grasslands, few studies have analysed the impact of ant activity on the floristic composition of grassland communities. Acosta et al. (1992) and López et al. (1993b) concluded that seed predation by ants hardly influenced the density of herbaceous cover. In fact, the influence of ants on the dynamics of soil seed banks has not been studied yet although several authors attribute to this process the great disparity between the number of seeds produced in spring and the

number that remain in autumn when the pasture regenerates (King 1966, Espigares et al. unpublished results).

The objective of this study is to determine if seed predation by ants affects the floristic composition of vegetation and soil seed banks in annual Mediterranean pastures of central Spain. We expect that ant activity will influence both floristic composition of the herbaceous community in spring and of the autumn soil seed banks.

MATERIAL AND METHODS

Study area

The study area was located at "El Encín" estate, near Alcalá de Henares (central Spain). The climate is continental Mediterranean, with a mean annual precipitation of 472.7 mm and 13.5 ºC of mean annual temperature. Soils have alluvial origin and sandy-loam texture. According to the Soil Taxonomy System (USDA 1985) they are *Xerochrept calcixerollic*. Vegetation consists of a Mediterranean pasture dominated by annual species established after the abandonment of agricultural practices.

Experimental design

In February 2002, before ants initiated their activity, eight 1x1m plots were randomly established, with the proviso that they had a similar distance to ant nest holes and avoiding that any would fall within the plots. Half of these plots were subjected to ant exclusion treatment with a double fence of 40 cm high aluminium planks placed 10 cm deep in soil. Besides, an initial formicide dose was applied to ensure the total elimination of ants. Control plots lacked any fences and were only marked with woody sticks at the corners.

In 2002 and 2003 springs, pasture floristic composition was sampled in each plot by using two squares of 40 x 40 cm, in which the abundance of each species was recorded. 2002 sampling represented the floristic composition of the pasture before applying ant exclusion, while 2003 sampling showed the floristic composition after one growing season of applying ant treatments. To evaluate the impact of ant exclusion on the soil seed bank, at the beginning of 2002 autumn, before the arrival of the rains that provoke germination, we collected two soil samples (60 cm^2 x 4 cm depth) randomly established in each plot. Each of these samples was subdivided into 7 subsamples that were placed in the upper part of small pots, on a vermiculate substrate. The floristic composition of the soil seed banks was determined by means of germination under controlled conditions in a greenhouse.

Data analysis

Differences in species richness and abundance of each species between plots were analysed by using ANOVA tests. We studied these differences in two stages: soil seed bank and spring floristic composition. At the same time, differences in density of seeds in the soil seed bank were explored by using the same test.

Non-metric multidimensional scaling (NMDS) analyses were carried out with the floristic composition data of the spring community and the autumn soil seed banks. The graphic representation of the samples in the ordination space enabled us to measure the differences in floristic composition between plots subjected to different ant treatments. These differences were estimated as the Euclidean distances calculated from the ordination graphs.

Our premise is that differences in floristic composition between the autumn soil seed banks respond to two principal components: (i) initial differences due to pasture spatial heterogeneity; and (ii) differences due to ant activity. By measuring the floristic composition of the grassland community at different stages of its dynamics we could quantify the amount of variation assigned to these two different sources. We can express this premise through this formula:

$$D_{final} = D_{ants} + D_{initial} \qquad (1)$$

where: D_{final} represents the final differences in floristic composition, i.e. the differences observed between the autumn soil seed banks from plots subjected to different ant treatments. D_{ants} represents the differences in floristic composition due to ant activity, to be determined. $D_{initial}$ represents the initial

differences in floristic composition due to spatial heterogeneity of the herbaceous community, which will be estimated from the differences in floristic composition between plots in the vegetation of the previous spring, as it was the primary source of the seeds collected in autumn.

From formula (1), we can calculate the differences in floristic composition due to ant activity in this way:

$$D_{ants} = D_{final} - D_{initial} \qquad (2)$$

Thus, we will estimate the differences in floristic composition due to ant activity between each pair of plots by calculating the difference between the Euclidean distances obtained from the NMDS with the data of the autumn seed banks and the same distances calculated from the NMDS obtained with the data of floristic composition in spring 2002 (initial spring), as Fig. 1 indicates. The differences in floristic composition between plots obtained in this way will be mainly due to ant activity, since noise from initial spatial heterogeneity was eliminated. In this way, if our initial hypothesis is correct, we expect that the distances in floristic composition between pairs of samples subjected to the same ant treatment will be different from those between pairs of samples subjected to a different treatment. To carry out this analysis we used a Mann-Whitney U-test.
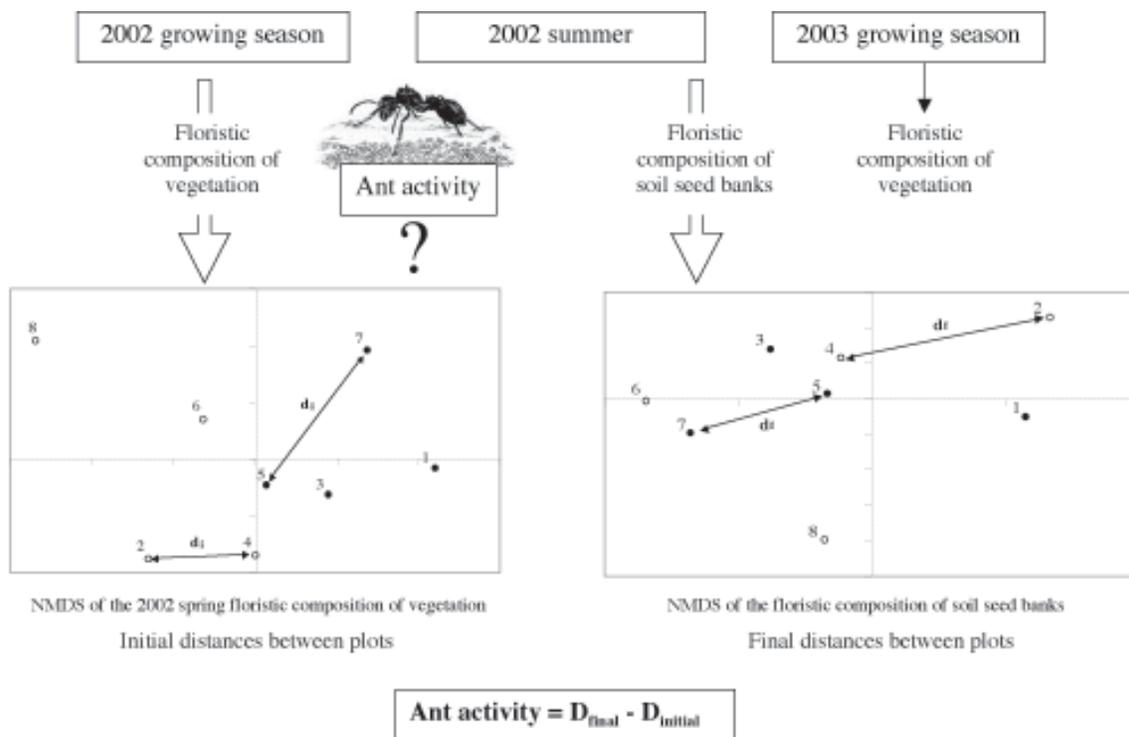

Fig. 1: Representation of the sampling and methodology of calculation of ant effect on soil seed banks. Ordination graphs represent the NMDS performed upon the floristic composition data of the spring 2002 vegetation (left) and autumn soil seed banks (right). Black dots: control plots; white dots: ant exclusion plots. Arrows indicate Euclidean distances between plots (d_i: initial distance, d_f: final distance). Numbers represent plots.

Representación esquemática del muestreo y de la metodología de cálculo utilizada para estimar el efecto de las hormigas sobre los bancos de semillas del suelo. Los gráficos de ordenación representan los NMDS realizados a partir de los datos de composición florística de la vegetación en la primavera de 2002 (izquierda) y de los bancos de semillas en otoño (derecha). Círculos negros: parcelas control; círculos blancos: parcelas de exclusión de hormigas. Las flechas indican las distancias euclídeas entre las diferentes parcelas (d_i: distancia inicial, d_f: distancia final). Los números representan las parcelas.

All multivariate analysis were performed with PC-ord package (McCune & Mefford 1997), and for the other statistical analysis we used STATISTICA package (Statsoft Inc. 1996).

RESULTS

We found 38 different species in the sampling of floristic composition of vegetation in spring 2002, and 30 different species in the autumn soil seed banks. Forty-four species were found in the sampling of vegetation during spring 2003.

The ANOVA tests performed to explore differences in species richness and species abundance between plots only found significant differences in the case of *Cerastium semidecandrum* L. abundance in the soil seed banks, i.e., there were more *Cerastium* seeds in the ant exclusion plots than in those with ant activity (with a mean of 1,666.7 seeds m^{-2} versus 458,3 seeds m^{-2}, $F_{1,14} = 4.23$, $P = 0.05$). Although without an acceptable significance level, the tendency in the case of the other main conspicuous species and of species richness agreed with this result, as more abundance and more species richness appeared in the exclusion plots.

Figure 1 shows the NMDS ordinations with the data of the floristic composition of vegetation in spring 2002 and of the autumn seed banks. After calculating the Euclidean distances between pairs of plots in each ordination, we applied formula (2) as described in Material and methods section. Differences in floristic composition due to ant activity between pairs of plots subjected to the same ant treatment (control-control, exclusion-exclusion) had an average (± SE) of 0.0140 ± 0.0086 (n = 12). The same differences between plots subjected to different ant treatments (control-exclusion) showed an average (± SE) of −0.0105 ± 0.0052 (n = 16). The Mann-Whitney U-test found significant differences between these two groups of distances (U = 48, P = 0.02).

The same procedure was followed to detect ant effect on the adult herbaceous community of spring 2003, calculating the Euclidean distances between spring 2002 and spring 2003 ordinations. Differences in floristic

composition due to ant activity between pairs of plots subjected to the same ant treatment (control-control, exclusion-exclusion) had an average (± SE) of 0.00305 ± 0.0103, (n = 12). The same differences between plots subjected to different ant treatments (control-exclusion) showed an average (± SE) of −0.00229 ± 0.0708, (n = 16). In this case the Mann-Whitney U-test was not able to find significant differences between these two groups of distances (U = 48, P = 0.458).

DISCUSSION

The analysis of the floristic composition of soil seed banks subjected to different treatments of ant control has shown that ant activity can modify the floristic composition of soil seed banks in the period between seed production in spring and the time of pasture regeneration in autumn, thus confirming our initial hypothesis.

Although this result seems to contradict Acosta et al. (1992) and López et al. (1993b, 2000), who concluded that seed predation by ants barely influences the dynamics of Mediterranean pastures, these authors analysed the effect of ants on the density of pasture cover. This can explain their results, since granivorous ants do not act directly upon density of pasture cover but predate on seeds. In fact, it is more likely to find the influence of seed predation by ants on the soil seed banks, as many authors have described for different arid and semiarid environments. For example, Inouye et al. (1980) studied the influence of seed predation by ants in the dynamics of annual species in the Sonoran desert, and found an increase of seedlings in the ant exclusion plots. Also, Mull & MacMahon (1996) analysed how seed predation by ants affected seed density and its distribution in semiarid areas of Wyoming. We have found that *Cerastium semidecandrum* seeds are severely affected by seed predation, as density of seeds in the plots subjected to ant activity was almost four times smaller than in the exclusion plots. In the same vein, Azcárate et al. (in press) also found that *Messor* ants consumed *Cerastium semidecandrum* seeds in a similar system.

Density of pasture cover or plant species cover are too coarse measures to reflect changes induced at the individual level, at least

in so short a time. As the comparison between floristic composition of the herbaceous community prior to and after ant exclusion treatment shows, more than a year would be needed for the changes in the soil seed banks to be detectable at vegetation level. Many processes lie between the initial soil seed bank and the adult community, both biotic and abiotic. Competition, facilitation and herbivory can further modify the number of individuals and their biomass distribution, and this in turn can be directly affected by meteorological conditions, local availability of water and nutrients, or shading. It would be needed the cumulative effects of several ant predation episodes upon each species' number of seeds to produce a consistent and detectable shift in their biomass proportion. The number of episodes required would depend on the particular characteristics of each community (species assembly and interactions). This could also explain the fact that we only found significant differences in the species abundance of the soil seed bank but not in the spring floristic composition.

Spatial heterogeneity can play an important role in the detectability of ant predation effects. This factor is especially important in Mediterranean pastures, where the annual predominant strategy makes them highly sensitive to factors operating at a microscale level. As these communities rely on seed germination for their regeneration, microtopography (Sterling et al. 1984), patchiness in light and nutrient distribution (Karssen & Hilhorst 1992, Pons 1992), and local dispersal of many species can strongly affect the initial floristic composition. This initial community is immediately subjected to the above-mentioned processes, that will give rise to the adult community in spring. In this context, ant predation is just another process operating at the microscale level at the beginning of community regeneration. As spatial heterogeneity changes the spatial pattern of seed accumulation, ant predation would probably be spatially modified through ant foraging behaviour, becoming a subordinate process. This could lead to the masking-up of its effects, as other authors have reported (Reichman 1984, Henderson et. al. 1988, Guo et. al. 1998). Therefore, it is essential to account for the spatial

heterogeneity of vegetation, especially to detect the effects of microscale-operating processes such as ant granivory in short time spans.

LITERATURE CITED

ACOSTA FJ, F LÓPEZ & JM SERRANO (1992) The dynamics of a therophytic community in relation to self-regulation, herbivores and environmental variation. Vegetatio 98: 59-71.

ANDERSEN AN (1987) Effects of seed predation by ants on seedling densities at a woodland site in SE Australia. Oikos 48: 171-174.

AZCÁRATE FM & B PECO (2003) Spatial patterns of seed predation by harvester ants (*Messor* Forel) in Mediterranean grassland and scrubland. Insectes Sociaux 50: 120-126.

AZCÁRATE FM, L ARQUEROS, AM SÁNCHEZ & B PECO (in press) Seed and fruit selection by harvester ants *Messor barbarus* in Mediterranean grassland and scrubland. Functional Ecology.

AZCÁRATE FM, AM SÁNCHEZ, L ARQUEROS & B PECO (2002) Abundance and habitat segregation in Mediterranean grassland species: the importance of seed weight. Journal of Vegetation Science 13: 159-166.

BROWN JH, OJ REICHMAN & DW DAVIDSON (1979) Granivory in desert ecosystems. Annual Review of Ecology and Systematics 10: 201-227.

CERDA X & J RETANA (1994) Food exploitation patterns of two sympatric seed-harvesting ants *Messor bouviery* (Bond.) and *Messor capitatus* (Latr.) (Hym. Formicidae) from Spain. Journal of Applied Entomology 117: 268-277.

DE PABLO CL, B PECO, EF GALIANO & FD PINEDA (1982) Space-time variability in Mediterranean pastures through the analysis of diversity parameters. Vegetatio 50: 113-125.

DETRAIN C & JM PASTEELS (2000) Seed preferences of the harvester ant *Messor barbarus* in a Mediterranean mosaic grassland (*Hymenoptera: Formicidae*). Sociobiology 35: 35-48.

ESPIGARES T & B PECO (1993) Mediterranean pasture dynamics: the role of germination. Journal of Vegetation Science 4: 189-194.

ESPIGARES T & B PECO (1995) Mediterranean annual pasture dynamics: impact of autumn drought. Journal of Ecology 83: 135-142.

FARJI-BRENER AG & L GHERMANDI (2000) Influence of nests of leaf-cutting ants on plant species diversity in road verges of northern Patagonia. Journal of Vegetation Science 11: 453-460.

FIGUEROA ME & AJ DAVY (1991) Response of Mediterranean grassland species to changing rainfall. Journal of Ecology 79: 925-941.

GÓMEZ C & X ESPADALER (1998) Seed dispersal curve of a Mediterranean myrmecochore: influence of ant size and the distance nests. Ecological Research 13: 347-354.

GÓMEZ JM, R ZAMORA, JA HÓDAR & D GARCÍA (1996) Experimental study of pollination by ants in Mediterranean high mountain and arid habitats. Oecologia 105: 236-242.

GORB SN & EV GORB (1995) Removal rates of seeds of five myrmecochorous plants by the ant *Formica polyctena* (Hymenoptera: Formicidae). Oikos 73: 367-375.

GORB SN, EV GORB & P PUNTTILA (2000) Effects of redispersal of seeds by ants on the vegetation pattern in a deciduous forest: a case study. Acta Oecologica 21: 293-301.

GUO Q, PW RUNDEL & DW GOODALL (1998) Horizontal and vertical distribution of desert seed banks: patterns, causes and implications. Journal of Arid Environments 38: 465-478.

HANDEL SN & AJ BEATTIE (1990) Seed dispersal by ants. Scientific American 263: 58-64.

HENDERSON CB, KE PETERSEN & RA REDAK (1988) Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. Journal of Ecology 76: 717-728.

HENSEN I (2002) Seed predation by ants in south-eastern Spain (Desierto de Tabernas, Almería). Anales de Biología (Spain) 24: 89-96.

HOWE HF & J SMALLWOOD (1982) Ecology of Seed Dispersal. Annual Review of Ecology and Systematics 13: 201-228.

INOUYE RS, GS BYERS & JH BROWN (1980) Effects of predation and competition on survivorship, fecundity and community structure of desert annuals. Ecology 61: 1344-1351.

KARSSEN CM & HWM HILHORST (1992) Effect of chemical environment on seed germination. In: Fenner M (ed) Seeds. The ecology of regeneration in plant communities: 327-348. CAB International, Oxon, United Kingdom.

KING LJ (1966) Weeds of the world, biology and control. Leonard Hill, London, United Kingdom. xvii+253 pp.

LÓPEZ F, FJ ACOSTA & JM SERRANO (1993a) Responses of the trunk routes of a harvester ant to plant density. Oecologia 93: 109-113.

LÓPEZ F, FJ ACOSTA & JM SERRANO (1993b) Foraging territories and crop production of a Mediterranean harvester ant in a grassland ecosystem. Acta Oecologica 14: 405-414.

LÓPEZ F, FJ ACOSTA & JM SERRANO (2000) Asymmetric interactions between plants and seed-harvesting ants in a Mediterranean pasture. Ecological Research 15: 449-452.

LÓPEZ-PINTOR A, T ESPIGARES & JM REY-BENAYAS (2003) Spatial segregation of species caused by *Retama sphaerocarpa* influence in a Mediterranean pasture: a perspective from the soil seed bank. Plant Ecology 167: 107-116.

LOUCKS O, M PLUMB-MENTJES & D ROGERS (1985) Gap processes and large-scale disturbance in sand prairies. In: Pickett STA & PS White (eds) The ecology of natural disturbance and patch dynamics: 72-82. Academic Press, New York, New York, USA.

McCUNE B & MJ MEFFORD (1997) Multivariate analysis of ecological data version 3.18. MJM Software, Gleneden Beach, Oregon, USA. xxiii+197 pp.

MONTIEL S & C MONTAÑA (2003) Seed bank dynamics of the desert cactus *Opuntia rastrera* in two habitats from the Chihuahuan desert. Plant Ecology 166: 241-248.

MULL JF & JA MACMAHON (1996) Factors determining spatial variability of seed densities in a shrub-steppe ecosystem: the role of harvester ants. Journal of Arid Environments 32: 181-192.

ORTEGA M, C LEVASSOR & B PECO (1997) Seasonal dynamics of Mediterranean pasture seed banks along environmental gradients. Journal of Biogeography 24: 177-195.

PECO B (1989) Modelling Mediterranean pasture dynamics. Vegetatio 83: 269-276.

PECO B, C LEVASSOR, MA CASADO, EF GALIANO & FD PINEDA (1983a) Influences météorologiques et géomorphologiques sur la succession de pâturages. Ecologia Mediterranea (France) 9: 63-76.

PECO B, C LEVASSOR & FD PINEDA (1983b) Diversité et structure spatiale de pâturages méditérraneens en cours de succession. Ecologia Mediterranea (France) 9: 223-234.

PECO B, T ESPIGARES & C LEVASSOR (1998a) Trends and fluctuations in species abundance and richness in Mediterranean annual pastures. Applied Vegetation Science 1: 21-28. (Sweden).

PECO B, M ORTEGA & C LEVASSOR (1998b) Similarity between seed bank and vegetation in Mediterranean grassland: a predictive model. Journal of Vegetation Science 9: 815-828.

PINEDA FD, JP NICOLÁS, A POU & EF GALIANO (1981a) Ecological succession in oligotrophic pastures of central Spain. Vegetatio 44: 165-176.

PINEDA FD, JP NICOLÁS, M RUIZ, B PECO & FG BERNÁLDEZ (1981b). Succession, diversité et amplitude de niche dans les pâturages du centre de la péninsule ibérique. Vegetatio 47: 267-277.

PINEDA FD, MA CASADO, B PECO, C OLMEDA & C LEVASSOR (1987) Temporal changes in therophytic communities across the boundary of disturbed-intact ecosystems. Vegetatio 71: 33-39.

PONS TL (1992) Seed responses to light. In: Fenner M (ed) Seeds. The ecology of regeneration in plant communities: 259-284. CAB International, Oxon, United Kingdom.

REICHMAN OJ (1984) Spatial and temporal variation of seed distributions in Sonoran desert soils. Journal of Biogeography 11: 1-11.

REYES-LÓPEZ JL & J FERNÁNDEZ-HAEGER (2001) Some factors determining size-matching in the harvester ant Messor barbarus: food type, transfer activity, recruitment rate and size –range. Insectes Sociaux 48: 118-124.

RUIZ M (1980) Características de la variación de pastizales en zonas graníticas del Centro de la Península Ibérica. Ph.D. Thesis, Facultad de Biología, Universidad Autónoma de Madrid, Madrid, Spain. xxi+269 pp.

M RUIZ, B PECO, C LEVASSOR, F PARRA & A POU (1980) Estructura de una dehesa en el área basal del Guadarrama y su relación con factores abióticos. Anales de Edafología y Agrobiología (Spain) 40: 91-110.

STATSOFT INC (1996) Statistica for Windows (Computer Program Manual). StatSoft Inc., Tulsa, Oklahoma, USA. xiv+177 pp.

STERLING A, B PECO, MA CASADO, EF GALIANO & FD PINEDA (1984) Influence of microtopography on floristic variation in the ecological succession in grassland. Oikos 42: 334-342.

USDA (1985) Soil taxonomy. Agriculture handbook 436, Washington, District of Columbia, USA. xvi+367 pp.

WILLOTT SJ, SG COMPTON & LD INCOLL (2000) Foraging, food selection and worker size in the seed harvesting ant *Messor bouviery*. Oecologia 125: 35-44.

WOODELL S & T KING (1991) The influence of tumulo-building ants on British lowland vegetation. In: Huxley C & Cutler D (eds) Ant-plant interactions: 521-535. Oxford University Press, Oxford, United Kingdom.