

Postdispersal seed predation in a Mediterranean patchy landscape

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Received: 22.3.96

Accepted: 19.9.96

Abstract

Seed predation rates of *Pistacia lentiscus* (Anacardiaceae) were determined at within and between site spatial scale in an Eastern Spanish Mediterranean landscape, a mosaic of scrubland and field patches. At within site scale, no differences in seed predation rates were found regarding the spatial location of the seed within scrubland patches (under parent plant, on the bare soil and under other woody perch different than *P. lentiscus*) nor within field patches (under woody perches and on the bare soil). Other significant factors related to seed predation in both fields and scrubland patches emerged at between site scale. In field patches, seed predation was higher in abandoned than cultivated fields. In scrubland patches, seed predation increased as the perimeter/surface ratio of the patch increased, as habitat fragmentation theory predicts due to the immigration of the ecotonic predators inside the patch. Also, seed predation rates were high at both low and high woody plant cover of the scrubland patches. Detectability of the seed would explain high seed predation rates at low woody plant covers, whereas the total seed density of the seeds and/or the presence of refuges for seed predators would explain high seed predation rates at high woody plant covers. A decreasing pattern of seed predation rates was found from scrubland patches through distant fields, suggesting a scrubland patch-specific behaviour of seed predators.

Keywords: Cultivated fields, old fields, *Pistacia lentiscus*, scrublands, seed predation, spatial scale.

Résumé

Les taux de prédation des graines de *Pistacia lentiscus* (Anacardiaceae) ont été déterminés à deux échelles, sur sites et entre sites dans un paysage méditerranéen de l'est de l'Espagne, mosaïque de fourrés et de parcelles de culture. A l'échelle du site même, les taux de prédation des graines ne diffèrent pas en fonction de la localisation spatiale des graines dans les fourrés (sous la plante-mère, sur le sol nu et sous des espèces ligneuses autres que *P. lentiscus*) ou dans les parcelles de culture

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(sous ligneux et sur sol nu). D'autres facteurs significatifs liés à la prédation des graines aussi bien dans les parcelles de culture que boisées apparaissent à l'échelle inter-sites. Dans les parcelles de culture, la prédation des graines est plus importante dans les champs abandonnés que dans les champs cultivés. Dans les fourrés, la prédation des graines augmente à mesure que le ratio périmètre/surface de la parcelle augmente, comme le prédit la théorie des habitats fragmentés, en raison de l'immigration des prédateurs de lisière vers l'intérieur de la parcelle. De plus, les taux de prédation des graines sont élevés, que le couvert ligneux des parcelles de fourrés soit faible ou important. La visibilité des graines expliquerait des taux élevés de prédation pour des couverts végétaux faibles, alors que la densité totale de graines et/ou la présence de refuges pour les prédateurs expliquerait des taux de prédation élevés pour un couvert végétal important. On a trouvé un patron décroissant des taux de prédation des graines des parcelles de fourrés vers les champs éloignés, ce qui suggère un comportement des prédateurs spécifique aux parcelles de fourrés.

INTRODUCTION

Agricultural activity has fragmented the Mediterranean landscape into a mosaic of scrubland and field patches (NAVEH & DAN, 1973; DI CASTRI, 1981; but see LEPART & DEBUSSCHE, 1992 for other landscape patterns). However, recent land abandonment is allowing scrubland vegetation to recolonize fields (PONS & QUEZEL, 1985; DEBUSSCHE & LEPART, 1992). Bird-dispersed plants are important field colonizers (DEBUSSCHE *et al.*, 1982).

The spatial pattern of seed distribution in bird-dispersed plants originally results from the interaction between plants and avian frugivores (HERRERA 1984 *a*, 1984 *b*, 1995; SNOW & SNOW, 1988; DEBUSSCHE & ISENMANN, 1992). The final pattern of seed distribution can be modified by postdispersal seed predation (JANZEN, 1971; HERRERA, 1984 *c*; WEBB & WILLSON, 1985; WILLSON & WHELAN, 1990; WHELAN *et al.*, 1991).

After dispersal, seed density decreases logarithmically with the distance from the seed source (DEBUSSCHE *et al.*, 1982, 1985; McDONNELL & STILES, 1983; MURRAY, 1988; WILLSON, 1993). It is a common pattern that seeds are often clumped around perches where birds stay and defecate or regurgitate (DEBUSSCHE *et al.*, 1982; McDONNELL & STILES, 1983; IZHAKI *et al.*, 1991; DEBUSSCHE & ISENMANN, 1994; HERRERA *et al.*, 1994; VERDÚ & GARCÍA-FAYOS, 1996). In the Mediterranean region, perches are isolated bushes or trees with tips arising from the vegetation layer (DEBUSSCHE *et al.*, 1982, 1985; IZHAKI *et al.*, 1991). In the patchy Mediterranean landscape, the demographic fate of the seed may be very different depending on the patch where it is dispersed (VERDÚ, 1994). Regarding postdispersal seed predation, the final fate of the seed differs depending on the habitat where the seed was dispersed because factors affecting postdispersal seed predation are different within the scrubland patch (WSP) and within the field patch (WFP). The main WSP effect refers to location of the seed: (1) beneath the parent plant, (2) beneath another perch, and (3) on the bare soil (see JANZEN (1970) and CONNELL (1971) for a model on seed predation changes with the distance from the parent plant). Because seeds are clumped beneath perches and parent plants, seed predators may be attracted to these clumps. The same differences would be expected regarding WFP, but only between two locations due to the lack of parent plants in fields: (1) beneath another perch and (2) on the bare soil.

In addition, new effects can emerge at different spatial scales. For example, SCHUPP (1992) argues that density- and distance-dependent seed survival on the local scale around the parent tree does not necessarily translate into density-dependent seed survival on the scale of a population. Similarly, in the patchy Mediterranean landscape, seed predation between sites (scrubland and field patches) does not necessarily respond to the same factors as within-site predation. These new factors affecting seed predation between-scrubland patches refer to (1) the ratio perimeter/surface of the scrubland patch and (2) overall woody plant cover. The effects of an increasing perimeter/surface ratio of the patch are widely known in habitat fragmentation studies and are related to high availability of perimeter per area for ecotonic predators (WÄSTLJUNG, 1989; TELLERÍA *et al.*, 1991). Overall woody cover of the patch can affect seed detectability, total seed density in soil and the presence of refuges for granivores. All of these variables are related to granivore behaviour (PRICE & JENKINS, 1986; GETTY & PULLIAM, 1993).

Another between-site effect may be the distance of the field to the scrubland patch acting as source of the seed. If predators are "scrubland patch-specific", seed predation rate would be greatest in the scrubland patch and decrease in intensity when seeds are dispersed far from it.

The aim of this paper is to test the factors affecting within-site and between-site postdispersal seed predation in a Mediterranean fragmented landscape for the bird-dispersed plant *Pistacia lentiscus*.

MATERIAL AND METHODS

The plant species

Pistacia lentiscus L. (Anacardiaceae) is a dioecious shrub common in Mediterranean sclerophyllous scrublands. This plant is evergreen and wind-pollinated. Females produce many one-seeded drupes in late summer and autumn. The colour of their fruits is strongly associated with seed viability: black fruits are ripe and contain viable seeds whereas red ones are unripe and contain non-viable seeds (JORDANO, 1988, 1989).

Frugivorous birds disperse the seeds from September to March (HERRERA, 1984 *a*; JORDANO, 1989; VERDÚ & GARCÍA-FAYOS, 1994). Rodents (*Apodemus sylvaticus*, *Mus spretus*, *Eliomys quercinus*) and granivorous birds (*Carduelis chloris*, *Fringilla coelebs*) are the main postdispersal seed predators.

Study sites

The study sites are located in Valencia (Eastern Spain), always less than 20 km to the coast, at an altitude ranging from 0 to 400 m a.s.l. The region has a dry and semi-arid Mediterranean climate with average annual rainfall ranging from 350 to 550 mm and the average annual temperature is ca. 16°C. The landscape is characterized by a mosaic of scrubland patches mixed with cultivated and old fields, a common pattern in the eastern Spanish Mediterranean landscapes.

Six scrublands with *Pistacia lentiscus* and nineteen fields (seven cultivated and twelve abandoned) were selected as study patches within this landscape. We considered that cultivated fields were the first step in the colonization process, while abandoned fields, with many weeds (Asteraceae, Fabaceae) and small shrubs (Lamiaceae) were considered the second step of the process.

Scrubland patches soils were mollisols and chromic luvisols whereas field patches were haplic calcisols and calcareous regosols (FORTEZA *et al.*, 1995). *Pistacia lentiscus*, *Pinus halepensis*, *Juniperus oxycedrus*, *Quercus coccifera*, *Rosmarinus officinalis*, and *Cistus albidus* are the main woody species in the scrublands. *Ceratonia siliqua*, *Prunus dulcis*, *Vitis vinifera*, and *Olea europaea* are common species in the fields. The age of abandonment for old fields ranged from 3 to 10 yr. In all of them, the trees or vines remained alive and the vegetation structure was dominated by annual and perennial herbs but small woody shrubs like *Thymus vulgaris*, *Helichrysum stoechas* and *Phagnalon saxatile* were also present. The scrubland patches structure consisted of a maquis with an average vegetation height of 1-3 m and different woody cover (see table I for environmental characteristics of each scrubland patch).

TABLE I. – Environmental characteristics and seed predation rates within the scrubland and field patches.

| Scrublands | | | | | | |
|------------|-----------------------|---------------------------------------|---------------------------------------|------|------------------------------|-------------------------------|
| Site | Woody plant cover (%) | Perimeter/surface of the path (km/Ha) | % of seed groups visited by predators | | | % of seeds eaten in the patch |
| | | | Parent | Soil | Perch | |
| S1 | 90 | 0.17 | 89 | 100 | 100 | 90.5 |
| S2 | 10 | 0.12 | 100 | 78 | 100 | 29.5 |
| S3 | 80 | 0.24 | 70 | 80 | 90 | 66.7 |
| S4 | 75 | 0.14 | 90 | 50 | – | 90.7 |
| S5 | 35 | 0.02 | 60 | 20 | 40 | 68.9 |
| S6 | 65 | 0.06 | 40 | 50 | 25 | 31.1 |
| | | Average | 74.6 | 61.1 | 71.7 | 62.9 |
| Fields | | | | | | |
| Site | Field stage | Distance from scrubland patch | % of seed groups visited by predators | | % of seed eaten in the patch | |
| | | | Perch | Soil | | |
| F1 | Cultivated | Near (> 300 m) | 60 | 60 | 38.3 | |
| F2 | Cultivated | Near | 0 | 30 | 5.0 | |
| F3 | Cultivated | Near | 80 | 60 | 48.3 | |
| F4 | Cultivated | Far (> 300 m) | 10 | 0 | 5.0 | |
| F5 | Cultivated | Far | 30 | 43 | 19.6 | |
| F6 | Cultivated | Far | 10 | 20 | 8.3 | |
| F7 | Cultivated | Far | 10 | 10 | 3.3 | |
| F8 | Abandoned | Near | 10 | 10 | 10.0 | |
| F9 | Abandoned | Near | 50 | 60 | 46.7 | |
| F10 | Abandoned | Near | 100 | 78 | 52.6 | |
| F11 | Abandoned | Near | 20 | 20 | 18.3 | |
| F12 | Abandoned | Near | 70 | 40 | 50.0 | |
| F13 | Abandoned | Near | 100 | 80 | 75.0 | |
| F14 | Abandoned | Near | 30 | 70 | 38.3 | |
| F15 | Abandoned | Far | 44 | 38 | 25.5 | |
| F16 | Abandoned | Far | 20 | 20 | 15.0 | |
| F17 | Abandoned | Far | 30 | 20 | 16.7 | |
| F18 | Abandoned | Far | 20 | 25 | 14.8 | |
| F19 | Abandoned | Far | 37 | 63 | 29.2 | |
| | | Average | 35.8 | 38.9 | 27.4 | |

Experimental design and data analysis

We quantified seed predation rates by placing seeds in the field and determining the number of eaten seeds. The experimental unit was a group of three seeds. This decision was based on the following observations:

– The modal class in both faeces in the field and seed regurgitations of caged individuals of *Erethacus rubecula*, one of the most abundant bird disperser species in the study area (VERDÚ *et al.*, 1989; VERDÚ & GARCÍA-FAYOS, 1994), was three seeds per “dispersal event”.

– Predation experiments with 0-15 seeds per experimental unit showed that variation in the number of seeds did not modify the results.

The seeds used in the experiment were taken from black fruits to ensure seed viability and prevent differential seed predation rates due to seed predator preferences. As JORDANO (1990) reported, seed predators can detect unfilled seeds and reject them by bill-weighing.

Experimental units were placed on the ground, not hidden under the litter. In this way, every seed had the same accessibility to predators. The seeds beneath perches were placed 1 m from the trunk.

As seed predation may be performed *in situ* or *ex situ*, we considered both missing seeds and the presence of seed coat remnants as evidence of predation. Secondary dispersal of *P. lentiscus* seeds, to our knowledge, is performed only sporadically by ants (ARONNE & WILCOCK, 1994) but it is unknown the generality of this phenomenon (HERRERA, 1995). However, ant activity was not observed during the winter months in which the experiment ran.

Results were not considered when the wind blew intensely or it rained enough to produce runoff during the experiment. After two weeks, the number of seeds depredated was recorded. This periodicity was chosen because previous exploratory experiments showed that differences among treatments could be perceived in that amount of time. More time than this did not bring further information and even increased the risk of accidental seed losses.

All experiments were performed during the seed dispersal season, early winter of 1992-1993. Two periods of 2 weeks were used for the experiments, the first along December 1992 and the second along January 1993 but no differences in average seed predation rates were found between both periods ($t = -1.23$; $p = 0.2$; two-tailed paired-samples *t*-test).

A woody plant higher than 1 m with upper branches standing out the surrounding vegetation was considered a perch, *i.e.* *Juniperus communis*, *Quercus coccifera*, *Cistus albidus* and *Rosmarinus officinalis* (height ranging from 1 to 3 m) in the scrubland sites and *Ceratonia siliqua*, *Vitis vinifera* and *Prunus dulcis* (height ranging from 1 to 5 m) in the field sites.

Within site predation

Scrubland sites

Groups of three seeds were placed in three treatments: (1) beneath *P. lentiscus* females, (2) on the bare soil beneath no plant and (3) beneath a woody perch, other than *P. lentiscus*. The third treatment was lacking in one of the six scrubland sites.

Ten replicates of each treatment were made, which meant a total of 510 seeds ($[(5 \text{ scrublands} \times 3 \text{ treatments}) + (1 \text{ scrubland} \times 2 \text{ treatments})] \times 10 \text{ replicates} \times 3 \text{ seeds} = 510 \text{ seeds}$).

Adjacent groups of seeds were at least 5 m apart, ranging from 5 to 10 m, ensuring independence of the replicates (BURKEY, 1994). For this reason, each group of three seeds represents one independent record and therefore an individual degree of freedom. Moreover, the treatments are not paired within each site. These premises enable us to analyze the data with logistic regression procedures (HOSMER & LEMESHOW, 1989).

A logistic regression model was built with seed predation as the dependent variable, location (beneath *P. lentiscus*, on the bare soil, and beneath other perch) as the independent variable, and the scrubland patch as a block. Seed predation was coded as 0 if no seed was depredated and 1 if one

or more of the three seeds were depredated. Location was modelled as a dummy variable with the following codes: 0 0 for bare soil, 1 0 for *P. lentiscus* females and 0 1 for perch. The Wald statistic was used to test the null hypothesis that the coefficient B in the logistic regression model is zero.

Field sites

Groups of three seeds were placed in two treatments: (1) beneath a tree, and (2) on the bare soil beneath no plant.

Ten replicates of each treatment were made within each of the 19 fields, which meant a total of 1 140 seeds (19 fields \times 2 treatments \times 10 replicates \times 3 seeds = 1 140 seeds). Adjacent groups of seeds were also at least 5 m apart, and therefore the premises and analysis were the same as those of the scrubland sites.

The dependent variable in the logistic regression model (seed predation) was also coded as 0, 1, the independent variable was location (beneath of perch and on the bare soil), and field was the block. Location was modelled as a dummy variable with the codes 0 for bare soil and 1 for perch.

Between site predation

Because the study scale was changed from within to between site, the experimental unit had also to change from the 3-seeds group to study site. Thus, in this analysis each study site corresponds to one degree of freedom, yielding 6 d.f. for scrubland analysis and 19 d.f. for field analysis. Thus, the 10 replicates of the treatments were used to get the proportion of eaten seeds per site. This measure is significantly correlated with that used in within site experiment ($r = 0.62$; $p < 0.01$; $n = 37$; values from present plus previous experiments) and therefore the conclusions of this study will be unaffected by the kind of measure. Furthermore, we are concerned only with relative and not with absolute predation.

As these data are not binomially distributed, logistic regression cannot be applied. To test seed predation across the different scrubland sites, we used least squares regression, with seed predation percentage the dependent variable and the perimeter/surface ratio of the patch and overall woody cover independent variables.

Seed predation across the different field patches was similarly tested with least square regression. Successional stage (abandoned or cultivated) was the independent variable.

To test seed predation across the different study sites (scrubland mixed with field patches), we classified (1) the scrubland patches as distance zero ($d = 0$), (2) fields surrounding a scrubland patch ($d < 300$ m) as "near", and (3) fields ranging from 300 to 3 000 m from the scrubland patch ($d > 300$ m) as "far". A oneway analysis of variance was performed, comparing seed predation among the three distance levels. A *a priori* orthogonal contrast was used to test differences between the three levels of the variable distance. The *a priori* test was used because a previous hypothesis was formulated. This hypothesis postulates that seed predation is more intense in the scrubland patch and decreases away from it (in the "near" and "far" fields). Thus, coefficients for the orthogonal polynomial were 1 0 -1 and 1 -2 1.

Seed predation was log-transformed. Normality of residuals was examined by plotting them against the observed values and homogeneity of variances was checked with Cochran's test.

Statistical tests were one-tailed when the direction of the alternative hypothesis was known *a priori*, and two-tailed when the direction was unknown.

RESULTS

Within site seed predation

Scrubland sites

Seed predation did not differ significantly beneath *P. lentiscus* female, on the bare soil, nor beneath perch other than *P. lentiscus* (table II), indicating that seed

TABLE II. - Statistics from the logistic regression model for seed predation within the scrubland patches.

| Variable | B | S.E. | Wald | df | Exp (B) |
|-----------------------|-------|------|-------------------|----|---------|
| Site | | | 31.1** | 5 | |
| - Site (1) | - 1.8 | 0.5 | 9.4* | 1 | 0.1 |
| - Site (2) | - 1.9 | 0.6 | 9.7* | 1 | 0.1 |
| - Site (3) | 1.7 | 1.1 | 2.4 ^{ns} | 1 | 5.8 |
| - Site (4) | 1.1 | 0.8 | 1.8 ^{ns} | 1 | 3.2 |
| - Site (5) | - 0.4 | 0.6 | 0.4 ^{ns} | 1 | 0.6 |
| Location | | | 3.1 ^{ns} | 2 | |
| - <i>P. lentiscus</i> | 0.8 | 0.4 | 2.9 ^{ns} | 1 | 2.2 |
| - Perch | 0.6 | 0.5 | 1.3 ^{ns} | 1 | 1.8 |
| Constant | 0.9 | 0.5 | 3.2 ^{ns} | 1 | |

*: $p < 0.01$; **: $p < 0.001$; ns not significant.

predation was not greater beneath perches or parent plants where seeds usually accumulate.

Some sites showed significant Wald statistics, revealing differences in seed predation among scrubland patches regarding the characteristics of each patch. Scrubland patches differ on characteristics like woody plant cover and the ratio perimeter/surface (table I) and differences of seed predation rates regarding these characteristics are analyzed under "between site seed predation" section.

Field sites

In fields, seed predation is similar beneath a perch and on the bare soil, indicating that seed predation within fields was not affected by the location of the seed (table III).

Some sites showed significant Wald statistics, revealing differences in seed predation among field patches regarding the characteristics of each patch. Field patches differ on characteristics like the successional stage (table I) and differences of seed predation rates regarding these characteristics are analyzed under "between site seed predation" section.

Between site seed predation

Scrubland sites

The relationship between the ratio perimeter/surface of the scrubland patch and seed predation is significant ($r = 0.78$; $t = 2.5$; $p = 0.03$; one-tailed test). The greater the ratio perimeter/surface, the greater the seed predation rate (fig. 1 a).

Woody plant cover is significantly correlated with seed predation rates fitting a U-shaped curve (fig. 1 b). Both linear and quadratic terms in the regression model are significant ($t = -4.6$; $p = 0.01$ for the linear term and $t = 4.8$; $p = 0.01$ for the quadratic term; two-tailed tests; $r = 0.94$; $F = 12.0$; $p = 0.03$ for the complete model).

TABLE III. - Statistics from the logistic regression model for seed predation within the field patches.

| Variable | B | S.E. | Wald | df | Exp (B) |
|-------------|----------|------|-------------------|----|---------|
| Site | | | 68.1** | 18 | |
| - Site (1) | 2.1 | 0.7 | 7.6* | 1 | 8.5 |
| - Site (2) | -0.4 | 0.9 | 0.2 ^{ns} | 1 | 0.6 |
| - Site (3) | -1.2 | 1.2 | 1.0 ^{ns} | 1 | 0.2 |
| - Site (4) | 1.1 | 0.8 | 2.0 ^{ns} | 1 | 3.1 |
| - Site (5) | 0.3 | 0.8 | 0.1 ^{ns} | 1 | 1.4 |
| - Site (6) | -0.4 | 0.9 | 0.2 ^{ns} | 1 | 0.6 |
| - Site (7) | 1.9 | 0.7 | 6.3* | 1 | 6.9 |
| - Site (8) | 2.5 | 0.7 | 10.5** | 1 | 13.2 |
| - Site (9) | 1.7 | 0.7 | 5.0* | 1 | 5.6 |
| - Site (10) | -5.4E-16 | 0.8 | 0.0 ^{ns} | 1 | 1.0 |
| - Site (11) | 0.6 | 0.8 | 0.6 ^{ns} | 1 | 1.8 |
| - Site (12) | 0.4 | 0.8 | 0.3 ^{ns} | 1 | 1.6 |
| - Site (13) | 1.7 | 0.8 | 4.6* | 1 | 5.6 |
| - Site (14) | 1.3 | 0.7 | 3.0 ^{ns} | 1 | 3.9 |
| - Site (15) | 3.9 | 0.9 | 16.3*** | 1 | 51.2 |
| - Site (16) | 1.9 | 0.7 | 6.3* | 1 | 6.9 |
| - Site (17) | 0.3 | 0.8 | 0.1 ^{ns} | 1 | 1.4 |
| - Site (18) | 2.2 | 0.7 | 8.4** | 1 | 9.7 |
| Location | 0.1 | 0.2 | 0.4 ^{ns} | 1 | 1.1 |
| Constant | -1.8 | 0.6 | 8.1** | 1 | |

*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; ns : not significant.

Field sites

The percentage of seeds eaten in abandoned fields (32.7 ± 5.8) is significantly higher than that in cultivated fields (18.3 ± 6.9) ($t = 2.27$; $p = 0.03$; two-tailed t -test for log-transformed data).

Distance effect

Figure 2 shows the mean values of seed predation rates in each of the study distances. A one-way analysis of variance revealed significant differences in seed predation rates as a function of the distance from the scrubland patch ($F = 7.3$; $p = 0.003$). A linear decreasing distance gradient in seed predation is found when the differences between levels of distance were tested by means of an orthogonal polynomial ($t = -3.8$; $p = 0.0004$ for the 1 0 -1 contrast and $t = 0.7$; $p = 0.38$ for the 1 -2 1 contrast; one-tailed tests), indicating that seed predation followed a decreasing trend from the scrubland patch through distant fields. Despite that the balance of both abandoned and cultivated fields was not exact between the levels of distance ("near" class contains 30% of cultivated and 70% of abandoned fields whereas "far" class contains 44.4% of cultivated and 55.6% of abandoned fields), this result is not a confounding effect with field stage because the same trend was found when abandoned fields are excluded from the analysis ($t = -3.9$; $p = 0.001$ for the 1 0 -1 contrast and $t = 0.4$; $p = 0.32$ for the 1 -2 1 contrast; one-tailed tests) or when cultivated fields are excluded ($t = -3.7$; $p = 0.0009$ for the 1 0 -1 contrast and $t = 0.05$; $p = 0.48$ for the 1 -2 1 contrast; one-tailed tests).

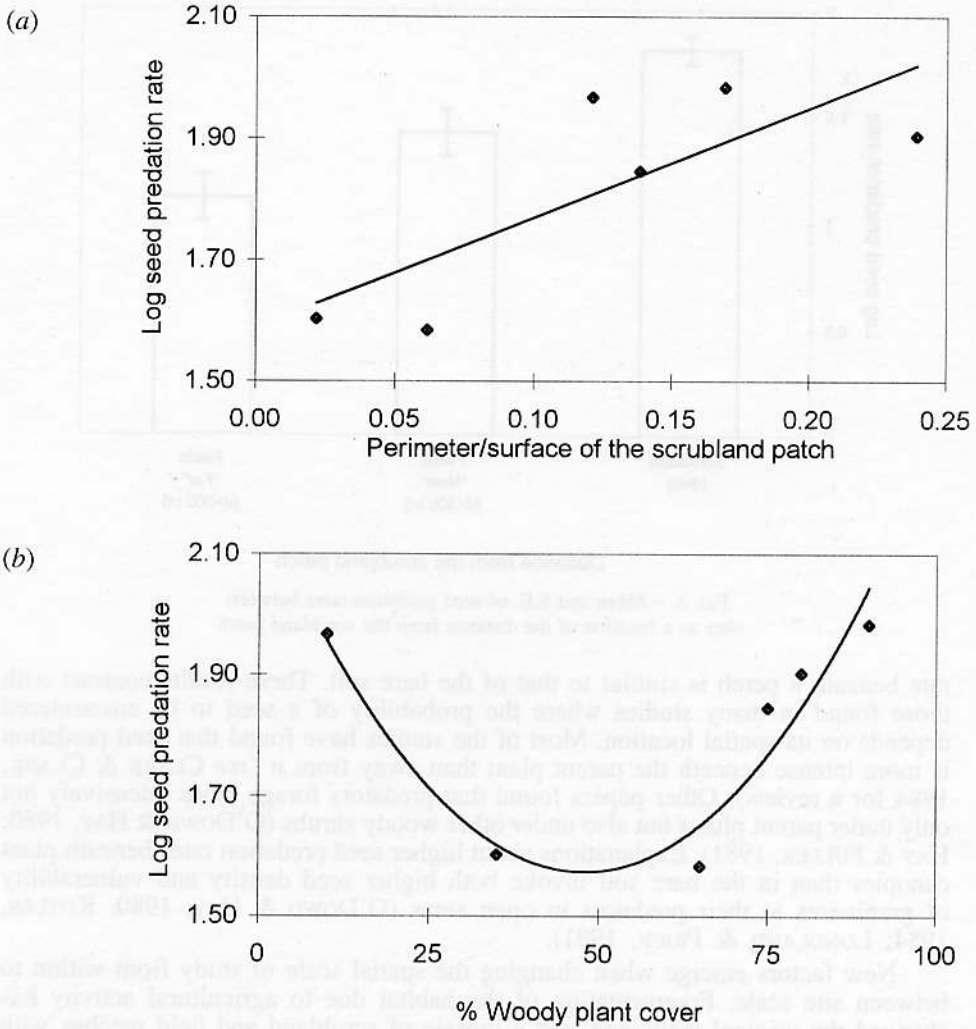


FIG. 1. – Relationship between seed predation rate and a) the ratio perimeter/surface of the scrubland patch and b) the overall woody cover of the scrubland patch.

DISCUSSION

Many studies have documented spatial variability in seed predation (WILLSON & WHELAN, 1990; WHELAN *et al.*, 1991; BURKEY, 1994). We found different seed predation patterns when changing spatial scale from within to between site scale.

Seed predation rates within the scrubland patches are similar beneath *P. lentiscus*, on the bare soil and beneath another woody perch, suggesting that granivores were not attracted by perches where seeds are usually accumulated by dispersers. The same result is found within the field patches, where seed predation

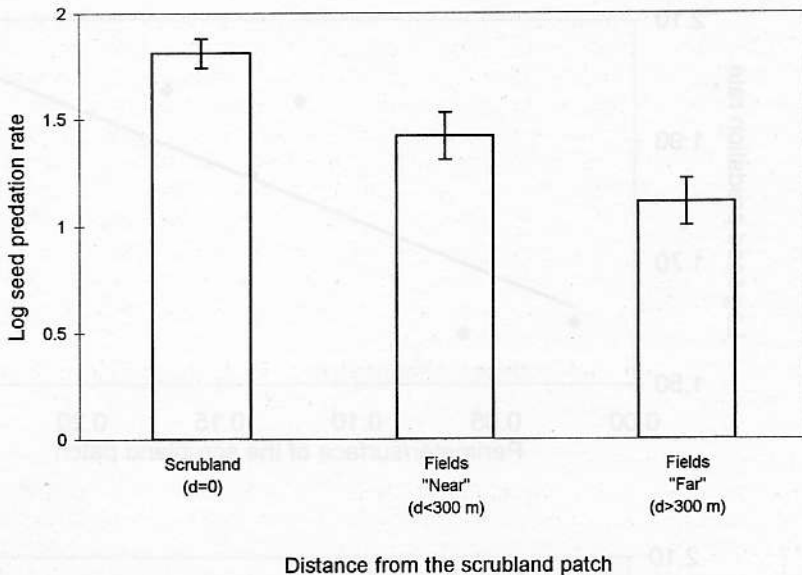


FIG. 2. – Mean and S.E. of seed predation rates between sites as a function of the distance from the scrubland patch.

rate beneath a perch is similar to that of the bare soil. These results contrast with those found in many studies where the probability of a seed to be encountered depends on its spatial location. Most of the studies have found that seed predation is more intense beneath the parent plant than away from it (*see* CLARK & CLARK, 1984 for a review). Other papers found that predators forage more intensively not only under parent plants but also under other woody shrubs (O'DOWD & HAY, 1980; HAY & FULLER, 1981). Explanations about higher seed predation rates beneath plant canopies than in the bare soil invoke both higher seed density and vulnerability of granivores to their predators in open areas (O'DOWD & HAY, 1980; KOTLER, 1984; LONGLAND & PRICE, 1991).

New factors emerge when changing the spatial scale of study from within to between site scale. Fragmentation of the habitat due to agricultural activity has changed the original landscape into a mosaic of scrubland and field patches with different characteristics potentially affecting seed predation. One consequence of habitat fragmentation is an increase in the perimeter/surface ratio of the scrubland patch. A higher immigration of ecotonic animals to the fragmented patch when this ratio increases has been documented (JANZEN, 1983). Thus, the immigration of seed predators increases the predation rate inside the patch (WÄSTLJUNG, 1989; TELLERÍA *et al.*, 1991). Effectively, we found that the greater the perimeter/surface ratio of the scrubland patch, the greater the seed predation.

We found that seed predation rates in scrubland patches were higher at both low and high woody plant covers. Different behaviours of granivores regarding habitat structure have been interpreted as responses to predation risk, dependence of stable refuges, and/or food accessibility (DÍAZ, 1994). GETTY & PULLIAM (1993) found that granivores search more intensively where seeds are most detectable than

where they are more abundant. Total seed density and/or the presence of refuges are also correlated with seed predation (*see* PRICE & JENKINS, 1986 for a review). Our data would be explained if several processes are operating in the scrubland patches. Thus, seed predation would be intense at high woody plant cover because of the total seed density and/or the presence of the refuges in the scrubland patch. Because plant cover in the scrubland patches includes other attractive species for seed predators, a high density of seeds should enhance granivores activity. In contrast, low woody plant cover would allow granivores to detect easily the seeds.

Seed predation in abandoned fields is significantly higher than in cultivated fields, suggesting that total seed density in soil and not seed detectability is the main variable affecting seed predation in these habitats. Similar results have been reported in MITTELBACH & GROSS (1985).

Results of within and between site predation in both scrubland and field patches indicate that the main seed predation processes are not operating at the microhabitat spatial scale (location of the seed) but at the macrohabitat spatial scale (patch characteristics).

In summary, we found different seed predation rates across sites resulting in a pattern of decreasing seed predation from the scrubland patch through distant fields. If predators are "scrubland patch-specific", seed predation rate should be greatest in scrubland and decrease away from scrubland. Many studies have shown that both scrubland and field seed predator communities are different (BLONDEL, 1981; CARRASCAL & TELLERÍA, 1985; PRICE & JENKINS, 1986). During the winter period, rodents depend on shrubby areas for safe and stable refuges (DIAZ, 1994). Even though the scrubland predator community is "patch-specific", it is not necessarily restricted to the scrubland patch, as BARTHOLOMEW (1970) has shown in California chaparral. In this community, predators forage in habitats surrounding the scrubland patch. The decreasing seed predation pattern found in our study can be explained if the specific-patch predators forage more intensively within scrubland and with lesser intensity away from it. This indicates that the probability for a seed to survive is greater when dispersed away from the scrubland patch. Consequently, seed predators can potentially affect plant establishment and successional processes.

ACKNOWLEDGEMENTS

We thank Rosa M^a LÓPEZ for field assistance. J. BURGOS, C. COLINAS, C. M. HERRERA, F. LÓPEZ-SANTOVEÑA, M. J. MOLINA, V. MONLEÓN, S. S. S. SARMA, A. TRAVSET and C. J. WHELAN helped to improve the manuscript. The Oficina Técnica Devesa-Albufera provided logistic assistance. This study was partially supported by the Institució Valenciana D'Estudis i Investigació (project 02-046). Caixa Sagunt provided a study grant to the first author. Additional support was provided by the Spanish Comisión Interministerial de Ciencia y Tecnología (project NAT91-0741).

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