

# Old-field colonization by *Daphne gnidium*: seedling distribution and spatial dependence at different scales

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**Abstract.** This paper deals with the spatial distribution pattern of the bird-dispersed plant *Daphne gnidium* in a 10-yr abandoned field under Mediterranean conditions. Colonization of Mediterranean old-fields by bird-dispersed plants is expected to fit a theoretical model in which (1) seed dispersal follows a negative exponential curve with the distance from the seed source and (2) seedlings are better established under perches (nucleation *sensu* Yarranton & Morrison 1974). However, post-dispersal processes such as seed predation, seed germination and seedling establishment are also spatial-dependent and can lead to spatial autocorrelation in the seedling distribution within an old-field.

Results show that both processes in the model (curve of seed dispersal and nucleation) significantly explained the spatial distribution of the seedlings, but some spatial variance remained unexplained. The semivariogram with the statistical residuals of the model detected spatial dependence at small (< 20 m) and large (> 250 m) distance intervals, indicating that some mechanisms with spatial components, apart from the curve of seed dispersal and nucleation under perches, also determined the distribution of seedlings colonizing fields. At scales below 20-m intervals, semivariance increased indicating that similarity between plots is lost when distance increases between them. This pattern may be explained because the favourable micro-environmental conditions for establishment produced under perches could be extended towards neighbour plots where perches were absent. A flat semivariogram between 20-m and 250-m intervals shows spatial independence along this range. From 250 m on, the semivariance increased again, indicating spatial dependence at coarse-scale. It is possible that the colonization model failed at this scale because different spatial processes to those included in the model (perch presence and distance to the shrubland) could be controlling seed colonization at coarse-scale.

**Keywords:** Geostatistics; Mediterranean; Nucleation; Seed dispersal; Seedling establishment.

**Nomenclature:** Tutin et al. (1964-1980).

## Introduction

Since the beginning of this century, cultivated areas in many regions of Mediterranean Europe are being recolonized by natural vegetation, due to the 'rural exodus' (Brouwer 1991; Debussche et al. 1996). Seed dispersal by frugivorous birds is one of the main processes involved in the colonization of Mediterranean old-fields (Debussche et al. 1982, 1985; Ne'eman & Izhaki 1996). As frugivorous birds have a marked preference for trees and shrubs acting as perches (Debussche et al. 1985; Debussche & Lepart 1992), colonization of abandoned fields can be produced by means of this directional dispersal from the source of the seeds towards the field. Both the curve of seed dispersal with distance from the seed source and the presence of nucleating trees (*sensu* Yarranton & Morrison 1974) are the two main processes analysed to fit the colonization models followed by bird-dispersed plants.

Taking into account these two processes and the size and behaviour of the dispersers, Debussche & Lepart (1992) proposed two models of seed shadows generated by birds. These models are: (1) small-sized birds that usually consume small fruits produce seed shadows following a negative exponential decrease from the seed source over a distance of up to 50 m and localized increases under perches; (2) Medium-sized birds that usually consume large fruits produce seed shadows clumped under the roosting place that can be located far away from the seed source.

The first process of the model, i.e. the curve of seed dispersal with distance from the seed source, has been widely studied. Willson (1992, 1993) reviewed data from the literature and found that seed dispersal curves usually follow a leptokurtic distribution where the slope decreases exponentially from the peak, or, less commonly, they fit a negative power function. Even though the tail distribution has been less studied, it can be fitted to algebraic and/or exponential types (Portnoy & Willson 1993).

As to the second process of the model, nucleation around trees, in Mediterranean habitats the role of perches

as attractors to frugivorous birds has long been documented (Izhaki et al. 1991; Debussche & Isenmann 1994). Thus, dispersed seeds are clumped under these perches.

As Debussche & Lepart (1992) noted, the colonization of Mediterranean old-fields is expected to fit their first model. However, post-dispersal processes such as seed predation, seed germination and seedling establishment can also be spatially dependent and alter the spatial distribution pattern of colonizing seedlings.

Seed predation may alter the spatial pattern of seed shadows generated by birds at different spatial scales (Janzen 1971; Webb & Willson 1985; Willson & Whelan 1990). At fine scales, predators may be attracted by clumps of seeds around perches and forage selectively around them. However, Verdú & García-Fayos (1996a) documented that even though seeds are distributed in clumps, seed predation within Mediterranean old-fields is not higher beneath perches than outside. At coarser scales, a significant spatial component of seed predation was found, because the seed predation rate decreased from shrubland patches through distant fields.

The spatial component of seed germination is linked to the distribution of microsites. Microsites may affect plant community composition through germination and survival of propagules (Eriksson & Ehrlén 1992; Smalldge & Leopold 1995). Similarly, seedling establishment has a spatial component linked to the presence of competing vegetation and favourable soil conditions. Berkowitz et al. (1995) found in several habitats, including old-fields, that seedling growth limitation was produced because of the competition with vegetation in high-quality sites whereas limitation in unfavourable sites was due to physical stress. In Mediterranean old-fields, germination and seedling establishment are favoured under perches, due to the micro-environmental conditions beneath their canopies (Verdú & García-Fayos 1996b).

These spatially dependent processes, which are not dependent on the disperser's behaviour, can lead to spatial autocorrelation in the seedling distribution within an old-field. For example, spatial autocorrelation in seedling populations of weeds and annual grasses – where bird behaviour is not relevant in the dispersal process – has been documented in agricultural fields (Cardina et al. 1996). Because variation in the colonization process may occur at different scales, spatial scaling methods are needed to study this (Webster 1985).

The aim of this paper is to test over a long distance range (575 m), in an olive grove which was abandoned 10 yr ago and subsequently colonized by the fleshy-fruited plant *Daphne gnidium*:

- (1) the colonization model with the two classical parameters (dispersal curve and nucleation);
- (2) the occurrence of spatial autocorrelation in the seedling distribution after fitting the colonization model.

## Methods

*Daphne gnidium* (*Thymelaeaceae*) is a sclerophyllous and evergreen hermaphroditic sub-shrub pollinated by insects, with one-seeded fleshy fruits dispersed by birds (J. Herrera 1987; C.M. Herrera 1992).

Sampling was carried out in the Parque Nacional de Cabañeros, located in the province of Ciudad Real, central Spain. The climate is Mediterranean, with hot and dry summers and mild winters. This park is a natural reserve of Mediterranean shrubland; it also includes large cultivated fields, which were abandoned in 1984. Mediterranean shrubland expands on the slopes whereas the fields are located at the bottom of the valleys.

We selected a 575 m × 160 m olive grove at the edge of the shrubland to test both parameters of the colonization model, dispersal curve and nucleation. Due to the location of the field and the presence of cultivated areas around the olive grove, seed dispersal was necessarily unidirectional; therefore we could determine the origin and the distance travelled by the seed. This assumption could also be made because none of the *D. gnidium* individuals colonizing the old-field were reproductive. By selecting an olive grove we could also test the nucleation parameter of the colonization model by considering the olive trees as perches.

We sampled the field in 5 m × 5 m plots, which should yield  $575/5 \times 160/5 = 3680$  sampling units; however, because the cultivated area entered into some plots at the end of the abandoned field, the final sample size was 3616 plots. In each 5 m × 5 m plot, we recorded: (1) the coordinate of the plot, being the origin of coordinates in the upper left corner of the imaginary grid; (2) presence or absence of perches, and (3) presence or absence of *D. gnidium* individuals. The size of the plots was selected so as to include the whole canopy of the olive tree in one plot. All the olive trees were similar in both canopy diameter (5 m × 5 m) and height (3 - 4 m).

The density of *D. gnidium* in the shrubland was  $0.046 \pm 0.005$  ind/m<sup>2</sup> whereas the density in the field was 0.001 ind/m<sup>2</sup>. Other fleshy-fruited plants were

<i>Arbutus unedo</i>	<i>Asparagus acutifolius</i>
<i>Crataegus monogyna</i>	<i>Ligustrum vulgare</i>
<i>Olea europaea</i> var. <i>sylvestris</i>	<i>Phyllirea angustifolia</i>
<i>Pistacia lentiscus</i>	<i>Rubus</i> sp.

The main species colonizing the field was *D. gnidium*, followed by *Asparagus acutifolius*:  $0.004 \pm 0.002$  ind/m<sup>2</sup> in the shrubland and  $0.0007$  ind/m<sup>2</sup> in the field. Probably, chemical defences in *D. gnidium* (Stout et al. 1970) and mechanical defences in *Asparagus acutifolius* allow these species to escape from deer (*Cervus elaphus*) herbivory and therefore they are able to colonize the old-field. Deer predation on the seedling and saplings of the rest of fleshy-fruited species was very strong.

## Statistical analysis

The premise of decreasing seedling density as a function of distance from the seed source was tested by fitting the equation  $\ln y = mx + b$ , where  $y$  is the seedling density occurring at a given distance from the seed source. Three lines of  $5 \text{ m} \times 5 \text{ m}$  plots were pooled to obtain seedling densities. Therefore, as each distance interval corresponded to 15 m from the seed source and the field width was 160 m, seedling density was referred to an area of  $15 \text{ m} \times 160 \text{ m} = 2400 \text{ m}^2$ .

A logistic regression model (Hosmer & Lemeshow 1989) was built with seedling presence within the  $5 \text{ m} \times 5 \text{ m}$  plot as the dependent variable, and perch presence and distance of the plot to the shrubland patch as the independent variables. Seedling presence usually occurred at the density of one individual per plot. Therefore, the value 0 was assigned to a plot if seedlings of *D. gnidium* were absent, and 1 if at least one seedling was present within the  $5 \text{ m} \times 5 \text{ m}$  plot. Perch presence was coded as 0 if there was no perch, and 1 if the perch was present within the plot. The distance from the plot to the shrubland patch was considered as a continuous variable. The Wald statistic was used to test the null hypothesis that the coefficient  $B$  in the logistic regression model is zero. The general equation of logistic regression is:

$$\text{Probability (event)} = 1 / [(1 + \exp(- (B_0 + B_1 X_1 + B_2 X_2 + \dots + B_x X_k))] \quad (1)$$

To detect if some spatial variation in seedling distribution still remained after removing the variance explained by the variables in the logistic regression equation – perch presence and distance of the plot to the shrubland patch – we constructed a semivariogram with the 3616 statistical residuals produced by the logistic regression. If data are spatially independent (two nearby points are, on average, no more likely to be similar than two distant points) a horizontal semivariogram at all scales is expected (Palmer 1988). For the semivariogram, distance was considered in discrete distance classes of 5 m, corresponding to the size of the sampling plots. The active lag of the semivariogram was 383 m, which represented 2/3 of the maximum lag (575 m). The last third of the semivariogram was not used, as recommended by Legendre & Fortin (1989). The percentage of spatially structured variance was measured as the proportion of model sample variance (the semivariogram asymptote or sill, or  $C_o + C$ ) explained by structural variance  $C$ .

Logistic regression was performed using SPSS (Norusis 1990) and geostatistical calculations were run with the program GS+ (Anon. 1995).

## Results

The density of *D. gnidium* seedlings decreased exponentially with distance from the seed source (Fig. 1). The regression was statistically significant ( $t = -5.4$ ;  $p < 0.001$ ;  $df = 34$ ). This decreasing trend was also illustrated in the logistic regression model, where the distance to the shrubland showed a significant, negative value for the parameter  $B$  (Table 1).

Nucleation was found under olive trees, where the probability of seedling establishment was  $138.5 \times$  higher than that outside the perch (Table 1).

After removing the variance associated with both the dispersal curve and nucleation, some variance still remained spatially structured, as the semivariogram constructed with the statistical residuals of the above logistic regression shows (Fig. 2). The semivariogram was fitted to theoretical semivariogram models, obtaining the best fit for the Gaussian model and indicating that 29 % of the variance was spatially structured within a range of 210.9 m (Table 2). The semivariogram showed a ‘nugget effect’ (amount of variance at infinite small separation distances), and illustrated three different trends, marked with numbers in the graph.

The ‘nugget effect’ corresponded to a semivariance around 0.015. The first trend shown in the semivariogram was a spatial dependence on a scale finer than 20 m. At this scale, semivariance increased to 0.0161. After this increment, the second trend in the semivariogram is shown by a flat semivariance that stabilized around 0.160 along the lags 20 and 250, indicating spatial independence. The third trend revealed, for distance intervals longer than 250 m, a linear increment in the semivariance, reaching a value of 0.180 within the active lag of the semivariogram.

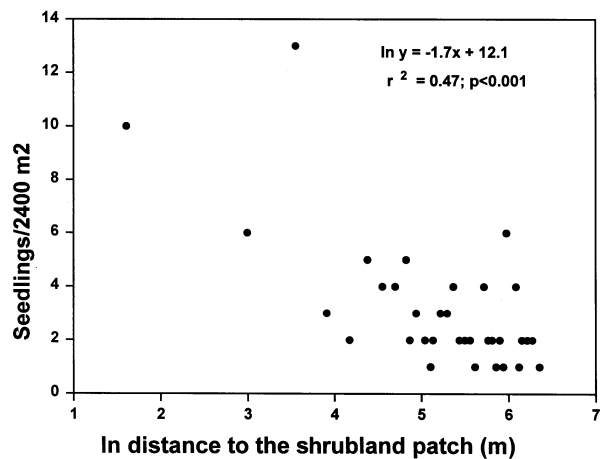


Fig. 1. Density of *Daphne gnidium* seedlings in the olive field as a function of the distance from the shrubland (seed source).

**Table 1.** Effects of distance to the shrubland patch and perch presence on the probability of the establishment of *Daphne gnidium* seedlings.

Variable	B	S.E.	Wald stat.	df	Exp(B)
Distance to the shrubland patch	-0.02	0.003	43.54*	1	0.98
Presence of a perch	4.93	0.359	188.28*	1	138.59
Constant	-4.85	0.351	191.58*	1	

\*  $p < 0.0001$ .

## Discussion

Colonization of old-fields by bird-dispersed plants has been analysed by taking into account only two parameters: (1) the curve of seed dispersal with distance from the seed source and (2) the presence of nucleating trees. The results of this study show that both parameters reasonably well explained the seedling spatial distribution of *Daphne gnidium* colonizing an olive grove, but that some variance with a spatial component remained unexplained.

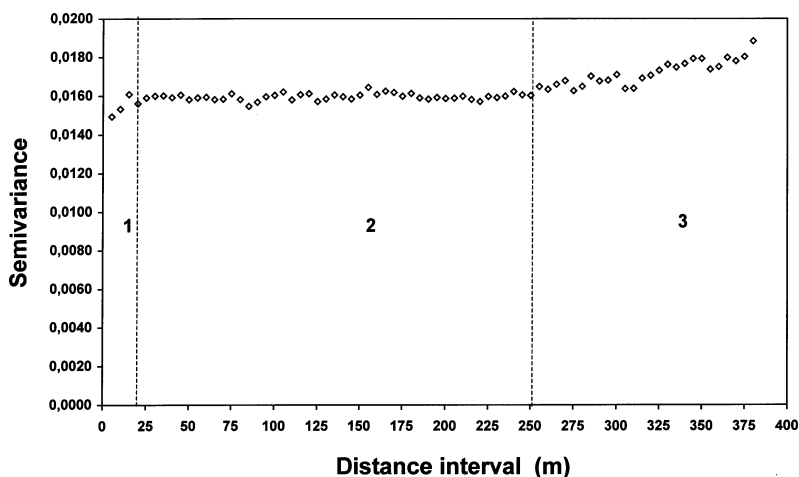
Seedling density significantly decreased as a function of the distance from the shrubland acting as seed source. Post-dispersal processes such as seed predation, germination and seedling survival can modify the spatial pattern of seed shadows produced by frugivorous birds. However, the seedling curve as a function of distance obtained in this study followed a negative semilog equation (with a slope of  $-0.54$ , like seed dispersal curves from individual plants in Mediterranean old-fields (*Sambucus nigra*: Debussche et al. 1985; Debussche & Isenmann 1994; *Buxus sempervirens*: Debussche & Lepart 1992). This fact suggests that the spatial distribution pattern of colonizing *D. gnidium* seedlings has not been strongly affected by post-dispersal processes.

**Table 2.** Semivariogram model parameters for the statistical residuals extracted from the logistic regression model explaining seedling distribution as a function of both perch presence and distance to the shrubland (seed source).

Model	$C_0$	$(C_0 + C)$	Range (m)	$r^2$
Linear	0.0153	$> 0.0174$	$> 76.60$	0.652
Linear/sill	0.0153	0.0208	204.10	0.652
Spherical	0.0153	0.0192	210.00	0.639
Exponential	0.0153	0.0219	210.90	0.620
Gaussian	0.0156	0.0220	210.90	0.757

$C_0$  = nugget variance;  $(C_0 + C)$  = variogram asymptote or sill; Range = distance over which structural variance is expressed.

The other factor analysed in the model is nucleation under perches; this is also fitted in this study because the seedling presence was linked to that of the perch. Both attraction of seed dispersers and favourable micro-environmental conditions for germination and seedling establishment can explain the nucleation process under perches (Verdú & García-Fayos 1996b). Nucleation pattern is very extended not only in Mediterranean old-fields (Debussche et al. 1985; Debussche & Lepart 1992) but also in tropical old-fields (Willson & Crome 1989), and North-American old-fields (McClanahan & Wolfe 1993).

**Fig. 2.** Semivariogram for the statistical residuals extracted from the logistic regression model explaining seedling distribution as a function of both perch presence and distance from the shrubland (seed source). Numbers inside the graph indicate three different trends in the semivariance.

Nevertheless, not all the variation is explained by those two processes (unidirectional dispersal and nucleation) because spatial dependence appeared at small (< 20 m) and large (> 250 m) distance intervals. This fact indicates that some mechanisms with a spatial component, apart from the curve of seed dispersal with distance and nucleation under perches, are also determining the distribution of seedlings colonizing fields.

A theoretical semivariogram model should pass through the origin because semivariance at distance zero is expected to be nil unless the 'nugget effect' was affecting the model. 'Nugget effect' refers to the semivariance at infinite small separation distances, and it can be attributed to either measurement error or to spatial dependence at scales finer than those examined (Legendre & Fortin 1989). We believe that measurement errors were negligible in this study because the variables were easy to record (presence/absence data and distance from the shrubland). For this reason, most of the 'nugget effect' can be attributed to spatial dependence at a finer scale than that used in this study (5 m × 5 m). We have no data to elucidate the kind of very fine-scale process that should be acting in the establishment of *D. gnidium*. Soil properties of agricultural ecosystems have been shown to display a great variability at fine spatial scales including physical, chemical and biological attributes (Sterling et al. 1984; Robertson et al. 1997). Some of this large amount of variation could be responsible for the variance found at finer scales in our study. Physical variability can be linked to microtopography. It is widely known that microtopography had a marked effect on the establishment of the seedlings (Harper 1977 and references therein). For example, the place and position in which the seed lands can affect its germination (Sheldon 1974).

The first trend shown in the semivariogram is that semivariance increased for the first distance intervals, indicating that close neighbour plots were more similar to each other than plots in general. Perhaps the favourable micro-environmental conditions produced under the canopy of the perch could be extended towards neighbour plots where perch is absent but seedlings can establish for this favourable condition. This effect should be diluted in more distant plots. According to this idea, the increasing trend in semivariance is broken at distance intervals of 20 m. From this distance interval, the semivariogram remained flat (spatial independence) until distance intervals of 250 m. From 250 m onwards, the semivariance increased again, indicating spatial dependence at coarse-scale. This trend indicates that distant plots became more different when the distance separating them, increased. Therefore, the colonization model fails to explain dispersal over a great distance. Long distance dispersal is a less frequent event (Debussche &

Isenmann 1994) and therefore it is expected that perch presence and/or the distance to the shrubland do not explain the probability of a seed to colonize long distances.

In conclusion, the results illustrate that only at medium spatial scales (from 20 to 250 m distance intervals), *Daphne gnidium* fitted the model proposed by Debussche & Lepart (1992), in which small-sized birds produce seed-shadows decreasing exponentially from the seed source and produce localized increases under perches. At fine and coarse spatial scales the model fails to explain the spatial variation, probably because different mechanisms with spatial components are involved in the distribution of seedlings.

**Acknowledgements.** We thank Rosa M. López and José Luis Echevarría for helping with data collection and Derek Wotton for language correction. José Antonio Palazón helped us with geostatistics and Francisco Lloret, S. Nandini, and S.S.S. Sarma reviewed the manuscript. The director of the Parque Nacional de Cabañeros gave us permission to work within the park. Financial support was provided by the IVEI (project 02-046) and Caja de Ahorros de Sagunto (Spain).

## References

- Anon. 1995. *GS+: geostatistical software for the agronomic and biological sciences, version 2.3*. Gamma Design. Plainwell, MI.
- Berkowitz, A.R., Canham, C.D. & Kelly, V.R. 1995. Competition vs facilitation of tree seedling growth and survival in early successional communities. *Ecology* 76: 1156-1168.
- Brouwer, F.M. (ed.) 1991. *Land use changes in Europe: processes of change, environmental transformations and future patterns*. Kluwer Academic Publishers. Dordrecht.
- Cardina, J., Sparrow, D.H. & McCoy, E.L. 1996. Spatial relationships between seedbank and seedling populations of common lambsquarters (*Chenopodium album*) and annual grasses. *Weed Sci.* 44: 298-308.
- Debussche, M. & Isenmann, P. 1994. Bird-dispersed seed rain and seedling establishment in patchy Mediterranean regions. *Oikos* 69: 414-426.
- Debussche, M. & Lepart, J. 1992. Establishment of woody plants in Mediterranean old fields: opportunity in space and time. *Landscape Ecol.* 6: 133-145.
- Debussche, M., Escarré, J. & Lepart, J. 1982. Ornithochory and plant succession in Mediterranean abandoned orchards. *Vegetatio* 48: 255-266.
- Debussche, M., Lepart, J. & Molina, J. 1985. La dissémination des plantes à fruits charnus par les oiseaux: rôle de la structure de la végétation et impact sur la succession en région méditerranéenne. *Acta Oecol.* 6: 65-80.
- Debussche, M., Escarré, J., Lepart, J., Houssard, C. & Lavorel, S. 1996. Changes in Mediterranean plant succession: old-fields revisited. *J. Veg. Sci.* 7: 519-526.
- Eriksson, O. & Ehrlén, J. 1992. Seed and microsite limitation

- of recruitment in plant populations. *Oecologia (Berl.)* 91: 360-364.
- Harper, J.L. 1977. *Population biology of plants*. Academic Press, London.
- Herrera, C.M. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in mediterranean woody plants. *Am. Nat.* 140: 421-446.
- Herrera, J. 1987. Flower and fruit biology in southern Spanish Mediterranean shrublands. *Ann. Mo. Bot. Gard.* 74: 69-78.
- Hosmer, D.W. & Lemeshow, S. 1989. *Applied logistic regression*. John Wiley & Sons, New York, NY.
- Izhaki, Y., Walton, P.B. & Safriel, U.N. 1991. Seed shadows generated by frugivorous birds in an eastern mediterranean scrub. *J. Ecol.* 79: 575-590.
- Janzen, D. 1971. Seed predation by animals. *Annu. Rev. Ecol. Syst.* 2: 465-492.
- Legendre, P. & Fortin, M.J. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80: 107-138.
- McClanahan, T.R. & Wolfe, R.W. 1993. Accelerating forest succession in a fragmented landscape. *Conserv. Biol.* 7: 279-288.
- Ne'eman, G. & Izhaki, I. 1996. Colonization in an abandoned East-Mediterranean vineyard. *J. Veg. Sci.* 7: 465-472.
- Norusis, M.J. 1990. *SPSS/PC Advanced statistics +4.0*. SPSS, Inc., Chicago, IL.
- Palmer, M.W. 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. *Vegetatio* 75: 91-102.
- Portnoy, S. & Willson, M.F. 1993. Seed dispersal curves: behavior of the tail of the distribution. *Evol. Ecol.* 7: 25-44.
- Robertson, G.P., Klingensmith, K.M., Klug, M. J., Paul, E.A., Crum, J.R. & Ellis, B.G. 1997. Soil resources, microbial activity, and primary production across an agricultural ecosystem. *Ecol. Appl.* 7: 158-170.
- Sheldon, J.C. 1974. The behavior of seeds in soil. III. The influence of seed morphology and the behavior of seedlings on the establishment of plants from surface lying seeds. *J. Ecol.* 62: 47-66.
- Smallidge, P.J. & Leopold, D.J. 1995. Watershed liming and pit and mound topography effects on seed banks in the Adirondacks, New York, USA. *For. Ecol. Manage.* 72: 273-285.
- Sterling, A., Peco, B., Casado, M.A., Galiano, E.F. & Pineda, F.D. 1984. Influence of microtopography on floristic variation in the ecological succession in grassland. *Oikos* 42: 334-342.
- Stout, G.H., Balkenhol, W.G., Poling, M. & Hickernell, G.L. 1970. The isolation and structure of Daphnetoxin, the poisonous principle of *Daphne* species. *J. Am. Chem. Soc.* 92: 1070-1071.
- Tutin, T.G. et al. (eds.) 1964-1980. *Flora Europaea*. Cambridge University Press, Cambridge.
- Verdú, M. & García-Fayos, P. 1996a. Postdispersal seed predation in a Mediterranean patchy landscape. *Acta Oecologica (Berl.)* 17: 379-391.
- Verdú, M. & García-Fayos, P. 1996b. Nucleation processes in a Mediterranean bird-dispersed plant. *Funct. Ecol.* 10: 275-280.
- Webb, S.L. & Willson, M.F. 1985. Spatial heterogeneity in post-dispersal predation on *Prunus* and *Uvularia* seeds. *Oecologia (Berl.)* 67: 150-153.
- Webster, R. 1985. Quantitative spatial analysis of soil in the field. *Adv. Soil. Sci.* 3: 1-70.
- Willson, M.F. 1992. The ecology of seed dispersal. In: Fenner (ed.) *Seeds. The ecology of regeneration in plant communities*, pp. 61-85. CAB International, Wallingford.
- Willson, M.F. 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107/108: 261-280.
- Willson, M.F. & Crome, F.H.J. 1989. Patterns of seed rain at the edge of a tropical Queensland rain forest. *J. Trop. Ecol.* 5: 301-308.
- Willson, M.F. & Whelan, C.J. 1990. Variation in postdispersal survival of vertebrate-dispersed seeds: effects of density, habitat, location, season and species. *Oikos* 57: 191-198.
- Yarranton, G.A. & Morrison, R.G. 1974. Spatial dynamics of a primary succession: nucleation. *J. Ecol.* 62: 417-428.

Received 16 May 1997;

Revision received 12 May 1998;

Accepted 22 June 1998.