



Seed dispersal in *Erythronium dens-canis* L. (Liliaceae): variation among habitats in a myrmecochorous plant

Pablo Guitián*, Mónica Medrano and Javier Guitián

Departamento de Biología Vegetal, Universidad de Santiago de Compostela, Facultad de Farmacia, Campus Sur s/n, E-15782 Santiago de Compostela, Spain; *Author for correspondence (e-mail: bvpabgui@usc.es; fax: +34 981 59 49 12)

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Abstract

Erythronium dens-canis is a geophyte which produces a single flower each season. The fruits produce small seeds with relatively large elaiosomes. We performed experiments to investigate primary and secondary seed dispersal mechanisms of this species in different habitats in the western part of the Cantabrian Range in northwest Spain. Sticky traps were used to measure primary dispersal of seeds up to 0.5 m from mother plants. Seed cafeteria experiments were performed in different habitats to examine the role of ants and rodents in secondary seed transport and seed predation. Our results indicate that: (a) primary seed dispersal is positively skewed (99% of seeds fall within 20 cm of the mother plant) and seed dispersal distances vary significantly among plants; (b) secondary dispersal is exclusively by myrmecochory, although the proportion of seeds removed by ants differs significantly among habitats; (c) ant species composition and abundances vary among habitats; and (d) freshly dropped seeds are more likely to be removed than seeds that have begun to dry out. We conclude that secondary dispersal of seeds is greatly influenced by habitat but not by small-scale microhabitat.

Introduction

Seed dispersal by ants (myrmecochory) has been the object of increasing interest in recent years, both in the general research context of plant-animal interactions and in the more specific context of the morphological and ecological adaptations of plants and ants that interact.

In plants with ant-dispersed seeds, the inherent advantages of dispersal *per se* (i.e. reduced population density in the proximity of the mother plant, improved gene flow, etc.; see Weiblen and Thomson (1995) for a recent review) are complemented by the specific advantages of myrmecochory, i.e. increased nutrient levels in ant nests, and protection against fire (Beattie and Culver (1982) and Beattie (1985), Oostermeijer (1989), Ruhren and Dudash (1996), Gorb et al. (1997); see however Rice and Westoby (1986)).

Dispersal by ants is common in a wide range of habitats, ranging from the communities of eastern

Australia and southern Africa to the temperate forests of North America and Europe (Berg 1975; Handel and Beattie 1998). There have been recent studies of myrmecochory in temperate deciduous forests in countries including Denmark (Mark and Olesen 1996), Japan (Ohkawara et al. 1996), and Ukraine (Gorb et al. (2000) and references therein). The plant's habitat can be expected to play an important role in seed dispersal processes. On the one hand, disperser abundance, and/or ant community composition typically vary with habitat type (Culver and Beattie 1978; Smith et al. 1989a; Le Corff and Horvitz 1995; Gorb and Gorb 1999), and on the other hand the length of time during which seeds remain attractive to dispersers will depend on degree of exposure to the sun, and thus on plant cover (Smith et al. 1986; Mark and Olesen 1996). In the longer term, habitat will play a key role in seed germination and seedling establishment.

An understanding of the seed dispersal ecology of a given species in a given area requires analysis of both the primary dispersal mechanism (by which the seeds separate from the mother plant) and the secondary dispersal mechanism (by which the diaspora reach their final locations); both stages in seed dispersal are key determinants of population gene flow and structure (Fenster 1991). In recent studies of *Erythronium grandiflorum* Pursh. and *Erythronium japonicum* Decne., both primary and secondary dispersal distances showed marked variation (Weiblen and Thomson 1995; Ohkawara et al. 1996).

In the present study, we studied the dispersal of seeds of *Erythronium dens-canis*, a common geophyte in mountainous habitats in the northwest Iberian Peninsula. As well as evaluating the primary mechanism of seed dispersal and dispersal distances, we investigated whether ants are the only dispersers of the seeds of *E. dens-canis*, and whether dispersal ecology varies among habitats. Finally, we attempted to assess whether there are between-habitat differences in disperser spectrum.

Erythronium dens-canis is well suited for a study of this type, since it occurs in diverse habitats, ranging from roadside verges to woodlands and scrub communities. In addition, its seeds have a prominent elaiosome.

Methods

The plant and the study area

Erythronium dens-canis L. (Liliaceae) is a characteristic geophyte of deciduous woodlands, scrub communities and meadows in mountainous areas of Europe, ranging from the Alps to the Cantabrian Range (Richardson 1980). The bulb gives rise to two broad leaves and a scape that produces a single pink flower at the end of winter. Fruiting occurs in late spring (May-June) with the production of a dehiscent capsule containing several small seeds (mean \pm s. d. = 16.8 ± 8.9 ; $n = 66$) with relatively large elaiosomes. The scape is 11.4 ± 2 cm long (range = 6.6–15.8 cm). Mean seed length is 4.52 ± 0.48 mm (range = 3.35–5.55 mm). The elaiosome is 1.85 ± 0.33 mm long (range = 0.92 ± 2.48 mm). The mean ratio of seed length to elaiosome length is thus 2.54 ± 0.67 .

Erythronium dens-canis is self-compatible, but requires insect visits for seed production. It is pollinated basically by *Bombus* bumblebees, and fruit set is typ-

ically close to 100% (Gutián et al. 1999). The green seed capsules are often ingested by ungulates, though seed losses for this reason show very pronounced spatial and temporal variation (J. Gutián, unpublished data).

The study was performed in the Sierra del Caurel, at the western end of the Cantabrian Range (Lugo, northwest Spain; $42^{\circ}36'$ N, $7^{\circ}19'$ W), close to O Alto do Couto, at three different sites separated by 800–1500 m, at altitudes between 1300 and 1450 m a.s.l.: A, a semi-abandoned track with almost no vegetation, in the higher part of the study area (henceforth “Camino del Couto”); B, an open *Brachypodium rupestre* (Host) Roemer & Schultze meadow with clearings and rocky areas alternating with patches of scrub (henceforth “Peña Salvatore”); C, a mixed deciduous woodland of *Quercus robur* L., *Betula alba* L. and *Corylus avellana* (C. Koch.) Winkl. (henceforth “Rogueira”). These three study sites were chosen as representative of different habitats with different plant densities (pers. obs.)

Experimental design

Primary dispersal

In May 1996 fifteen *Erythronium dens-canis* plants with a mature fruit ready to dehisce were randomly selected with the aim of studying their primary seed dispersal distances. Over each plant we placed a 50-cm-diameter aluminium tray with a circular hole cut at the centre (to fit over the scape). Fifty-cm-diameter trays were used because preliminary observations had shown that primary dispersal distance was generally less than 25 cm. The trays were thickly coated with glue, to ensure adherence of fallen seeds. Of the total of 15 trays, 2 showed significant loss of seeds over the experimental period due to tray damage as a result of ungulate activity, and were excluded from the final analysis. The total number of seeds collected on the remaining 13 trays was 276. Seed dispersal distances (i.e. distances from the mother plant) were recorded within 1-cm bands.

Secondary dispersal

In 1996 secondary seed dispersal was investigated in the field using selective exclusion experiments, (“cafeteria method”, modified from Turnbull and Culver (1983)), with four treatments: (1) *Free Exposure* – 25 seeds placed directly on the ground; (2) *Ant Exclusion* – 25 seeds placed on metal-mesh trays whose borders (1 cm) were impregnated with glue to prevent

ant entry, but permitting the access of rodents and other larger animals; (3) *Rodent Exclusion* – 25 seeds placed underneath a metal-mesh tray, allowing access of ants but not of rodents or other larger animals; (4) *Ant+Rodent Exclusion* – 25 seeds placed underneath a metal-mesh tray whose borders were impregnated with glue (i.e. treatments 2 and 3 combined). Each group of 25 seeds was regularly spaced over an area of 15 × 15 cm. The four groups of seeds were placed at the corners of a 1-metre quadrat, and four replicate quadrats were placed at each site (Camino del Couto, Peña Salvatore, and Rogueira). All treatments were maintained for a total of 3 days. Every 12 h during this period, we recorded the number of seeds that had been removed from each group, and when necessary replaced them with fresh seeds to bring the total number up to 25. These experiments were performed simultaneously at the three sites.

Ant species and seed durability

At each of the two sites in which ant activity was detected (Peña Salvatore, the meadow site, and Rogueira, the woodland site), we estimated ant population density on the basis of trapping. Specifically, we sunk four plastic cups, containing water with detergent, at each of the corners of a 1×1 m square. The traps were collected after 24 h, for laboratory determination and counting of the species present. These experiments were performed on sunny rain-free days during the normal seed-dispersal period.

In parallel with the ant-trapping, we performed experiments to investigate how long seeds in the natural habitat remain “fresh”, since preliminary observations (not shown) had indicated that dry seeds were not dispersed. To this end we placed four groups of 50 seeds in each habitat, subsequently recording at regular intervals the number of seeds that remained in good condition. A seed was classed as fresh if its surface remained smooth.

Data analysis

Primary dispersal distances were compared among mother plants by the Kruskal Wallis nonparametric test. Dispersal spectra were compared among the different habitats by chi-square heterogeneity tests (Zar 1996). The significance of the effects of selective exclusion (factor “Treatment”) and of the habitat where the seeds were placed (factor “Site”) on the proportion of seeds remaining after each 12 h period were analysed using generalized linear mixed models and

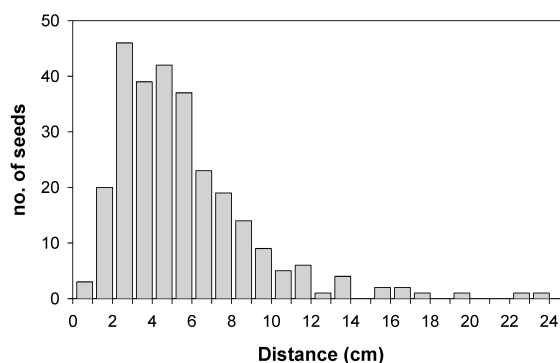


Figure 1. Frequency histogram of primary dispersal distances of seeds of *E. dens-canis*.

the SAS Macro program GLIMMIX (Littell et al. (1996); see Herrera (2000) for further details and applications in the context of plant reproduction studies). The response variable (“proportion of remaining seeds”, i.e. the proportion of initial seeds that were not removed after each 12-h exposure period) was modelled as a binomial response. “Treatment” and “Site” were considered as fixed effects in the model, while “Quadrat” (nested within “Site” and “Treatment”) was considered as a random effect. The results of the *Ant Exclusion* and *Ant+Rodent Exclusion* treatments were not included in the analysis, since no seed movements whatsoever were observed in either case.

Results

Primary dispersal

The primary dispersal of seeds of *E. dens-canis* occurs by gravity following capsule dehiscence. The primary dispersal curve obtained is strongly skewed to the left (Figure 1). None of the total of 276 seeds recovered travelled more than 23 cm from the base of the scape (Figure 1): 99% of seeds fell within 20 cm of the scape, and 91% within 10 cm of the scape. Primary dispersal distance varied significantly among mother plants ($H = 132.4$; $P < 0.0001$). Taken together, these results suggest that primary dispersal is generally of limited importance, with primary dispersal distance often being less than the height of the mother plant.

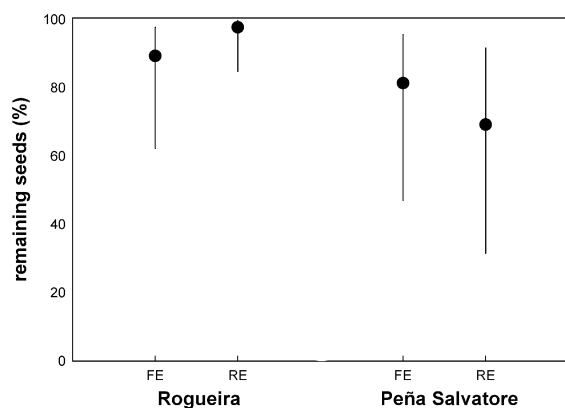


Figure 2. Percentage of *E. dens-canis* remaining seeds, of an initial total of 25, after exposure for 12 h at the two sites (Rogueira and Peña Salvadore) and the two treatments (*Free Exposure* – FE – and *Rodent Exclusion* – RE –) in which seed removal were observed. Values plotted are model-adjusted means obtained by fitting a generalized linear mixed model to the data. Vertical lines denote the 95% parametric confidence intervals around the means.

Secondary dispersal

The results of our selective exclusion experiments show that ants are the only dispersers of seeds of *E. dens-canis*, and furthermore that the seeds are not eaten by mice. At the Camino del Couto site, none of the seeds disappeared during the experimental period, indicating that there is negligible secondary dispersal in this type of habitat. At the other two sites, about 12% and 4% (Rogueira), and 23% and 38% (Peña Salvadore) of seeds were removed respectively in the *Free Exposure* and *Rodent Exclusion* treatments (Figure 2), but all seeds remained in both the *Ant+Rodent Exclusion* and *Ant Exclusion* treatments. The results of the GLIMMIX analysis (Table 1) revealed significant differences among sites (Rogueira vs Peña Salvadore), but not among treatments (*Rodent Exclusion* vs *Free Exposure*), in the proportion of seeds remaining after the 12-h exposure period. In addition, neither the Site \times Treatment interaction nor the nested factor Quadrat had significant effects ($P = 0.17$ and 0.08 , respectively).

Ant species and seed durability

Our results indicate significant differences between the two sites in both species composition and abundance ($\chi^2 = 109.5$, $P < 0.0001$, for the four most frequent species) (Table 2). At the woodland site, the most frequent species was *Formica lugubris*, while at

Table 1. Summary of significance tests for the effects of Treatment (*Free Exposure* vs. *Rodent Exclusion*), Population (Rogueira vs. Peña Salvadore) and their interaction on seed remotion (probability of seed remotion, modeled as a binomial process).

Effect in the model	Significance test		
	df	F	P
Treatment	1,12	0.38	0.55
Population	1,12	5.21	0.04
Treatment \times Population	1,12	2.11	0.17

Table 2. Number of ant captures at the two study sites (Rogueira, woodland, and Peña Salvadore, meadow) in which ant community composition and abundance were studied.

Species	Rogueira	Peña Salvadore
Total no. of individuals	197	101
<i>Myrmica scabrinodis</i> Nyl.	9 (4.5%)	41 (40.6%)
<i>Lasius niger</i> L.	7 (3.6%)	38 (37.6%)
<i>Formica fusca</i> L.	3 (1.5%)	9 (8.9%)
<i>Formica lugubris</i> Zett.	162 (82.2%)	–
<i>Formica gerardi</i> Bond.	7 (3.6%)	–
<i>Aphaenogaster</i> sp.	3 (1.5%)	–
<i>Camponotus</i> spp.	3 (1.5%)	–
<i>Lasius flavus</i> Fab.	2 (1%)	–
<i>Formica rufibarbis</i> Fab.	–	12 (11.9%)
<i>Pheidole pallidula</i> Nyl.	–	1 (1%)
Unidentified	1 (0.5%)	–

the meadow site the most frequent species were *Myrmica scabrinodis* and *Lasius niger*.

Seeds remained attractive to ants for significantly longer at the woodland site than at the meadow site (at Rogueira, 97% of non-dispersed seeds remained fresh after 24 h, versus none at Peña Salvadore and Camino del Couto).

Discussion

Our results indicate that primary dispersal of *E. dens-canis* seeds is negligible, since most seeds fall within 10 cm of the mother plant. This dispersal mechanism has been denominated semachory (Van der Pijl 1982), and is the most frequent both in the northwest Iberian Peninsula (Buide et al. 1998) and in temperate regions in general (Gutián and Sánchez 1992). Short primary dispersal distances have likewise been observed for *E. japonicum* (Ohkawara et al. 1996), a plant of similar size to *E. dens-canis*, in which most

seeds (excluding those that are transported to ant nests) are found within 30 cm of the mother plant. In *E. grandiflorum*, most seeds fall within 40 cm of the mother plant, though some reach distances of up to 80 cm (Weiblen and Thomson 1995). In any case, the primary dispersal distance for most seeds is less than the height of the mother plant's scape (up to 45 cm in *E. grandiflorum*). The primary dispersal curve in all three species is positively skewed, with seed density declining with distance from the mother plant.

Our observations suggest that ants are the only secondary dispersers of *E. dens-canis* seeds. The seeds have a large elaiosome. Ants clearly prefer fresh seeds to seeds that have started to dry out (see for example Mark and Olesen (1996)). The time during which the seed remains fresh is related to exposure to the sun, and to the seed's microclimate in general; clearly, the likelihood that a seed will remain fresh is much greater in a woodland habitat than in open meadow. It has recently been shown that, in temperate deciduous woodlands, ants may deposit seeds underneath the litter layer along the return path to the nest, providing protection against drying out and improving germination rate (Ohkawara et al. 1996).

In our secondary seed dispersal experiments, there were no significant differences in seed removal efficiency between the *Free Exposure* treatment and the *Rodent Exclusion* treatment, confirming that there was no predation in either habitat. The fact that there was no seed removal in the *Ant Exclusion* treatments (i.e. rodent access only) provides additional support for this conclusion. During the study period, we did not observe any other dispersers of *E. dens-canis* seeds. In some species, it has been reported that other arthropods (e.g. beetles) may eat the elaiosomes or the whole seeds without acting as dispersers (Ohara and Higashi (1987) and Ohkawara et al. (1996); see however Jules (1996)). Studies of secondary seed dispersal mechanisms in other species of *Erythronium* have produced diverse findings. In *E. grandiflorum* ant dispersal occurs but is of negligible importance (Weiblen and Thomson 1995). In *E. japonicum*, by contrast, ants rapidly disperse a large proportion of seeds (Kawano et al. 1982; Ohkawara et al. 1996). Ants are also the primary removers of *E. americanum* Ker-Gawl. seeds and remove significantly more seeds ($\approx 25\%$) than predators ($\approx 1\%$) over the first 48 h following seed release (Ruhren and Dudash 1996). In *E. dens-canis*, the rate and efficiency of secondary dispersal is highly variable, and depends on site characteristics. At one of the sites studied by us (Camino

del Couto), we did not observe any seed removal whatsoever; in the other two sites about 8% (Rogueira, woodland) and 30% (Peña Salvatore, rocky meadow) of seeds were removed, with this difference in percentage removal being statistically significant. These findings seem to indicate that the secondary dispersal of seeds of *E. dens-canis* is greatly influenced by habitat (track, rocky meadow, woodland), but not by small-scale microhabitat. The interaction between the factors Treatment and Site was not significant, indicating that the treatments had not different effects at the different sites. Previous studies of various species have found differences in dispersal effectiveness depending on site- or habitat-related factors, including seed density (Smith et al. 1989b; Gorb and Gorb 2000), ant abundance, ant activity or the presence/absence of ant nests (Horwitz and Schemske 1986; Smith et al. 1989a; Kalisz et al. 1999), and the taxonomic composition of the ant community (Le Corff and Horvitz 1995). By contrast, other authors have not detected site- or habitat-related effects: for example, Heithaus (1986) did not detect any significant differences in dispersal effectiveness among six populations of *Asarum canadense* L. with different spatial densities, while Ruhren and Dudash (1996) found that seed removal rates for *Erythronium americanum* did not vary between sites (floodplain and hilltop).

Some variations in dispersal effectiveness (i.e. proportion of seeds removed by ants) were observed among the quadrats of each treatment at each site. These variations were not statistically significant, and in any case may reflect small-scale spatial variation in ant activity rather than the distribution of ant nests (see Hughes and Westoby (1990)). The rate at which seeds are removed by ants may be of critical importance in habitats in which temperature rises sharply during the central hours of the day, leading to destruction of the elaiosome and thus reduced attractiveness of the seed to ants. When seed removal is relatively slow, so that there is competition between seeds for dispersers, fresh seeds may have a marked advantage over seeds that were dropped some time ago (Kjellsson (1985) and Mark and Olesen (1996); see however Hughes and Westoby (1990)). The rate of seed removal is also likely to be important when there is significant seed predation (Turnbull and Culver 1983). Although we have data only for a single year, and have not investigated variation over time within this year (see Ruhren and Dudash (1996)), our results suggest two clearly defined patterns of seed dispersal

in *E. dens-canis*. In open habitats, some seeds are dispersed very rapidly, while those that remain soon lose their attractiveness to ants. In shaded habitats, by contrast, the seeds tend to be dispersed more slowly, but remain attractive to ants for a longer period.

In conclusion, the results of this study confirm that the efficiency of dispersal of seeds of *E. dens-canis* varies among habitats. This may be due to differences in ant abundance, differences in seed removal rates, and/or differences in seed durability. The consequences of the different dispersal patterns for seedling establishment and population dynamics have not been evaluated in the present study, but the current distribution and abundance of this species in the Cantabrian Range is likely to depend heavily on among-habitat differences in dispersal efficiency.

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References

- Beattie A.J. 1985. The Evolutionary Ecology of Ant-Plant Mutualism. Cambridge University Press, Cambridge.
- Beattie A.J. and Culver D.C. 1982. Inhumation: how ants and other invertebrates help seeds. *Nature* 297: 627.
- Berg R.Y. 1975. Myrmecochorous plants in Australia and their dispersal by ants. *Australian Journal of Botany* 23: 475–508.
- Buide M.L., Sánchez J.M. and Guitián J. 1998. Ecological characteristics of the flora of the Northwest Iberian Peninsula. *Plant Ecology* 135: 1–8.
- Culver D.C. and Beattie A.J. 1978. Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. *Journal of Ecology* 66: 53–72.
- Fenster C.B. 1991. Gene flow in *Chamaecrista fasciculata* (Leguminosae). I. Gene dispersal. *Evolution* 45: 398–409.
- Gorb E.V. and Gorb S.N. 2000. Effects of seed aggregation on the removal rates of elaiosome-bearing *Chelidonium majus* and *Viola odorata* seeds carried by *Formica polyctena* ants. *Ecological Research* 15: 187–192.
- Gorb S.N. and Gorb E.V. 1999. Effects of ant species composition on seed removal in deciduous forest in eastern Europe. *Oikos* 84: 110–118.
- Gorb S.N., Gorb E.V. and Sindarovskaya Y. 1997. Interaction between the non-myrmecochorous herb *Galium aparine* and the ant *Formica polyctena*. *Plant Ecology* 131: 215–221.
- Gorb S.N., Gorb E.V. and Punttila P. 2000. Effects of redispersal of seeds by ants on the vegetation pattern in a deciduous forest: A case study. *Acta Oecologica* 21: 293–301.
- Guitián J. and Sánchez J.M. 1992. Seed dispersal spectra of plant communities in the Iberian Peninsula. *Vegetatio* 98: 157–164.
- Guitián J., Guitián P., Medrano M. and Sánchez J.M. 1999. Variation in floral morphology and individual fecundity in *Erythronium dens-canis* (Liliaceae). *Ecography* 22: 708–714.
- Handel S.N. and Beattie A.J. 1998. Semillas dispersadas por hormigas. In: *Los Recursos de las Plantas. Investigación y Ciencia*, Barcelona, pp. 36–43.
- Heithaus E.R. 1986. Seed dispersal mutualism and the population density of *Asarum canadense*, an ant-dispersed plant. In: Estrada A. and Fleming T.H. (eds), *Frugivores and Seed Dispersal*. Dr W. Junk Publishers, Dordrecht, The Netherlands, pp. 199–210.
- Herrera C.M. 2000. Flower-to-seedling consequences of different pollination regimes in an insect-pollinated shrub. *Ecology* 81: 15–29.
- Horwitz C.C. and Schemske D.W. 1986. Seed dispersal of a neotropical myrmecochore: variation in removal rates and dispersal distance. *Biotropica* 18: 319–323.
- Hughes L. and Westoby M. 1990. Removal rates of seeds adapted for dispersal by ants. *Ecology* 71: 138–148.
- Jules E.S. 1996. Yellow jackets (*Vespa vulgaris*) as a second seed disperser for the myrmecochorous plant, *Trillium ovatum*. *American Midland Naturalist* 135: 367–369.
- Kalisz S., Hanzawa F.M., Tonsor S.J., Thiede D.A. and Voigt S. 1999. Ant mediated seed dispersal alters pattern of relatedness in a population of *Trillium grandiflorum*. *Ecology* 80: 2620–2634.
- Kawano S., Hiratsuka A. and Hayashi K. 1982. Life history characteristics and survivorship of *Erythronium japonicum*. *Oikos* 38: 129–149.
- Kjellsson G. 1985. Seed fate in a population of *Carex pilulifera* L. I. Seed dispersal and ant-seed mutualism. *Oecologia* 67: 416–423.
- Le Corff J.L. and Horvitz C.C. 1995. Dispersal of seeds from chasmogamous and cleistogamous flowers in an ant-dispersed neotropical herb. *Oikos* 73: 59–64.
- Littell R.C., Milliken G.A., Stroup W.W. and Wolfinger R.D. 1996. SAS System for Mixed Models. SAS Institute, Cary, North Carolina, USA.
- Mark S. and Olesen J.M. 1996. Importance of elaiosome size to removal of ant-dispersed seeds. *Oecologia* 107: 95–101.
- Ohara M. and Higashi S. 1987. Interference by ground beetles with the dispersal by ants of seeds of *Trillium* species (Liliaceae). *Journal of Ecology* 75: 1091–1098.
- Ohkawara K., Higashi S. and Ohara M. 1996. Effects of ants, ground beetles and the seed-fall patterns on myrmecochory of *Erythronium japonicum* Decne. (Liliaceae). *Oecologia* 106: 500–506.
- Oostermeijer J.G.B. 1989. Myrmecochory in *Polygala vulgaris* L., *Luzula campestris* (L.) DC. and *Viola curtissi* Forster in a Dutch dune area. *Oecologia* 78: 302–311.

- Rice B. and Westoby M. 1986. Evidence against the hypothesis that ant-dispersed seeds reach nutrient-enriched microsites. *Ecology* 67: 1270–1274.
- Richardson I.B.K. 1980. *Erythronium* L. In: Tutin T.G., Heywood V.H., Burges N.A., Valentine D.H., Walters S.M. and Webb D.A. (eds), *Flora Europaea*, 5. Cambridge University Press, Cambridge.
- Ruhren S. and Dudash M.R. 1996. Consequences of the timing of seed release of *Erythronium americanum* (Liliaceae), a deciduous forest myrmecochore. *American Journal of Botany* 83: 633–640.
- Smith B.H., Ronsheim M.L. and Swartz K.R. 1986. Reproductive ecology of *Jeffersonia diphylla* (Berberidaceae). *American Journal of Botany* 73: 1416–1426.
- Smith B.H., Forman P.D. and Boyd A. 1989a. Spatial patterns of seed dispersal and predation of two myrmecochorous forest herbs. *Ecology* 70: 1649–1656.
- Smith B.H., De Rivera C.E., Bridgman C.L. and Woida J.J. 1989b. Frequency-dependent seed dispersal by ants of two deciduous forest herbs. *Ecology* 70: 165–1648.
- Turnbull C.L. and Culver D.C. 1983. The timing of seed dispersal in *Viola nuttalli*: attraction of dispersers and avoidance of predators. *Oecologia* 59: 360–365.
- Van der Pijl L. 1982. *Principles of Dispersal in Higher Plants*. 3rd edn. Springer-Verlag, Berlin.
- Weiblen G.D. and Thomson J.D. 1995. Seed dispersal in *Erythronium grandiflorum* (Liliaceae). *Oecologia* 102: 211–219.
- Zar J.D. 1996. *Biostatistical Analysis*. 3rd edn. Prentice-Hall, New Jersey, USA.