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Original article

Red fox (*Vulpes vulpes* L.) favour seed dispersal, germination and seedling survival of Mediterranean Hackberry (*Celtis australis* L.)

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ABSTRACT

Seeds of the Mediterranean Hackberry *Celtis australis* are often encountered in fox faeces. In order to evaluate the effect of gut transit on the size of seeds selected, the rates and speed of germination and on the survival of the seedlings, Mediterranean Hackberry seeds from fox faeces were germinated in a greenhouse. The results were compared with those of seeds taken from ripe, uneaten fruits. Fox-dispersed seeds were smaller and lighter than the control ones and had higher (74% vs. 57%) and more rapid germination (74.5 days vs. 99.2 days). Seedlings from fox-dispersed seeds showed significantly greater survival by the end of the study period (74.1% vs. 43.6%) than the control ones. Survival in seedlings from fox-dispersed seeds was related to germination date, late seedlings showing poorer survival. This relationship was not observed away in the control seedlings. Seed mass did not affect seedling survival. Seedling arising from fox-dispersed seeds grew faster than control ones. These results suggest that fox can play a relevant role as seed disperser of Mediterranean Hackberry.

1. Introduction

Fruit dispersal by frugivorous animals is beneficial to both parties (Herrera and Jordano, 1981; Herrera, 1987, 1995). The animals gain from consuming fleshy fruits, energy-rich on account of their high sugar content. The plants benefit because i) dispersal distances seeds from their parents, where predation rates tend to be high (Janzen, 1970) and parent/offspring competition may be intense (Crawley and Long, 1995; Rey and Alcántara, 2000), ii) dispersal may allow seeds to end up in favourable sites for germination (Harper et al., 1965; Fowler, 1988) where their survival chances are higher (Howe and Smallwood, 1982) and iii) gut-transit may accelerate germination or increase germination rates (Barnea et al., 1991; Traveset and Verdú, 2002). These benefits are not mutually-exclusive; rather their relative importance depends on the habitat involved (Howe and Smallwood, 1982; Stiles, 1992), on the dispersing animals and on the particular requirements of the plant species concerned (Verdú and Traveset, 2004). Seed dispersal by frugivores thus influences the distribution and abundance of plant species and the dynamics and survival of their populations (Schupp and Fuentes, 1995; O'Hara and Weisse, 1999; Kollman, 2000; Arrieta and Suárez, 2005).

Gut transit destroys numerous seeds, both during consumption and during their passage through the digestive tract (Malo and Suárez, 1995; Herrera, 1989; Schupp, 1993; Ar-

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rieta and Suárez, 2001). However, these hazards are superceded by the higher rates and speed of germination of seeds dispersed by frugivores, resulting from the removal of pulp and by both mechanical and chemical abrasion during consumption and transit through the gut (Barnea et al., 1991; Clergeau, 1992; Traveset and Verdú, 2002). Early germination has been associated with reduced post-dispersal exposure to seed predators (Schupp, 1993) and with enhanced seedling survival. This last may be due to a higher availability of resources, especially light in deciduous forests (Ross and Harper, 1972; Seiwa, 1998), a reduced incidence of pathogens (Seiwa, 1997, 1998), or to early rooting which increases the ability of seedlings to withstand water stress in summer (Seiwa, 2000).

In addition to influences on rates and speed of germination, a range of studies in Mediterranean regions (see review in Herrera, 1995) note a certain selectivity of particular fruit and/or seed characteristics by dispersers (Traveset and Verdú, 2002). For example, birds feed chiefly on small-fruited species (Herrera 1995), whereas carnivorous mammals seem to be drawn to larger-fruited ones (Herrera, 1989). Selection of a particular size range also occurs intraspecifically occasionally (Herrera, 1988; Jordano, 1987; Alcántara et al., 2000). Whether selection is predispersive or it results from selective damage in transit through the gut, the fact that the size characteristics of the dispersed seeds may differ from those of the population as a whole may have demographic consequences. These may result from changes in the proportions which germinate and in the speeds at which they do so, as well as from differential seedling survival, especially if there is a relationship between seed size and seedling growth (Seiwa, 2000; see, however, Herrera, 1988, 1995; Izhaki, 2002).

Despite the relative abundance of descriptive studies, the effects of dispersal by vertebrates on seedling survival and seedling growth have been little studied, especially for fleshy-fruited plants (Herrera, 1995). In particular, few studies analyse the intraspecific effects of gut transit on seed sizes, speeds of germination and seedling survival and growth. In addition, most studies involve avian dispersers (Jordano, 1987; Alcántara et al., 2000), the effects of dispersal by carnivorous mammals being little known (see nevertheless Traveset et al., 2001).

This study explores various aspects of germination and first stages of regeneration of a Mediterranean tree, the Mediterranean Hackberry *Celtis australis* L. (Ulmaceae), from seeds dispersed in the dung of Red Foxes *Vulpes vulpes* L. (Carnivorae). The fleshy fruits of the Mediterranean Hackberry and its distribution as solitary individuals or in small groups could be related to the dispersal of its seeds by frugivores. The Mediterranean Hackberry probably belongs to the broad majority of Mediterranean species whose seeds are dispersed primarily by birds and fortuitously by other vertebrates. Its fruits do not offer abundant nutritional rewards since the pulp fraction is small (40-50 kg/100 kg of fruit, Catalán, 1991), and it has a relatively low water, lipid, fibre and protein content (24%, 0.9%, 10.6% and 3.7%, respectively) in comparison with the mean of other Mediterranean fleshy fruits, but it has a high sugar content (81.5%, Herrera, 1987). However, the dispersal ecology of this species is unknown, with the exception of empirical data showing the frequent presence of its seeds in fox faeces at certain times of year. The following hypotheses are proposed: i) Mediterranean Hackberry fruit consumption by foxes will select for small seed sizes, larger ones being rejected or spat-out (Yanes, 1997) or destroyed to a greater extent during mastication and digestion (Herrera, 1989); ii) seeds dispersed in fox faeces will germinate better and more rapidly than those which have not passed through guts, as a result of abrasion during chewing and digestion; and iii) despite germinating better and more rapidly, the smaller size of the seeds dispersed by foxes will tend to affect negatively the subsequent survival and height of seedlings in the first stages of growth.

2. Methods

2.1. Species

The Mediterranean Hackberry is a medium-sized tree inhabiting mild Mediterranean regions (southern Europe and northern Africa) extending to Southeast Asia. It occurs across the major part of the Iberian Peninsula, from the Pyrenees to the sierras of Algeciras, generally sparsely. It prefers deeper moist soil where it may attain its greatest size. However, it is often found in poor soils on the dry, south-facing, rocky slopes of inland sierras, but never above 1,200 m (Costa et al., 1998). It fruits in autumn, the fruits being spherical drupes of 9–12 mm diameter each containing a single seed, comprising about 38% of the dry mass of the fruit (Herrera, 1987). The fruits remain on the tree until well into winter.

The Red Fox is an opportunistic carnivore whose dietary flexibility is due as much to its generalist nature as to the seasonal and distributional variation of food availability in Mediterranean areas (Rau et al., 1985; Calisti et al., 1990; Serafini and Lovari, 1993; Fedriani, 1996), which makes it an occasional seed disperser (Herrera 1989).

2.2. Study area and methods

The study area was on one of the slopes of the Garganta de Santa María, Sierra de Gredos, Candeleda (Ávila) (40°10′N; 5° 15′W; 600–700 m). It holds one of the most important populations of Mediterranean Hackberries in the Iberian Peninsula, with over 500 individuals on the sun-facing slopes. The Mediterranean climate of the area is subject to Atlantic influences, reflected in a mean temperature (15.8 °C) and rainfall (954 mm) which are somewhat higher than is usual on the meseta.

During late winter 1995, mature fruits ($N > 300$) were collected from Mediterranean Hackberries trees ($N = 30$) located inside a whole study area of more than 250 ha. In the same dates 30 fox faeces with visually apparent seeds inside were collected in the same area during three consecutive days, searching the whole study area and avoiding previously visited sites. Minimum distance between faeces collected the same day was 500 m.

Both seeds from fruits and faeces were cleaned carefully in the laboratory and were subjected to flotation tests to determine their viability. Those which showed obvious signs of insect damage were discarded. They were then weighed on a balance sensitive to 0.01 mg and their largest and smallest diameters measured with callipers to the nearest 0.01 mm. Seeds were kept in dark, dry storage until the following autumn; they may be stored for 2 years without any reduction in germination rates (Catalán, 1991). Although seeds which did not germinate were not tested for viability, we have assumed that between-treatment differences in rates of germination were not attributable to existing differences in initial seed viability.

In order to test the effects on rates and speed of germination of the different treatments, 100 seeds were randomly selected and exposed to stratification in damp sand kept at 4 °C for 75 days (Catalán, 1991), after which they were set to germinate in a greenhouse. Another 100 seeds were used as controls and set to germinate without previous treatment. The same was done with seeds from fox faeces, although here the number of intact, undamaged seeds was lower ($N = 73$).

All seeds were individually sown in pots of commercial compost and kept in an unheated greenhouse where they were inspected daily. Watering was provided when necessary by capillarity so as to keep the compost moist (Catalán, 1991). The pots were reshuffled randomly once a week to avoid place effects. Each seedling was carefully labelled, noting the date of germination and death, if it happened. Alive seedlings were measured after 8 weeks from germination, using callipers to record the length from its base to the nearest 0.01 mm. The hypocotyl and epicotyl were measured separately but the lengths were combined for the analysis to give the total height attained. The plants were monitored until 31 July, when watering ceased.

2.3. *Statistical analyses*

To analyse whether dispersal via gut transit has a differential effect on seed size we used t-tests for independent samples between seed mass, diameter and roundness index (smallest diameter/largest diameter) of seeds present in fox faeces ($N = 73$) and the corresponding values from non-dispersed seeds (controls + stratified samples; $N = 200$). We transformed logarithmically the data to prevent for non-normality and heterocedasticity. Additionally, and to avoid replication errors, we tested the correlation between mass, smallest and largest diameter and roundness index.

The differences between rates of germination between control, stratified and fox-dispersed seeds were analysed by $\chi 2$ tests. The difference in time of germination between control and fox-dispersed seeds was analysed by a one-way ANOVA with seed mass as a covariable.

Seedling survival (number of days of survival) of seedlings from fox-dispersed seeds compared with those from controls was analysed using a log-rank test (Parmar and Machin, 1996), censuring those individuals which remained alive by the end of the study period. The influence of mass and germination date on seedling survival was analysed via a proportional hazard Cox regression (Le, 1997), for control and fox-dispersed samples independently.

Finally, differences in seedling height between the control and fox-dispersed seed samples were analysed by an ANOVA, with seed mass and number of days of seedling survival included as covariables. The seedlings were not all the same age when measured as a result of differences in germination dates (mean age in days ± 1 S.E.; controls: 53.2 ± 0.9; fox-dispersed: 55.3 ± 0.6). Although these differences between samples proved not significant (t-test for independent samples, $t = -1.9$; $P = 0.06$) the observed trend suggested the inclusion of this variable as a covariable too. The quadratic term of the number of days studied was also used as a covariable, to control for non-linear relationships between seedling height and survival. The Statistica programme (StatSoft, 1998) was used for all analyses.

3. Results

Fox-dispersed seeds were significantly smaller and lighter than the non-dispersed ones (Table 1). Nevertheless, differences in seed diameters remained small (low than 3.1%), being more relevant for seed mass (10%). Seed mass was significantly positively correlated with maximum diameter ($r = 0.63$; $P < 0.001$), minimum diameter ($r = 0.78$; $P < 0.001$) and roundness ($r = 0.25$; $P < 0.001$) and so only mass was used as an indicator of size in the remaining analyses. Control and fox-dispersed coefficient of variance were both similarly high (25% and 20%, respectively). Frequency distributions of both control ($N = 200$) and fox-dispersed seeds ($N = 73$) were different either testing them with an F test either with a non-parametric test.

3.1. *Rates and time of germination*

Fox-dispersed seeds showed a significantly higher rate of germination than the control (74% vs. 57%; $\chi 2 = 10.64$; $P < 0.01$) or the stratified seeds (74 vs. 6.7%; $\chi 2 = 92.25$; $P < 0.001$). Due to their low germination rate, stratified seeds

Table 1 – Results of *t*-tests comparing the morphological variables (mean ± 1 S.D. and coefficient of variance) of non-dispersed seeds (control and afterwards stratified seeds; *N* = 200) and fox-dispersed seeds (*N* = 73). Tests are based on logarithmically transformed data

	Control	C.V.	Fox-dispersed	C.V.	t-value	*P*
Mass (mg)	0.154 ± 0.038	24.95	0.140 ± 0.029	20.65	2.77	< 0.01
Largest diameter (mm)	7.407 ± 0.455	6.15	7.279 ± 0.502	6.90	2.05	< 0.05
Smallest diameter (mm)	6.380 ± 0.474	7.43	6.183 ± 0.462	7.47	3.07	< 0.01
Roundness index	0.863 ± 0.058	6.72	0.852 ± 0.069	8.12	1.28	0.20

Table 2 – Time of germination (mean ± 1 S.D.) for seedlings from control and from fox-dispersed seeds, and ANOVA results with log-transformed mass as covariable

	Control	Fox-dispersed	F	P
Speed of germination	99.17 ± 24.39	74.54 ± 20.88	31.25	< 0.001
Mass (covariable)			0.20	0.655

were excluded from the remaining analyses. Fox-dispersed seeds germinated sooner than the control ones (by an average of 25 days), independently of seed size (Table 2). Seeds first to germinate were 55 days after the experiment began (four fox-dispersed seeds) and some germinated up to 190 days afterwards. Although the cumulative germination curves approximated in both cases to logistic curves (Fig. 1), most of the fox-dispersed seeds germinated significantly earlier than the control ones (55–90 days vs. 75–110 days; log-rank test statistic: –4.837; $P < 0.001$).

3.2. *Survival and seedling size*

Seedlings from fox-dispersed seeds showed significantly higher survival by the end of the study period than those from control seeds (74.1% vs. 43.6%; log-rank test statistic: 3.46; $P < 0.001$; Fig. 2). Both sets showed the highest mortality during the first month (Fig. 2). Survival was related to germination date in the fox-dispersed sample (Cox's regression, beta = 0.019 ± 0.008; log Likelihood = –56.947; $\chi 2 = 4.071$; $P = 0.044$), later germinators showing poorer survival. This relationship was not observed in the control seedlings (beta = 0.004 ± 0.009; log Likelihood = –148.040; $\chi 2 = 0.195$; $P = 0.659$). Seed mass did not affect seedling survival (Cox's regression, $P = 0.830$ and $P = 0.600$ for fox-dispersed and control sets, respectively).

Seedlings from fox-dispersed seeds grew significantly larger than those from the control seeds by the end of the period studied (Table 3). This superior height was independent of seed size ($F = 2.533$; d.f. = 1; $P = 0.118$) but was positively related to the linear term of the number of days of life (beta = 10.137; $t = 2.055$; $P < 0.05$) and showed an inverse tendency with the quadratic term (beta = –9.869; $t = –1.999$; $P = 0.051$).

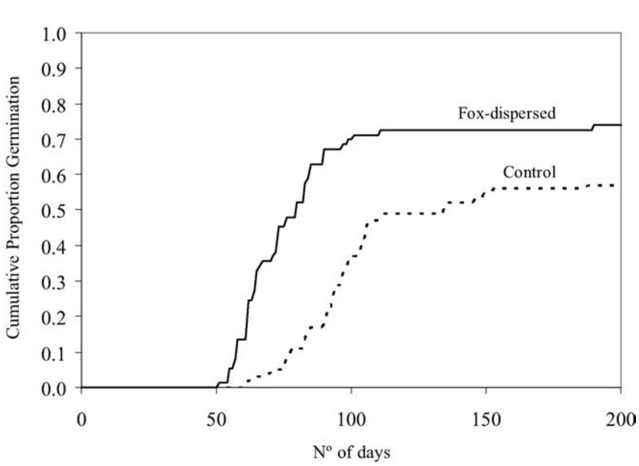

Fig. 1 – Cumulative % germination of fox-dispersed (solid line) and control seeds (broken line).

4. Discussion

The results show that fox-dispersed seeds are smaller, and germinate faster, than non-consumed seeds, thus confirming the first two hypotheses suggested. In addition, and contrary to predictions, fox-dispersed seeds produced seedlings which survived better and grew taller than the controls, at least during the early stages of growth. Taken together these effects suggest that fox could be an active disperser of Mediterranean Hackberry seeds.

The Mediterranean Hackberry was not known to figure in fox diets until now (see among others Calisti et al., 1990). The abundance of Mediterranean Hackberry seeds in fox faeces, frequently with seeds of Juniper (*Juniperus oxycedrus*), confirms that fox is an opportunistic and generalist seasonally-available resources consumer (Fedriani, 1996), acting as a seasonal seed disperser (e.g. Herrera and Jordano, 1981; Herrera, 1995).

4.1. *Seed morphological characteristics*

Mediterranean Hackberry seeds dispersed by foxes were smaller than those available, either because foxes select

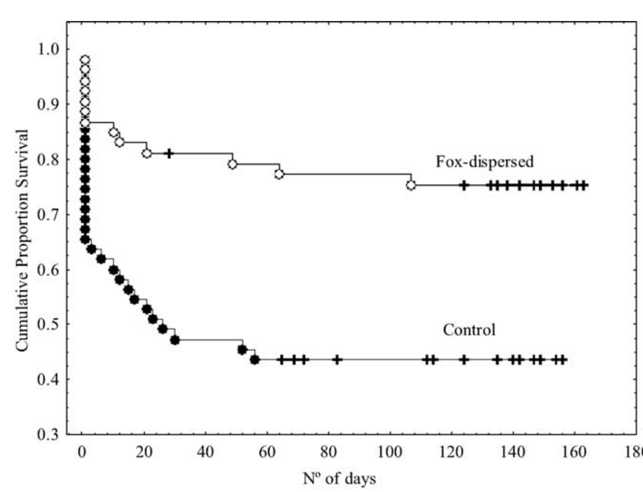

Fig. 2 – Cumulative percentage survival of seedlings derived from fox-dispersed (hollow circles, continuous line) and control (filled circles, broken line) seeds. Observations of individuals which survived until the end of the study period are included (crosses).

Table 3 – Seedling heights after 8 weeks (mean ± 1 S.D.) of seedlings from control and from fox-dispersed seeds and ANOVA results with log-transformed mass and the linear and quadratic terms of survival periods as covariables

	Control	Fox-dispersed	F	P
Heights (mm) after 8th week	64.6 ± 12.98	73.2 ± 9.02	6.584	0.014
Mass (covariable)			0.934	0.339
Survival period (covariable)			4.225	0.046
Survival period quadratic term			3.999	0.051

smaller fruits by rejecting or spitting-out larger ones (as observed in other mammals, such as the Rabbit *Oryctolagus cuniculus* feeding on *Capparis spinosa*, Yanes, 1997), or because larger seeds tend to suffer higher rates of destruction by chewing (Herrera, 1989). Although differences between control and fox-dispersed seeds were small, at least for both diameters (low than 3.1%), fox-dispersed seed mass was 10% lower than control ones, indicating that small changes in seed dimensions provoked bigger changes in seed mass.

Several studies of seed dispersal by birds have found evidence towards a small-fruited species selection, even within-species, being this selection no relevant over the plants' reproductive success (Jordano, 1987; Herrera, 1988). Intraspecific studies relating seed size to germination rates and seedling growth have found that large seeds are advantageous where resources are limited or where there is strong competition (Gross, 1984) although smaller seeds may be more competitive in other circumstances (Matilla, 2004).

4.2. *Rates and time of germination*

Ingestion by foxes has been shown to accelerate Mediterranean Hackberry seed germination in comparison to that observed in scarified or control seeds. The germination rate of the control seeds (57%) was very similar to that observed earlier in this species (40–60%, Catalán, 1991), although lower to that of fox-dispersed seeds (74%). Stratification accelerated neither the rate (7%) nor speed of germination.

The promotion of germination by gut transit has been described for other species and attributed to scarification during chewing and to the action of gastric juices on seed coats (Barnea et al., 1991; Traveset and Verdú, 2002). Nevertheless, the acceleration of germination of fox-dispersed seeds by nearly a month, in comparison to the controls, is much greater than the average effect reported by similar studies (Traveset and Verdú, 2002). The positive effects of gut transit are generally higher in cases of bird- and bat-dispersal than in those involving other dispersers, such as terrestrial mammals (Traveset and Verdú, 2002), where the promotion of germination has not usually been so well detected as in our study (Traveset et al., 2001). Aronne and Russo (1997) found a similar enhancement of germination in fox-dispersed seeds of Myrtle *Myrtus communis*, which was greater than that involving other mammals such as martens *Martes* sp. On the other hand, some authors have noted an intraspecific tendency for smaller seeds to germinate sooner (Cavers and Harper, 1966; Matilla, 2004), suggesting that different size categories within a species may vary in their germination requirements. In the case of Mediterranean Hackberry, no significant trend related to seed size has been found.

Seeds which germinate early have an advantage over later germinators since their seedlings obtain a larger share of resources (water and nutrients, Ross and Harper, 1972), take more light in the understorey of deciduous forests and are less exposed to predators and pathogens (Seiwa, 1997; 1998). The advance on germination date of only a few days may have little significance (Traveset and Verdú, 2002), but the advance of nearly a month here observed in the fox-dispersed seeds could confer significant advantages for the growth period preceding the summer drought (Traveset et al., 2001), although field studies are needed to confirm their effects in natural conditions.

4.3. *Survival and seedling height*

The initial hypothesis proposed that seedlings from small seeds (as those fox-dispersed) would have poorer survival and lesser height than those from larger seeds, which have greater food reserves (Piper, 1986; Seiwa, 2000). Nevertheless, the results showed the seedlings from fox-dispersed seeds to survive better than the control ones, at least during the study period, despite both samples having had equal access to resources and standardised growing conditions in the greenhouse. Most mortality occurred within 1 month of germination. Part of this enhanced survival may be due to early germination, according to the Cox regression. It is possible that, if the experiment not ended before the plants had to encounter the worst rigours of summer, the proportion of survival between early and late germinators would might have been more balanced (Seiwa, 2000). Although surviving longer only to die in summer is ecologically insignificant, the fact that a larger proportion of seedlings reach that difficult season enhances the probability of a higher final net incorporation into the population.

In addition, the seedlings from fox-dispersed seeds showed greatest height at the end of the study period, (independently of germination date, since all seedlings were measured in their 8th week), which implies a higher competitiveness. The lack of a relationship between seed size and final seedling height is contrary to our initial hypothesis, although this has been observed in other species (Gross, 1984). Some authors have related the higher survival and height of early germinators with the better light conditions and less exposure to pathogens and predators during early growth stages (Seiwa, 1998) together with their experiencing a longer period of favourable conditions (Seiwa, 2000), independently of seed size (Piper, 1986; Seiwa and Kikuzawa, 1996), although this is possibly species-specific (Seiwa, 2000). These suggestions need to be tested in the field.

5. Conclusion

Our findings, although resulting from a greenhouse-based experimental study, have shown that Mediterranean Hackberry may benefit from seed-consumption by foxes, since dispersed seeds, despite being smaller and lighter, showed higher rates and speeds of germination than control seeds, which allows the seedlings a longer period of exposure to available resources. The fact that gut-transited seeds produce seedlings which survive longer and grow taller may indicate a relevant role played by fox in the first stages of regeneration of Mediterranean Hackberry. Field studies on these aspects are needed to corroborate these questions.

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