OIKOS 71: 152–162. Copenhagen 1994

Cumulative effects on the reproductive output of Pistacia terebinthus (Anacardiaceae)

Anna Traveset

Traveset, A. 1994. Cumulative effects on the reproductive output of *Pistacia terebinthus* (Anacardiaceae). – Oikos 71: 152–162.

This study identifies the factors that influence the reproductive output (number of viable seeds dispersed) of *Pistacia terebinthus* (Anacardiaceae), examines the magnitude and variability of their effects, and considers how plant traits affect the relative importance of each factor in reducing reproductive potential. Pre-dispersal reproductive losses were measured in a total of 28 individuals from anthesis to seed dispersal. Post-dispersal seed predation was estimated as well by placing seeds in different locations and checking them periodically.

A total of eight factors were found to reduce plant reproductive potential during the pre-dispersal phase. Ordered according to the importance of their effects these factors were: abortion of flowers and latent ovaries, abortion of seeds, fruit dryness (mainly caused by hemipterans that suck the fruit pulp), parthenocarpy (production of empty seeds), consumption of viable fruits by non-legitimate seed dispersers, fruit damage by psyllids, seed damage by chalcidoid wasps, and fruit damage by fungi.

There was much inter-individual variability in the effects of all those factors. That variation, however, was in most cases independent of the plant traits examined (plant size, fecundity, distance to males, flowering synchrony, peak date of fruit ripening). The most relevant associations were found between plant fecundity and (1) proportion of wasp-damaged seeds (larger fruit crops experienced greater seed predation by these insects) and (2) proportion of fruits removed by non-legitimate seed dispersers (smaller fruit crops with greater proportions of viable seeds had higher bird predation rates). Also, plants that had most fruits ripen in early September had more viable seeds removed by non-legitimate dispersers than those that had most fruits ripen in late September.

A key factor analysis showed that factors intrinsic to the plant, such as flower and ovary abortion and seed inviability, accounted for low among-plant variation in total reproductive losses, even though their relative contribution to such losses was great. Extrinsic factors such as fruit or seed damage by animals accounted for a low reproductive loss but for great among-plant variation in the number of viable seeds dispersed, and appeared to act as selective agents on plant fecundity.

Post-dispersal seed predators (mainly field mice, chaffinches, and ants) removed a significant proportion of the seeds placed in different locations where birds can drop them, indicating that seedling recruitment in a given site is largely determined by the abundance of these animals at that site.

A. Traveset, Estación Biológica de Doñana, Apdo. 1056, E-41080 Sevilla, Spain (present address: Institut d'Estudis Avançats de les Illes Balears, Crtra. de Valldemossa Km. 7'5, E-07071 Palma de Mallorca, Spain).

Most studies that identify the importance of different agents on the reproductive output of plants consider only a single stage in the whole plant life cycle – either pollination, herbivory (including seed predation) or seed dispersal – while very few consider the additive or multiplicative effects that all these processes have on plant

Acepted 14 March 1994

Copyright © OIKOS 1994
ISSN 0030-1299
Printed in Denmark – all rights reserved

fitness. A number of studies have demonstrated that the final effect on fitness cannot be predicted considering these factors separately (e.g. Green and Palmbald 1975, Heithaus et al. 1982, Louda 1982, Hainsworth et al. 1984, Herrera 1984a, b, 1988, Jordano 1987, 1989, Schemske and Horvitz 1988, Campbell 1991), and that it is not possible to assign more importance to one or another process unless the net result of all of them is known. The selective pressures that different factors exert on plant reproductive output may be counteracting each other, and this may only be detected by considering the different stages as linked and dependent on each other (Primack 1987).

An interaction will be evolutionarily important in a plant population only if there is individual variation in the reproductive output due to that particular interaction. Even if it only has a small effect on the dynamics of a population, inducing a small demographic change, the interaction may have a great evolutionary importance (Heithaus et al. 1982). To determine whether a factor exerts a relevant selective pressure on a particular plant trait we need to know whether and to what degree the demographic change produced by that factor translates into an adaptive change.

Here I intend to determine 1) what factors limit the production of seeds in *Pistacia terebinthus* L. (Anacardiaceae), a fleshy-fruited tree/shrub dispersed by birds, 2) the relative importance of each factor that affects its reproductive potential from anthesis to seed dispersal, 3) the variation, between and within populations, in the effect of those factors during the whole reproductive phase, and 4) how such variation relates to particular traits of the plant. The factors examined are both intrinsic to the plant (such as flower and ovary abortion, parthenocarpy and seed abortion) and extrinsic to it (such as fruit damage by fungi and plant-animal interactions).

Natural history of the plant

Pistacia terebinthus is a dioecious woody shrub or small tree, occasionally reaching 10 m in height. It is distributed around the Mediterranean, from Portugal to Turkey and from Morocco to Cyrenaica, and as far north as the southern Alps (Zohary 1952). It produces small wind-pollinated flowers from mid April through the beginning of June. Inflorescences of 3–ca 50 flowers are always grouped in panicles. A panicle may contain up to 20 inflorescences and up to 800 flowers, although 100–400 flowers are usual. A branch may bear up to 10 panicles, grouped in turn in several distal clusters. Males tend to start flowering somewhat earlier than females.

About a month after anthesis, the ovary (but not the ovule) grows continuously until reaching its maximum size. The endocarp becomes woody one or two weeks later. Along with the endocarp, the pericarp also develops before and independently of the ovule (or embryo if it has been fertilized). As in other species of *Pistacia* (Grundwag 1976), there is probably a delay in syngamy (Grundwag and Fahn 1969), which causes an extended dormancy of the zygote.

The fruit is a drupe that measures, on average, 6.6 ± 0.7 (s.d.) mm in length and 5.9 ± 0.7 mm in diameter ($n = 575$). A viable seed fills the entire fruit locule with a green endosperm. Fruits lacking viable seeds are either parthenocarpic (i.e. come from unpollinated flowers) or are the result of embryo abortions that can occur at different stages of development. Information on the causes of these types of seeds can be found in Grundwag and Fahn (1969) and Grundwag (1975, 1976).

Final-sized fruits with inviable seeds are retained on the plant for several months. Their color is red, being indistinguishable from other immature fruits. After maturation, viable fruits turn a blueish-green color. As found in *P. lentiscus* (Jordano 1989), fruit ripening is strongly associated with seed viability (Traveset 1993a). Mature fruits have a pulp approximately tenfold richer in lipid content than red fruits (35.8 ± 8.7% vs. 3.9 ± 1.6%, respectively) (Traveset 1993a).

Fruits are consumed by at least 20 species of birds, some of which are migratory. Half of these species are legitimate seed dispersers, five act as seed predators, and five consume only the fruit pulp, usually dropping the seeds under the parent plant (Traveset 1993a). Birds that swallow entire fruits and pulp-eaters prefer mature fruits over red fruits because of their much greater amount of lipids; likewise, seed predators prefer green over red fruits because they have more endosperm. The same has been found in *P. lentiscus* by Jordano (1989). Carnivores, mainly the red fox (*Vulpes vulpes*), may also feed upon the fallen fruits; they usually act as seed predators of this plant since only seed fragments have been found in their faeces (Herrera 1989). The field mouse, *Apodemus sylvaticus*, also eats fruits as evidenced by bitten seeds found below the fruiting shrubs. I have observed several species of ants (*Aphaenogaster iberica*, *Pheidole pallidula*, *Crematogaster auberti*, *C. sardidula*, *Camponotus cruentatus* and *Messor barbarus*) on the fruits (both red and green) of *P. terebinthus*. One of the most common, *A. iberica*, is seen carrying mature fruits, and probably acts as a secondary disperser since intact seeds can be often found near or inside its nests (C. M. Herrera and P. Hulme, pers. comm.). The other species, except the granivorous *M. barbarus*, are usually observed eating the pulp, mainly of ripe fruits, completely peeling them but not dispersing the seeds.

Study site

The study took place at Parque Natural de Cazorla, Segura y Las Villas (southeastern Spain) between April and November of 1990. Previous data on the proportion of viable and inviable seeds was available from 1989, and additional observations were made during 1991. Two populations of *P. terebinthus* were studied. One was in

Agracea, an area located in the Guadahornillos Valley, between 1100 and 1200 m. This site is occupied by dense Mediterranean forest constituted mainly by *Quercus*, *Phillyrea*, *Arbutus* and *Juniperus*. Here *P. terebinthus* tends to grow in small gaps or along trails and its density is not greater than 15 individuals per ha. The other study site, Las Navillas, is located about 5 km from the Vadillo-Castril village and 15 km from Agracea, at about 1000 m in altitude. This site is a large secondary scrub, until recently used intensively for sheep and goat grazing. *P. terebinthus*, *Quercus rotundifolia* and *Pinus pinaster* are the dominant trees in this terrain, which is calcareous and very rocky.

Mean monthly temperatures of the coldest (January) and hottest (August) months are 4°C and 21°C, and mean annual precipitation is ca 1200 mm. During 1990, mean temperature was 11.4°C; this year was especially dry, having a total precipitation of only 553 mm.

Methods

Pollination limitation

To assess the degree of pollination limitation I used experimental hand-pollination in 1990. I haphazardly selected a total of 30 individual plants, 17 from Las Navillas and 13 from Agracea. From each plant, I randomly chose and marked six panicles, pollinating half of them and leaving the other half as controls. Pollinations began on 6 May and lasted until 26 May due to plant flowering asynchrony among individuals. Fresh pollen was collected from different males and applied with a thin paintbrush to the stigmas of opened flowers. This was repeated 2–3 d later to ensure that all stigmas were receptive when flowers were pollinated. The average number of flowers pollinated per panicle was 274 ± 127 (s.d.) ($n = 168$). Some inflorescences were lost because of a big storm on 4 June and had to be eliminated from the analyses.

On 8–9 June I recorded the number of full-sized fruits in the marked panicles. By 30 June, I again counted the total number of fruits in the panicle, recording the number attacked by fungi or dried up (presumably due, at least in part, to hemipterans sucking on the pulp). At the beginning of September, I started to record the number of fruits that ripened from each panicle. This was done every 2–5 d to ensure that no fruit would be missed because of removal by birds.

For each plant studied, I measured different variables to examine whether they were associated with fruitset. The variables considered were: plant size (height and canopy diameter), fecundity (total number of flowers produced), distances to the two nearest males that flowered synchronously with it, and number of males among the five nearest neighbors. I also estimated an index of flowering synchrony for each individual, calculating the overlap in its flowering period with that of the male individuals. The method used was taken from Augspurger (1983):

$$X_i = [1/(n-1)]\ (1/f_i) \sum_{j=1}^{n} e_{j\neq i}$$

where n is the number of male individuals in the population; $e_{j\neq i}$ is the number of days during which individuals i and j are flowering simultaneously; f_i is the number of days during which individual i flowers; and X_i is the index of synchrony, which varies from 0 (when there is no overlap) to 1 (in the case of total synchrony).

Losses due to psyllids (Agonoscena targionii)

Psyllids appear on the fruits after these are full-sized; they usually attack entire panicles, sucking the fruit pulp and leaving a honeydew that is eaten by ants. Heavily attacked fruits dry up quickly, turn yellow and usually fall off. For each studied plant, I recorded the absolute number of fruits damaged by these insects.

Losses due to parthenocarpy, abortion and wasp seed predation

On 21–22 August, I collected 50 fruits from each of the studied plants. By this time, no fruits had ripened, and inviable fruits were indistinguishable from those containing a viable seed. All the fruits were dissected, recording the number of those with 1) no embryo (parthenocarpic), 2) an aborted embryo, at any stage of development, 3) a wasp larva or exit hole, or 4) a viable seed.

In order to find a possible association between some plant traits and the incidence of parthenocarpy, seed abortion, seed predation by wasps, and/or fruit attack by psyllids, the following plant variables were recorded: total number of fruits produced, number of fruits that ripened, average distance to the two nearest fruiting neighbors, and number of fruiting individuals in a 10 m radius.

Losses due to bird seed-predators

Direct observations of feeding visits by birds to 13 haphazardly selected plants were used to estimate the proportion of mature (viable) fruits that are consumed by legitimate dispersers. Except for one individual, these plants were not the same used for the pollination experiment, mainly because of the difficulties of making observations on them without disturbing the birds, or because of the low number of mature fruits produced. Plants were observed from late September through beginning of November for a total period of 163.25 h. Watches were made from 08:30 to 18:30. The average proportion of seeds removed by non-legitimate dispersers was obtained from the observed plants, and used to estimate the absolute

Table 1. Analyses of variance of (A) full-sized fruits:flowers ratio and (B) mature fruits:flowers ratio. Area and treatment are fixed effects whereas plant is a random effect. Data were normalized with an angular transformation before analyses. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Source of variation	(A)			(B)		
	df	MS	F	df	MS	F
Area	1	0.001	0.01	1	0.379	12.85**
Plant (Area)	26	0.092	3.12***	24	0.028	11.04***
Treatment	1	0.001	0.03	1	0.004	0.49
Area × Treatment	1	0.133	5.21*	1	0.008	1.05
Treatment × Plant (Area)	26	0.025	0.86	23	0.008	3.04***
Error	95	0.029		64	0.003	

number of seeds not dispersed. Direct and indirect observations (made by marking branches and recording fruit removal rates) showed that birds remove all mature fruits from most individuals (Traveset 1993a). Those few that fall off for some reason are also promptly picked up by birds, usually chaffinches (Traveset, pers. obs.). In contrast to what happens with red fruits, green (viable) fruits do not have time to dry up on the trees.

The following variables were recorded from each observed plant in order to find any associations with the relative or absolute number of fruits removed by either legitimate or non-legitimate dispersers: plant size (area of the vertical canopy projection), fecundity (total fruit crop, total number of fruits that ripen), and phenology (date at which the maximum number of ripe fruits was present on the plant).

Losses to post-dispersal seed predators

On 2 October, when fruits were already being consumed intensively, I placed four groups of five viable seeds (with the pulp removed) of *P. terebinthus* under each of the 13 plants that had ripened fruits in Las Navillas. The groups were placed on 10 × 10 cm pieces of plastic netting, one at each cardinal point; two of them were covered by a vertebrate-exclusion cage made of 1 cm mesh to distinguish removal by ants from removal by mammals and birds. The seeds were checked after 1, 3, 10 and 20 d. I also set the experiment under five trees from Agracea, even though they had not ripened a single fruit. This was done to determine whether viable seeds would have a different probability of survival in an area with different vegetation.

In a parallel experiment set on 4 October, I placed a total of 450 viable seeds in three different sites: a) under oaks, b) under pines, and c) on uncovered soil, simulating places where birds can drop the seeds. Two groups, 30 cm from each other, of five seeds were placed (on plastic netting and without any cage) under each of 10 oaks, 10 pines, and in 10 open sites in Las Navillas, and under 5 oaks, 5 pines and in 5 open sites in Agracea. The seeds were checked 1, 10 and 20 d after placement.

Data analyses

All analyses of variance were performed using the GLM procedure in SAS (1985). Correlations (both Spearman and Pearson's tests) and multiple regression analyses were executed also with this program using the CORR and REG procedures, respectively. Multiple regressions were performed considering as the dependent variables: a) fruit set (number of full-sized fruits relative to number of flowers produced, estimated from the marked panicles); b) mature fruitset (number of mature fruits relative to number of flowers produced, estimated from absolute counts in the entire plant), and c) proportion of fruit crop that ripened (estimated from absolute counts in the entire plant). The independent variables considered in the model were: plant height, total number of flowers produced, average distance to the two nearest males, number of males among the five closest neighbors, and index of flowering synchrony with males. All these independent variables were logarithmically transformed before performing the analyses. For b) and c), only plants from Las Navillas were included in the analyses since only one individual ripened fruits in Agracea.

The relative contribution of the factors that influence the plant reproductive potential was estimated by using key factor analysis (Podoler and Rogers 1975). In such an analysis, the quantified reproductive loss at each phase is regressed against the total loss of reproductive structures, and the slopes of the regressions are used to determine the relative influence that each factor has on among-plant variation in total pre-dispersal losses (see Heithaus et al. 1982 and Jordano 1989 for similar analyses). Standard deviations are given with the means throughout the paper.

Results

Pollination limitation

Fruit set (defined as the number of full-sized fruits relative to the number of flowers) in *P. terebinthus* varied between 0.29 and 0.81, averaging 0.49 ± 0.15 (N = 28 plants). The hand-pollination experiment demonstrated that pollen was not limiting the production of fruits since

Table 2. Parameters of multiple regression relating (A) fruit set (full-sized fruits/flowers), (B) mature fruitset (mature fruits/flowers) and (C) proportion of fruit crop that ripened, to traits of *P. terebinthus*. The dependent variables were normalized with the angular transformation. * $P < 0.05$.

Variables	b ± se	Std.coef.	t	r_s^2
Intercept	0.75	–	–	–
Plant height	0.0004±0.0008	0.14	0.53	0.07
Total no. of flowers	–0.00001±0.000006	0.50	1.80	0.19
Min. dist. to males	–0.00001±0.00005	0.08	0.29	0.0004
Male neighborhood	–0.01±0.04	0.09	0.31	0.006
Flowering synchrony	0.11±0.18	0.13	0.63	0.09
(A) $F_{5,20} = 1.38$, $P = 0.27$, $R^2 = 0.07$				
Intercept	–0.13	–	–	–
Plant height	0.0005±0.0004	0.34	0.27*	0.01
Total no. of flowers	0.000003±0.000003	0.27	0.97	0.001
Min. dist. to males	0.000001±0.00003	0.006	0.02	0.003
Male neighborhood	0.03±0.02	0.58	1.68	0.03
Flowering synchrony	0.02±0.14	0.05	0.18	0.05
(B) $F_{5,8} = 3.23$, $P = 0.07$, $R^2 = 0.46$				
Intercept	–0.70	–	–	–
Plant height	0.003±0.001	0.58	2.32*	0.005
Total no. of flowers	0.000004±0.00001	0.10	0.39	0.0003
Min. dist. to males	0.00001±0.0001	0.04	0.14	0.009
Male neighborhood	0.09±0.06	0.55	1.70	0.006
Flowering synchrony	0.06±0.44	0.03	0.13	0.06
(C) $F_{5,8} = 3.79$, $P = 0.05$, $R^2 = 0.52$				

no significant differences were observed between pollinated and control panicles (0.49 ± 0.19, N = 74, and 0.48 ± 0.19, N = 77, respectively; see Table 1A). Fruit set was similar in the two populations (0.48 ± 0.20, N = 73 in Las Navillas and 0.49 ± 0.18, N = 78 in Agracea). However, the effect of hand-pollination differed slightly between areas: whereas fruitset was 0.46 ± 0.19 in control panicles and 0.52 ± 0.16 in treated panicles in Las Navillas, it was 0.51 ± 0.18 and 0.46 ± 0.21, respectively, in Agracea. No differences in the effect of hand-pollination were found among plants within a population (Table 1A).

The number of fruits that reached maturity relative to the number of flowers was also similar between treatment and controls, although it differed significantly between the two areas (0.03 ± 0.07, N = 22 and 0.04 ± 0.07, N = 20, respectively, in Las Navillas, and 0.0004 ± 0.002, N = 36 and 0.0002 ± 0.001, N = 37, respectively, in Agracea; Table 1B). The average absolute number of ripe fruits in Las Navillas was 442 ± 669 (range 0–2525, N = 15 plants), which represented only 10.3 ± 11.2% of the total individual crop. In Agracea, except for one individual that ripened 3% of its crop, the plants did not ripen a single fruit.

Neither fruit set nor mature fruit set were significantly influenced by any of the variables measured from each plant (Table 2). For the former variable, the model explained a negligible fraction (< 10%) of the variance, whereas for the second, that fraction increased considerably (46%). In the third regression, the model is nearly significant, explaining 52% of the variance in the proportion of fruits that mature from a crop, and plant height alone accounts for 34% of such variance; taller plants in Las Navillas matured a greater proportion of their crop than shorter plants.

Losses to dryness, psyllids and fungi

The number of full-sized fruits per plant, recorded on 8–9 June, varied between 650 and 9350, averaging 4024 ± 2775 (N = 28 plants). From this date to time of maturation, significant amounts of fruits were lost due to different causes:

a) pulp dryness (resulting in a lack of maturation) was observed in all plants in varying proportions. A species of hemipteran, *Gonocerus acuteangulatus* Goeze (F. Coreidae), which was often observed on the drupes sucking the pulp content, was presumably the main cause of such dryness. However, fruit dryness might also be related to some extent to seed inviability; in *Pistacia lentiscus*, inviable fruits dry up sooner than viable ones (P. Jordano, pers. comm.). The absolute number of dried fruits per crop was estimated to be on average 489 ± 400, ranging between 52 and 1661 (N = 28 plants), not differing significantly between the two areas studied ($F_{1,26}$ = 0.08, P > 0.05). It was not significantly associated with fruit crop size (r = 0.47, P = 0.10). However, the proportion of the crop that dried up was negatively correlated with the absolute number of fruits produced (r = –0.51, P = 0.006); that is, larger crops had a lower proportion of

Table 3. Parameters of multiple regression relating number of viable seeds consumed by birds that are not legitimate dispersers. Data were log transformed. $R^2 = 0.74$ ($F_{5,7} = 9.42$ $P = 0.004$), df = 12.

Variable	b + se	std.coef.	t	r^2
Intercept	11.42±5.83	–	–	–
No. mature fruits	0.70±0.30	0.69	2.38*	0.76
Basal area	–0.22±0.67	–0.07	–0.33	0.30
Isolation	0.36±0.24	0.26	1.52	0.10
Ripening peak date	–1.66±1.50	0.26	1.10	0.45

* $P<0.05$.

dried fruits. There were no significant correlations between number of dried fruits and the other variables measured from each plant.

b) *Agonoscena targionii* (Licht.) (Psyllidae) was present on 10 of the 28 plants examined and, on average, it attacked a low proportion of the total fruit crop, 3.8 ± 9.0% (N = 28 plants), although it damaged up to 42% of the fruit crop in one individual. No differences in the number of psyllid-damaged fruits were found between areas ($F_{1,26} = 0.98$, $P>0.05$). The presence of psyllids on a plant was not associated with the variables describing size, fecundity or proximity to neighbors.

c) Fungi were present on 18 of the 28 trees studied. The average absolute number of fruits attacked by fungi was 51 ± 72 (N = 28). Larger crops had more fruits damaged ($r = 0.70$, $P = 0.0001$), although the probability that a fruit was attacked by fungi was independent of crop size ($r = 0.27$, $P>0.05$). There were significant differences between the two areas ($F_{1,26} = 15.2$, $P = 0.0006$), fungi being more commonly found in Agracea (97 ± 83 fruits attacked per crop; N = 13) than in Las Navillas (10 ± 22; N = 15).

Note that the reproductive losses due to these three factors are somewhat overestimated as not all fruits damaged would contain a viable seed. Thus, these estimated losses must be considered as potential decreases in the reproductive output.

Losses to parthenocarpy, abortion and wasp seed-predation

The dissection of fruits collected from each of the 28 individuals in August, before any fruit had ripened, showed that an average of 484 ± 486 fruits were parthenocarpic, which represented 18 ± 14% of the total crop. The proportion of fruits with no embryo was similar between the two populations examined (19.2 ± 12.2% and 16.4 ± 15.4% in Agracea and Las Navillas, respectively) and ranged between 2 and 60% of the crop. It was not significantly correlated with either plant size, fecundity (production of fruits) or flowering synchrony with males.

The number of fruits that contained a seed aborted at any stage of development represented, on average, a high proportion (70 ± 13%) of the fruit crops. The average absolute number of aborted fruits per crop was 2369 ± 1832 (range 158–6464; N = 28). That proportion was not significantly different between the two populations (73.2 ± 7.2% and 67.3 ± 16.4% in Agracea and Las Navillas, respectively) and was not significantly correlated with the plant variables measured.

Chalcidoid wasps damaged an average of 4.6 ± 6.3% of the fruits per crop (N = 28). There was much variability between individual plants, the intensity of attack ranging from 0 to 24%. The proportion of wasp-damaged seeds did not differ significantly between areas, being 5.4 ± 6.7% in Agracea and 3.9 ± 6.1% in Las Navillas. Fruit crop size had a significant effect on the proportion of wasp-damaged seeds ($F_{1,26} = 10.21$, $P<0.01$), explaining 25.4% of the variance. Larger crops experienced a significantly greater damage. None of the other variables measured from each individual had a significant influence on either the relative or absolute number of wasp-damaged seeds.

Losses to avian seed-predators

Percent removal of ripe fruits by birds averaged 98.9 ± 2.9% (range 88.2 – 100%). This removal took place between mid September and the end of October. Avian seed predators, including those that crack the seeds (*Fringilla coelebs*, *Sitta europaea*, *Carduelis chloris*, *Coccothraustes coccothraustes* and *Dendrocopos major*) and those that consume only the fruit pulp, dropping most seeds under the parent plant (*Parus ater*, *P. caeruleus*, *P. major*, *P. cristatus* and *Aegithalos caudatus*) were responsible for a large proportion (X = 71.7 ± 29.6%; range = 14.3–100%; N = 13 plants) of the ripe fruit removal. Thus, only 28.3 ± 29.6% of the viable fruits were consumed by legitimate dispersers.

There was much variability among individual plants in the absolute number of ripe fruits consumed by bird seed-predators, ranging from 156 to 11 375 (N = 13 plants). The results of multiple regression analysis between plant traits and the number of viable fruits consumed by bird seed-predators are summarized in Table 3. The whole set of variables accounted for a significant fraction of variance in the number of seeds not dispersed ($R^2 = 0.74$, $F = 9.42$, $P = 0.004$). The absolute number of mature fruits had a highly significant effect on the de-

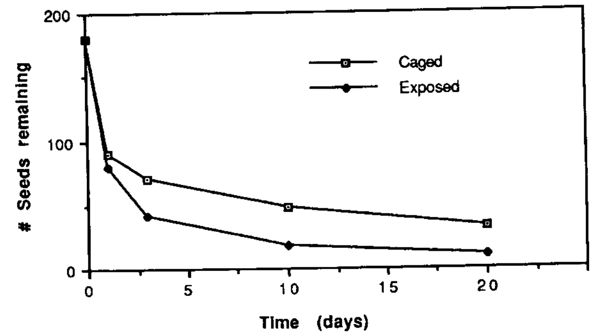

Fig. 1. Removal of seeds from underneath the shrubs of *P. terebinthus* by field mice, chaffinches, and ants. Caged treatments allowed only seed removal by ants.

pendent variable, showing also the highest value of the standardized coefficients. Plants with larger mature fruit crops had an increased number of viable seeds preyed upon by birds. The correlation between number of ripe fruits preyed upon by birds and number of ripe fruits produced was $r=0.82$ ($P=0.0006$). The correlation was also significant between number of ripe fruits consumed by bird seed predators and proportion of the crop that ripen ($r=0.66$, $P=0.01$). In contrast, it was not significant between number of viable seeds consumed by legitimate dispersers and mature fruit crop ($r=0.49$, $P=0.09$).

Losses to post-dispersal seed predators

Fig. 1 shows the removal of seeds through time from underneath the shrubs by both vertebrates and ants. Seeds were removed quite quickly after day of placement, and after 20 d only 9.2% and 19% were left in Las Navillas and in Agracea, respectively.

A 2-way ANOVA, using area and presence of exclusion cage as main effects, and number of seeds remaining at day 1, 3, 10 and 20 after placement as the dependent variables, showed that seed removal was significantly lower in the vertebrate-excluded groups of seeds than in those exposed to both vertebrates and ants. This was detected at day 10 ($F_{1,68}=6.11$, $P=0.02$), although three d after seed placement the difference was already nearly significant ($F_{1,68}=3.42$, $P=0.07$). At day 20, the number of seeds remaining was still greater in the caged than in the exposed groups of seeds (Fig. 1). During the first 10 days after placement, seeds were removed faster in Las Navillas than in Agracea ($F_{1,68}=5.85$, $F_{1,68}=7.65$, $F_{1,68}=5.43$, all $P<0.05$, for day 1, 3, and 10, respectively). At day 20, no differences were found between these areas ($F_{1,68}=2.34$, $P>0.05$), probably because most seeds were already gone. The interaction between the two effects (area and presence of exclusion cage) was not significant in any case. The proportion of seeds removed during the 20 days varied among plants from 40% to 100%. In 8 of the 18 studied plants not a single seed was left. Seed removal by ants, field mice or birds (chaffinches) from the ground was not correlated with any of the plant traits (fruit crop, basal area, average distance to the two closest fruiting conspecifics) that might be relevant to such plant-animal interaction.

Table 4. Number (and percentage in parentheses) of seeds remaining in the three different sites after 1, 10 and 20 d since placement. Initial number of seeds at each site = 150. Two groups of five seeds were placed at each location.

Day	Under oaks	Under pines	Open sites
1	49 (32.7)	44 (29.3)	39 (26.0)
10	16 (10.7)	24 (16.0)	28 (18.7)
20	1 (0.7)	15 (10.0)	19 (12.7)

As mentioned above, whereas seeds removed by mice and chaffinches are killed, some of those taken by ants may undergo secondary dispersal. Therefore, post-dispersal seed predation was here somewhat overestimated.

In the second experiment, no significant differences in seed removal were observed between locations ($F_{1,84}=0.46$, $F_{1,82}=0.39$ and $F_{1,82}=2.20$, all $P>0.05$, for day 1, 10 and 20, respectively) or among areas ($F_{1,84}=0.09$, $F_{1,82}=0.02$, $F_{1,82}=0.12$, all $P>0.05$), and there were no significant interactions between effects (Table 4). The great majority (70.7%) of seeds disappeared during the first day; 20 d after seed placement, only 7.8% of the seeds remained. Again, most of these seeds were probably killed by mice, birds or granivorous ants, only a small fraction undergoing secondary dispersal.

Cumulative reductions in the reproductive potential during the pre-dispersal phase

I identified a total of eight factors that affected the reproductive potential of *P. terebinthus* during the pre-dispersal phase (Table 5). The cumulative effect of such factors is expressed as the proportion of the initial crop size (number of female flowers) that will not become dispersed seeds. The relative importance of losses at each stage is quantified as the proportion of the initial crop size lost during that stage.

The initial flower crop sizes (ranging from 1300 to 22727) were greatly reduced to a minimum of 0 and a maximum of 2525 viable seeds dispersed (Fig. 2). Abortion of flowers and latent ovaries accounted for most of the losses (51% of the initial crop size; Fig. 2). All monitored plants suffered the greatest loss during this stage. The next important cause of reproductive loss was seed abortion (27.5% of the initial crop size), followed by fruit dryness (7.6%) and by lack of ovule fertilization (6.1%). Fruit or seed damage by psyllids, wasps and birds represented a total of 6.4% of loss, showing extreme between-plant variation in magnitude (CV > 100%), compared with the factors that are intrinsic to the plants

Table 5. Factors that contribute to the losses in the reproductive output of *P. terebinthus* during the pre-dispersal phase, and results of the key factor analysis. The key factor slope indicates the relative influence of each factor on variation in total losses; the correlation coefficient parallels between total losses and losses due to each factor. Data (the two areas are pooled) were log transformed before analysis.

			Key factor analysis	
	X[1]	CV	Slope[2]	r
1. Abortion of flowers and latent ovaries	0.5100	30.0	−0.016	−0.05
2. Fruit dryness	0.0764[3]	97.9	0.1458	0.45**
3. Fruit damage by fungi	0.0058[3]	134.5	−0.0109	−0.24
4. Fruit damage by psyllids	0.0232[3]	249.6	0.1155	0.35
5. Parthenocarpy	0.0606	62.5	0.0545	0.14
6. Seed abortion	0.2749	43.8	−0.0070	−0.03
7. Seed damage by wasps	0.0195	133.8	0.3610	0.39*
8. Consumption of viable fruits by non-legitimate dispersers	0.0210	150.9	0.3578	0.39*

[1] Proportion of the initial crop size lost at each stage.

[2] Calculated by regressing the reduction in the reproductive potential for each phase against the total loss of reproductive structures (sum of the losses at each phase).

[3] Value somewhat overestimated, as some of the fruits were already inviable (parthenocarpic or aborted).

such as abortion or parthenocarpy (see Table 5). Fruit damage by fungi was nearly negligible (<1% of total losses) and also showed an enormous variation between plants.

The key factor analysis shows that factors associated with interactions with animals (fruit/seed damage and consumption by non-legitimate seed dispersers) have steeper slopes than factors intrinsic to the plant (flower and ovary abortion and seed inviability) (Table 5). The highest slopes indicate that the greatest contribution to among-plant variation in total loss of reproductive potential is due to the extrinsic factors (plant-animal interactions), even though these factors account for a lower reproductive loss than the intrinsic factors (Table 5).

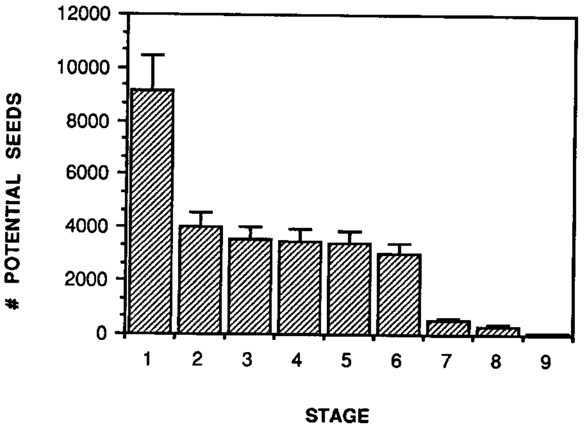

Fig. 2. Reduction of the reproductive potential of female plants throughout the successive phases of the life cycle. 1: initial flower crop size, 2: fruit crop size or number of full-sized fruits, 3: number of remaining fruits (NRF) after subtracting those that dry up, 4: NRF after subtracting those damaged by fungi, 5: NRF after subtracting those damaged by psyllids, 6: NRF after subtracting the parthenocarpic, 7: NRF after subtracting those that abort their seeds, 8: NRF after subtracting those attacked by wasps, or number of viable fruits (seeds), and 9: number of fruits consumed by legitimate dispersers.

Discussion

Factors limiting reproductive output

Eight factors were found to reduce the reproductive potential of *P. terebinthus* during the pre-dispersal phase. These factors were both intrinsic to the plant (flower and ovary abortion, parthenocarpy and seed abortion) and extrinsic (fruit damage by fungi and the plant-animal interactions). Moreover, post-dispersal seed predation by animals also influences the final number of seeds that can recruit and germinate.

The greatest loss took place between the flower stage and the final-sized fruit stage. The abortion of flowers and latent ovaries represented, on average, about half of the initial number of flowers produced. This is very similar to the figure (55%) found by Jordano (1989) in *P. lentiscus*. Such low fruit:flower ratio might be attributed to any of the causes usually found in other species: pollination limitation, nutrient limitation, bet hedging and/or selective abortion (e.g. Stephenson 1981, Bawa and Webb 1984, Sutherland 1986a, b, Wiens et al. 1987, Haig and Westoby 1988, Krusi and Debussche 1988, Charlesworth 1989, Ehrlén 1991). The hand-pollination experiment performed here, however, showed that, at least in 1990, pollen was not limiting the production of fruits.

The low proportion of fruits that ripen is also found in other congeneric species (Grundwag 1975, 1976, Jordano 1988, 1989) and it is mainly due to the large number of developed fruits that contain inviable seeds, which come either from unpollinated flowers (parthenocarpic fruits) or are the result of embryo abortions at some stage of development.

Dryness of full-size fruits represented a reproductive loss of about eight percent of the initial flower crop. Hemipterans suck the pulp-content of the fruits which dry up and fall off the plant; they may even be sucking the seed contents from some of the fruits, although this is unknown. In a study that mimicked damage by hemipterans in *Sesbania*, Marshall et al. (1985) found that there was selective seed abortion of more heavily damaged fruits and of younger fruits. It is possible that a fraction of the developing ovaries of *P. terebinthus* were lost due to hemipteran-sucking, although these insects were not observed until fruits were full-sized.

Fruit damage by *Agonoscena targionii* was usually low, never reducing the number of viable seeds more than 10%. The incidence of psyllid attack on an individual plant was extremely variable. Large differences between individual plants in susceptibility to attack have also been found for other psyllids (Journet 1980) and aphids (Snow and Stanton 1988, Akimoto 1990) and have been attributed to physiological or biochemical differences among individuals.

The attack by fungi on the fruits of *P. terebinthus* represented a reproductive loss lower than 1%. The same species of fungus attacked also the leaves of the plant. Whether the leaf damage had an additive effect on reproduction is unknown.

Parthenocarpy represented about 6% of the reproductive loss. The production of fruits from unfertilized flowers is commonly found in the genus *Pistacia* and in other species within the family Anacardiaceae (Grundwag 1976, Jordano 1988), and it seems to be due to the independent development of the pericarp and the ovule (Grundwag and Fahn 1969, Grundwag 1976). The proportion of fruits with no embryo was highly variable between plants. The relative importance of parthenocarpy varies among years, probably depending upon the weather conditions during the flowering period. In 1989, the incidence of parthenocarpy was much greater than in 1990 (31 ± 16% vs 18 ± 14% of the crop, respectively), probably due to the better conditions for pollination in 1990 (precipitation in 1989 during April and May was 235.5 mm whereas in 1990 it was only 94.5 mm).

About 27% of the initial number of flowers became fruits that contained aborted seeds. The main cause of seed abortion has been attributed to a limitation in resource availability (Stephenson 1981; but see Wiens et al. 1987), although other authors have found selective abortion depending upon paternity (e.g. Bookman 1984) or upon genetic deficiencies (Wiens et al. 1987). Dry climatic conditions have also been found to influence seed abortion (e.g. Lee and Bazzaz 1986, Jordano 1988). In the present case, the dry conditions of 1990 might also be responsible, at least in part, of the much greater proportion of aborted seeds (70 ± 13% of the crop) compared to the proportion observed in 1989 (38 ± 16%).

Seed predation by chalcidoid wasps caused, in general, a low (about 2%) reproductive loss, even though their incidence in some individual plants was high (being up to 24% of the fruit crop). Larger fruit crops harbored a greater proportion of wasp-damaged seeds than smaller fruit crops. Other studies (e.g. Roitberg et al. 1982, Courtney and Manzur 1985, Jordano 1987) have also reported density dependence in insect infestation of fruits or seeds. Wasps might locate larger crops more easily than smaller ones, therefore selecting for crops with a low absolute number of fruits. Wasps seem to survive well in seeds aborted at a late stage of development (Traveset 1993a); therefore, the number of seeds damaged by wasps might be somewhat overestimated. A negative correlation was found between incidence of wasp-damaged seeds and incidence of parthenocarpy per crop (Traveset 1993b).

The removal of fruits with viable seeds by birds was quite intense. However, most (72%) of those fruits were removed by birds that do not act as legitimate dispersers but as seed predators (consuming either the pulp alone or cracking the seeds). The total reproductive loss (referred to the initial flower crop size) due to bird seed predators was only about 2%, being extremely variable between individual plants; some plants had most fruits consumed by legitimate dispersers whereas others had a null or almost null dispersal success. Plants that produce a large final mature crop do not necessarily have more seeds dispersed successfully than others which suffer greater losses during the previous reproductive stages and have small mature crops. Indeed, it appeared that larger mature crops had greater number of ripe fruits consumed by avian seed predators. The reproductive success of an individual plant, therefore, is importantly controlled by the type of frugivores that eat its fruits, and not only by the losses during the pre-dispersal phase. Such results contrast with those reported by Jordano (1989) who found that the effect of frugivorous birds visiting *P. lentiscus*, in southwestern Spain, did not offset variation arising from both pollination and fertilization constraints of the pre-dispersal phase. The reason for such different results is very likely the negligible effect that bird seed predators had in his system, reducing seed dispersal success with less than 4%.

The key factor analysis showed that the influence of a factor on among-plant variation in total reproductive loss cannot be predicted by the magnitude of predispersal losses in reproductive potential caused by that factor. The same was found by Podoler and Rogers (1975) and Heithaus et al. (1982) in their systems. The effects of animals on the plant accounted for the greatest between-plant variation in total loss of reproductive potential, even though they caused a lower reproductive loss than the factors intrinsic to the plant (flower and ovary abortion and seed inviability). Seed damage by wasps and fruit consumption by bird seed predators were the most important factors in explaining differences among individuals in the number of viable seeds dispersed.

The seeds that fall beneath the plant have a low probability of survival since most are preyed upon by chaffinches, field mice or ants. Some of the seeds, however, may be secondarily dispersed by species such as *Aphaenogaster iberica*. These species account also for a high removal of seeds of other plants such as *Daphne laureola* (Hulme 1992). The recruitment of seeds of *P. terebinthus* far from the parent plant seems to be greatly affected by such post-dispersal predators, as has been found for other species and in other habitats (e.g. Howe et al. 1985, Schupp 1988, Willson 1988, Traveset 1990, Whelan et al. 1991, Hulme 1992). The experiment in which seeds were placed in different locations (on open sites, under oaks or under pines), showed that the large majority (92%) of them disappear soon after being dropped. Both chaffinches and mice are abundant in the study sites, evidenced by the seed remains found near the plants. Ants are also abundant and frequently observed during the whole fruiting period. Whether seeds in open sites are more likely to be removed by ants than by vertebrates and the fate of those seeds that are taken to ant nests are questions that remain still open.

Selection on plant traits

Of the eight factors that decrease the reproductive potential of the plant, only 1) fruit dryness, 2) seed predation by wasps, and 3) seed predation by birds showed to be potential selective agents on plant fecundity. The other plant traits measured appeared to not significantly affect the losses at each stage. Larger fruit crops had a lower proportion of dried fruits although they harbored a greater proportion of wasp-damaged seeds. Also, larger number of mature fruits per crop had a greater consumption by avian seed predators. Considering that seed losses due to dryness are greater than the losses due to wasps and birds and that this is consistent through time, we may predict that selection will favor larger crops. Therefore, even though the plant-animal interactions appear to not induce an important demographic change in reproductive output compared to the factors intrinsic to the plant, they do show to be relevant from an evolutionary viewpoint.

Conclusion

The reproductive output of *P. terebinthus* appears to be influenced by a number of factors that reduce the potential number of viable seeds dispersed in different degrees. Intrinsic factors such as flower and ovary abortion and seed inviability were the most important in reducing the reproductive potential of the plant. However, they accounted for a low among-plant variation in total reproductive losses. In contrast, factors extrinsic to the plant (such as fruit or seed damage by animals) did not greatly reduce the reproductive potential but did contribute notably to the among-plant variation in the number of viable seeds dispersed and appeared to act as selective agents on plant fecundity. Therefore, the study supports the argument by Heithaus et al. (1982) that one interaction may have a great evolutionary importance even if it has only a small effect on the dynamics of a population.

The final contribution of each individual plant to the population seed production was largely determined at the pre-dispersal phase. Nonetheless, the interaction with frugivorous birds was able to override its net result. This was mainly due to the variable proportion of viable fruits removed by non-legitimate seed dispersers.

Once seeds have been dispersed, they are still exposed to different species of post-dispersal predators that ultimately determine whether the seeds will or will not recruit at a given site. In the present study, these animals appeared to play an important role.

Acknowledgements – I especially thank P. Jordano for convincing me that the genus *Pistacia* was an interesting one to study. The Agencia del Medio Ambiente, Junta de Andalucía, provided valuable logistic support in Cazorla. I thank the people at the Estación Biológica de Doñana who helped in different ways during the study. I am also grateful to P. Jordano, M. F. Willson, and C. R. Altaba for constructively criticizing earlier versions of the manuscript. Financial support came from the Ministry of Education and from DGICYT grant PB87–0452.

References

Akimoto, S. 1990. Local adaptation and host race formation of a gall-forming aphid in relation to environmental heterogeneity. – Oecologia 83: 162–170.
Augspurger, C. K. 1983. Phenology, flowering synchrony, and fruit set of six neotropical shrubs. – Biotropica 15: 257–267.
Bawa, K. S. and Webb, C. J. 1984. Flower, fruit and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. – Am. J. Bot. 71: 736–751.
Bookman, S. S. 1984. Evidence for selective fruit production in *Asclepias*. – Evolution 38: 72–86.
Campbell, D. R. 1991. Effects of floral traits on sequential components of fitness in *Ipomopsis aggregata*. – Am. Nat. 137: 713–737.
Charlesworth, D. 1989. Why do plants produce so many more ovules than seeds? – Nature 338: 21–22.
Courtney, S. P. and Manzur, M. I. 1985. Fruiting and fitness in *Crataegus monogyna*: the effects of frugivores and seed predators. – Oikos 44: 398–406.
Ehrlén, J. 1991. Why do plants produce surplus flowers? a reserve-ovary model. – Am. Nat. 138: 918–933.
Green, T. W. and Palmbald, I. G. 1975. Effects of insect seed predators on *Astragalus cibarius* and *Astragalus utahensis* (Leguminosae). – Ecology 56: 1435–1440.
Grundwag, M. 1975. Seed set in some *Pistacia* L. (Anacardiaceae) species after inter- and intraspecific pollination. – Isr. J. Bot. 24: 205–211.
– 1976. Embryology and fruit development in four species of *Pistacia* L. (Anacardiaceae). – Biol. J. Linn. Soc. 73: 355–370.
– and Fahn, A. 1969. The relation of embryology to the low seed set in *Pistacia vera* (Anacardiaceae). – Phytomorphology 19: 225–235.
Haig, D. and Westoby, M. 1988. On limits to seed production. – Am. Nat. 131: 757–759.
Hainsworth, F. R., Wolf, L. L. and Mercier, T. 1984. Pollination and pre-dispersal seed predation: net effects on reproduction and inflorescence characteristics in *Ipomopsis aggregata*. – Oecologia 63: 405–409.

Heithaus, E. R., Stashko, E. and Anderson, P. K. 1982. Cumulative effects of plant-animal interactions on seed production by *Bauhinia ungulata*, a neotropical legume. – Ecology 63: 1294–1302.

Herrera, C. M. 1984a. Selective pressures on fruit seediness: differential predation of fly larvae on the fruits of *Berberis hispanica*. – Oikos 42: 166–170.

– 1984b. Seed dispersal and fitness determinants in wild rose: combined effects of hawthorn, birds, mice, and browsing ungulates. – Oecologia 63: 386–393.

– 1988. The fruiting ecology of *Osyris quadripartita*: individual variation and evolutionary potential. – Ecology 69: 233–249.

– 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. – Oikos 55: 250–262.

Howe, H. F., Schupp, E. W. and Westley, L. C. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). – Ecology 66: 781–791.

Hulme, P. E. 1992. The ecology of a temperate plant in a mediterranean environment: post-dispersal seed predation of *Daphne laureola*. – Proc. VI Int. Conf. Medit. Climate Ecosystems: 281–286.

Jordano, P. 1987. Avian fruit removal: effects of fruit variation, crop size, and insect damage. – Ecology 68: 1711–1723.

– 1988. Polinización y variabilidad de la producción de semillas en *Pistacia lentiscus* L. (Anacardiaceae). – An. J. Bot. Madrid 45: 213–231.

– 1989. Pre-dispersal biology of *Pistacia lentiscus* (Anacardiaceae): cumulative effects on seed removal by birds. – Oikos 55: 375–386.

Journet, A. R. P. 1980. Intraspecific variation in food plant favourability to phytophagous insects: psyllids on *Eucalyptus blakelyi* M. – Ecol. Entomol. 5: 249–261.

Krusi, B. O. and Debusche, M. 1988. The fate of flowers and fruits of *Cornus sanguinea* L. in three contrasting habitats. – Oecologia 74: 592–599.

Lee, T. D. and Bazzaz, F. A. 1986. Maternal regulation of fecundity: non-random ovule abortion in *Cassia fasciculata* Michx. – Oecologia 68: 459–465.

Louda, S. M. 1982. Inflorescence spiders: a cost/benefit analysis for the host plant, *Haploppapus venetus* Blake (Asteraceae). – Oecologia 55: 185–191.

Marshall, D. L., Levin, D. A. and Fowler, N. L. 1985. Plasticity in yield components in response to fruit predation and date of fruit initiation in three species of *Sesbania* (Leguminosae). – J. Ecol. 73: 71–81.

Podoler, H. and Rogers, D. 1975. A new method for the identification of key factors from life-table data. – J. Anim. Ecol. 44: 85–114.

Primack, R. B. 1987. Relationships among flowers, fruits, and seeds. – Annu. Rev. Ecol. Syst. 18: 409–430.

Roitberg, B. D., Lenteren, J. C., Alphen, J. J. M., Galis, F. and Prokopy, R. J. 1982. Foraging behaviour of *Rhagoletis pomonella*, a parasite of hawthorn (*Crataegus viridis*), in nature. – J. Anim. Ecol. 51: 307–325.

SAS 1985. SAS User's Guide: Statistics, Version 5 Ed. – SAS Inst. Inc., Cary, NC.

Schemske, D. W. and Horvitz, C. C. 1988. Plant-animal interactions and fruit production in a neotropical herb: a path analysis. – Ecology 69: 1128–1137.

Schupp, E. W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. – Oikos 51: 71–78.

Snow, A. A. and Stanton, M. L. 1988. Aphids limit fecundity of a weedy annual (*Raphanus sativus*). – Am. J. Bot. 75: 589–593.

Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. – Annu. Rev. Ecol. Syst. 12: 253–279.

Sutherland, S. 1986a. Patterns of fruit-set: what controls fruit-flower ratios in plants? – Evolution 40: 117–128.

– 1986b. Floral sex ratios, fruit-set, and resource allocation in plants. – Ecology 67: 991–1001.

Traveset, A. 1990. Post-dispersal predation of *Acacia farnesiana* seeds by *Stator vachelliae* (Bruchidae) in Central America. – Oecologia 84: 506–512.

– 1993a. Weak interactions between avian and insect frugivores: the case of *Pistacia terebinthus* L. (Anacardiaceae). – Vegetatio 107/108: 191–203.

– 1993b. Deceptive fruits reduce seed predation by insects in *Pistacia terebinthus* L. (Anacardiaceae) – Evol. Ecol. 7: 357–361.

Whelan, C. J., Willson, M. F., Tuma, C. A. and Souza-Pinto, I. 1991. Spatial and temporal patterns of postdispersal seed predation. – Can. J. Bot. 69: 428–436.

Wiens, D., Calvin, C. L., Wilson, C. A., Davern, C. I., Frank, D. and Seavey, S. R. 1987. Reproductive success, spontaneous embryo abortion, and genetic load in flowering plants. – Oecologia 71: 501–509.

Willson, M. F. 1988. Spatial heterogeneity of post-dispersal survivorship of Queensland rainforest seeds. – Aust. J. Ecol. 13: 137–145.

Zohary, M. 1952. A monographical study of the genus *Pistacia*. Palest. J. Bot. Jerus. Ser. 5: 187–238.