Ecological causes, function, and evolution of abortion and parthenocarpy in *Pistacia lentiscus* (Anacardiaceae)

Miguel Verdú and Patricio García-Fayos

Abstract: Parthenocarpy (the production of seedless fruits) and abortion of reproductive structures at different developmental stages are important processes limiting female fecundity in *Pistacia lentiscus* (Anacardiaceae), a Mediterranean endozoochorous dioecious shrub. This paper (*i*) tests the effects of water and pollen as the ecological causes of abortion and parthenocarpy, (*ii*) tests the function of abortion and parthenocarpy regarding the uncertainty of resources and predispersal seed predation, and (*iii*) reviews the evolution of parthenocarpy across the phylogeny of the genus *Pistacia* and the family Anacardiaceae. Using experimental manipulations, we examined the effects of pollen and water availability on female fecundity. The components of female fecundity were the four sequential developmental stages in the reproductive cycle: (*i*) flower survival after pollination, (*ii*) latent ovary survival, (*iii*) final-sized fruit survival, and (*iv*) seed viability. The survival of reproductive structures along the four developmental stages in response to pollination was highly variable. The survival of pollen-excluded flowers was negligible. Water addition increased the survival of reproductive structures in the first two developmental stages but this effect was lost in the other two stages. However, irrigation had a delayed effect, significantly increasing the number of viable seeds per number of flowers at the following reproductive season. The irrigated females significantly increased the percentage of viable seeds, whereas nonirrigated females did not. These data support the hypothesis that the adjustment of progeny size to the available resources is an individual feature inherent to the life history of each individual and therefore independent of the present resource level. This adjustment may have an adaptive value in relation to uncertainty of water availability. An advantage for parthenocarpy in terms of reducing seed predation was not found and it may be a nonadaptive plesiomorphic character within the genus *Pistacia* and within the family Anacardiaceae. A significant negative relationship was found between the rate of seed abortion and predispersal seed predation by wasps, suggesting that abortion reduces insect predation. In support of this hypothesis, we found that fruits with aborted seeds abscised in a lower proportion than expected, while fruits with seeds parasitized by wasps fell in a greater proportion than expected.

Key words: abortion, parthenocarpy, predispersal seed predation, seed production.

Résumé : La parthénocarpie (la production de fruits sans graine) et l’avortement des structures reproductrices à différents stades du développement sont des processus importants qui limitent la fécondité femelle chez le *Pistacia lentiscus* (Anacardiaceae), un arbuste endozoochore méditerranéen. Dans ce travail (*i*) on vérifie les effets de l’eau et du pollen comme causes écologiques de l’avortement et de la parthénocarpie; (*ii*) on vérifie la fonction de l’avortement et de la parthénocarpie eu égard à l’incertitude des ressources et à la prédation des graines avant la dispersion; et (*iii*) on revoie l’évolution de la parthénocarpie au cours de la phylogénie du genre *Pistacia* et de la famille des Anacardiaceae. À l’aide de manipulations expérimentales, les auteurs examinent les effets du pollen et de la disponibilité de l’eau sur la fécondité femelle. Les composantes de la fécondité femelles comportent les quatre stades séquentiels de développement du cycle vital : (*i*) survie de la fleur après la pollinisation, (*ii*) survie latente de l’ovaire, (*iii*) survie du fruit à son plein développement, et (*iv*) viabilité de la graine. La survie des structures reproductrices tout au long des quatre stades de développement est très variable. La survie des fleurs non pollinisées est rare. L’apport en eau augmente la survie des structures reproductrices aux deux premiers stades du développement, mais cet effet est perdu aux deux autres stades. Cependant, l’irrigation a un effet à retardement, ce qui augmente significativement le nombre de graines viables par nombre de fleurs à la saison de reproduction suivante. Les plantes femelles irriguées augmentent significativement leurs pourcentages de graines viables alors que les plantes femelles non-irriguées ne le font pas. Ces données supportent l’hypothèse que l’ajustement de la dimension de la progéniture aux ressources disponibles est une caractéristique individuelle inhérente au cycle vital de chaque individu et conséquemment indépendant de l’importance actuelle de la ressource. Cet ajustement pourrait avoir une valeur adaptative en relation avec l’incertitude de la disponibilité de l’eau. Un avantage pour la parthénocarpie en termes de réduction de la prédation sur les graines n’a pas pu être observé et pourrait être un caractère plésiomorphe non-adaptif dans le genre *Pistacia* et dans la famille des Anacardiaceae. Les auteurs ont observé une relation inverse significative entre le taux d’avortement et de prédation par les

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guêpes des graines avant dispersion, ce qui suggère que l'avortement réduit la prédation par les insectes. Comme confirmation de cette hypothèse, les auteurs ont trouvé que les fruits comportant des graines avortées s'excisaient dans une proportion plus faible qu'attendue, alors que les fruits comportant des graines parasitées tombaient dans une plus forte proportion qu'attendue.

Mots clés : avortement, parthénocarpie, prédation des graines avant dispersion, production de graines.

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Introduction

Flowering and fruiting are the two key processes in plants that ensure the transfer of genetic material from one generation to the next. However, in some species only a small proportion of the available ovules develop ultimately into viable seeds (Sutherland 1986). The main process that controls the number of successful ovules is the abortion of flowers and fruits during different developmental stages (Stephenson 1981; Sutherland 1986; Charlesworth 1989). Another process that limits female fertility is parthenocarpy, the growth of seedless fruits without fertilization (Schwabe and Mills 1981).

Most studies concerning the causes of abortion and parthenocarpy have focused on the four theoretical determinants proposed by Tinbergen (1963) for the study of the biological problems: causes (physiological, genetical, and ecological), development, evolution, and function. Several hypotheses concerning causes and function of abortion have been formulated (Stephenson 1981), but parthenocarpy has received much less attention.

The primary causes of seed abortion are thought to be resource or pollen limitation (Bierzychudek 1981; Lee and Bazzaz 1982; Campbell 1985; Herrera 1990; Johnston 1991; Obeso 1993; Campbell and Halama 1993). Hypotheses concerning the function of abortion can be placed into three groups, (*i*) environmental uncertainty about resources, pollen, and flower and seed predation, (*ii*) the male role of hermaphroditic flowers, and (*iii*) the improvement of the quality of seed produced through selective abscission (Stephenson 1981).

Possible causes of parthenocarpy include frost damage to the ovule, stimulation by foreign pollen, changes in the competitive balance between vegetative and reproductive structures, and (or) a spatial or temporal failure on auxin synthesis (Schwabe and Mills 1981; Goldwin 1993; Gillaspy et al. 1993). Willson and Burley (1983) consider that parthenocarpic fruits may develop when resources are not limiting, or when there is a developmental error. The function of parthenocarpy has also been considered as an exaptation related to the uncertainty of seed predation (Zangerl et al. 1991; Traveset 1993*a*).

Abortion and parthenocarpy in *Pistacia lentiscus* L. as biological problems have been unevenly studied at the four approaches proposed by Tinbergen (1963). Development is the best known subject and has been described in detail by Grundwag (1975, 1976). Regarding their ecological causes, pollen availability is positively related to seed survival, but the effects of resource availability have not been studied. However, the role of water as the limiting resource has been indirectly invoked to explain the proportion of both aborted and parthenocarpic fruits (Jordano 1988). Jordano (1988) has examined the relationship between parthenocarpy and abortion rates and annual rainfall. As water is a major limiting resource in Mediterranean habitats (Mooney and Dunn 1970; Aerts 1995; Hobbs et al. 1995), it is expected that female fecundity could be constrained by water availability. Function (adaptive value) of abortion and parthenocarpy in *Pistacia lentiscus* has not been documented (Jordano 1988) but, in *Pistacia terebinthus,* parthenocarpy may play an important role as a defense against seed predators in at least some years (Traveset 1993*a*). In *Pistacia terebinthus,* parthenocarpic fruits appear to reduce seed predation because predators cannot discriminate between viable and parthenocarpic (deceptive) fruits, as ovules have not enlarged at the time of oviposition. Seed predators waste time and energy ovipositing in parthenocarpic berries where larvae cannot survive because there is no endosperm (Traveset 1993*a*). Regarding the evolution of abortion and parthenocarpy, both processes have been considered to be ontogenetic constraints with a strong phylogenetic inertia within the genus *Pistacia* (Jordano 1989).

The objective of the present paper is to study abortion and parthenocarpy in *Pistacia lentiscus* under the following approaches.

1. Ecological cause: does pollen and (or) water availability determine the rates of abortion and parthenocarpy?
2. Function: do abortion and parthenocarpy have an adaptive value concerning the environmental uncertainty about resources (water), pollen, or fruit predation?

We also consider the evolution of parthenocarpy within *Pistacia* and, more generally, in the family Anacardiaceae to discuss if phylogenetic inertia may explain the presence of this ontogenetic process in these taxa.

Methods

Study species

Pistacia lentiscus is a dioecious shrub, common in Mediterranean sclerophyllous scrublands (see Zohary 1952 for morphological traits and taxonomy). It is evergreen and wind pollinated. Flowering of male and female plants overlaps, usually between March and May (Jordano 1988; Correia et al. 1992).

Male flowers have 8–10 stamens, produce 47 000 – 60 000 pollen grains per flower, and are grouped in inflorescences of 8–10 flowers (Jordano 1989). Pollen grains are subcircular or elliptic with a major diameter of 25–30 μm and a minor diameter of 22–27 μm (Ballouche 1986). Female flowers have a tricarpellar and unilocular ovary filled by one anatropous ovule (Scaramuzzi 1957) and are grouped in inflorescences of 4–21 flowers.

Vegetative growth starts after the flowering period. Following pollination, the zygote remains dormant for several weeks and, finally, fruits grow quickly in mid and late summer until they reach their final size. Females produce many one-seeded drupes. The colour of the fruits is strongly associated with seed viability: black fruits usually contain viable seeds, whereas white and red fruits contain nonviable seeds (owing to abortion or parthenocarpy) (see Jordano (1988, 1989) for more details and Grundwag (1976) for embryology and fruit development).

Frugivorous birds disperse the seeds from September to March (Herrera 1984; Jordano 1989; Verdú and García-Fayos 1994). Ants can act as secondary dispersers (Aronne and Wilcock 1994). Pre- and post-dispersal seed predation is mainly performed by chalcidoid wasps, granivorous birds, and rodents (Jordano 1989, 1990; Verdú and García-Fayos 1996*a*). Seed germination is favoured beneath trees and shrubs (named perches) because of the microclimatic conditions produced under their canopy (Verdú and García-Fayos 1996*b*).

Field observations

Field observations of fruit-set under different pollen densities were made during September 1992 in five Mediterranean sclerophyllous scrublands, located in eastern Spain (Pujol, Porta-Coeli, Duna Punta, Sagunto, and Petrer), that differ in density of *Pistacia lentiscus* individuals. Fruit-set estimations were made at these sites assuming that pollen density was correlated with *Pistacia lentiscus* density. Sex ratios of the populations were also estimated to make a more accurate estimate of pollen availability. Estimates of fruit-set were computed by dividing the number of final sized fruits by the number of initial flowers. The number of initial flowers was estimated as the sum of the number of final sized fruits plus the number of scars left by both flowers and fruits fallen by abscission. Sex ratio was calculated by counting 150 reproductive individuals. Sex ratio could not be estimated in the populations where densities were so low that females were isolated.

Ecological causes of abortion and parthenocarpy: irrigation and pollination experiment

The irrigation and pollination experiment was carried out in 1993 in a single population (Porta-Coeli, Valencia, East Spain), a site 20 km inland, at 200 m elevation, with soils developed on limestone. The vegetation is secondary scrub, dominated by *Pistacia lentiscus*, *Pinus halepensis, Quercus coccifera*, and *Rosmarinus officinalis*. The climate is Mediterranean, with hot, dry summers and mild winters.

A total of 28 females were selected in the population within a 500 × 400 m area. To avoid differences in reproductive success due to resource levels, water distribution, or interspecific competition, females on the same type of soil, on flat topography, and with little or no vegetation beneath them were chosen for comparison. Female size was computed as $\pi R_1 R_2 h/6$, where R_1 and R_2 are the length of the major and minor axes of the vertical projection of the canopy, respectively, and h is the shrub height (Philips and MacMahon 1981). Females were assigned to each of two irrigation treatments (10 irrigated and 18 non-irrigated), balancing the size of the females between both groups ($5.31\ \text{m}^3 \pm 1.10\ \text{m}^3$ and $5.68 \pm 0.84\ \text{m}^3$ for irrigated and nonirrigated females, respectively). Each plant in the irrigation treatment was watered every 2 weeks, from April to September, with 10 L/m^2 of tap water. A total of 110 L/m^2 of water was added to the 107 L/m^2 that rained during the study period.

We selected 15 branches per female with 10 inflorescences per branch to apply the three pollination treatments: pollen exclusion, hand-pollination, and control (28 females × 3 treatments per female × 5 branches per treatment × 10 inflorescences per branch). To avoid an excessive manipulation of the inflorescences, we assumed that the number of flowers per inflorescence was constant for each female. Previous measurement indicated that the variation in the number of flowers per inflorescence within each female was very low (the mean of flowers per inflorescences ranged from 6.7 to 16.6 and CV from 11 to 34%). All inflorescences, except the control ones, were protected with paper bags before anthesis to prevent pollination. When all the flowers had opened, we hand-pollinated them with abundant pollen collected from 10 males from the same population. After the male flowering period, all inflorescences were protected by a gauze bag to prevent fruit predation.

We recorded the number of surviving reproductive structures at the time of each developmental stage considered by Jordano (1988). We recorded (*i*) number of surviving flowers after pollination, (*ii*) number of flowers with latent ovaries before fruit growth, (*iii*) number of final sized fruits, and (*iv*) number of viable seeds.

Because the resources available for a flower are a function of the number of both reproductive and vegetative structures requiring those resources, the following variables were also measured for each of the studied females.

1. Fruit-set: the number of fruits was estimated in September and was divided by the number of initial flowers.
2. Vegetative growth: measured using an index that considered both the length of new shoots and the quantity of new leaves. The average length of 10 shoots was multiplied by either 1, 2, or 3, depending on whether the quantity of new leaves was considered to be low (less than 33% of the plant canopy had new leaves), medium (from 34 to 66% of the plant canopy had new leaves), or high (more than 66% of the plant canopy has new leaves). The plants were measured in late April, when vegetative growth started (Correia et al. 1992), and in September, at the end of the experiment. Initial (April) vegetative growth was substracted from the final (September) vegetative growth to obtain a standardized index for each individual for the period of the experiment.

The number of flowers and viable seeds per female were estimated again in 1994, the year following the experiment, to test whether irrigation influences future reproduction.

Data analysis

The following mixed model ANOVA was run in SPSS statistical package (Norusis 1990) to analyze the data of the four developmental stages

$$[1]\quad Y_{ijkl} = \mu + \mathrm{I}_i + \mathrm{P}_j + \mathrm{IP}_{ij} + \mathrm{F}_{k(i)} + \mathrm{PF}_{jk(i)} + \varepsilon_{l(ijk)},$$

$$i = 1{,}2;\ j = 0{,}..2;\ k = 1{,}..28;\ l = 1{,}..5(ijk)$$

where I (irrigation) and P (pollination) are considered as fixed effects and F (female) as random effects. The experimental error $\varepsilon_{l(ijk)}$ was the surviving percentage of flowers or fruits of each branch. The "pollen exclusion" level of the pollination treatment was not included in the ANOVA of viable seeds, because viable seeds cannot develop without pollination. Other common statistical tests are referred to in the text.

Function of abortion and parthenocarpy

To study the function of both abortion and parthenocarpy, we checked the viability of approximately 50 seeds of each of 33 females from five populations. These populations were the same Mediterranean scrublands where the exploratory observations about fruit-set were made. Fruits were collected in September, 1992 and split to classify them as containing viable seeds, parthenocarpic, or containing aborted seeds, following the information given by Jordano (1989), or as damaged when a little hole was present in the seed coat or a larva of a chalcidoid wasp (*Megastigmus pistaciae*) was found inside (see Traveset 1993*a* for the life cycle of the wasp).

We test for selective abscission of fruits (i.e., retention of aborted and (or) parthenocarpic fruits on branch to reduce wasp predation) by checking seed viability of abscised fruits along the 1992–1993 dispersal season and comparing it with that of fruits on the branch at the start of the dispersal season. The hypothesis of selective abscission of fruits predicts that, if parthenocarpic and (or) fruits with aborted seeds reduce seed predation by wasps, then a lower proportion than expected by random is expected to fall. We placed plastic trays covered with wire mesh under control infrutescences from 29 females in three populations (11 in Pujol, 5 in Duna Punta, and 13 in Porta-Coeli) to collect the abscised fruits while excluding secondary dispersers and predators. Seeds from 2440 fruits (1438 from abscised and 1002 from fruits at the branch) were split to check viability. Fruits were classified as containing viable seed, containing aborted seed, parthenocarpic, containing larva of *Megastigmus pistaciae*, or infected with fungi.

We tabulated the variable "seed viability" into five categories (viable seeds, aborted seeds, parthenocarpic fruits, seeds containing larva, and seeds infected with fungi) and computed a chi-square (χ^2) statistic based on the differences between the observed frequencies (percentage of abscised fruits in each category) and the expected fre-

Table 1. Mean fruit-set (mean ± SE) of five populations with different varying densities of *Pistacia lentiscus*.

Population	Density (individuals per 10 ha)	Fruit-set % (mean ± SE)	*N*
Pujol	250.0	52.95±5.01	16
Porta-Coeli	180.0	51.60±3.43	16
Duna Punta	1.0	30.87±6.11	6
Sagunto[a]	0.5	19.42	1
Petrer [a]	0.006	9.29	1

Note: *N*, number of females studied.
[a]Isolated females.

Table 2. Descriptive statistics of the irrigation and pollination treatments on survival of reproductive structures in *Pistacia lentiscus* females.

	Non-irrigated			Irrigated		
	Pollen excluded	Hand pollinated	Control	Pollen excluded	Hand pollinated	Control
% Flowers after pollination	0.28±0.02	0.78±0.04	0.95±0.01	0.65±0.06	0.96±0.01	0.97±0.01
% Latent ovaries	0.003±0.010	0.42±0.04	0.62±0.03	0.005±0.000	0.57±0.05	0.74±0.04
% Final sized fruits	0.02±0.03	0.54±0.04	0.73±0.03	0.00±0.00	0.45±0.04	0.52±0.04
% Viable seeds	—	0.29±0.04	0.34±0.03	—	0.33±0.05	0.20±0.04

Note: Values are mean ± SE. For non-irrigated females, $N = 18$, and for irrigated females, $N = 10$.

quencies (percentage of fruits in each category counted on the branch at the start of the dispersal season).

Evolution of abortion and parthenocarpy

Evolution of parthenocarpy was reviewed from the literature for the presence of this character in *Pistacia* and other genera of Anacardiaceae. The presence of parthenocarpy in Burseraceae, a sister group of Anacardiaceae (Cronquist 1981; Terrazas 1994; Gadek et al. 1996), was checked in *Bursera fagaroides* and *Bursera morelensis* seeds collected in Atotonilco El Grande (Estado de Hidalgo, Mexico) and Coxcatlan (Estado de Puebla, Mexico), respectively.

Results

Ecological causes of abortion and parthenocarpy: irrigation and pollination experiment

Field observations revealed that fruit-set in *Pistacia lentiscus* increased along with population density and stabilized at high densities ($r = 0.98$; $p = 0.004$; both parameters log-transformed. Data is shown in Table 1). Sex ratio (males to females) for the population of Pujol was 39:61, whereas for Porta-Coeli it was 44:56, which yields 97.5 males per 10 ha in Pujol and 79.2 males per 10 ha in Porta-Coeli, allowing us to assume that more plants mean more males producing pollen. Fruit-set data at different population densities suggest that female reproduction could be constrained by pollen availability at low population densities, although other alternative explanations are also possible (e.g., low-density populations are sparse because they grow under adverse environmental conditions, which could also adversely affect fruit-set). The experimental data supported the pollen limitation explanation at low population density, because the lowest survival of flowers always corresponded to the pollen exclusion group (Table 2). However, there was a significant statistical interaction between female and pollination treatment in the four phases of the experiment (Table 3), indicating that survival of reproductive structures (flower, ovaries, fruits, or seeds) in response to pollination depended on the female.

Irrigation increased the survival of reproductive structures in the first two developmental stages (flowers after pollination and latent ovaries), but not at the later ones (final sized fruit and viable seeds; Table 2). The flowers of the irrigated plants had a higher survival rate than those of the nonirrigated group across the three levels of pollination treatment. However, this increase was quantitatively different across the three levels of pollination (Table 2), and therefore the interaction between irrigation and pollination treatments was statistically significant (Table 3). Survival of latent ovaries from the irrigated plants was higher than survival from the nonirrigated plants, and the effect of irrigation was similar across the three levels of the pollination treatment, as the nonsignificant interaction between irrigation and pollen treatments at this stage revealed (Table 3). Most of the pollen-excluded flowers died at this stage.

Surprisingly, irrigation significantly decreased the survival of final sized fruits. The negative effect of irrigation on fruit survival was consistent across the three pollination treatments (Table 2). Pollen-excluded flowers only survived and developed into parthenocarpic fruits in nonirrigated females, although in a negligible number.

At the last stage (viable seeds), there was a significant interaction between the irrigation and pollination treatments, although the main effect was not significant (Table 3). Irrigation increased seed viability in the hand-pollinated group, but not in the control group (Table 2).

The vegetative growth index in irrigated females did not differ significantly from that of nonirrigated females (142.5 ± 20.5 and 174.4 ± 14.1, respectively; $U = 62$; $W = 117$; $Z = -1.34$; $p = 0.18$; *U* Mann–Whitney test). Similarly, fruit-set on the irrigated females was not different from that on the nonirrigated females (41.2% ± 8.5% and 38.4% ± 7.8%, respectively; $t = -0.23$; df = 26; $p = 0.81$; 2-tailed *t* test).

The increment in the number of viable seeds per number of flowers of the irrigated females in 1994, the year following irrigation, compared with 1993, was highly significant (from 0.06 ± 0.07% in 1993 to 0.32 ± 0.28% in 1994; $t = -3.12$;

Fig. 1. Relationship between seed predation by wasps and (*a*) parthenocarpic fruits and (*b*) aborted seeds, expressed as the percentage of total fruit crop per tree. Data were pooled from five populations. Overlapped data points could not be shown.

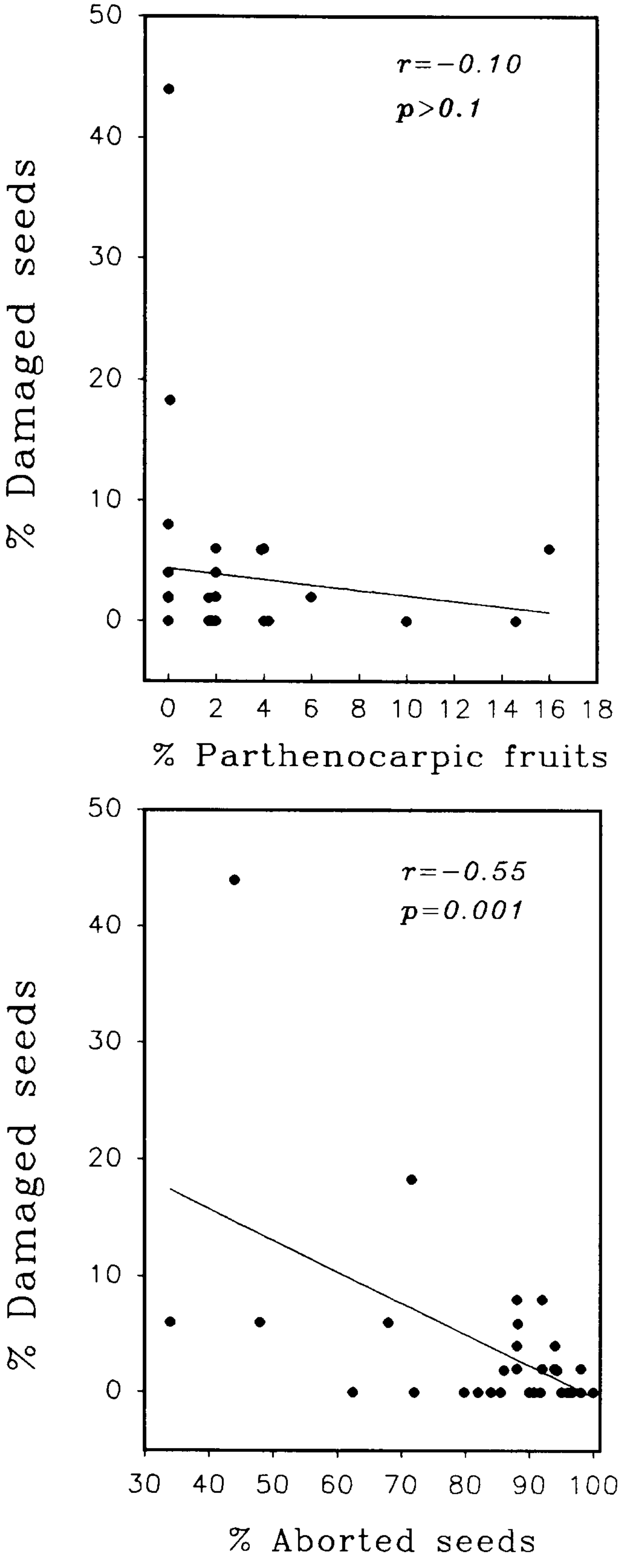

Table 3. Effects of the irrigation and pollination treatments on survival of reproductive structures of *Pistacia lentiscus* females.

Variable	Source of variation	SS	df	*F*
Flowers after pollination	Irrigation	2.93	1	9.98**
	Pollen	21.84	2	66.57**
	Female(Irrigation)	7.63	26	8.23**
	I×P	1.87	2	5.70**
	F(I)×P	8.53	52	4.60**
	Error	11.13	312	
Latent ovaries	Irrigation	0.80	1	5.13*
	Pollen	30.14	2	14.7**
	Female(Irrigation)	4.05	26	3.24**
	I×P	0.36	2	1.37$^{\text{ns}}$
	F(I)×P	6.83	52	2.73**
	Error	14.99	312	
Final sized fruits	Irrigation	1.06	1	6.92*
	Pollen	29.36	1	128.5**
	Female(Irrigation)	3.98	26	2.58**
	I×P	0.61	2	2.67$^{\text{ns}}$
	F(I)×P	5.94	52	1.93**
	Error	18.30	309	
Viable seeds	Irrigation	0.17	1	0.53$^{\text{ns}}$
	Pollen	0.03	1	0.05$^{\text{ns}}$
	Female(Irrigation)	8.34	26	5.66**
	I×P	0.53	1	6.20*
	F(I)×P	2.22	26	1.51**
	Error	12.01	212	

Note: *, $p < 0.05$; **, $p < 0.01$; ns, nonsignificant ($p > 0.05$).

df = 9; $p = 0.01$; 2-tailed paired *t* test), whereas for the nonirrigated females it was not (from 0.15 ± 0.04% in 1993 to 0.27 ± 0.7% in 1994; $t = -1.25$; df = 17; $p = 0.22$; 2-tailed paired *t* test).

Function of parthenocarpy and abortion

The rate of parthenocarpy in natural populations was very low and was not correlated with the rate of seed predation by insects (Fig. 1*a*). However, the abortion rate was high in the same populations. Approximately 70% of the seeds had an early abortion. An inverse relation was found between abortion and predation rates; the greater the rate of abortion, the lower the rate of damaged seeds (Fig. 1*b*). The possibility of an outlier effect in the regression was checked but the relation was still significant after removing one ($r = -0.37$; $p < 0.05$) or two extreme values ($r = -0.38$; $p < 0.05$). Residuals distributed normally ($Z = 1.24$; $p > 0.05$; Kolmogorov–Smirnov test of normality). Crop size (log-transformed) was not correlated to the rate of damaged seeds ($r = -0.07$; $p = 0.69$).

Viability of abscised fruits along the dispersal season was significantly different to that of fruits on the branch at the start of the dispersal season (Table 4). Fruits with aborted seeds abscised in a lower proportion than expected (70.76 vs. 83.17%), whereas parthenocarpic fruits, fruits containing viable seeds, and fruits with seeds containing larvae and fungi fell in a greater proportion than expected.

Table 4. Seed viability of abscised fruits along the dispersal season compared with that of fruits on the branch at the start of the dispersal season in 29 *Pistacia lentiscus* females from three different populations.

Seed viability	Observed frequencies (abscised fruits) (%)	Expected frequencies (fruits on the branch) (%)
Viable seeds	13.37	10.50
Aborted seeds	70.76	83.17
Parthenocarpic fruits	6.09	2.78
Seeds containing larva	7.49	2.92

Note: $\chi^2 = 181.9$; df = 4; $p < 0.0$

Discussion

Pollen and resource limitation may lead to low fruit-sets because of abortion of reproductive structures and development of parthenocarpic fruits. The result of both ontogenetic processes are empty seeds that have been hypothesized to reduce seed predation by acting as a decoy mechanism to predators.

Fruit-set in *Pistacia lentiscus* was low in populations with a low density of individuals. This scarcity of fruits is presumably caused by low pollen availability, as shown by the pollination experiment: only 1 out of 28 individuals developed any fruits in the pollen-exclusion treatment and none of them contained viable seeds. Fruit-set increased as the density of individuals increased, and thus pollen limitation presumably disappeared. This was experimentally supported because hand pollination did not increase female fertility in populations with medium (present study) or high (Jordano 1988) density of individuals of *Pistacia lentiscus*. Similarly, Grundwag (1975) found that copious artificial pollination of several *Pistacia* species, including *Pistacia lentiscus*, did not significantly increase seed set in these species. He also documented a high percentage of abortion (over 50% depending on the species).

As Grundwag (1975) documented, abortion and parthenocarpy are important processes limiting fruit-set in *Pistacia* species. The proximate causes of abortion and parthenocarpy have been linked to pollen and water limitation, whereas the ultimate causes have been linked to the reduction of seed predation effects.

One hypothesis for the cause of parthenocarpy is that parthenocarpic fruits develop because resources are not limited (Willson and Burley 1983). In Mediterranean habitats, water is a major limiting resource (Mooney and Dunn 1970; Aerts 1995; Hobbs et al. 1995), and thus, increased water availability should result in increased rates of parthenocarpy. Jordano (1988) studied rates of parthenocarpy in a *Pistacia lentiscus* population during two consecutive years, and found that the higher rate corresponded to a wet year (47.9%) and the lower to a dry year (35.8%). However, we found that none of the irrigated females developed parthenocarpic fruits in the pollen-excluded flowers. Furthermore, the positive effect of irrigation on survival of reproductive structures during the first developmental stages was lost in the two later stages. Similar results have been found in *Lavandula latifolia*, where irrigation increased both the number of flowers per inflorescence and the fruit-set, but not the number of seeds per fruit (Herrera 1990, 1992). Herrera (1992) suggests that fruit-set is an inherent characteristic feature of individual plants, independent of current resource levels. Likewise, Zahoueh et al. (1991) concluded that reproductive effort and growth differences among individuals of *Pistacia terebinthus* are strongly linked to the life history of each individual (i.e., some individuals suffer more predation than others, individual rhythms and environmental conditions interact in different way across individuals, etc.) rather than to genetic or physiological features. Because uncertainty about water availability is produced along the whole life of each individual of *Pistacia lentiscus* and each individual has different life histories (sensu Zahoueh et al. 1991), then it is expected that fruit-set can be adjusted in different ways depending on the life history of each individual. The adjustment of progeny to the available water resources in *Pistacia lentiscus* is probably an individual feature inherent to the history of each individual, and therefore not exclusively dependent on the current resource level. For this reason, an immediate reproductive or vegetative response to current resource levels would not be expected and the response might be distributed along the life of the individual. We have not found an immediate response to irrigation, either reproductive or vegetative, but a delayed effect at the following reproductive season: irrigated females increased fruit-set from one year to the next in 21.3 percentage points and seed viability in 32.3, whereas non-irrigated females only increased fruit-set in 12.2 percentage points and seed viability in 15.2. This adjustment may have adaptive value in relation to uncertainty about resource availability (Stephenson 1981), because water resources are distributed along the life of each individual depending on their necessity, as suggests the increase of seed set in the next year after experiment.

Parthenocarpy in *Pistacia lentiscus* was not related to seed predation by insects, which contrasts with the results of Traveset (1993*a*) in *Pistacia terebinthus*.

Parthenocarpy is a common character within the genus *Pistacia*. It has been reported for *Pistacia lentiscus, Pistacia chinensis, Pistacia vera, Pistacia khinjuk, Pistacia × saportae, Pistacia atlantica*, and *Pistacia terebinthus* (Copeland 1955; Grundwag and Fahn 1969; Crane 1973, 1975; Grundwag 1975, 1976; Jordano 1984, 1988, 1989; Arista et al. 1990; Traveset 1993*a*, 1993*b*, 1994). There are no studies on parthenocarpy in *Pistacia palaestina*, *Pistacia mexicana, Pistacia falcata, Pistacia weinmannifolia*, and *Pistacia texana*. The most parsimonious hypothesis regarding the evolution of parthenocarpy is that it is a plesiomorphic character within the genus *Pistacia*. Species of other genera within the Anacardiaceae family, such as *Toxicodendron* (Copeland and Doyel 1940), *Rhus* (Grimm 1912 in Copeland and Doyel 1940), *Mangifera* (Kulkarni and Rameshwar 1978 in Schwabe and Mills 1981), and *Spondias* (E. Avitia, unpublished data) also develop parthenocarpic fruits. Overlapping parthenocarpy in the cladogram of Anacardiaceae generated by Terrazas (1994) shows that the most likely hypothesis is that parthenocarpy was already present in the ancestry of the family. However, it is also possible that parthenocarpy evolved in the family at least twice independently, since parthenocarpic genera occur in two different clades within the family. One of these clades contains *Spondias* and the other one the remaining genera. Parthenocarpic fruits are also present in *B. fagaroides* and *B. morelensis* of the family Burseraceae, a sister group of Anacardiaceae (Cronquist 1981; Terrazas 1994; Gadek et al. 1996). Therefore, an outgroup analysis would indicate that parthenocarpy did not evolve twice in Anacardiaceae, but rather the common ancestor already had this character. The ancient evolutionary origin of this character suggests that parthenocarpy could be present in contemporary populations as a result of phylogenetic inertia selected in the past for unknown reasons, or merely a developmental constraint without adaptive value. An alternative possibility is that parthenocarpy could have beneficial effects not addressed in this study.

Many fruits with aborted seeds remained attached to the plant, suggesting that they could have an adaptive value, perhaps by enhancing the conspicuousness of fruit display to dispersers. However, because crop size is not related to seed dispersal rate (Verdú and García-Fayos 1995), it suggests that the retention of fruits containing aborted seeds has not an adaptive value for attracting dispersers. Moreover, most fruits with aborted seeds are white or red, whereas dispersers show a strong preference for black, fertile fruits (Jordano 1984). However, these are observational data, and alternative explanations could be found, as Fuentes (1995), who carried out experimental tests of this hypothesis in *Pistacia terebinthus*, finding that unripe fruits, most of them containing empty seeds, attract dispersers but reduce accessibility to ripe fruits.

On the other hand, empty seeds have been documented to reduce predispersal seed predation by granivorous birds because there is a cost in manipulating fruits containing empty seeds, and therefore birds avoid plants with many empty seeds (Fuentes and Schupp 1998). These costs in *Pistacia lentiscus* may be associated to the bill-weighting behaviour displayed by granivorous birds, such as *Carduelis chloris*, to detect viable seeds (Jordano 1990). We did not address the hypothesis of predispersal seed predation by birds, but we did that of insect seed predation. We have found that the presence of aborted seeds reduced predispersal seed predation rates by insects (chalcidoid wasps) in the same way that Traveset (1993*a*) found in *Pistacia terebinthus*, where parthenocarpic fruits reduced seed predation. Like parthenocarpic fruits, early aborted seeds (approximately 70%) did not contain enough tissues for larval development.

Janzen (1971*a*, 1971*b*) argued that abortion could have an adaptive value in reducing seed predation if (*i*) abortion occurs early in the developmental period, and therefore should not produce a great cost to the plants, and (*ii*) if the number of damaged seeds is independent of the initial fruit-set, so that greater crops do not attract seed predators. In *Pistacia lentiscus*, (*i*) approximately 70% of the seeds had an early abortion and (*ii*) seed crop was not related to the percentage of damaged seeds. Therefore, both conditions are fulfilled in the case of *Pistacia lentiscus*, supporting the hypothesis that abortion may have an adaptive value in reducing seed predation by insects. Supporting this hypothesis, we have found that fruits with aborted seeds abscised in a lower proportion than expected, whereas fruits with seeds containing larvae fell in a greater proportion than expected. Thus, *Pistacia lentiscus* may benefit from the retention of aborted seeds by reducing seed predation effects, at least in the first wasp generation (see Traveset 1993*a*).

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