Deceptive fruits reduce seed predation by insects in *Pistacia terebinthus* L. (Anacardiaceae)

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Summary

The production of seedless fruits (parthenocarpy) is not yet understood from an evolutionary viewpoint, even though it is taxonomically widespread. Here I present a case in which parthenocarpy reduces the incidence of seed predation by insects. At least the first generation of chalcidoid wasps that oviposit in the fruits of *Pistacia terebinthus* L. (Anacardiaceae) cannot discriminate among viable and inviable fruits, allocating energy and time to oviposition on fruits that are not suitable for larval development.

Keywords: parthenocarpy; insect seed predation; chalcidoid wasps; *Pistacia terebinthus*; Anacardiaceae; western Mediterranean

Introduction

Parthenocarpic fruits, prevalent in plant families such as Umbelliferae, Anacardiaceae, Vitaceae, Rutaceae, Musaceae and Moraceae, have intrigued scientists since Darwin (1876). Willson and Burley (1983) have considered the phenomenon to be either a 'mistake', which suggests that there is no resource limitation during fruit development or the result of a developmental error. These authors argue, however, that a real function of parthenocarpy may be discovered, proposing the possibility of dilution of predation on seeds. Recently, Zangerl *et al.* (1991) have shown that parthenocarpic fruits in *Pastinaca sativa* can reduce the effect of insect herbivory, suggesting an adaptive value for them; a lepidopteran frugivore prefers seedless fruits because of their much lower concentration of deterrent furanocoumarins. In *Pistacia terebinthus* L. (Anacardiaceae), I have found that parthenocarpy also reduces insect seed predation, but through a different mechanism.

Methods

Study site and organisms

The study was carried out at Parque Natural de Cazorla, Segura y Las Villas, southeastern Spain, during the fruiting seasons of 1990 and 1991, although preliminary data were gathered in 1989. The study sites are mainly constituted by Mediterranean forest, the common vegetation being *Quercus*, *Phillyrea*, *Arbutus* and *Juniperus*. *Pistacia terebinthus* is a wild dioecious, wind-pollinated tree/shrub, with a circummediterranean distribution (Zohary, 1952). Its fruits (drupes) may result from (1) unpollinated flowers (parthenocarpic), (2) embryo abortions that can occur at different stages of development and (3) normally developed seeds (mature viable fruits) (Fig. 1). An unusual trait of this bird-dispersed species is that its immature fruits are red and become

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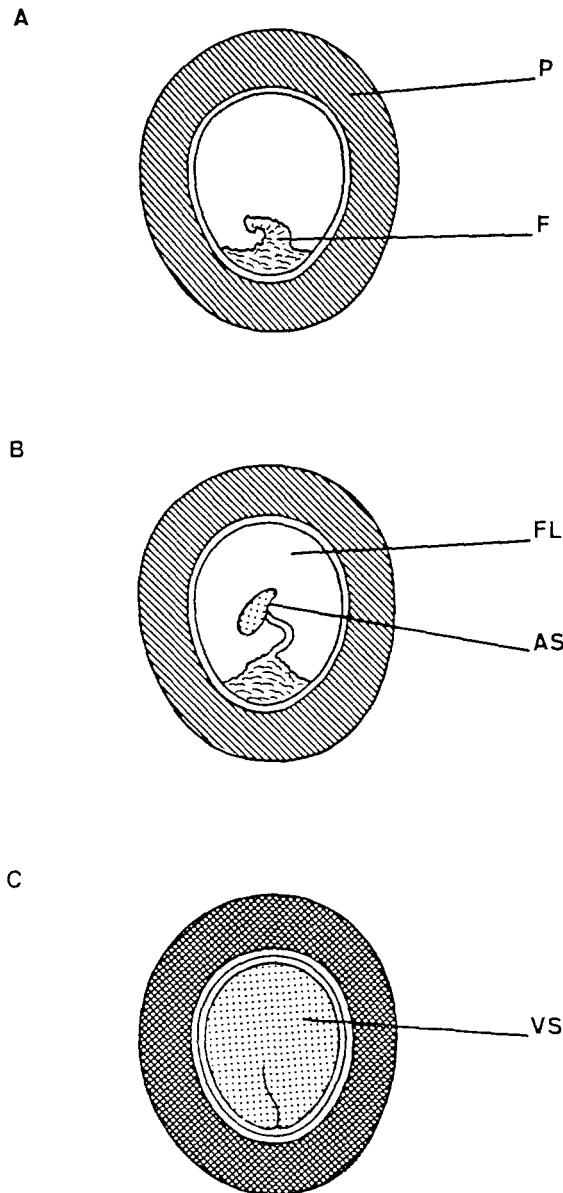
Figure 1. Sketch of the three types of fruits produced by *Pistacia terebinthus*, after removing half of the pericarp and endocarp. (a) Parthenocarpic fruit, with a seed that contains only vestiges of funiculus and ovule (F). (b) Aborted fruit, showing a partially developed seed (AS), still with a large fruit locule (FL). (c) Mature fruit, with a viable seed that fills the whole locule with the normally developed embryo and cotyledons (VS). The pericarp (P) of both parthenocarpic fruits and of immature or aborted fruits is red, which makes them indistinguishable from the outside, and is green in the mature fruits.

green or bluish green when ripe, a pattern opposite to that shown by many bird-dispersed plants. Fruits with inviable seeds are red and of the same size (6.6 ± 0.7 mm long and 5.9 ± 0.7 mm wide, $n = 575$) as the immature viable fruits and are indistinguishable to the human eye (however, they are clearly distinguished if X-rayed; personal observation). Fruit ripening is strongly associated with seed viability, as found in *P.lentiscus* (Jordano, 1989); except on very rare (1.5%) occasions, a green fruit always contains a viable seed, which fills the entire fruit locule. Mature fruits have a significantly higher weight (0.14 ± 0.03 g, $n = 147$) than inviable red fruits (0.09 ± 0.02 g, $n = 150$). Chemical analyses of the organic and mineral content of the pulp of red and green fruits indicate that the most significant difference between them is in their lipid content, almost ten-fold higher in the latter (Traveset, 1993). No differences in secondary compounds have been examined so far.

As in other species of *Pistacia*, parthenocarpy in *P.terebinthus* can occur because the pericarp and the endocarp develop independently of the ovule (Grundwag, 1976). Furthermore, there seems to be a delay in zygote division (Grundwag and Fahn, 1969) and the fertilized ovule reaches its final size several months after flower anthesis and shortly before fruit maturation. In *P.terebinthus*, ripening occurs during September, mature fruits lasting less than 2 months on the plants because of removal by birds. Most final-sized fruits with inviable seeds are retained on the plant for several months (July through to October), after which whole infructescences begin falling off, even before fruits desiccate (Traveset, 1993).

It is the end of June when several species of chalcidoid wasps emerge, the most common of which are *Megastigmus pistaciae* Walker 1871 (F. Torymidae) and *Sycophila* sp. (F. Eurytomidae). These wasps have overwintered as larvae inside the seeds of *P.terebinthus* (Davatchi, 1958; Traveset, 1993). The emerging adult females mate and start ovipositing in the fruits (which already have a hard endocarp). Adult females probably lay only one egg within each fruit because seeds bear a single larva; only on one occasion were two larvae found within a seed. Attacked fruits remain red and resemble intact ones. Pupation occurs within the seeds, second-generation adults emerging by mid-August (personal observation in the laboratory). *Sycophila* may produce a third generation before the end of the fruiting period, since adults keep emerging as late as mid October and females are observed to oviposit at this time (Traveset, 1993). A female wasp can visit many fruits per day, although it does not oviposit in all of them. It can spend up to 30 min on a single fruit before ovipositing (personal observation in the field), although this does not seem to be typical.

From each of 28 individuals selected randomly from two populations I dissected fruits (usually 50 per individual), both in 1990 and 1991, in order to determine the proportions of (1) parthenocarpic fruits, (2) fruits with aborted seeds, (3) wasp-damaged seeds and (4) fruits with viable seeds. Fruits were collected towards the end of August, before they had ripened and birds began removing them. Fruit crop (total fruit production) was recorded for each individual. In 1989, I dissected fruits from 74 plants, although I recorded only the proportion of seeds damaged by wasps.

Results and discussion

Parthenocarpy in *P.terebinthus* reduces seed predation by wasps. The higher the proportion of parthenocarpic fruits per crop, the lower is that of wasp-damaged seeds (Fig. 2). The wasps appear to be specific to *Pistacia* (Davatchi, 1958) and can damage almost 50% of the seed crop on some individuals, although the average level of damage is about 9% (± 9%, $n = 129$).

When laying an egg, a wasp embeds the entire ovipositor in the fruit pulp and the endocarp. Wasps of the first generation cannot distinguish between fruits that will contain a viable seed from
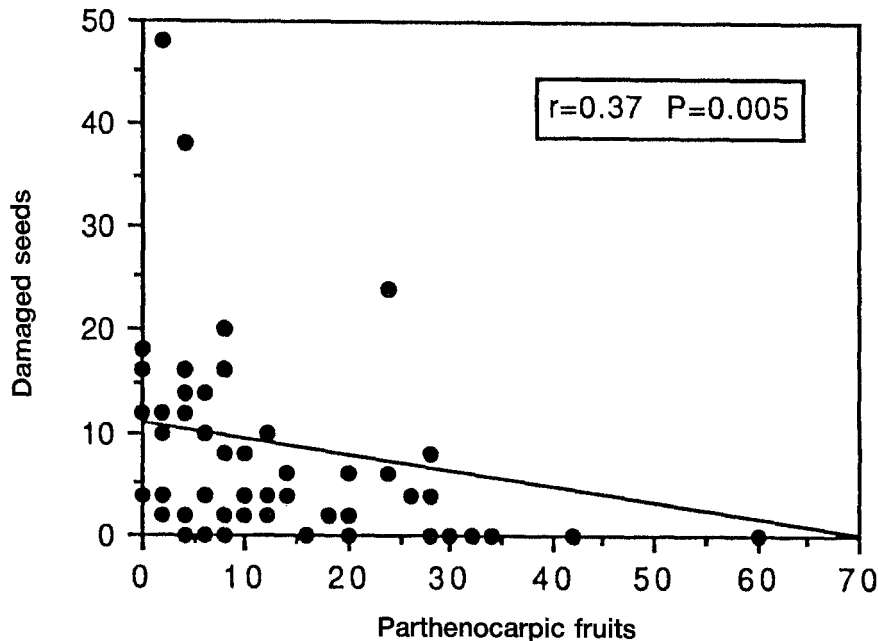
Figure 2. The inverse relationship between parthenocarpic fruits and seeds damaged by wasps, expressed as proportions of total fruit crop per tree. Data from 1990 and 1991 are pooled.

those that will not because, by that time (end of June), ovules are not enlarged yet and thus they must be making many 'mistakes' when ovipositing. In introducing the ovipositor, the wasp may detect differences in ovule sizes and avoid those that have not grown. However, this wasp decision, if it actually takes place, is only possible for the second wasp generation (that emerging in mid-August), when ovules have begun to enlarge. Wasps of the second generation appear to oviposit invariably in red fruits, even when green (ripe) ones are available. I have never observed a wasp ovipositing in a green fruit, which may be interpreted as a way to avoid being eaten by frugivorous birds (mainly by those that act as seed predators), since these usually consume all mature fruits (Traveset, 1993).

The proportion of parthenocarpic fruits found per crop indicates that indiscriminating wasps are wasting time and energy that might be allocated to fruits with viable seeds. That proportion can vary significantly among years, depending upon factors such as the weather conditions during the pollination period (April–May). In 1990, it averaged $18 \pm 14\%$ ($n = 28$ individuals), whereas in 1991 (with much less rain during those 2 months than the previous year) the mean was $8 \pm 8\%$ ($n = 27$). In some individuals, parthenocarpy can represent up to 60% of the total fruit production. The proportion of parthenocarpic fruits was not significantly correlated ($p > 0.05$) with fruit crop size in any of the 2 years.

From the wasps's perspective, the first generation (end of June) experiences a mistake rate equivalent to the ratio of number of parthenocarpic fruits : total number of red fruits (total crop). This mistake rate was on average $18 \pm 14\%$ ($n = 28$) in 1990 and $8 \pm 8\%$ ($n = 27$) in 1991. If the second wasp generation does not distinguish between fruits suitable for development and unsuitable ones, the mistake rate will increase through the season, as fruits ripen and become green-coloured. Assuming those wasps do not discriminate, the rate in mid-September rose only slightly (and insignificantly, due to the usually low proportion of the crop that matures) to $19 \pm$

14% in 1990 and to 10 ± 11% in 1991. If the wasps recognize perfectly well the fruits with no embryos and avoid ovipositing in them, that mistake rate obviously decreases to zero. Wasps can develop well in late-aborted seeds, which contain some green endosperm (Traveset, 1993), but cannot in early-aborted seeds. Therefore, the mistake rate will be even higher when considering that a proportion (not estimated here) of the embryos abort at an early stage and are not suitable for wasp development.

The possibility that parthenocarpic fruits might also attract a higher number of seed dispersers cannot be dismissed (Jordano, 1989); however, no evidence has been found in this species (and has never been reported for others) that plants with a greater proportion of empty fruits attract a larger coterie of dispersers or increase the removal of viable fruits (Traveset, 1993).

Parthenocarpy in *P.terebinthus* currently has an adaptive value by reducing offspring mortality. Nevertheless, its origin is probably not related to seed predation. Within the genus *Pistacia*, fruit traits are remarkably conservative (Grundwag, 1976; Jordano, 1989), suggesting developmental controls established long before the existence of current ecological conditions. Furthermore, the production of fruits with inviable seeds may be triggered by the particular conditions that a plant experiences during the pollination period (Crane, 1975; Jordano, 1989) or during the process of fertilization and early growth of fruits (Grundwag and Fahn, 1969; Grundwag, 1976). Parthenocarpy may have its origin in these physiological mechanisms, in some past selective pressure (being an exaptation) or even in a quirk of fate. Yet, it appears to play an important role in some cases as a defence against seed predators.

Acknowledgements

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