

# Reproductive biology of *Phillyrea angustifolia* L. (Oleaceae) and effect of galling-insects on its reproductive output

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Manuscript received April 1993, accepted for publication October 1993

TRAVESET, A. 1994. **Reproductive biology of *Phillyrea angustifolia* L. (Oleaceae) and effect of galling-insects on its reproductive output.** The breeding system of *Phillyrea angustifolia* is examined in several Spanish populations, both in the southeastern Iberian Peninsula and in the Balearic Islands. Hand-pollination experiments performed on one of the mainland and on one of the island populations demonstrated that the plant is functionally androdioecious. Pollen from males was several times more fertile than pollen from hermaphrodite flowers or self-pollen in the island population, but not so in the Iberian Peninsula. The interpretation of such a result is that androdioecy must have an adaptive advantage in an island system, where inbreeding depression is expected to be greater. Male individuals are much less common than hermaphrodites in all populations studied, thus supporting the prediction made by the models for the maintenance of androdioecy. Sex expression in an individual plant differs between populations. The frequency of sexes was purely bimodal in one population, whereas it was not so in another. Pollen from both male and hermaphrodite flowers appears to be morphologically different, although it remains unknown at what stage of the fertilization process the difference becomes functional. Fruitset in the hermaphrodite individuals was always less than 10%. Most fruits abort at an early stage and there is also a great flower abscission. Fruitset does not appear to be influenced by any of the plant traits describing size or fecundity. A high unpredictability of flowering in an individual was also observed in all populations. *P. angustifolia* is attacked by a cecidomyiid fly that induces the formation of galls in the ovaries (producing 'deformed' fruits which have been confused until recently with parthenocarpic fruits), thus reducing the plant reproductive output. The production of such galls (most of them in the hermaphrodite individuals but a small proportion also in males) is highly variable among plants and among populations, representing from 0 to 97% of the initiated fruits. Such variability in gall incidence does not respond to variability in plant size, fecundity, distance to flowering conspecifics or time that flowers are available for fly oviposition. A high consistency in gall production was found in both the mainland and the island populations. The greater abundance of galls in the islands compared with the mainland populations is interpreted as a result of the higher temperatures in the former which might influence the activity period of the flies.

**ADDITIONAL KEY WORDS:**—Androdioecy – breeding systems – sex expression – Cecidomyiidae – insect galls – southeastern Spain – Balearic Islands.

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## INTRODUCTION

Androdioecy (the presence of male and hermaphrodite individuals in a breeding population) has been shown to be extremely rare in plants (Darwin, 1877; Lloyd, 1975; Yampolsky & Yampolsky, 1922). The phenomenon has been claimed in some floras and botanical studies for a number of species (Charlesworth, 1984). For most of the reported cases, however, the species have proved to be andromonoecious—with males and hermaphrodites on the same individual—(see Charlesworth, 1984), or functionally dioecious—with hermaphrodites producing non-viable pollen (see Anderson & Symon, 1989; Haber & Bawa, 1984; Kevan, Longair & Gadawski, 1985).

Models for the maintenance of androdioecy predict that the frequency of male plants should be much lower than that of hermaphrodites, but that they should be at least twice as fertile (Charlesworth, 1984; Charlesworth & Charlesworth, 1978; Lloyd, 1975). Such requirements make this breeding system unlikely to be evolutionarily stable, and that is why Charlesworth (1984) even questions whether functional androdioecy exists at all, arguing that only the morphological features of the species described as androdioecious are correct. Anderson *et al.* (1988) have found that the palm *Orbignya phalerata* Mart. is morphologically androdioecious but functionally subdioecious. Likewise, Thomson *et al.* (1989) report *Ricinocarpus pinifolius* Desf. as an androdioecious species, even though the species would be best categorized as simply monoecious given the continuous distribution of floral gender that it displays.

According to Liston *et al.* (1990) and to Fritsch & Rieseberg (1992), the only documented case in which androdioecy occurs and is maintained is *Datisca glomerata* (Datisceae). Rieseberg *et al.* (1992) further argued against the traditional prediction that androdioecy is an intermediate step in the formation of dioecy from hermaphroditism, maintaining rather that androdioecy may be derived from dioecy, at least in the Datisceae.

Recently, in a study carried out in southern France, Lepart & Dommée (1992) reported *Phillyrea angustifolia* L. (Oleaceae) to be functionally androdioecious in one population and functionally dioecious in another. They considered androdioecy in this species as a kind of 'leaky' dioecism, suggesting that the ability of hermaphrodites to be functionally male and female could be particularly adaptive in founding populations.

In the present study, sex expression and the breeding system of *Phillyrea angustifolia* was examined in various populations in southeastern Spain and also in the Balearic Islands. Cross hand-pollinations were made to assess whether androdioecy is maintained by a higher fertility of male pollen than of hermaphrodite pollen.

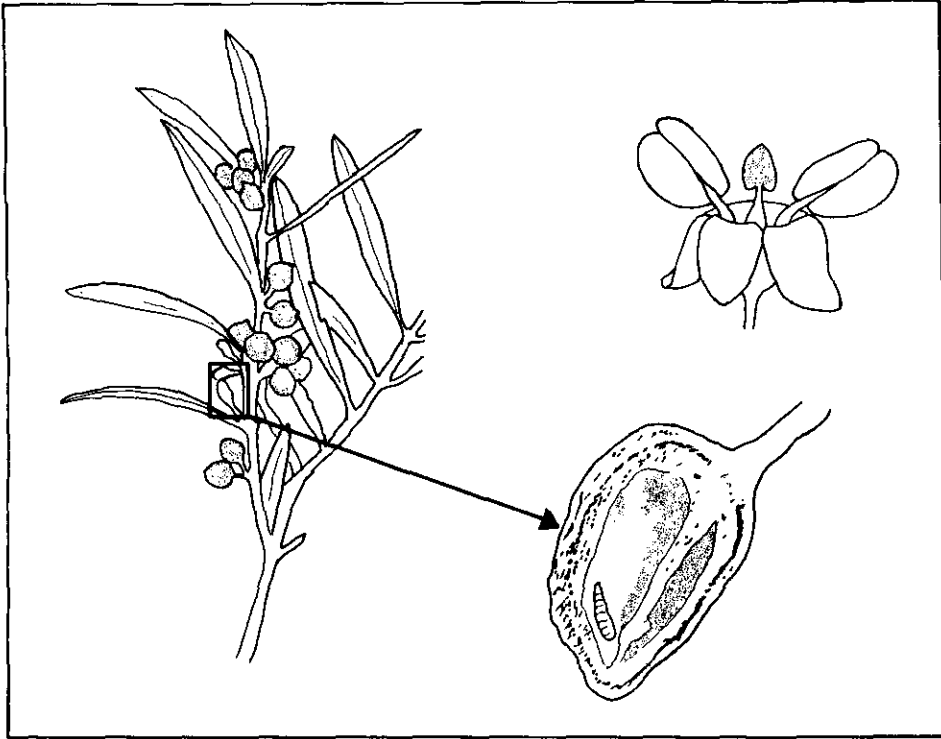


Figure 1. Diagram of a branch of *Phillyrea angustifolia* bearing full-size fruits and insect galls, and sketch of a longitudinal section of a gall showing the fly larva inside. A hermaphroditic flower is also shown at the upper right corner.

*Phillyrea angustifolia* presents another particular phenomenon which is the presence of insect-galls that replace fruits (Fig. 1). These galls look like green deformed fruits (without seeds and bearing a minute insect larva inside) and have been confused with parthenocarpic fruits (Campbell, 1915; Lepart & Dommée, 1992). Given the abundance of such galls in some individuals, another goal of this study was to determine (1) their negative effect on the plant reproductive output, (2) the variability within and among populations in the number of galls per plant, and (3) the consistency of gall incidence in an individual plant in successive years.

#### MATERIAL AND METHODS

##### *Study sites*

Between 1989 and 1991, the study was undertaken at Parque Natural de Cazorla, Segura y las Villas (southeastern Spain). Two populations of *P. angustifolia* were examined, one in El Agracea (AG hereafter) and the other in Hoyos de Muñoz (HM hereafter). Both sites are located in the Guadahornillos Valley, between 1100 and 1200 m. They are occupied by dense mediterranean forest, mainly comprising *Quercus*, *Phillyrea* (both *latifolia* and *angustifolia*), *Arbutus* and *Juniperus*. Detailed descriptions of the vegetation and climate of the area can be found in Polunin & Smythies (1973: 83–89). Mean monthly temperatures

range from 4° (January) to 21°C (August). Mean annual precipitation at the nearest station is about 1200 mm.

In autumn 1991 and during 1992, *P. angustifolia* was examined in the Balearic Islands, mainly in Cabrera. This island has an area of only 1500 ha. and is largely mediterranean scrubland, with a vegetation dominated by *Pistacia lentiscus*, *Phillyrea*, *Olea*, *Juniperus phoeniceae* and *Euphorbia dendroides*, among others. *Pinus halepensis* is also commonly found in some parts of the island. Two sites were chosen for the study, one being a section of the main trail around the harbour (Port hereafter) and the other being in front of Cala Gandulf (CG hereafter). The mean monthly temperatures range from 8° (January) to 28°C (August). Total annual precipitation is low; in 1992 it was only about 300 mm.

The pollination experiment in 1992 was performed on Mallorca Island, in a population near Port des Canonge (PC hereafter) where this plant grows among other mediterranean taxa such as *Quercus*, *Erica*, *Arbutus* and *Cistus*.

#### Study organisms

*Phillyrea angustifolia* L. is an evergreen shrub or small tree 1–5 m tall found all over the western Mediterranean region. It is common in maquis formations both in the Iberian Peninsula and in the Balearic Islands. The anemophilous flowers are white-yellowish, 3–4 mm in diameter, and clustered in groups of four to ten in the leaf axils. Anthesis is asynchronous in an individual plant (even within a raceme) and the flowering period lasts between two and four weeks (Fig. 2). Flowering occurs generally between mid-March and mid-April, although in colder years it may be extended to mid May (pers. obs. in Cazorla in 1990 and 1991). Both male and hermaphrodite individuals start flowering simultaneously, and the flowers are open for 3–7 days (pers. obs.). Styles and

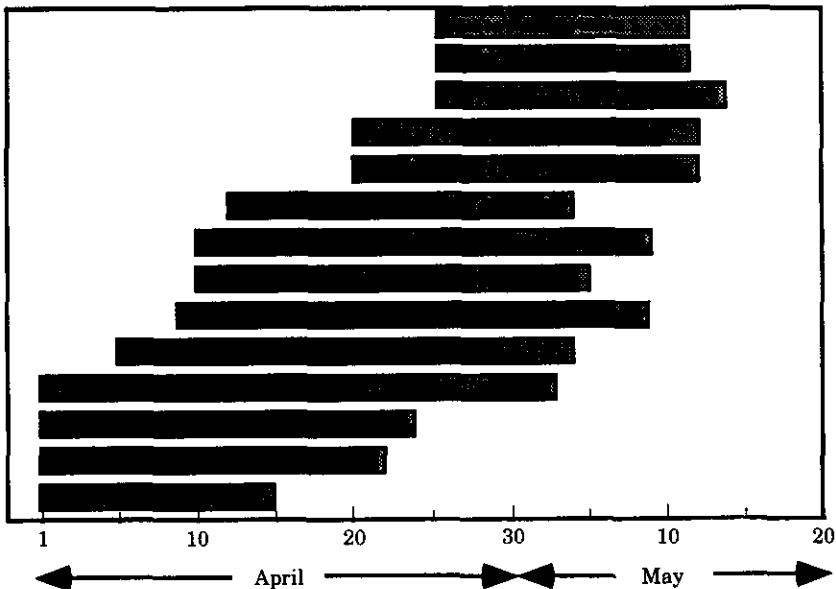


Figure 2. Flowering phenology of 14 individuals of *P. angustifolia*. Data from 1990. Each line represents the entire period during which flowers are open.

stigmas reach full size two or three days before stamens dehisce. The stigma of a flower is globular (bilobate); it is receptive for 2–3 days, appearing with a spongy texture and being able to receive its own pollen (Lepart & Dommée, 1992, and pers. obs.). The ovary is bilocular, each loculus bearing two seminal primordia; generally, however, only one primordium per flower is fertile (Herrera, 1987). The pistils of male flowers are clearly different from those of hermaphrodite flowers; the ovary is not well developed, the style is shorter and the stigma has a brownish colour and lacks the latter's spongy texture.

The ovaries start growing after fertilization, reaching full size towards the end of August. Mature fruits are bluish-black drupes, 4–8 mm in diameter, and are dispersed by birds during the autumn. The plant does not flower consistently every year, and in some flowering hermaphrodite individuals not a single fruit ripens. In general, fruitset is low, and those fruits that are initiated have a high probability of abortion before reaching maturity. In the Balearic Islands, some seeds have been found bearing an exit hole of an insect not yet identified.

During the flowering period, adults of the cecidomyiid fly, *Schizomyia phillyreae* Tavares (Diptera: Cecidomyiidae) oviposit into the open flowers of *P. angustifolia*. The gall begins to form 6 to 8 weeks after flower fertilization. Before this time, galls are indistinguishable from intact small fruits. The larva grows slowly inside the ovary and remains there for a long period that can reach three years (Traveset, 1992). Not all flies from the same cohort, even within a plant, emerge the same year, which is interpreted as an adaptation to the unpredictability of flowering in *P. angustifolia* in a given year (Traveset, 1992). The same species of fly inducing the same type of galls has been usually observed in *P. latifolia* in Cabrera island (in Cazorla, however, plants of this species only rarely bear galls; pers. obs.). Flies have been observed on both male and hermaphrodite individuals. Whether and how they discriminate between the two type of flowers remains unknown.

#### *Pollination experiment*

In April 1991, seven hermaphrodite individuals, bearing enough buds to carry out the hand-pollination experiment, were chosen from the AG population. Several branches were bagged (with white paper bags) from each plant, and were checked periodically for flower anthesis. When enough flowers were open and had receptive stigmas, pollination was initiated. One control group of 30 individual flowers, distributed on different branches, was marked and left unbagged to determine fruitset in normal conditions. Three treatment crosses, of 30 flowers each, were made: (1) *geitonogamous cross* (flowers were pollinated with pollen of other flowers in the same plant), (2) *male cross* (with pollen coming from male flowers of male individuals) and (3) *hermaphrodite cross* (with pollen coming from hermaphrodite flowers of hermaphrodite individuals). Pollinations were performed between April 30 and May 8, by means of a thin paintbrush, depositing pollen directly on recently receptive stigmas. All treated flowers were individually labelled. The branches were again bagged after pollination; bags were removed 5–6 days later, when fertilization had already taken place. The number of initiated fruits from each marked flower was counted on June 22. Fruits were later checked for abortion and maturation on July 25 and again on August 28.

The same experiment was repeated on April 4–6 1992, with three plants in the PC population. The number of initiated fruits was recorded on June 6, and fruits were subsequently checked on July 25 and August 23.

#### *Sex expression*

In order to determine the proportion of flowers of each sex per individual plant, the sex of all flowers on a minimum of five twigs was recorded for a total of 55 individuals in Cabrera island (24 from the CG population and 31 from the Port population) and for 11 plants in Mallorca island (PC population).

#### *Fruitset and gall incidence*

To evaluate fruitset and proportion of initiated fruits that became galls, the total number of flowers in five marked branches from a total of 32 individuals from AG and 8 individuals from HM were counted on April 23–24 1990. On May 30–31, records of the number of initiated fruits, and on July 23–24, the number of fruits and galls produced in each marked branch and also the total per plant was taken. Plant height, crown diameter, flower crop and average distance to the two nearest conspecific flowering plants were measured in 13 individuals to determine whether they had any influence on fruitset and number of galls per plant. Also, from a sample of 14 plants, the period during which flowers were open and available for fly oviposition was recorded in order to know if the number of galls per plant was correlated with it.

Fruitset was again obtained on May 8 1991, from a total of 19 hermaphrodite plants (7 from AG and 12 from HM). The number of initiated fruits was recorded on June 22 and the number of maturing fruits and galls on August 28. In AG, all flowers in six male individuals were also counted on May 8, and later checked for any initiated fruits.

The proportion of flowers that became fruits and galls was also determined in one of the populations (CG) of Cabrera island. On April 13 1992, the flowers on three marked branches in 12 hermaphrodite plants were counted, recording the number of initiated fruits on May 23 and the number of fruits and galls on July 1 and again on September 3. The incidence of galls in Cabrera island was examined in a total of 22 individuals from the Port population and in 17 individuals from the CG population.

Pollen from both male and hermaphrodite flowers from at least three plants was examined under the scanning electron microscope (SEM). Open anthers were placed on double-sided sticky tape on aluminium stubs, and after being dried they were coated with approximately 200 Å of gold for viewing. SEM micrographs were taken of each pollen morph.

Non-parametric tests (Spearman correlations) were used for data that were not normally distributed. All means are given with their standard deviations.

## RESULTS

### *Hand-pollination*

Of the pollinations performed during 1991 in Cazorla, no significant differences among treatments were obtained in the proportion of flowers that

initiated fruits in June ( $X^2=3.79$   $P>0.05$ ) or that developed into full-sized fruits ( $X^2=2.63$  and  $X^2=2.35$   $P>0.05$ , for the July and September fruit counts, respectively) (Fig. 3A). An average of only 16% of the flowers in the control group initiated fruits compared with about 40% in the hermaphrodite- and male-crosses. At the time of maturation that figure had fallen to 5% for the control flowers and to 24% and 18% for the hermaphrodite and male crosses, respectively. There was, however, much variation within each treatment.

In contrast, the pollinations performed in Mallorca island in 1992 showed highly significant differences among treatments (Fig. 3B;  $F_{3,8}=7.78$   $P<0.01$  in June,  $F_{3,8}=13.52$   $P<0.01$  in July, and  $F_{3,8}=4.15$   $P<0.05$  in September). Pollen from male individuals gave the greatest fruitset (43% of the flowers initiated fruits) whereas flowers pollinated with pollen from hermaphrodite individuals or self pollen gave a fruitset of 11% and 4%, respectively. By September

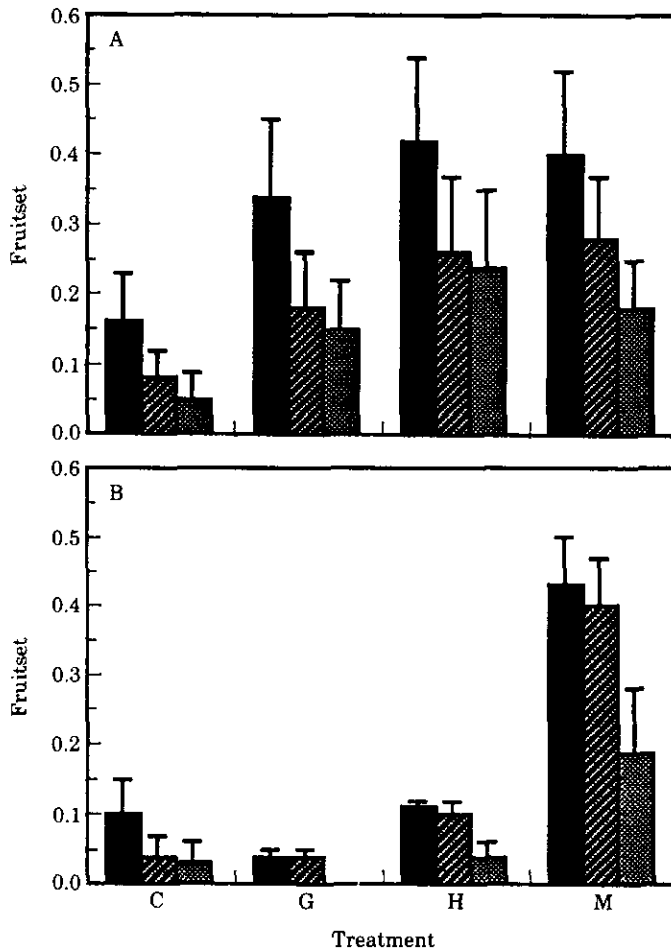


Figure 3. Number of fruits relative to number of flowers produced for each of the three treatments: G (geitonogamous cross), H (hermaphroditic cross) and M (male cross) and for the controls (C) in each of the two populations AG(A) and PC(B). Bars indicate the standard error of the mean. ■ June ▨ July ▩ September.

(maturation time), fruitset was about 20% in those flowers fertilized with male pollen and less than 5% in all other treatments and in the control group.

*Sex expression and sex ratio*

Figure 4 shows the relative frequencies of male flowers in both hermaphrodite and male individuals in the two populations studied in Cabrera island. It can be observed that while in the CG population there are hermaphrodite plants with nearly 50% of their flowers being male, and male plants with *c.* 25% of their flowers hermaphrodite, in the Port population the frequency distribution of sexes is much more bimodal, all males examined having 100% male flowers and hermaphrodite plants having a maximum of *c.* 15% male flowers.

In the Mallorcan population (PC), 9 of the 11 plants examined were hermaphrodites that had no male flowers, except for one individual which bore

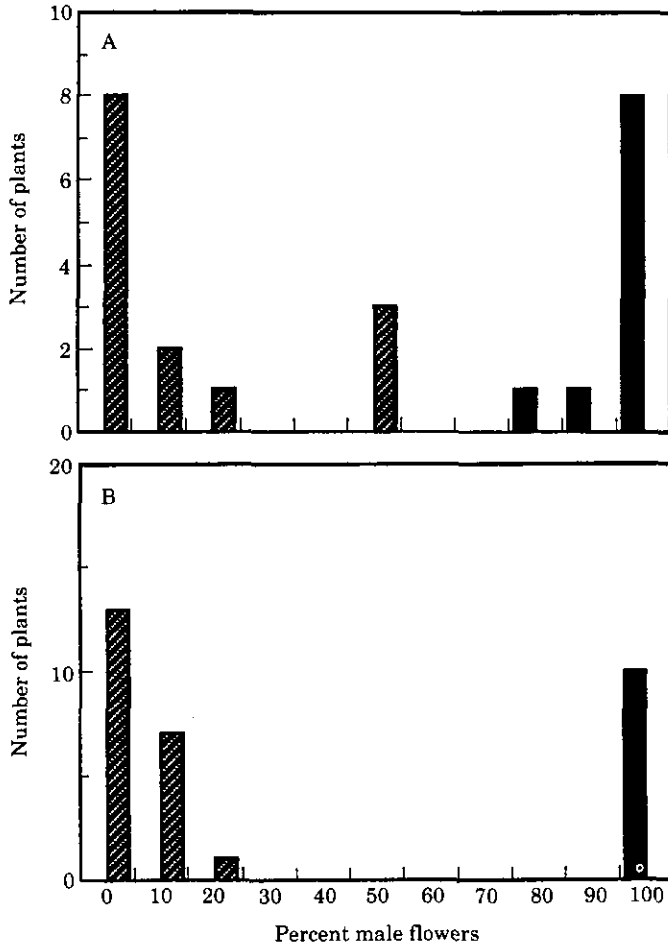


Figure 4. Relative frequencies of male flowers in hermaphrodite (striped columns) and male (black columns) individuals in the Cala Gandulf (A) and in the Port (B) populations.



3.1% male flowers; the other two were males, one having 100% and the other 72.8% male flowers.

The sex ratio in PC, estimated from all flowering individuals over an area of c. 2500 m<sup>2</sup>, was 27 hermaphrodites: 7 male plants.

In Cabrera island, the proportion of males was also lower than that of hermaphrodites. In the Port population sex ratio was about 21 hermaphrodites: 10 males while in CG it was 19 hermaphrodites: 12 males.

In the two populations of southeastern Spain, sex ratio was not determined; however, the great fructification of this species in both populations during 1989 showed that the large majority of individuals were hermaphrodite since they produced fruits.

#### *Fruitset and gall incidence*

In 1990, the proportion of flowers that initiated fruits was, on average, 21.1% ± 20.0% (*n* = 32) in AG and 6.0% ± 0.12% (*n* = 8) in HM. Except for three fruits in one plant and seven fruits in another from the former population, none of those initiated fruits reached maturity. More than half became galls (Table 1) and the rest were aborted at an early stage of fruit growth. The production of galls per plant was 68 ± 124, ranging from 0 to 548 (*n* = 40). In 1989, the proportion of initiated fruits that became galls was apparently lower than in 1990, especially in the AG population where galls represented less than 5% of the initiated crop (Table 1). This year, fruit crop was high in the two populations: 1319 ± 1881 (*n* = 40) in AG and 519 ± 905 (*n* = 50) in HM.

Neither fruitset nor number of galls per plant appeared to be significantly correlated with any of the plant traits measured: size (height and crown diameter), fecundity (flower crop) and average distance to flowering conspecifics (all *P* > 0.05; *n* = 13). The period during which flowers were open and available for fly oviposition in a plant did not appear to influence the incidence of galls either.

In 1991, fruitset in the hermaphrodite plants from AG and from HM was on

TABLE 1. Mean and standard deviation of the number of galls produced per plant during the years of study in the different populations. The proportion of the initiated fruit crops that became galls is given in parentheses. *n* is the number of plants examined

Population	1989	1990	1991	1992
Cazorla				
AG	19.3 ± 46.5 (3.2% ± 6.7%) <i>n</i> = 40	83.4 ± 134.7 (54.7% ± 22.6%) <i>n</i> = 32	38.4 ± 78.4 (34.8% ± 76.2%) <i>n</i> = 7	—
HM	85.4 ± 132.4 (33.0% ± 36.0%) <i>n</i> = 50	8.8 ± 12.3 (51.3% ± 41.3%) <i>n</i> = 8	104.0 ± 77.3 (63.6% ± 30.8%) <i>n</i> = 12	—
Cabrera				
Port	—	—	352.1 ± 342.3 (52.0% ± 35.7%) <i>n</i> = 27	227.2 ± 379.8 (—) <i>n</i> = 22
CG	—	—	192.0 ± 624.6 (36.9% ± 43.7%) <i>n</i> = 25	324.3 ± 768.3 (—) <i>n</i> = 17

average  $21.6\% \pm 15.0\%$  ( $n=7$ ) and  $28.8\% \pm 20.7\%$  ( $n=12$ ), respectively; none of the six males examined in AG produced a single fruit. The proportion of flowers that developed into mature fruits was only  $2.3\% \pm 2.9\%$  in AG and  $0.1\% \pm 0.3\%$  in HM. The number of galls per plant ranged from 0 to 257, being significantly higher in HM (Table 1). The average flower crop this year was  $628.76 \pm 464.06$  ( $n=25$ ) and was not correlated with either fruitset or gall abundance ( $P>0.05$ ).

In Cabrera island, mean flower crop in 1992 was  $4356 \pm 519$  ( $n=42$ ). The proportion of those flowers that initiated fruits was  $33.6\% \pm 27.4\%$  ( $n=12$  plants from CG population), and the proportion that became full-size fruits was only  $9.2\% \pm 12.6\%$ . In the Port population, fruit production was  $177 \pm 443$  ( $n=22$ ), representing only  $5.0\% \pm 5.8\%$  of the flower production. Fruit crop in 1991 had been  $1068 \pm 1734$  ( $n=25$ ) in CG and  $836 \pm 1499$  ( $n=27$ ) in the Port population.

#### *Consistency in flower, fruit and gall production over time*

Only 11.4% of the plants that flowered in 1989 produced flowers again in the two following years in the populations of southeastern Spain. Of the plants examined in AG and in HM in 1989, 68.4% and 50%, respectively, did not flower in the two subsequent years. Other plants (13.2% in AG and 34.0% in HM) flowered in 1989 and in 1991 but not in 1990.

In contrast, consistency in flower production between 1991 and 1992 was great in Cabrera island. Of the 25 flowering plants examined in 1991 in CG, 23 (92%) flowered again in 1992. In the Port population, all flowering plants examined in 1991 flowered again in 1992. However, none of those plants in the two populations flowered in 1993.

A significant correlation ( $r=0.87$ ,  $P=0.0002$ ,  $n=12$ ) was found between fruit production in 1990 and in 1991 in the populations of southeastern Spain, but not between that in 1989 and the other years. There was also a negative correlation between fruit crop in 1989 and flower crop in 1991 ( $r=-0.83$ ,  $P=0.01$ ,  $n=8$ ), but not with that in 1990. In the two populations of Cabrera, no significant correlations were observed between flower or fruit crops in 1991 and 1992.

Gall production in AG and HM was consistent between 1989 and 1991 ( $r=0.91$ ,  $P<0.01$ ,  $n=7$ ), but not in 1990. In Cabrera, there was a high correlation ( $r=0.72$ ,  $P<0.001$ ,  $n=37$ ) between number of galls produced in 1991 and in 1992.

## DISCUSSION

### *Breeding system*

*Phillyrea angustifolia* appears to have a labile breeding system which can differ even among populations that, at a geographical scale, are not much separated from each other. The results of the hand-pollination experiment performed in the populations of southeastern Spain showed that pollen from male individuals was not significantly more fertile than pollen from hermaphrodite individuals or self-pollen. Open pollination gave a significantly lower fruitset (number of initiated fruits: number of flowers), indicating that pollination in this species may be limiting the number of seeds produced, at least during some years, and

probably depending upon the weather conditions. In contrast, the results obtained in the Mallorcan population showed that male pollen was several times more fertile than pollen from hermaphrodites or self-pollen. The number of final-size fruits produced was also significantly higher in those flowers fertilized with male pollen. SEM micrographs show that pollen of male flowers is morphologically different from pollen of hermaphrodite flowers, the former being more porous than the latter (Fig. 5). Whether such porosity is of great importance during the fertilization process is unknown. Lepart & Dommée (1992) report that both types of pollen are viable and germinate *in vitro* at a similar rate.

Sex ratios in the studied populations appeared to be biased, male individuals being much less common than hermaphrodites, which supports the prediction made in the models for the maintenance of androdioecy (Charlesworth, 1984; Charlesworth & Charlesworth, 1978; Lloyd, 1975).

Interestingly, sex expression in an individual of *P. angustifolia* varies among populations. So, for instance, while in CG the frequency of sexes was not completely bimodal, the plants in the Port area, just a few kilometers apart, were purely (or almost purely) hermaphrodites or had 100% male flowers. Such results contrast with those reported by Lepart & Dommée (1992) who found that male individuals never produce hermaphrodite flowers and that most hermaphrodites bore male flowers at a low frequency.

The existence of hermaphrodites bearing male flowers could be considered, as Lepart & Dommée (1992) point out, to be an indication of andromonoecy, a breeding system commonly found in other species of the Oleaceae family such as *Olea europaea* (Brooks 1948; Fernández 1979; Uriu 1959). *Phillyrea media* and *P. latifolia* have been reported to be andromonoecious by Campbell (1922) and

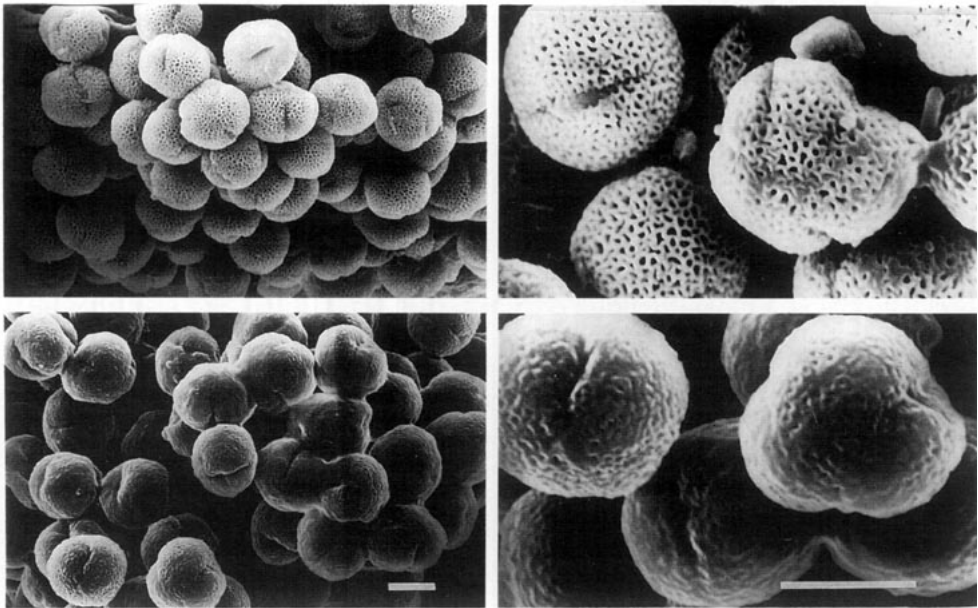


Figure 5. SEM photographs of pollen grains from male flowers (above) and hermaphrodite flowers (below). Scale bars = 10  $\mu\text{m}$ .

Armenise (1956), respectively. These two authors, however, examined only floral morphogenesis and not the overall sex expression of individual plants. My observations on *P. latifolia*, both in southeastern Spain and in the Balearic Islands, coincide with those made by Lepart & Dommée (1992) and show that this species has also male and hermaphrodite individuals, thus probably having the same breeding system as *P. angustifolia*.

Sexual expression probably has a strong genetic basis. Lepart & Dommée (1992) found no labile sexuality within an individual, remaining stable for its sexual type for at least three years. Data showing such consistency in sex expression could not be gathered in the present study because none of the flowering individuals in 1992 flowered again in 1993.

The fact that functional androdioecy is being maintained by at least a greater fecundity of pollen from male flowers in the Mallorcan population but not in the population of Cazorla could suggest an adaptive advantage of such a breeding system in an island environment, especially to avoid inbreeding depression which is expected to be greater in an island than in the continent. Androdioecy, in fact, has been considered as a form of leaky dioecism (Baker & Cox, 1984), a breeding system strongly associated with colonization and invasion processes.

The lower frequency of individuals found bearing both hermaphrodites and male flowers suggests that andromonoecy could well be a relict state in *P. angustifolia*, as pointed out by Lepart & Dommée (1992). Such a breeding system would evolve to androdioecy in particular conditions such as those of insularity and founding populations.

It seems to be more likely, although there is no evidence at present, that androdioecy in the present case is an intermediate state to dioecy via hermaphroditism rather than the opposite pathway found in *Datisca glomerata* (Fritsch & Rieseberg, 1992; Liston *et al.*, 1990; Rieseberg *et al.*, 1992). Possible explanations for the evolution towards dioecy would involve avoidance of inbreeding depression and differential resource allocation from one sex function to another (Charlesworth, 1984; Lloyd 1975). Pollen of hermaphrodites should become sterile or produce seeds with lower germination rates and/or seedlings with lower growth. Long period studies are required to assess that this is what actually happens in *P. angustifolia*. Lepart & Dommée (1992) report a greater flower production, a more regular and greater vegetative growth, and a higher survival rate in male plants compared with hermaphrodites in their populations of southern France. Vegetative growth and survival rate have not been examined in the Spanish populations, but no differences between sexual types in flower production have been observed so far, at least in the Balearic Islands.

#### *Fruit and gall production*

*P. angustifolia* appeared to have a low fruitset, and the number of fruits that reached full size and maturity was always less than 10% of the number of flowers produced. Most fruits abort at an early stage of development although there is also a large proportion of flower abscission. The reason for such a low fruitset is possibly a limitation of resources. Nevertheless, there is also the possibility of a selection favouring those hermaphrodite individuals that increase their male function by producing more flowers, even if these are not going to set fruit. If this is the case, it becomes more difficult to imagine an evolution towards dioecy.

Fruitset was not influenced by any of the plant traits measured describing size or fecundity. Fruit crop, however, was correlated with plant size (height and crown diameter), with larger plants producing greater crops.

The production of galls is highly variable among individuals. In some plants, flies greatly reduced the reproductive output and up to 97% of the initiated fruits became galls. In contrast, some plants bore no galls at all during the years of the study. Such variability in gall incidence, however, was not found to relate to variability in plant size, fecundity, distance to flowering conspecifics or time that flowers remain available for fly oviposition. In general, factors that may affect such variation may be environmental—for instance, it has been shown that host plant height (Walton *et al.*, 1990) or surface chemicals (Abrahamson *et al.*, 1989) can stimulate insect oviposition—and/or genetic (Anderson *et al.*, 1989 and references therein). Gall incidence may also be the result of previous levels of attack (e.g. Craig *et al.*, 1986) or simply the chance of discovery by a female insect with little dispersibility (McCrea & Abrahamson, 1987). A high consistency in gall production was found in Cabrera island between 1991 and 1992, and also in Cazorla between 1989 and 1991.

The number of galls per plant appeared to be greater in the island populations than in those in the Peninsula, which suggests that flies are either more abundant in the islands or they are active for a longer period of the day. The reason for a more prolonged activity might be the higher temperatures in the Balearic Islands compared with those in Cazorla.

The observation that galls can remain on the plant for long periods of time suggests that they may not represent a significant nutrient or energetic cost to the plant. By photosynthesizing, they might offset a large portion of their cost. However, these long periods might also indicate a low resource availability. Furthermore, the long generation time may be because galling insects often require embryonic tissues for development, or because by growing slowly and to a large size, they can produce highly fecund adults (Cornell, 1990). In the present system, a further selective force increasing generation time might be the low probability that a plant produces flowers during consecutive years. The reason why flies of a cohort do not emerge the same year may in fact be due to the unpredictability of flowering.

#### ACKNOWLEDGEMENTS

I am grateful to C. R. Altaba, J. A. Amat and C. Keller for their help in the field. The study was begun during a postdoctoral fellowship in the Estación Biológica de Doñana (CSIC), Sevilla. While there I greatly benefited from discussions with C. Domínguez, C. M. Herrera, P. Hulme and P. Jordano. Financial support came from DGICYT grants PB87-0452 to C. M. Herrera and PB88-0041 to J. A. Alcover. Ferrán Hierro helped with the SEM micrographs, and Fernando Campos made the drawing. I also thank the Agencia del Medio Ambiente (in Andalucía) and ICONA (in the Balearic Islands) for logistic support in Cazorla and Cabrera, respectively.

#### REFERENCES

- Abrahamson WG, McCrea KD, Anderson SS. 1989. Host preference and recognition by the goldenrod ball gallmaker *Eurosta solidaginis* (Diptera: Tephritidae). *American Midland Naturalist* **121**: 322–330.

- Anderson AB, Overal W, Henderson A. 1988.** Pollination ecology of a forest-dominant palm (*Orbignya phalerata* Mart.) in Northern Brazil. *Biotropica* **20**: 192–205.
- Anderson SS, McCrea KD, Abrahamson WG, Hartzel LM. 1989.** Host genotype choice by the ball gallmaker *Eurosta solidaginis* (Diptera: Tephritidae). *Ecology* **70**: 1048–1054.
- Anderson GJ, Symon DE. 1989.** Functional dioecy and andromonoecy in *Solanum*. *Evolution* **43**: 204–219.
- Armenise V. 1956.** Sull'aborto dell'ovario nella *Phillyrea latifolia* L. *Nuovo Giornale Botanico Italiano, n.s.* **63**: 444–445.
- Baker HG, Cox PA. 1984.** Further thoughts on dioecism and islands. *Annals of the Missouri Botanical Garden* **71**: 244–253.
- Brooks RM. 1948.** Seasonal incidence of perfect and staminate olive flowers. *Proceedings of the American Society for Horticultural Science* **52**: 213–218.
- Campbell C. 1915.** Sulla partenocarpia nella *Phillyrea media* L. *Annali di Botanica* **13**: 411–413.
- Campbell C. 1922.** Sulla riduzione dei costituenti il pistillo nella *Phillyrea media* L. *Annali di Botanica* **15**: 285–288.
- Charlesworth B, Charlesworth D. 1978.** A model for the evolution of dioecy and gynodioecy. *American Naturalist* **112**: 975–997.
- Charlesworth D. 1984.** Androdioecy and the evolution of dioecy. *Biological Journal of the Linnean Society* **23**: 333–348.
- Cornell HV. 1990.** Survivorship, life history, and concealment: a comparison of leaf miners and gall formers. *American Naturalist* **136**: 581–597.
- Craig TP, Price PW, Itami JK. 1986.** Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology* **67**: 419–425.
- Darwin C. 1877.** *The different forms of flowers on plants of the same species*. Chicago: The University of Chicago Press (facsimile).
- Fernández R. 1979.** Factores que afectan a la polinización y cuajado de frutos en olivo (*Olea europaea* L.). *Fundación Juan March, Serie Universitaria* **99**: 1–42.
- Fritsch P. & Rieseberg LH. 1992.** High outcrossing rates maintain male and hermaphrodite individuals in populations of the flowering plant *Datisca glomerata*. *Nature* **359**: 633–636.
- Haber WA, Bawa KS. 1984.** Evolution of dioecy in Saurauia (Dilleniaceae). *Annals of the Missouri Botanical Garden* **71**: 289–293.
- Herrera J. 1987.** Flower and fruit biology in southern Spanish mediterranean shrublands. *Annals of the Missouri Botanical Garden* **74**: 69–78.
- Kevan PG, Longair RW, Gadawski RM. 1985.** Dioecy and pollen dimorphism in *Vitis riparia* (Vitaceae). *Canadian Journal of Botany* **63**: 2263–2267.
- Lepart, J. & Dommée B. 1992.** Is *Phillyrea angustifolia* L. (Oleaceae) an androdioecious species? *Botanical Journal of the Linnean Society* **108**: 375–387.
- Liston A, Rieseberg LH, Elias TS. 1990.** Functional androdioecy in the flowering plant *Datisca glomerata*. *Nature* **343**: 641–642.
- Lloyd DG. 1975.** The maintenance of gynodioecy and androdioecy in Angiosperms. *Genetica* **45**: 325–339.
- McCrea KD, Abrahamson WG. 1987.** Variation in herbivore infestation: historical vs. genetic factors. *Ecology* **68**: 822–827.
- Polunin O, Smythes BE. 1973.** *Flowers of south-west Europe*. London: Oxford University Press.
- Rieseberg LH, Hanson MA, Philbrick CT. 1992.** Androdioecy is derived from dioecy in Datisceae. Evidence from restriction site mapping of PCR-Amplified chloroplast DNA fragments. *Systematic Botany* **17**: 324–336.
- Thomson JD, Shivanna KR, Kenrick J, Knox RB. 1989.** Sex expression, breeding system, and pollen biology of *Ricinocarpus pinifolius*: a case of androdioecy? *American Journal of Botany* **76**: 1048–1059.
- Traveset A. 1992.** Production of galls in *Phillyrea angustifolia* induced by cecidomyiid flies. *Proceedings of the VI International Conference on Mediterranean Climate Ecosystems*: 198–204.
- Uriu K. 1959.** Periods of pistil abortion in the development of the olive flower. *Proceedings of the American Society for Horticultural Science* **73**: 194–202.
- Walton R, Weis AE, Lichter JP. 1990.** Oviposition behavior and response to plant height by *Eurosta solidaginis* Fitch (Diptera: Tephritidae). *Annals of the Entomological Society of America* **83**: 509–514.
- Yampolsky C, Yampolsky H. 1922.** Distribution of sex forms in the phanerogamic flora. *Bibliotheca Genetica* **3**: 1–62.