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SEED SET IN THE 'MALE SYCONIA' OF THE COMMON FIG *FICUS CARICA* L. (CAPRIFICUS)

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SUMMARY

Artificial pollination experiments have been carried out with short-styled, female flowers (in functionally male syconia) of the common fig (*Ficus carica* L., Caprificus). The results support the contention that the short-styled flowers are fertile female flowers capable of producing normal seeds. Inhabitation of the short-styled flowers by the wasp *Blastophaga psenes* L. not only transformed the flower ovary into a gall and induced the development of parthenogenetic endosperm, but also exerted a significant influence on the development of the fruit. It is likely that consumption of the endosperm by the larvae developing within the ovaries is the stimulus for the development of the unique spongy tissue in the fruits of Caprificus at ripening. Seed-producing caprifigs develop juicy, sweet figs, very similar to ordinary female figs. These fruits are eaten by birds and bats whereas the spongy fruits are neglected.

INTRODUCTION

In the common fig (*Ficus carica* L.), as is usual in *Ficus*, the syconia produce three types of flowers: short- and long-styled female flowers, and male flowers. The short-styled female flowers, first described by Pontedera (1720), possess a hollow style and a funnel-shaped stigma into which the pollen vector, the agaonid wasp *Blastophaga psenes* L., oviposits. As a result of oviposition, the ovary becomes a gall which is the host to the developing wasp larva. In the long-styled female flowers the style is longer than the ovipositor of the wasp and consequently wasps cannot ovipost into them. Pollination results in normal seed setting.

All figs of the subgenus *Ficus*, to which the common fig belongs, are dioecious. The syconica of the female tree of *F. carica* contain long-styled female flowers, while those of the male tree, the Caprificus, contain male flowers as well as short-styled female flowers which are generally inhabited by the wasp and do not produce seeds. Hence, although it contains short-styled female flowers, the caprifig is functionally a male plant. It has long been known (Solms-Laubach, 1882) that upon germination, fig seeds give rise to equal numbers of female and Caprificus plants.

Eisen (1901) regarded the short-styled flowers as degenerated female flowers incapable of producing seeds, and named them 'gall flowers'. However, Gasparini (1845) found twenty normal seeds in forty summer figs (mammoni, Caprificus), while Rixford (1918) reported seventy-two seeds from a single such fig. Ravasini (1911), who thought that the short-styled

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flowers were not flowers at all but rather specific structures adapted to receive the eggs of the wasps, attributed seed production in mammoni figs to flowers with intermediate-sized styles. Since repeated examination of the female flowers in mammoni figs has not revealed such intermediate flowers, it is reasonable to assume that the seeds reported by Gasparini (1845) and Rixford (1918) were produced by ordinary, short-styled pistils which happened to be unoccupied by wasps.

Condit (1932) carried out anatomical studies of the various types of flowers and found that the internal structure of the ovary and ovules in the short- and long-styled flowers was the same, the differences between the styles and stigmas being superficial. Although anatomical and other studies provide evidence of the nature of the short-styled gall flowers, clear proof of their fertility requires artificial pollination experiments in the total absence of the wasps, and these have now been carried out.

MATERIALS AND METHODS

Our study was carried out on caprifig trees growing in the region of Safed (Upper Galilee, northern Israel). The syconia of the spring crop–the profichi–appear on the wood of the previous season's growth at the end of March. They ripen in June, producing plenty of pollen. The polleniferous profichi are the main source of pollen in the common fig. The syconia of the remaining two crops borne by the functionally male trees–the summer crop (= mammoni) and the winter crop (= mamme)–produce very little or no fertile pollen. They function as domiciles in which the wasps complete their life cycle.

The crops used for artificial pollination were the new profichi and the mammoni. Pollination of profichi was carried out in April with pollen, obtained from the ripe profichi of the previous year (June), which had been stored for about 10 months (in the freezer of a refrigerator) at $-10^{\circ}C$. For pollination, the pollen was suspended in 2% sucrose solution and injected into the receptive syconia through the ostiole. All syconia to be pollinated were bagged in advance in organdy to prevent the entry of wasps. To accelerate the development of the mammoni and provide receptive figs at the right time, the tips of the new-growth branches of Caprificus were lopped off in May (see Condit, 1947). As a consequence of pruning the mammoni figs on these branches appeared earlier than usual and reached the receptive stage while numerous profichi were still present on the trees.

The syconia for each experiment were divided into three groups: (1) unbagged syconia which were left on the trees without any treatment which became inhabited by *Blastophaga* wasps. (2) Syconia bagged in organdy and artifically pollinated. These figs were not inhabited by wasps. (3) Bagged syconia which were not pollinated. These figs, too, were free of *Blastophaga* wasps.

The figs of the three groups were systematically observed and when they were ripe, the specific gravity, dry weight, water content and taste were estimated. By means of 15-30 μm thick microtome sections, prepared by the paraffin method, the internal structure of figs was studied. As a final step, the seeds in each syconium were counted and the characteristics of the fruit were determined.

RESULTS

The development of profichi syconia under the various treatments is presented in Fig. 1. Generally, the unpollinated and uninhabited syconia dropped off after 5 weeks without

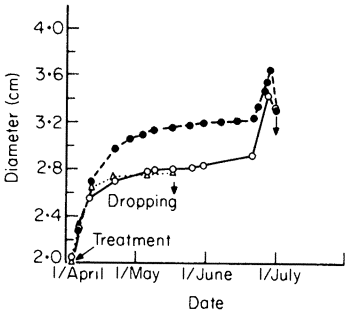

Fig. 1. Growth curves of variously treated Profichi syconia. •, Inhabited but unpollinated; ○, artifically pollinated but uninhabited; △, unpollinated and uninhabited.

Table 1. *Comparison of the specific gravity and dry weight of ripe profichi gall syconia and of fleshy female seed syconia. Dry weight is presented as percent of fresh weight*

	Specific gravity	Dry weight
Gall syconia	0.51 ± 0.03	13.55%
Seed syconia	0.97 ± 0.02	21.3%

further development of the flower-ovaries or the figs. The inhabited syconia, as well as the artificially pollinated ones, developed normally and ripened simultaneously at the end of June. Throughout the development, the inhabited syconia were larger than those artificially pollinated (Fig. 1). As usual in Caprificus, the gall syconia (unbagged) produced large, spongy, unsweet fruit (Plate 1, No. 1). Their sponginess and low specific gravity were due to the very large intercellular air spaces in the peel of the fruit (Plate 1, No. 3. For comparison the structure of the fleshy compact parenchyma in female fruit is shown in Plate 1, No. 4). In contrast, the seed-producing, pollinated male syconia were somewhat smaller. The intercellular spaces in the peel of the fruit were considerably smaller than those in the inhabited caprifigs. The flower peduncles and the perianth scales became juicy, so that the whole fruit turned more fleshy and sweet. The comparatively high specific gravity of ordinary female fruits, compared with the fruit produced from inhabited, unpollinated Caprificus syconia (Table 1), is due to their high sugar content (Crane and Brown, 1950). Seed-containing male fruits are thus intermediate between female and ordinary Caprificus fruits.

Pollinated male syconia of the two crops (profichi and mammoni) produced a large number of normal seeds. The profichi, pollinated with preserved pollen, each contained about 400 seeds, but the mammoni figs, pollinated with fresh pollen, were much more prolific, producing 500–700 seeds per syconium. The germination percentage of the seeds of the two types was 60 and 90 respectively.

DISCUSSION

Differentiation of the female flowers into long- and short-styled flowers, which produce seeds and galls, respectively, is common to all *Ficus* species. Such differentiation has a basic survival value because otherwise the ubiquitous wasps would proliferate in all the female flowers without leaving any for seed. Generally the only difference between the two types of flowers

is in the length of the style, but in several species the stigmas of the two types differ (as in *Ficus nota,* Baker, 1913; in *F. fistulosa,* Galil, 1973). In the common fig the differences between the two types are more pronounced. In spite of that, long-styled and short-styled flowers of all the species hitherto investigated, including *F. carica,* are normal, fertile female flowers (for *F. religiosa* see Johri and Konar, 1956; for *F. sycomorus*–Galil, Dulberger and Rosen, 1970).

Our results fully support Condit's opinion that the short-styled flowers of the common fig are fertile female flowers. Although regrettably the present study did not include studies of the winter syconia (mamme) of Caprificus, the remaining two crops, that is the spring syconia (profichi) and the summer syconia (mammoni), invariably produced normal seeds upon artificial pollination. The large number of seeds developed in mammoni syconia is in agreement with the view of Rixford (1918) that 'all short-styled flowers are fertile and susceptible to pollination'. The finding that seeds are produced in profichi figs as a result of artificial pollination is especially interesting. In nature, these syconia cannot be pollinated because viable pollen is lacking in the antecedent fig generation and consequently no seeds have been found in naturally developing profichi. Production of seeds in these syconia in our experiments shows that even in this case the short-styled flowers are normal fertile female flowers.

Condit (1932, 1947) stated that embryos of both fig and of wasp cannot be found simultaneously in a single ovule. He suggested that insertion of the wasp's ovipositor into the pistil injures the living cells of the narrow stylar canal and that the toxic substances generated thereby inhibit the growth of pollen tubes through the canal and prevent ovule fertilization. This view of Condit is untenable. In several *Ficus* species the pollinating wasps insert their ovipositors into both short- and long-styled pistils but without ovipositing into the latter (Galil, 1973; Galil and Snitzer-Pasternak, 1970; Galil *et al.,* 1973). Fertile seeds develop in all long-styled flowers, as well as in the short-styled flowers which have not been occupied by the wasps, or when the larvae died at an early stage (Galil and Eisikowitch, 1971). Since no apomixis of any type has yet been detected in *Ficus,* it is quite clear that mere insertion of the ovipositor into the style does not interfere with fertilization, in most figs so far investigated. In fact Johri and Konar (1957) found plant embryos, at the octant stage, alongside wasp larvae in the ovules of *F. religiosa.* In such cases, however, the plant embryo degenerates very quickly as a result of activities of the larva.

The influence of the wasps on the fig is not confined to gall induction and development of parthenogenetic endosperm in the ovules. Even in the total absence of pollination, oviposition by the wasp prevents untimely dropping of syconia and ensures development of the figs to final ripening. The viability and maturation of the unpollinated syconia, due to occupation by wasps, is therefore of vital importance to the annual life cycle of the insects. The alternative stimulus to maturation of the syconia, namely fertilisation, is never available to mamme and profichi and only infrequently to mammoni. Fruits which do not produce any seeds and whose development is induced solely by inhabitation by wasps have been named by Condit (1947) 'stimulatively parthenocarpic'. The fruit of *F. sycomorus* in the Middle East, which develops as a result of inhabitation by *Sycophaga sycomori* and not from pollination, belongs to the same category (Galil, 1968).

The considerable structural differences between ordinary Caprificus fruits and ones developed as a result of artificial pollination are intriguing. It is well known (Crane, Bradley and Luckwill, 1959) for the common fig that development of the fruit is regulated by the growing endosperm, both in pollinated syconia and in parthenocarpic ones. However, when

the endosperm is consumed by the larvae and does not increase, development of the fruit takes a different course, ultimately yielding the large spongy inedible fruit of typical profichi. In view of the development of fleshy, edible fruits which we have demonstrated in artificially pollinated but unoccupied mammoni figs, there is reason to think that the destruction of the endosperm in Caprificus by the wasp is connected with the change in the qualities of the fruit.

The characteristics of the seed-bearing and gall-bearing fruits are highly adaptive. Normal swelling and sweetening of the seed-containing syconia, both in Caprificus and in female fruits, is essential for effective seed dispersal by frugivorous bats and birds. On the other hand, production of unpalatable, inedible spongy fruits in the caprifigs insures the timely release of the wasps maturing in them. It is likely that the sponginess of such fruits and the atmospheric conditions which develop within the fig cavity are essential for normal pollen loading on the wasp body (Galil and Neeman, 1977).

Condit and Flanders (1945) did not accept the common epithet 'gall flower' for the short-styled female flowers of *Ficus* within whose ovaries the wasps developed. According to them 'there is no swelling or excrescence resulting from the presence of *Blastophaga* in the ovary. An inhabited flower cannot be distinguished from an uninhabited one'. For a wasp-inhabited ovary they proposed the name 'psenocarp'. This opinion of Condit and Flanders is unjustified. The inhabited ovaries are in many respects distinguishable from seed-producing ovaries (Mani, 1964). They produce a unique nourishing tissue, the sclerification of the endocarp is unlike the cover of the seed and, finally in many *Ficus* species inhabitation by sycophilous insects causes moderate to considerable swelling of the ovary.

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REFERENCES

BAKER, C. F. (1913). A study of caprificertion in *F. nota. The Philipine Journal of Science,* **8,** 63.
CONDIT, I. J. (1932). The structure and development of flowers in *Ficus carica* L. *Hilgardia,* **6,** 443.
CONDIT, I. J. (1938). Parthenocarpy in the fig. *Proc. Amer. Soc. Hort. Sci.,* **36,** 401.
CONDIT, I. J. (1942). The croisic (cordelia) fig. *Proc. Amer. Soc. Hort. Sci.,* **40,** 255.
CONDIT, I. J. (1947). *The Fig.* Waltham Mass., U.S.A.
CONDIT, I. J. & FLANDERS, S. E. (1945). 'Gall flowers' of the fig–a misnomer. *Science,* **102,** 128.
CRANE, J. C., BRADLEY, M. V. & LUCKWILL, L. C. (1959). Auxins in parthenocarpic and nonparthenocarpic figs. *J. hort. Sci.,* **34,** 142.
CRANE, J. C., & BROWN, J. G. (1950) Growth of the fig fruit, *Ficus carica* var mission. *Amer. Soc. Hort. Sci. Proc.,* **56,** 93.
EISEN. (1901). The fig. *U.S. Dept. Agr. Div. Perm. Bul.,* **9,** 1.
GALIL, J. (1968). An ancient technique for ripening sycomore fruit in East Mediterranean countries. *Economic Bot.,* **22,** 178.
GALIL, J. (1973). Pollination in dioecious figs: pollination of *Ficus fistulosa* by *Ceratosolen hewitti. Gard, Bull. Singapore,* **26,** 303.
GALIL, J., DULBERGER, R. & ROSEN, D. (1970). The effect of *Sycophaga sycomori* L. on the structure and development of syconia in *Ficus sycomorus* L. *New Phytol.,* **69,** 103.
GALIL, J. & EISIKOWITCH, D. (1971). Studies on the mutualistic symbiosis between syconia and sycophilous wasps in monoecious figs. *New Phytol.,* **70,** 773.
GALIL, J. & NEEMAN, D. (1977). Pollen transfer and pollination in the common fig (*Ficus carica* L.). *New Phytol.,* **79,** 163.

GALIL, J., RAMIREZ, B. & EISIKOWITCH, D. (1973). Pollination of *Ficus costaricana* and *F. hemsleyana* by *Blastophaga esterae* and *B. tonduzi* in Costa Rica. *Tijdschr. Entomol.*, **116**, 175.

GALIL, J. & SNITZER-PASTERNAK, Y. (1970). Pollination of *Ficus religiosa* L. as connected to the structure and mode of action of the pockets of *Blastophaga quadratideps* Mayer. *New Phytol.*, **19**, 775.

GASPARINI, G. (1845) Ricerche sulla natura del caprifico e del fico, e sulla caprificazione. *Accad. delle Sci. Napoli, Rend.*, **4**, 321.

JOHRI, B. M. & KONAR, C. W. (1956). The floral morphology and embryology of *Ficus religiosa*. *Phytomorphology*, **6**, 97.

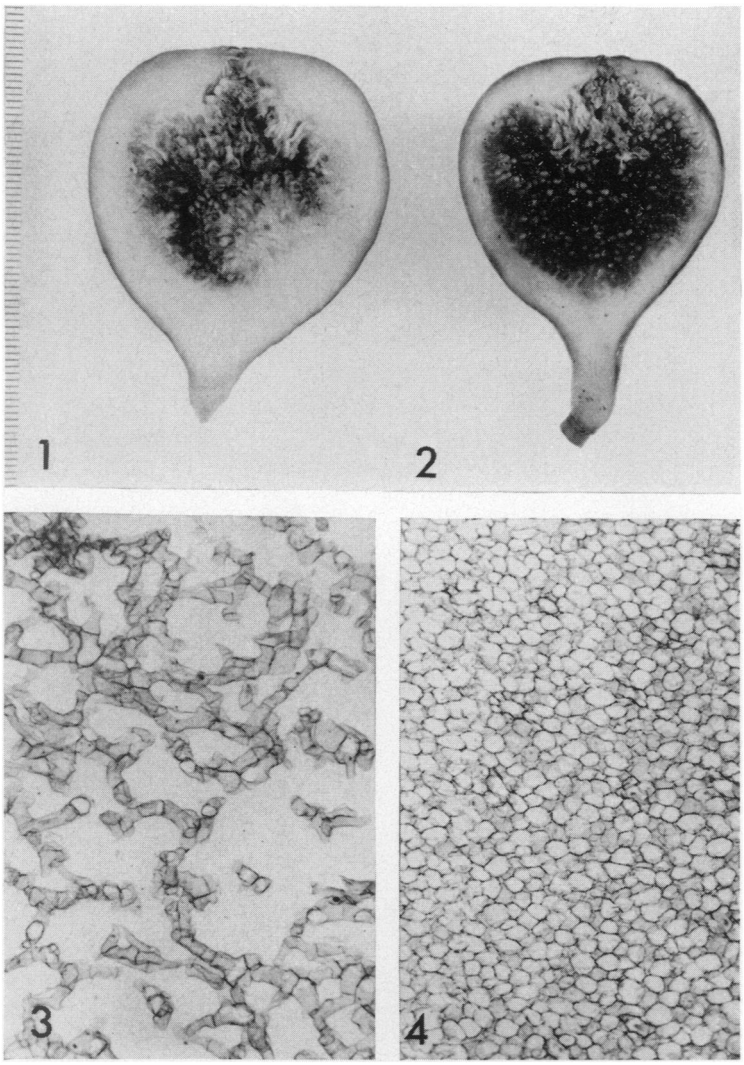
MANI, M. S. (1964). *Ecology of Plant Galls.* V. Junk, Hague.

PONTEDERA, G. (1720) Anthologia, sive de flors natura. *Typ. Seminarii, Patavii.* **26**, 230.

RAVASINI, R. (1911). *Die Feigenbäume Italiens.* Akademische Buchhandlung von Max Drechsel, Bern.

RIXFORD, G. P. (1918). Smyrna fig culture. *U.S.D.A. Bull.*, **732**, 1.

SOLMS-LAUBACH, H. G. (1882). Die Herkunft, Domestication und Verbreitung des gewöhnlichen Feigenbaüme (*Ficus carica* L.) *Abhandl. Konigl. Ges. Wiss. Göttingen.* **28**, 1.



Nos 1–2. Ripe fruit of variously treated *proficht syconia*. No. 1, spongy fruit (inhabited but not artificially pollinated); No. 2, fleshy fruit (pollinated but uninhabited).
Nos. 3–4. Microtome sections through the peel of ripe syconia of male and female *Ficus carica*. No. 3, spongy tissue of inhabited but unpollinated *proficht syconium*; No. 4 compact fleshy tissue of pollinated female syconium.