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Hybridization of Ficus religiosa with F. septica and F. aurea (Moraceae)

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Resumen: Se encontró híbridos naturales y producción de semillas viables entre el cruce de Ficus religiosa L. (sección Urostigma, subgénero Urostigma) del Viejo Mundo y F. aurea Nutt. (sección Americana, subgénero Urostigma) del Nuevo Mundo en Florida, y entre F. religiosa (Asia Continental) y F. septica Burn. f. (Australasia) en las Islas Filipinas. Al contrario de F. religiosa y F. aurea, F. septica es una especie terrestre y gino-dioica que pertenece a la sección Sycocarpus (subgénero Ficus). En la naturaleza y sus respectivas áreas de distribución cada una de estas especies de higo tiene polinizadores diferentes (Hymenoptera: Agaonidae). Se informa por primera vez sobre la presencia de Platiscapa quadraticeps en las Filipinas. Ninguno de los agaonidos estudiados se reprodujo en los hospederos extraños. Se postula que F. aurea, F. religiosa y F. septica producen "sinomonas" similares, las cuales confunden a sus polinizadores simbióticos respectivos. Todas esas especies tienen ostiolos con escamas helicoidales que permiten la entrada de los agaonidos extraños. También se postula que la hibridación en Ficus ocurre porque sus especies no han evolucionado mecanismos genéticos de aislamiento, puesto que tienen polinizadores específicos y constantes.

Key words: Hybridization, Ficus religiosa, septica, aurea Moraceae, pollination.

There is strong evidence that the agaonid wasps (Agaonidae) are very specific to their fig hosts (Wiebes 1963, 1986, Hill 1967, Ramírez 1971). Introduced species normally fail to set viable seeds when their own wasps are absent (Ramírez 1971, Ramírez and Montero 1988). Ramírez (1970) reported that agaonids occasionally enter syconia of species other than their usual host.

There are only a few records of reproduction of figs by artificial pollination (Condit 1950, Ramírez, 1986). Ramírez and Montero (1988) reported that *F. benjamina* L. of section *Conosycea* (Old World) was fertilized by the symbiotic wasp of *F. padifolia* H.B.K. of section *Americana* (New World). They also mentioned that the syconia of *F. religiosa* (Old World) were fertilized by the pollinator of *F. aurea* Nutt. (in Florida, U.S.A.). Both crosses produced hybrid seedlings. Ficus species which evolved in diferent geographic areas could have developed chemically similar attractant pheromones (synomones) (Ramírez and Montero 1988). This article reports the hybridization of *F. religiosa* with *F. septica* and *F. aurea*.

F. religiosa (Figs. 1 and 2) is characterized by having monoecious figs with ostiolar male flowers, a caudate lamina with a long tip (25-90 mm) and a petiole as long as or longer than the lamina (Corner 1965). *F. septica* (Fig. 2) is a dioecious fig which also has ostiolar male flowers, but the lamina is shortly acuminate and has a short petiole (about 20 mm). *F. aurea* (Fig. 1) has monoecious syconia with dispersed male flowers; an acuminate lamina with a short tip and a short petiole (less than 20 mm).

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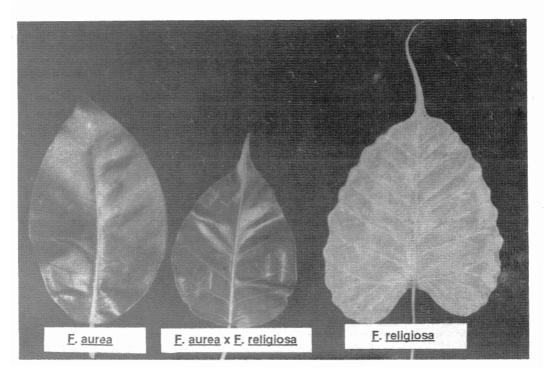


Fig. 1. Ficus leaves from Florida, U.S.A. (center: seedling; rest: adults). These leaves of F. religiosa and F. septica are representative.

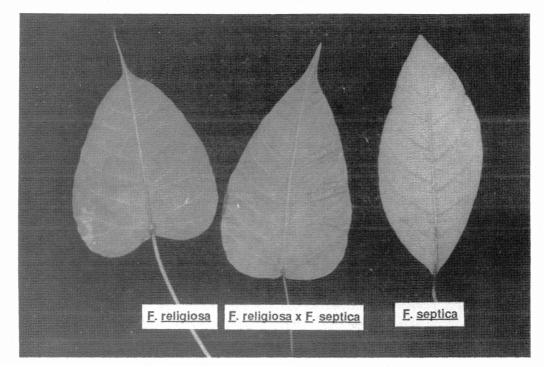


Fig. 2. Ficus leaves from Manila, Philippines (center: seedling; rest: adults). These leaves of F. aurea and F. religiosa are representative.

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Taxonomic and geographical distribution of F. regliosa, F. septica and F. aurea and their pollinators: F. religiosa is a monoecious strangler fig in section Urostigma, subgenus Urostigma. It is found naturally in the sun-Himalayan forests from Rawalpindi to Continental China, SE Asia and North Thailand (Corner 1965) and is widely cultivated in most tropical and subtropical areas. F. septica is a dioecious terrestrial species which belongs to section Sycocarpus, subgenus Ficus. It is found in Philippines, and other islands in the Western Pacific and Queensland. F. septica v. salicifolia Corner occurs in the Philippines (Luzon, Samar, Mindanao) and Celebes (Corner 1965). F. aurea is an strangler endemic to Florida which belongs to section Americana, subgenus Urostigma.

According to Merril (1923), *F. religiosa* was cultivated in Manila, Cebu, and perhaps other large towns of the Philippines as a very recent introduction from India; however, he did not mention the presence of its pollinator.

F. religiosa is normally pollinated by (Platyscapa) quadraticeps (Mayr) (Wiebes, 1977) and F. aurea is pollinated by Secundeisenia mexicana Ashmead =Pegoscapus mexicanus. (Ashmead) Wiebes (1986). Wiebes (1983) stated that the pollinators of F. aurea in Florida and F. jimenezii Stand. in Costa Rica are conspecific. Nevertheless, F. jimenezii is known as a Central American species; it ranges from Costa Rica northward to Guatemala (Burger 1977) and is pollinated by P. jimenezii (Grandi). (Ramírez 1970)... F. septica is pollinated by Ceratosolen jucundus Grandi (1927) in the Philippines.

Hybridization and penetration of a foreign pollinator in Florida: Ramírez and Montero (1988) reported syconia of *F. religiosa* to be penetrated and pollinated by the symbiotic agaonid of *F. aurea* in Miami, Florida. Abundant hybrid seedlings about one meter tall were found growing naturally. The hybrids had leaves of intermediate shape between those of *F. aurea* and *F. religiosa* (Fig. 1). Syconia of one *F. septica* tree planted at the Subtropical Horticultural Research Station (U.S. Dept. of Agriculture, Miami, Florida) was found by the author to be penetrated by the pollinator or *F. aurea*, *P. mexicanus* but no seedlings were found. Wiebes (pers. comm. 1986) identified the pollinator wasps, in syconia of the same F. septica tree as P. mexicanus.

Hybridization in Manila, Philippines: F. septica v. salicifolia is a small native terrestrial tree growing in downtown Manila and probably the most common species found in open places of the forest and along roads in Philippines. In the city F. septica grows commonly in sidewalk cracks and gardens in street isles. F. religiosa is introduced and abundantly planted as a shade tree along streets and parks. Most planted trees are 10 or more years old. Botanical specimens (all with asynchronous syconia) have been collected and deposited at the herbarium of the Systematic Laboratory of the the University of Philippines at los Baños after 1950. Generally the planted trees of F. religiosa growing in Manila and other towns of Luzon bloom asynchronously. Until recently the trees did not produce ripe pollinated figs since the pollinator did not exist in Manila. However, its pollinator has become established recently and now Manila has many F. religiosa seedlings growing in sidewalk cracks, elevated bridges and other structures. Ripe fruits from introduced F. religiosa (collected in Manila, November, 1989), were found pollinated and inhabited by its pollinator P. quadraticeps. It is possible that P. quadraticeps was accidentally introduced into Manila about ten years ago, and that this wasp was probably transported by airplanes coming from the Asian mainland.

Two small hybrid trees (F. religiosa x F. septica) were also found in Manila sidewalks. Both were about two meters tall. The leaves (Fig. 2) had a laminar shape intermediate between those of the parent species; the same was found in the hybrid between F. aurea and F. religiosa in Florida (Fig. 1).

Considering the relatively constant number of chromosomes and the frequent absence of hybrids in nature (Ramírez 1971), one may ask what has been the role of hybridization in the evolution of *Ficus*. How is each species kept as a separate biological unit in spite of being insect pollinated, particularly considering that many species are sympatric and trees of different species may bloom synchronously?

As shown, viable seeds can be produced when a foreing species is introduced into the range of a local species. However, both species must have some physiological, morphological and genetic characters in common. Fig species also hybridize when artificially pollinated (Condit 1950, Ramírez 1986).

P. mexicanus, pollinator of *F. aurea* in Florida, is attracted by *F. religiosa* syconia, and viable seeds are produced. It also penetrates figs of an introduced *F. septica* tree in Florida, although apparently it does not produce viable seeds. Possibly these figs produce attracting synomones which are similar enough to confuse the symbiotic wasps of *F. aurea*. They also have ostiola with similar morphology which allows them to enter their syconia. *P. quadraticeps* has not been found in the New World.

Occassional hybridization may occur in nature because many species of figs have a common chromosome number (26). They probably lack genetic isolating mechanisms, since they have very faithful specific pollinators. Hybridization and polyploidy do not seem to have had any important role in the speciation of *Ficus* (Ramírez 1971). Accoding to Kjelberg *et al.* (1986), in a teleological approach, the mutualistic interactions between the wasps and the fig seem to explain why the system is stable and allows the existence of some 700 fig species

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