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BREEDING SYSTEM IN *FICUS CARICA*, THE COMMON FIG. I. FLORAL DIVERSITY¹

N. G. BECK AND E. M. LORD

Department of Botany and Plant Sciences, University of California, Riverside, California 92521

ABSTRACT

Coevolution in *Ficus carica* (Moraceae) and the fig wasp (*Blastophaga psenes*, Agaonidae, Chalcidoidea) has resulted in a complex breeding system involving two tree morphs (Caprifig and Edible fig), three floral forms (long-styled female, short-styled female, and male flowers) and the insect pollinator. The two female floral forms have been reported to differ only in style length and stigma shape. In the present study, we demonstrate that the two female flowers differ from inception—short-styled flower primordia are smaller and exhibit significantly greater individual variation than do those of the long-styled flower, and the relative growth rate of each flower type differs. Mature forms exhibit disparity in style length, in stigma characteristics, and in degree of fusion of styler lobes. Female flowers of both tree morphs are unisexual from inception. Male flowers of the Caprifig tree morph are initiated as hermaphrodites and gynoecium abortion occurs before megaspore mother cell stage. A single inflorescence therefore expresses two pathways to unisexuality. Hermaphrodite flower primordia were repeatedly found in the supposedly unisexual female syconium of the Edible fig tree morph. Based on its developmental morphology, *Ficus carica* appears to be of gynomonocious ancestry.

A FEW ANGIOSPERM breeding systems show a mutual symbiosis in which the plant acts as a host for its animal pollen vector. One such relationship is that found between *Ficus* species and their pollinator wasps. The majority of the 1800 *Ficus* species have a single, specific wasp pollinator (Grandi, 1923; Baker, 1961; Hill, 1967; Ramirez, 1970, 1974; Valdeyron and Lloyd, 1979; Kjellberg et al., 1987); each wasp can undergo its life cycle only in specially adapted flowers of its particular host (Hill, 1967; Wiebes, 1979). *Ficus* has evolved several features which favor development of its symbiont pollinator: 1) female flowers specifically adapted for oviposition (short-styled flowers, SS) versus flowers specifically adapted for pollination (long-styled flowers, LS); 2) synchronization of female receptivity and wasp emergence; and 3) synchronization of anther dehiscence and wasp emergence (Ramirez, 1970, 1974). The fig wasp also has developed specializations which coordinate with those of its host; the most notable specialization is the development, in the female wasp, of an ovipositor which matches the length of the styles (Condit, 1932; Ramirez, 1970; Storey, 1975, 1985). This closed-circle breeding system has resulted in the evolution of an unusual amount

of morphological diversity in *Ficus carica*, the common fig. Old World figs have two tree morphs; in *Ficus carica*, these morphs are called the Edible fig (EF) producing syconia with LS flowers only, and the Caprifig (CF) producing syconia with SS, as well as male, flowers. The EF is referred to as the female tree and the CF, the male tree, since the SS flowers function mainly as an oviposition site and not as a seed source. In this sense, the system can be called dioecious or structurally gynodioecious (Valdeyron and Lloyd, 1979).

Flowers are located on the inside surface of the syconium, a false fruit consisting of shortened internodes (Penzig, 1894). The SS female flowers were at one time considered galls, a result of the gall-making abilities of the agaonid *Blastophaga psenes*, the wasp pollinator (Solms-Laubach, 1882; Eisen, 1896; Condit, 1922). This was invalidated when pollen blown into a CF syconium gave rise to seed-containing short-styled fruit (Rixford, 1918; Condit, 1932; Ramirez, 1974; Galil, 1977; Valdeyron and Lloyd, 1979; Murray, 1985). Morphological work on *Ficus carica* indicated no difference in the two female forms beyond that of style length and stigma shape (Condit, 1932) even though their functions are so markedly different (Murray, 1985).

The general belief is that species such as *F. carica*, with their functional dioecious breeding system, evolved from a monoecious ancestor

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carica, with their functional dioecious breeding system, evolved from a monoecious ancestor (Corner, 1978). Since remnants of a gynoeceium have been documented for the male flowers of a CF (Longo, 1909; Ravasini, 1911; Cotte and