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An overview on *Ficus* pollination with some notes on *Ficus carica*

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L'impollinazione dei *Ficus* con riferimenti a *Ficus carica*

Riassunto. Le specie di *Ficus* sono caratterizzate da un'impollinazione specializzata effettuata da vespe della famiglia Agaonidae. L'impollinazione comprende l'ingresso di femmine in un'infiorescenza sferica (siconio) attraverso una piccola apertura (ostiolo), che è l'unico punto d'ingresso verso i fiori. Ciascun siconio contiene centinaia di fiori unisessuati lungo le pareti interne. Una volta entrata nel siconio la vespa agonide effettua i servizi di impollinazione e di ovideposizione in questi fiori entro il siconio. La vespa spesso muore all'interno del siconio dopo l'impollinazione. L'impollinazione e il successivo sviluppo del frutto possono avvenire solo se si verifica questa interazione specializzata. La progenie delle vespe impollinatrici non si può sviluppare in assenza dei siconi dell'ospite *Ficus*. Lo stesso meccanismo di impollinazione è noto in tutte le specie del genere *Ficus*, costituito da 750 specie che crescono in habitat che vanno dai tropici ai sub-tropici e mostrano sistemi riproduttivi sia monoici che (gino)dioici. Nelle specie monoiche i semi e le vespe si sviluppano all'interno dello stesso siconio, mentre in quelle (gino)dioiche la pianta dà origine a semi o vespe impollinatrici a seconda del suo sesso. L'impollinazione in *Ficus* è mediata da segnali chimici (composti volatili emessi dall'ospite) e la modalità di impollinazione può essere attiva o passiva. Originari della regione Mediterranea temperata, i fichi eduli comuni (*Ficus carica*) sono stati coltivati sin da epoche preistoriche. Allo stato spontaneo il fico comune passa attraverso un'interessante e complessa serie di stadi di sviluppo e riproduttivi della vespa, probabilmente legati alle condizioni di clima temperato. I fichi coltivati producono frutti con l'aiuto della vespa impollinatrice *Blastophaga psenes* e la propagazione è per seme. Comunque, durante la lunga interazione tra fichi e uomo, molte varietà partenocarpiche sono state sviluppate e propagate clonalmente per talea. Inoltre, l'impollinazione artificiale con polline da diversi donatori ha consentito di ottenere nuove cultivar e persino nuovi ibridi di fichi.

Parole chiave: Fico, Caprifico, Gino(dioico), impollinazione passiva.

Introduction

The genus *Ficus* (Family: Moraceae) with over 750 species contributes to the highest number of species within the family Moraceae (Rohwer, 1993; Datwyler and Weiblen, 2004). Species of *Ficus* grow mostly in the tropics with a few exceptions that grow in the subtropics (Berg, 1989; www.figweb.org). They vary widely in their growth form that can range from tall trees above ten meters in height to shrubby plant less than a few meters that can be found in a variety of habitats such as tropical forest to desert (Hill, 1967; Berg and Wiebes, 1992; http://www.figweb.org). Often *Ficus* species are popularly called figs.

The aim of this paper is to shed more light on pollination of *Ficus carica*, the common fig. In order to understand pollination in *Ficus carica* it is important to know about figs and the interaction of figs with its pollinator. The next section is, therefore, devoted to introduce figs and pollinators of figs, the fig wasps.

The fig

All species of figs have two distinguishing features:

- a unique inflorescence resembling an urn shaped structure commonly called a syconium, with hundreds to thousands of unisexual flowers hidden within the syconium (Kugler, 1955; Barth, 1985) (fig. 1a);

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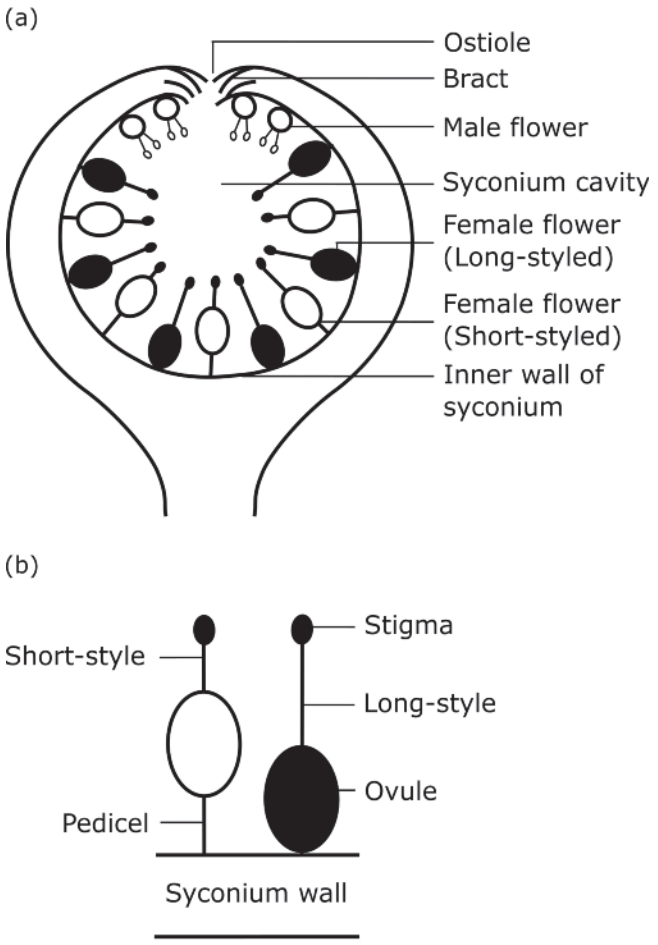

Fig. 1 - (a) Cross-section of a syconium showing unisexual flowers arranged along the syconium wall. Both male and female flowers can be found within a syconium. The bract lined ostiole leads to syconium cavity. (b) Two types of female flowers found within syconium. Flowers with long-style have no pedicel (or sometimes short pedicel) and flowers with short-style have long pedicel.
Fig. 1 - (a) Sezione trasversale di un siconio con fiori unisessuali disposti lungo la parete del siconio. Nel siconio si possono trovare sia i fiori maschili che quelli femminili. L'ostiolo conduce alla cavità del siconio. (b) Due tipi di fiori femminili sono presenti nel siconio. I fiori longistili non hanno peduncolo (o talvolta lo hanno breve), quelli brevistili hanno un peduncolo lungo.

- specialized pollination that is carried out only by wasps of the family Agaonidae (Superfamily: Chalcidoidea).

The association between fig and fig wasps is dated approximately 60-100 million years (Rønsted *et al*., 2005; Cruaud *et al*., 2012); the interaction between fig and its pollinator is a classic example of mutualism and co-evolution.

As the syconium is a closed structure and the flowers are concealed within it, access to the flowers by the pollinators is possible only through an opening called the ostiole. The ostiole is present on top of the syconium that in turn leads to a bract lined tunnel and eventually into the syconium cavity; inside this cavity along the inner wall of the syconium are arranged unisexual male and female flowers (fig. 1a). The male flowers are either dispersed among the female flowers or present near the ostiole. The female flowers are of two kinds - short-styled with long pedicel and long-styled without pedicel (sometimes a short pedicel) (Johri and Konar, 1956; Galil and Eisikowitch, 1968) (fig. 1b). The stigma of all the flowers are, however, present at the same level. In some species of *Ficus,* the surface of the stigma forms an interwoven mat called as the synstigma (Galil and Eisikowitch, 1968). Figs are protogynous i.e., the female flowers mature earlier than the male flowers.

In nearly half of the known species of *Ficus*, the male flowers as well as the female flowers of both kinds are found within the same syconium. Such figs are referred to as monoecious figs (Berg, 1989) (fig. 2a) and the remaining species are known as (gyno)dioecious. (Gyno)dioecious species have separate trees that function as pollen donor (male tree) and pollen acceptor (female tree); the female trees bear syconia with only the long-styled female flowers whereas syconia on the male tree have functional male flowers and female flowers of short-style length (Kugler, 1955; Galil, 1973) (fig. 2b,c). *Ficus carica* is an example of (gyno)dioecious species (Condit, 1947).

The fig wasps

Fig wasps are specialized for pollination of only *Ficus* spp. (Weiblen, 2002). They are mostly species specific, i.e., each pollinator species pollinates only one species of *Ficus,* however there are exceptions also (Molbo *et al*., 2003; Su *et al*., 2008). Fig wasps are sexually dimorphic, females have wings and males are wingless (Berg and Wiebes, 1992). Only the female fig wasps are capable of pollinating the flowers.

These female wasps are small in size with the total body length spanning up to only a few millimeters (for example, *Blastophaga psenes* the pollinator of common fig is ca. 1.8 mm) and their average lifespan is 24-48 hours as inferred from studies under laboratory as well as field conditions (Kjellberg *et al*., 1988; Berg and Wiebes, 1992; Ghara and Borges, 2010). Though they have limited lifespan they can disperse more than hundred kilometers for pollination, as recorded for an African fig wasp (Ahmed *et al*., 2009). Pollinators are guided to pollen receptive syconia by volatile signals emitted by these syconia (van Noort *et al.*, 1989; Hossaert-McKey *et al*., 1994; Ware and Compton, 1994). Upon arriving on a syconium the pollinator wasps inspect the syconium followed by entry into the syconium.

Once inside a syconium the wasps are known to pollinate actively, i.e., they "deliberately" pollinate

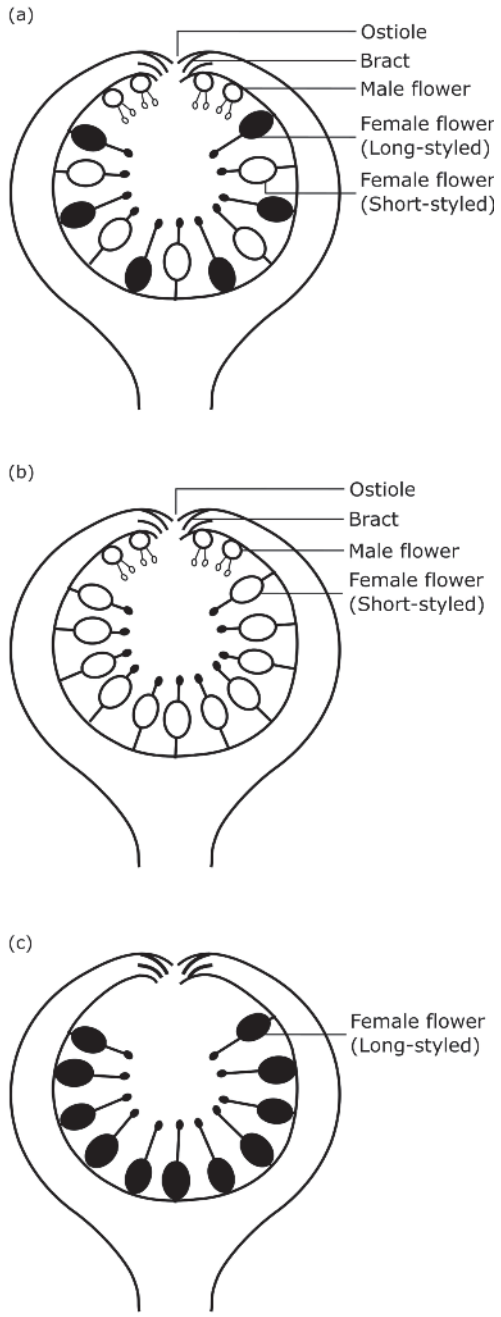

Fig. 2 - Cross-section of syconia representing different breeding systems: (a) monoecious with male flowers and both kinds of female flowers. (b) Gyno(dioecious) male with male flowers and short-styled female flowers. (c) Gyno(dioecious) female syconium with only long-styled flowers and no male flowers.
Fig. 2 - Sezione trasversale di siconi che mostra vari tipi di incrocio: (monoico con fiori maschili ed entrambi i tipi di fiori femminili. (b) siconio gino(dioico) maschile con fiori maschili e fiori femminili brevistili. (c) Siconio gino(dioico) femminile con soli fiori femmnili longistili (senza fiori maschili).

flowers with the pollen stored in their pollen pockets, or, in a few systems, passively whereby the pollen on the body of the wasp falls passively on the stigma as the wasp moves inside the syconium, thus, pollinating the flowers. The wasps mostly die within the syconium upon pollination, though in certain cases they can exit and pollinate other syconia (Gibernau *et al*., 1996). In return for pollination services the wasps oviposit (lay eggs) in some of the flowers by inserting their ovipositor through the style and the wasp offspring complete their development cycle inside modified fig flowers also called a gall; they develop by feeding on ovary or hypertrophied endosperm (Condit, 1932; Jansen-González *et al*., 2012). However, because of the constraints of the ovipositor length the wasp cannot oviposit in all the flowers (primarily, the long-styled flowers) and therefore the long-styled flowers mostly produce seeds whereas due to successful oviposition the short- styled flowers nurture the wasp offspring.

Thus, the fig provides a nursery for the wasp offspring, and hence this mutualism is also called as nursery pollination mutualism (Sakai, 2002; Dufaÿ and Anstett, 2003). The pollinator is, therefore, in a mutualistic interaction with its host fig species, where the development and survival of each partner depends on the other (Condit, 1920, 1947). In the wild, figs can produce seeds only if the pollinator exists and the pollinator offspring can develop only if the host species of fig exists.

Pollination in *Ficus carica*

Pollination in *Ficus carica* was described for the first time in detail by Condit (1947) and later by Galil and Neeman (1977) in Israel and Kjellberg *et al*. (1987) in France. Species specific pollinator *Blastophaga psenes* L. pollinates *Ficus carica*. Using mark-recapture technique with florescent dyes, Kjellberg *et al*. (1988) found that the adult pollinators can live up to 48 hours in the wild.

In order to understand pollination process in genus *Ficus*, Galil and Eisikowitch (1968) divided the development cycle of the fig into five different stages (stage A-E) for the monoecious species *Ficus sycomorus*; the details of the stages are as follows:

- Stage A (Pre-female): The syconium is young prior to opening of ostiole.
- Stage B (Female): Flowers are mature, the scales on the ostiole loosen; pollinator wasps enter the syconium, pollinate and oviposit.
- Stage C (Interfloral): Larvae of wasps and seeds develop.
- Stage D (Male): Male flowers mature; adult male wasps emerge from the galls, mate with the female wasps still inside the galls and assist the female wasps to leave the syconium.
- Stage E (Post-floral): Seeds in the syconia are ready for dispersal. Later these stages were also

used for the (gyno)dioecious species *Ficus carica* (Galil and Neeman, 1977; Galil, 1989).

We describe the stages of pollination in *Ficus carica* in the wild as observed in Israel. In *Ficus carica*, the female trees called the *fichi* produce only one crop annually; this crop is produced during the spring season. The syconia on *fichi* have only long-styled flowers. The male tree is called *caprificus*; syconia on *caprificus* have short-styled female flowers. Both flowers of *fichi* and *caprificus* have the potential of seed setting (Neeman and Galil, 1978).

Caprificus produces more than one crop per year, namely the spring crop *profichi*, the summer crops *mammoni I* and *mammoni II*, and the winter crop *mamme*. These crops have overlapping stages. The number of crops and their nomenclature might vary between different climatic zones (Condit, 1932). The stages of the development cycle in *Ficus carica* with respect to the *fichi* and *caprificus* are as follows.

Stage A (Pre-pollination)

Syconia are small and present as a small protuberance on the axil of the stem. The flowers within the syconia are immature. The ostiole remains closed and is overlapped with scales.

Stage B (Pollination)

Syconia on female trees *fichi* are ready to receive pollen. Adult wasp developing inside the syconium of the *profichi* crop of *caprificus* already swollen from hydration due the wet conditions within the syconium comes in contact with the pollen before emerging out of the syconium (Galil, 1984). Once outside the syconium environment, the wasp gets dehydrated and shrunken due to dry condition outside the syconium. The pollen on the body of the wasp thus gets concealed in intersegmental and pleural invaginations (Galil and Neeman, 1977). The pollinator wasp enters into the cavity of the syconium on the female tree through the ostiole (fig. 3). Since the ostiole has a nar-

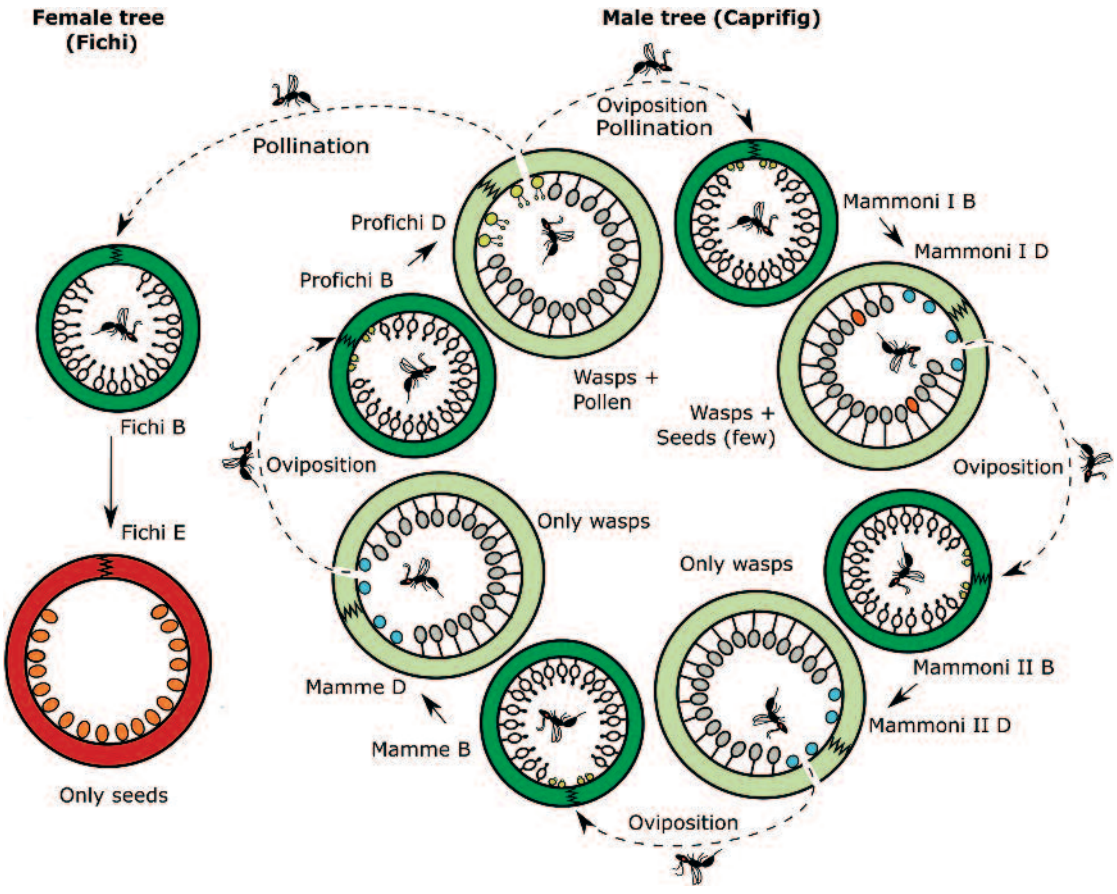

Fig. 3 - The fig and wasp cycle of *Ficus carica.* The male tree *caprificus* produces multiple crops –profichi, mammoni I, mammoni II and mamme. These crops have overlapping generations especially pollen receptive stage B (dark green) and wasp dispersal stage D (light green) respectively. Syconia on fichi ripen (red) and disperse seeds. Developing seeds (orange), wasps (grey) or both seeds and wasps can be observed within a syconium. The anthers produce pollen (yellow) or are rudimentary (blue).

Fig. 3 - Il ciclo fico-vespa di Ficus carica. L'albero maschile caprifico produce profichi, mammoni I, mammoni II e mamme. Questi raccolti hanno generazioni sovrapposte, specialmente lo stadio B recettivo del polline (verde scuro) e lo stadio D di dispersione della vespa (verde chiaro). I siconi sui fichi maturano 8rosso) e disperdono i semi. All'interno del siconio si osservano semi durante lo sviluppo (arancione), vespe (grigio) o entrambi. Le antere producono polline (giallo) o sono rudimentali (blu).

row space for entry into the syconium, the wasp, while attempting to enter, loses its wings and part of its antenna (Galil and Neeman, 1977). Once inside, the wasp gets rehydrated, the body swells, and concealed pollen is released, thus, carrying out passive pollination. Though the wasp attempts oviposition, eggs cannot be laid because the style length is longer than the length of the ovipositor.

The pollinator locates the pollen receptive fig using species specific volatile organic compounds (VOCs) released from the fig (Hossaert-McKey *et al*., 1994); female wasps show electrophysiological response to VOCs such as linalool, linalool oxide, b-caryophyllene and germacrene D (Soler *et al*., 2012). Bouquet comprising of twenty-six VOCs most of which are terpenoids in nature are emitted by the receptive figs. The female figs emit the same volatiles as the male figs (thus mimicking the male figs) and deceive the pollinators into entering the female fig. Both the male and the female figs share the same pollinator *B. psenes* (Soler *et al*., 2012). Though the receptivity of the syconium is a few days, upon lack of presence of pollinators the figs can wait and remain receptive for 2-3 weeks (Khadari *et al.*1995). A portion of wasps from *profichi* crop also enters syconia at B-stage of male trees, i.e., *mammoni I* inflorescences (fig. 3). The wasps oviposit in the short-styled flowers of *mammoni I*, flowers also get pollinated.

Stage C (Post-pollination)

Development of seeds from pollinated flowers takes place in *fichi*. In *mammoni I* syconia, wasp offspring and seeds develop together.

Stage D (Wasp dispersal)

Because of absence of developing wasps in *fichi*, the wasp dispersal stage is not valid for *fichi*. Seeds continue to develop in the *fichi.* On the male tree, the pollinator offspring are ready to emerge from *mammoni I*. Male wasps developing inside *mammoni I* syconia hatch from their galls and copulate with the females which remain arrested within the galls. Later on, these fertilized females crawl out from their galls and disperse from the natal syconium through the open ostiole (Galil and Neeman, 1977).

Stage E (Seed dispersal)

The syconia of *fichi* have seeds ready for dispersal. The fruit is sweet, fleshy, changes colour and becomes attractive to seed dispersal agents such as bats and birds (Neeman and Galil, 1978). Since there are no seeds to disperse from the syconia of *mammoni I* crop (though a few seeds are produced owing to pollen from *Profichi*), a significant change in colour is not observed. The fruit is spongy as well as less nutritious (Neeman and Galil, 1978).

In order to continue the wasp cycle, wasps from *mammoni I* enter the co-occurring receptive B stage syconia of *mammoni II* crop (fig. 3). Mammoni I does not produce pollen and hence *mammoni II* syconia are only used for oviposition and seeds are not produced, thus functioning exclusively as nursery for the wasps. However, Neeman and Galil (1978) found that artificially pollinated *mammoni II* can produce seeds indicating that lack of seeds in the wild from *mammoni II* crop is because of absence of pollen in the previous crop of *caprificus*.

Once the wasps are ready to emerge from *mammoni II*, syconia of next crop *mamme* are in B-stage. Thus wasps from *mammoni* II D-stage enter into the *mamme* B-stage. They also do not have any pollen on their body and hence only oviposition followed by wasp development takes place in the flowers of *mamme*. The D-stage of *mamme* crop overlaps with the *profichi* B-stage in which like *mamme* there is only wasp development. However, D-stage of *profichi* produces viable pollen that is carried by the wasps to the *fichi*. Thus, cycling of wasp takes place on multiple crops on the *caprifig* to have the wasps ready for pollination and seed production of *fichi*.

Importance of pollination

The edible fig *Ficus carica* is one of the few species of *Ficus* that has been cultivated (F. Kjellberg, personal communication). Cultivation of common fig is known since prehistoric times; fig seeds dated to 11,400-11,200 yrs. ago found in Jordan valley might have preceded domestication of cereals (Kislev *et al.*, 2006a, b; Lev-Yadun *et al*., 2006). During its long history of cultivation, the process of pollination is probably the path through which these figs pass as it can be found in native cultivars in Turkey, Greece or other countries in the region. Since the young syconia of the *Ficus carica* (Stage-B) is not hermetically closed (contrary to other figs), artificial pollination with an aid of puffer or syringe is enabled. The relatively easy possibility to pollinate *Ficus* without the aid of wasps enabled plant breeders to create new cultivars and even new hybrids of edible figs (Condit, 1950 and M. Flaishman personal communication). On the other hand, during thousands of years of cultivation of the common fig many parthenocarpic cultivars were selected. The ovaries of these cultivars turn into drupelets without fertilization. Since no seeds are formed in the parthenocarpic cultivars, propagation is totally

dependent on stem cuttings leading to clonal cultivars. Through traditional agriculture the diversity of such clonal varieties are maintained (Achtak *et al.*, 2010).

In conclusion, common fig is one of the few species that grow in sub-tropical areas that is exposed to greater fluctuation in climatic conditions. The wasps thus go through developmental arrest or multiple generations of breeding in different crops of figs. Once the female trees are ready for pollination they deceive the pollinators to enter the syconia on the female trees thus obtaining pollination services. This interaction is unlike the usual fig-fig wasp interaction especially in the monoecious system where the same syconium produces both seeds and wasp offspring.

Abstract

Ficus species are characterized by a specialized pollination by wasps of the family Agaonidae. Pollination involves entry of female wasps into an enclosed spherical inflorescence (syconium) with a minute opening (ostiole). Each syconium contains along the inner wall hundreds of unisexual flowers and the ostiole is the only point of access to these flowers. Upon entering the syconium the Agaonid wasp carries out pollination services as well as oviposition in these flowers within the syconium. The wasp often dies inside the syconium after pollination. Pollination and therefore seed development can occur only if this specialized interaction exists. Offspring of pollinator wasps cannot develop in the absence of syconia of the host *Ficus*. The same pollination mechanism is seen in all the members of genus *Ficus* that comprises of over 750 species growing in habitats ranging from the tropics to sub-tropics and exhibiting both monoecious and (gyno)dioecious breeding systems. In monoecious species seeds and wasps develop inside the same syconium, whereas in (gyno)dioecious species, the plant, based on its sex either produces seeds or pollinator wasps. Pollination in *Ficus* is mediated by chemical signals (volatiles emitted by the fig host) and the mode of pollination is either active or passive. Native to the temperate Mediterranean region, the edible figs (*Ficus carica*) have been cultivated since prehistoric times. In the wild, the edible fig goes through a complex yet interesting cycle of wasp development and wasp cycling likely owing to the temperate climate. The cultivated edible figs produce fruits with the aid of the pollinator wasp *Blastophaga psenes* and propagation is by seeds. However during the long interaction of edible figs with human beings, many parthenocarpic varieties have been developed that are propagated clonally by stem cutting. Also, artificial pollination with pollen from different pollen donors has enabled the creation of new cultivars and even new hybrids of edible figs.

Key words: Common fig, Caprifig, Fichi, Gyno(dioecious), Passive pollination.

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