CHAPTER 5

DISCUSSION

5.1 *Ficus* phenology

5.1.1 General leaf and fig phenology. Two main types of phenological patterns were identified amongst the dioecious *Ficus* species in this study. The first pattern can be termed the *F. carica* type, after Kjellberg *et al.* (1987) and includes the three species in the subgenus *Sycomorus*, section *Sycomorus*, subsection *Neomorphe* (*F. auriculata*, *F. oligodon* and *F. variegata*) and the two species in the subgenus *Ficus*, section *Eriosycea*, subsection *Eriosycea* (*F. fulva* and *F. triloba*). The general traits within this type are; i) peaks of receptive syconia produced at different times on 'male' and 'female' trees, ii) release of most pollen-laden wasps at the same time as peak production of receptive figs on female trees, iii) male figs least abundant when the conditions are unfavorable for wasp dispersal/reproduction, and iv) strong within-tree synchronous fig production. The second pattern can be termed the *F. hispida* type (after Patel, 1996) and includes *F. hispida* (subgenus *Sycomorus*, section *Sycocarpus*) and *F. semicordata* (subgenus *Sycomorus*, section *Hemicardia*). This type displayed completely asynchronous within-tree fig production, with receptive and wasp/seed production occurring all year-round.

Ficus variegata in seasonal wet tropical forest at Cape Tribution, Australia (Spencer *et al.*, 1996), *F. auriculata* in the tropical rainforests in Xishuangbanna, China (Peng *et al.*, 2004), *F. hispida* in India (Patel, 1996) and *F. fulva* in Sarawak, Malaysia (Harrison *et al.*, 2000) exhibited similar phenology to that of the same species in our study. Hence it seems that our study, based on a single year of observation, managed to catch the basic feature of the specie's phenology and that this phenology is rather stable over large distances.

Globally, only some species of subgenus *Sycomorus* presented *F. hispida*-type phenology, namely *F. semicordata*, a fig of section *Hemicardia* which taxonomically stands apart from *F. hispida* (section *Sycocarpus*) and *F. hispida* presented a *F. hispida*-type phenology. The whole data set also suggests that northern species of dioecious figs such as *F. auriculata*, *F. oligodon* and *F. triloba* more often have *F. carica* phenology, while the southern species probably may have *F. hispida* type. Whether or not these findings apply to all dioecious figs warrant further research.

At the population-level, all species displayed asynchronous fig production. Figs of most species were produced year-round (at the population level), but there were pronounced annual cycles in fig abundance. Year-round flowering has been widely reported in *Ficus* spp. trees and it is necessary to ensure survival of their short lived-span pollinators (Ramirez, 1974; Jansen, 1979; Kjellberg *et al.*, 1987; Compton *et al.*, 1994; Anstett *et al.*, 1997; Jia *et al.*, 2007). It is also necessary for efficient seed dispersal and to increase the probability of successful germination and seedling establishment, which require specialized micro-sites (i.e. large light gaps) for successful establishment (Milton, 1991).

Frequency dependent selection for year round fruiting in figs may be relaxed in seasonal climates leading to seasonal fruiting patterns (Kjellberg and Maurice, 1989). Indeed, like most tropical tree species, growing in seasonal dry areas, most species (*F. auriculata, F. fulva, F. hispida, F. oligodon, F. semicordata* and *F. variegata*) produced the main seed crops in the beginning of rainy season, the optimal period for germination and seedling establishment (Blakesley *et al.*, 2002a).

Normally, most *Ficus* species take 3-4 weeks to germinate (FORRU, 2006). Therefore, seedlings of most species would have about 4-5 months for the development of an expansive root system, essential to enable seedling to survive the dry, first cold (November-January) then hot conditions from February to April (dry season) which prevail in the area. However, most of the seeds of *F. triloba* were dispersed in September-October (late rainy season). *Ficus triloba* seedlings would therefore have only 1-2 months for establishment before the onset of the dry season. Therefore, survival of *F. triloba* seedlings is probably lower than that of other selected *Ficus* seedlings.

Before initiation of the peak fig crops, female trees of most species (particularly *F. fulva*, *F. oligodon* and *F. variegata*) shed their old leaves, and then produced both new leaves and new figs simultaneously, or fig initiation occurs soon after leaf flushing, to ensure that they have enough fresh energy sources to support development main seed crop (Zhang *et al.*, 2006). Also, peaks of wasp/pollen production of male trees often coincided with the peak of receptive figs on female trees (particularly for *F. auriculata*, *F hispida* and *F. oligodon*), which ensures enough pollinators for pollination success and avoids possible pollinator competition when wasps are unable to discriminate between the sexes of trees (Moore *et al.*, 2003).

Fig production on male trees of most species peaked in the dry season before the onset of the main seed crop of female trees (about 1-3 months depends on species) when the conditions are most favorable for wasp dispersal (i.e. high abundance of receptive female trees and favorable flight conditions). However, the timing of fig production on male trees of *F. auriculata*, *F. fulva*, *F. oligodon* and *F. variegata* created a bottleneck for wasp dispersal, particularly during rainy season, when the wasp-producing figs of male trees were least abundant. Kjellberg *et al.* (1987) proposed that this might be an adaptation to weather conditions, as *F. carica* grows in highly seasonal environments. The results presented here showed that male figs of most species only produce few figs during the rainy season. This could results in particularly unfavorable period for fig wasp survival. Indeed Peng *et al.* (2003) reported that fig wasps stopped hovering if the weather was rainy. Also rainfall may dilute the airborne chemicals that attract fig wasps to their host tree species (Zhang *et al.*, 2003). Indeed abortion of young figs of *F. auriculata* and *F. oligodon* occurred mainly in crops produced in the rainy season suggesting wasp limitation.

Further, most species which showed a bottleneck for wasp dispersal are ranked as rare in Doi Suthep-Pui National Park (Maxwell and Elliott, 2001). *Ficus* trees and their pollinator-wasps depend on each other to complete reproduction (Jia *et al.*, 2008). So, a shortage of pollinators (during the critical bottleneck periods) may also affect *Ficus* reproduction. In support of this assertion, Bronstein (1988b) found that seed set in *F. pertusa* L. is pollinator-limited and Harrison *et al.* (2000) suggested for dioecious figs that fig abortion of female trees is likely to reflect pollen limitation. Ma *et al.* (2009) also showed that the numbers and the proportions of fig seeds and female wasp offspring significantly increased with numbers of foundresses.

In the present study, *F. hispida* and *F. semicordata* had high ability to maintain their pollinator populations all year-round, even with small tree populations, because fig production in male trees was highly asynchronous. Jia *et al.* (2008) suggested that asynchrony enables *Ficus* spp. to maintain their pollinator population, by reducing pollinator mortality during flight between trees. In contrast, asynchronous fig production within male trees of *F. auriculata, F. fulva*, *F. oligodon*, *F. triloba* and *F. variegata* was rare, compelling their pollinator wasps to leave the natal trees to search for receptive figs on other trees. Therefore for *Ficus* species with synchronous fig production within male tree crowns, it is important in restoration projects to include sufficient numbers of male trees in order to ensure the persistence of local wasp populations. Indeed, Harrison (2000) showed that wasp populations are more local in dioecious figs than in monoecious ones.

5.1.2 Implications for forest restoration plans. Even though, data on fig-eating animals is limited, for the particular dioecious *Ficus* species selected for this study, it is still possible that they act as keystone species in tropical forest ecosystems, in that they can supply food to wildlife all year-round and thus qualify as framework tree species, likely to facilitate seed dispersal in forest restoration projects. Especially, *F. auriculata* produced ripe figs more abundantly when fruits of other tree species were in short supply (i.e. June, July and February in northern Thailand; Maxwell and Elliott, 2001; r=-0.631, p=0.034), fulfilling the definition of "keystone species", but statistical results for other *Ficus* spp. tested were inconclusive (Table 19). In particular, figs may maintain viable populations of fruit bats, which are known to feed on dioecious figs (Shanahan *et al.*, 2001b; Dumont *et al.*, 2004; Lomáscolo *et al.*, 2008, for *F. auriculata*, M. Hossaert-Mckey, unpublished observations, for *F. hispida*, Borges *et al.* 2008). Fruit bats are known to be vital for recovery of tree species richness in regenerating or planted forest (Corlett and Hua, 2000; FORRU, 2006).

Table 19 Results of Pearson's correlation test between the proportion of ripe female figs and the number of the other tree/treelet species producing ripe fruits in each month (Maxwell and Elliott, 2001)[a].

Pearson's Correlation	FIAU	FIFU	FIHI	FIOL	FISE	FITR	FIVA
r	-0.631*	-0.099	-0.271	-0.070	-0.118	0.754**	-0.132
p	0.034	0.758	0.394	0.830	0.715	0.005	0.682

* Correlation is significant at the 0.05 level, ** Correlation is significant at the 0.01 level.

[a] Data were calculated from 390 trees and 67 treelets in 'Vegetation and Vascular Flora of Doi Sutep-Pui National Park, Northern Thailand'. FIAU = *F. auriculata*, FIFU = *F. fulva*, FIHI = *F. hispida*, FIOL = *F. oligodon*, FISE = *F. semicordata*, FITR = *F. triloba* and FIVA = *F. variegata*.

Although, female trees of most species produced figs all year round, the optimal time for seed collection of most of the selected *Ficus* spp. (except for *F. triloba*) for nursery production of seedlings is at the beginning of the rainy season when the main seed crop is produced (from May to July). Seed collection is easiest in mixed forest types (elevations ranging from 800 to 1,200 m.) where the parent trees of all selected species are fairly common and it is easy to find seeds with minimum searching time.

In the case of *F. triloba*, the phenology of female trees is unfavorable for seed germination and seedling establishment, since the trees produced the main seed crop at the end of the rainy season, when the chances of seedling survival are low due to the long hot dry season. To maintain the population of *F. triloba* in the park, seedlings must be produced in the nursery and planted out when they are 30-60 cm tall in the optimal planting time, at the beginning of rainy season (May-June in northern Thailand; Elliott and Kuaraksa, 2008).

Ficus hispida, *F. oligodon* and *F. semicordata* can be planted to restore several types of degraded areas in the park, because the species distributions are wide (from dry deciduous forest to hill evergreen forest; Table 2, Fig. 7). Moreover, these species are evergreen, which is helpful in lowland restoration sites to suppress weed growth and to provide shade for wildlife, especially during the dry season when other tree species shed their leaves. Optimum planting sites for *F. auriculata* and *F. variegata* are degraded areas, higher than 800 m elevation. Also, optimal planting sites for *F. fulva* and *F. triloba* are in degraded areas of mixed forest, because their natural distribution is limited to that zone.

In order to maintain pollinator populations of *Ficus* species which had critical bottlenecks for wasp dispersal, it is especially important to increase the numbers of male trees, which are critical for year-round survival of local fig-wasp population (i.e. fruiting in the rainy season). However, in forest restoration projects, most plantlets are usually produced from seeds. In the case of dioecious fig species, it is not known how many of the seedlings are male and how many are female. Therefore, vegetative propagation (i.e. from leafy cuttings) derived from trees of known sex (and its phenological patterns) may be more necessary to ensure a fairly even sex ratio among the planting stock.

Phenological studies are also helpful for taxonomists or local staffs who are in charge in forest restoration projects to separate the two closely related species; *F. auriculata* and *F. oligodon* as distinct species. Indeed, their status as distinct species is in dispute and has not been sorted out by conventional taxonomy (Berg and Corner, 2005; Berg, 2007; Berg *et al.*, 2011). This paper shows clear differences between the two species that confirm their status as distinct species such as: habitat, abundance, distribution, and phenological patterns of figs and leaves. Furthermore, for all dioecious species, it is not possible to distinguish individuals of the two sexes from external characteristics, except when they are in flower or fruit (Valdeyron and Lloyd, 1979). However, for *F. fulva*, *F. triloba* and *F. variegata*, they showed different leafing patterns between the two sexes, which may useful for nursery staff to distinguish the sex of trees, even when they have no figs (i.e. for collection of cuttings).

5.2 Interaction between fig trees and their associated wasps

5.2.1 General interactions. At receptivity, female figs of most species were bigger male figs (Table 10), suggesting adaptation to attract pollinators into female figs to complete pollination, because wasps prefer larger figs when they have a choice (Anstett *et al.*, 1996). In addition, fig volatile chemical production increases fig diameter (Barker, 1985; Hossaert-Mckey *et al.*, 1994). In female figs of most species, the jelly-like substance which filled the cavity during ripening was probably an adaptation to attract seed dispersers and to deter egg laying by wasps. In all dioecious *Ficus* species studied, female figs produced more seeds than male figs produced wasps (Table 13), suggesting that selection might favor the evolution of differences in flower numbers between the sexes of dioecious fig species. Patel and Hossaert-Mckey (2000) reported that dioecious figs produce more flowers per fig in females than in males.

The numbers of seeds produced in most species were greater in the rainy season than in other seasons (Table 14). This may be an adaptation by fig trees to seasonal environments for their seed germination and seedling establishment success because both *Ficus* seed germination and *Ficus* seedling establishment depend on sustained moisture (Swagel *et al.*, 1997).

5.2.2 Pollinators. Pollination of all the selected *Ficus* was active, since pollinators had pollen pockets (Kjellberg *et al.*, 2001). Fig wasps of the subgenus *Vilisia* were the only species-specific pollinators for the subgenus *Ficus* (subsection *Eriosycea*), whilst the studied species of *Ficus* subgenus *Sycomorus* were pollinated by the genus *Ceratosolen* (Table 20). This supports the assumption that related *Ficus* species are generally pollinated by wasps belonging to the same genus (Wiebes, 1979; Thompson, 1989; Wiebes and Compton, 1990; Herre *et al.*, 1996; Berg and Corner, 2005). The phylogeny of pollinating fig wasps parallels that of their host trees, suggesting that the two groups have co-evolved (Wiebes, 1982; Weiblen, 2002). In confirmation of this, the molecular study of Kerdelhué *et al.* (1999) revealed that a robust phylogeny of the *Ceratosolen* associated with *Ficus* of the subgenus *Sycomorus*.

Table 20 The association between *Ficus* and Agaonidae morphological classification.

***Ficus* species**	**Subgenus**	**Section**	**Subsection**	**Agaonidae genus**	**Pollination mode** [a] (anther/ovule)
F. auriculata	*Sycomorus*	*Sycomorus*	*Neomorphe*	*Ceratosolen*	Active
F. oligodon	*Sycomorus*	*Sycomorus*	*Neomorphe*	*Ceratosolen*	Active
F. variegata	*Sycomorus*	*Sycomorus*	*Neomorphe*	*Ceratosolen*	Active (0.04)
F. hispida	*Sycomorus*	*Sycocarpus*	*Sycocarpus*	*Ceratosolen*	Active (0.04)
F. semicordata	*Sycomorus*	*Hemicardia*	*Hemicardia*	*Ceratosolen*	Active
F. fulva	*Ficus*	*Eriosycea*	*Eriosycea*	*Vilisia*	Active (0.14)
F. triloba	*Ficus*	*Eriosycea*	*Eriosycea*	*Valisia*	Active

[a] Based on Kjellberg *et al.*, (2001)

Previously, it was thought that the fig-wasp relationship was entirely species-specific obligate mutualism. However, recent studies have shown that up to 30-60% of fig-wasp relationship are not mono-specific, depending on the locality (Kerdelhue *et al.*, 1999; Molbo *et al.*, 2003; Harrison, 2006). Erroneous pollination events are known from isolated trees or from trees introduced to an area, which lack their natural pollinator (Parrish *et al.*, 2003). Previous authors predicted that non-one-to-one relationships might represent intermediate steps in the process of speciation (Wiebes, 1979; Anstett *et al.*, 1997). Some *Ficus* species are known to have more than one pollinator (Rasplus, 1986; Wiebes, 1994; Cook and Rasplus, 2003; Berg and Corner, 2005; Harrison *et al.*, 2008). As in *F. natalensis* in Uganda, four species of potential pollinators (viable seeds were produced) were recorded by Compton *et al.* (2009). Cook and Rasplus (2003) also found that *F. sur* has three pollinators with different geoghaphical distributions and *F. fulva* is reported to be pollinated by *V. compacta* and *V. inopinata* (Wiebes, 1994). The results of the study showed that a majority of fig species have only one specific pollinator. However, *F. hispida* was pollinated by two *Certosolen* species (Appendix D). If each *Ficus* species is pollinated by a single pollinator, the two pollinators found may have been collected from the two different varieties (*F. hispida* L.f. var. *hispida* and *F. hispida* var. *badiostrigosa* Corner; Chantarasuwan and Kumtong, 2005; Tarachai, 2008). However, if the pairs of pollinator species coexisted on the same trees, further studies are needed to explore outstanding questions such as which species is the true pollinator or both? Are the two pollinators equally successful at entering the figs? Do the two wasp species compete for oviposition sites?

There are also some cases of the same pollinator species being found in more than one *Ficus* species (Wiebes, 1994; Cook and Rasplus, 2003). Wiebes (1979) suggested that the apparent association of one wasp with two *Ficus* species may be due to geographical variation, whilst Weiblen (2002) suggested that the breakdown of host specificity is an alternative mode of speciation. Although the rates of pollinator sharing among dioecious fig species is low, compared with monoecious figs, about 1.5% of wasp species in the *Ceratosolen* group is known to have more than one host (Moe *et al.*, 2011). For example, *C. appendiculatus*, the pollinator of *F. variegata* in my study, is pollinates *F. viridicarpa* in peninsular Malaysia (Rasplus, 1996). Moreover, some fig wasp species (e.g. *Ceratosolen galili*) have lost the capacity to pollinate but still breed in figs so-called "cuckoos" (Galil and Eisikowitch, 1969; Berg and Wiebes, 1992; Kjellberg *et al.*, 2001). In this study, *F. auriculata* and *F. oligodon* shared the same pollinator *(C. emarginatus*), this implying that these two closely related species may be tightly linked, probably as a result of hybridization or speciation from the breakdown of host specificity. Analysis of molecular markers would be necessary to test this hypothesis.

The number of foundresses found in the gall and seed figs of most of the studied *Ficus* species was similar (Table 10). Weiblen *et al.* (2001) reported that foundresses are equally attracted to both gall and seed figs in functionally dioecious species. Grafen and Godfray (1991) suggested that pollinators are unable to differentiate between seed and gall figs. Indeed, wasps that enter female figs cannot lay any eggs, so they should avoid entering female figs (Moore *et al.*, 2003). I propose four reasons to explain the equal number of foundress entering female and male figs: i) differences in the seasonal phenology of female and male figs leave wasps with no choice between fig sexes (e.g. male and female figs of *F. carica* are very rarely receptive at the same time of the year; Kjellberg *et al.*, 1987; Anstett *et al.*, 1997), ii) similar volatile chemicals are produced from receptive female and male figs so that pollinators cannot distinguish between the two sexes (Grison-Pigé *et al.*, 2001; Chen *et al.*, 2009), iii) low tree density compels wasps to enter the first fig found (Cook and Rasplus, 2003) and iv) 'selection to rush'- because fig wasps live for only 1-2 days, they may not be able to afford the time to choose, thus wasps are tend to enter the first fig encountered (Cook and Rasplus, 2003; Moore *et al.*, 2003).

5.2.3. Non-pollinators. Clearly, the results showed that fig wasp communities of dioecious figs were less species rich than in monoecious figs. Cook and Rasplus (2003) reported that a single monoecious fig species can host up to 30 diverse NPFW species. Kjellberg *et al.* (2005) suggested that often figs produce more non-pollinating wasps than pollinating wasps in a single fig. However, this may be true only for monoecious figs, because most of the selected dioecious *Ficus* had higher production of pollinators than of non-pollinator (Table 10). This finding supports the assertion that dioecy in *Ficus* spp. evolved from monoecious species in order to avoid non-pollinating wasps (Kerdelhue and Rasplus, 1996). Also, Weiblen *et al.* (2001) found that in dioecious fig species, pollinators occurred in 93-100% of the crops, while in monoecious *F. microcarpa* pollinators were present in only 56%. However, in a single fig of *F. auriculata* and *F. fulva* (both are ranked as rare locally), the proportion of non-pollinating wasps was relatively high (Table 10), indicating that they may have a strong impact on the pollinator population size and the stable existence of the fig-wasp mutualism.

Most non-pollinators found in this study oviposited outside the figs and were specific to a host fig species (Table 11). However, Godfray (1988) stated that where tree specificity completely breaks down, some parasitoids, specificity sometimes extends to the species of wasp hosts. Previous authors reported that different species of non-pollinators had different effects on fig-fig wasp mutualisms, but the real nature of their relationship is still not clearly understood in many cases (Appendix I).

As a result of previous studies, larval biology of NPFWs in my data were divided into three major ecological groupings: gall-makers (*Platyneura* spp.), inquilines (*Philotrypesis* spp.) and true parasitoids (*Apocrypta* spp. and *Sycoscapter* spp., Fig. 27).

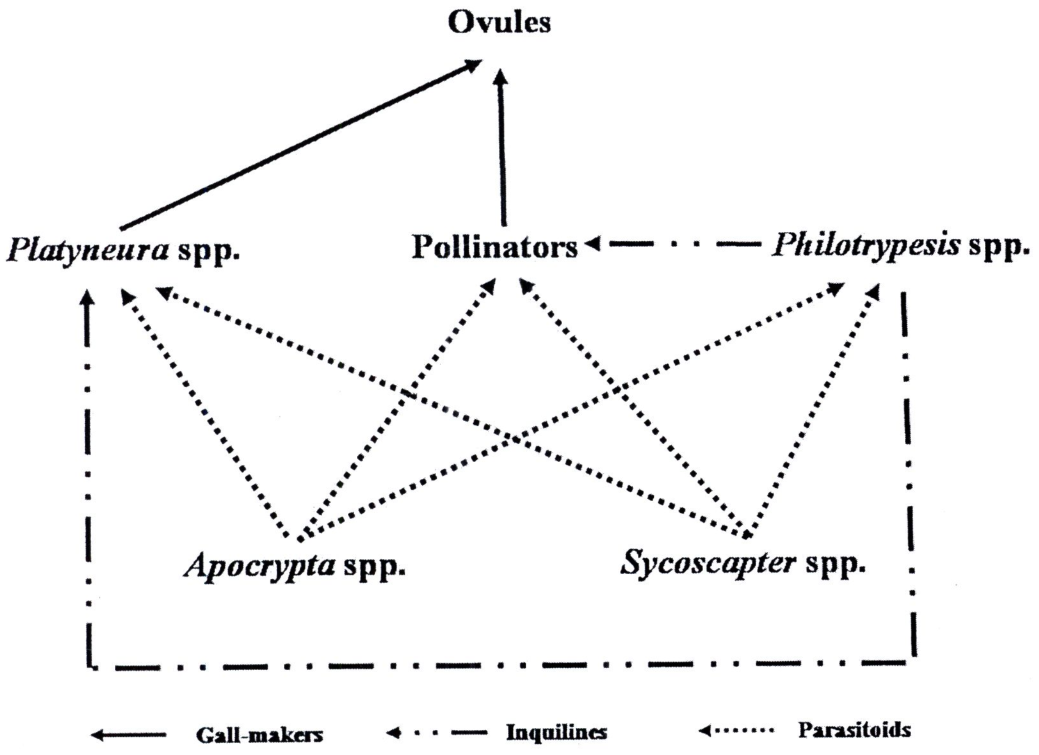

Figure 27 Relationship summarizing of the fig wasps associated with the *Ficus* species studied, in the Doi Suthep-Pui National Park, Thailand.

5.2.3.1 *Apocrypta* spp. (Sycoryctinae). The genus *Apocrypta* is recognized by the ploughshare-shaped sterna of the metasoma in the females (Ulenberg, 1985) and by the tubular type in the males (Murray, 1990). Ulenberg (1985) also reported that *Apocrypta* is related strictly to the *Ficus* sections *Ficus*, *Sycomorus* and *Sycocarpus*. However, in my results, I only found *Apocrpta* spp. in *F. hispida* (section *Sycocarpus*) and *F. semicoradta* (section *Hemicardia*), whereas it was absence in figs of section *Ficus* and *Sycomorus*, suggesting that *Apocypta* spp. are related with each *Ficus* species and are probably independent of a fig tree's taxonomic affiliation. Previous studies have considered *Apocrypta* spp. as a true parasitoid, which predated on pollinators (Jansen, 1979; Kerdelhué and Rasplus, 1996). Several authors also found that *Apocrypta* spp. were the parasitoids of other non-pollinating wasps. They cannot oviposit in figs unless the figs are already occupied by either pollinators or the non-pollinators (Ansari, 1967; Abdurahiman and Joseph, 1978; Weiblen *et al.*, 2001; Wang and Zheng, 2008). Silvieus *et al.* (2007) mentioned that *Apocrypta* are specifically associated with *Platyneura* gallers, while Peng *et al.*, (2005) found that *Apocrypta* has a significant effect on both *Philotrypesis* and *Ceratosolen*. In the fig species studied, I found *Apocrypta*, *Platyneura* and *Philotrypesis* together in a single fig of *F. semicordata*. I also found *Apocrypta* sp. in *F. hispida* in which the genus *Platyneura* was absent, suggesting that *Apocrypta* spp. are not the only species-specific with *Platyneura* gallers but they can also be a parasitoids of *Ceratosolen* and *Philotrypesis*. Xu *et al.* (2003) suggested that when the number of *Apocrypta* spp. increased, the population of pollinating fig wasps would decrease. The oviposition behavior of this genus varied among species due to ovipositor length and syconial wall thickness, as *Apocrypta* sp. founded in *F. semicordata* had a shorter ovipositor than *A. bakeri* in *F. hispida*, which correlates with the thinner syconial wall of its host fig (Appendixes D, F). Ramirez (1997) noted that male *Apocrypta* sp. emerge from the gall where they developed before the males of other species (e.g. *Ceratosolen* and *Philotrypesis*) which probably to prevent overcrowding and to avoids damage by males of fighting species.

5.2.3.2 *Philotrypsis* spp. (Sycoryctinae). Among the NPFWs, *Philotrypesis* species were very common in most selected figs of both subgenus *Sycomorus* and *Ficus* (Table 11). Although, the biology of most *Philotrypesis* spp. is poorly known, many authors regard *Philotrypesis* spp. as inquilines, while a few regard them as parasites (Appendix I). Shi *et al.* (2006) and Zhai *et al.* (2008) considered *Philotrypsis* spp. as inqualine of the pollinating wasps, whilst Peng *et al.* (2005b) considered *Philotrypsis* is an inquiline of NPFW when it feeds on the developing galls of *Apocryptophagus* sp. He also mentioned that the genus *Philotrypesis* appears to have no significant impact on the pollinator population. On the other hand, several studies have considered that members of genus *Philotrypesis* were parasitoids because they depend on the presence of pollinator larvae to complete development (Abdurahiman, 1986; Weiblen *et al.*, 2001; Silvieus *et al.*, 2007). In confirmation of this, Joseph (1958, in Jiang *et al.*, 2006) reported that *Philotrypesis caricae* has been shown to be a parasitoid of the pollinator *Blastophaga psenes* and feeds on the surrounding ovular tissue, called cleptoparasitoid. *Philotrypesis* is highly host species-specific (Jousselin *et al.*, 2004) but some fig species may host several *Philotrypesis* species as in this study (Table 11).

5.2.3.3 *Platyneura* spp. (Sycophaginae). The name *Platyneura* takes priority over *Apocryptophagus* (Silvieus *et al.*, 2007) but the taxonomic affinity of this subfamily is currently unclear (Herre *et al*., 2008). They are considered to be gall-makers in *Sycomorus* figs (Silvieus *et al*., 2007). They started to visit figs at pre-female phase, before arrival of pollinator wasps, and they deposit eggs in un-pollinated flowers (Kerdelhué and Rasplus, 1996; Peng *et al*., 2005b; Shi *et al*., 2006; Sun *et al*., 2008). However, some species of *Platyneura* lay eggs in the developing phase figs through the fig wall (Kerdelhué and Rasplus, 1996). All *Platyneura* species found in my study seemed to oviposit through the fig wall from the outside of the fig because the female morphological characters are not suitable for entry through the ostiole (e.g. large body, long ovipositor). In a single fig, I sometimes found multiple *Platyneura* species that differed in ovipositor length. Silvieus *et al*. (2007) reported that *Platyneura* species with short ovipositors lay eggs prior to pollination when figs are small in diameter, whereas species with long ovipositors lay eggs after pollination when figs are larger. Elias *et al.* (2008) mentioned that *Platyneura* species with a long ovipositors are either inquilines or parasitic on the pollinators or other NPFWs. However, several studies have considered *Platynuera* groups as the parasites of fig seeds when they could oviposit in the external ovaries of the long-styled florets, which had been destined to produce seeds (Compton *et al*., 1991; Kerdelhué and Rasplus, 1996; Xu *et al*., 2003; Silvieus *et al*., 2007). My data showed that females *Platyneura* oviposited on the female figs of *F. oligodon* and produced viable offspring (Appendix E), especially while male figs were least abundant. Thus, I confirmed that *Platyneura* does not depend on pollinator larvae for inducing galls. However, Peng *et al*. (2005b) suggested that *Platyneura* sp. prefer to oviposit on male figs than that of female figs. Only when few or no male figs are available does it shift its reproduction to female figs. The fact that *Platyneura* sp. oviposited on both male and female figs, suggests that they may have negative effects on the production of seeds, even though they inflict a small cost in terms of ovules destroyed and only for a few months each years. *Platyneura* is not only the competitor of pollinator for floral resources, but is also a parasite on fig seeds (Weiblen *et al.*, 2001). However, Galil and Eisikowick (1968) also predicted that the females of *Platyneura* may carry pollen. If this is confirmed, they may able to prevent female figs which did not receive pollinating wasps from aborting, especially where pollinator is a limitation, and they may provide benefit to animals who feed on figs in general.

5.2.3.4 *Sycoscapter* spp. (Sycoryctinae). I found *Sycoscapter* spp. in several figs throughout the subgenus *Sycomorus* and *Ficus*, which is in accordance with the observation of Compton and van Noort (1992) as *Sycoscapter* group has the large size of their host figs and generally not depend on the taxonomic factors of their host figs. The females are easily recognizable by their green metallic luster, red eyes and very long ovipositor (Appendixes C, E-H). *Sycoscapter* species are considered to be parasitoids (Weiblen *et al.*, 2001), the larvae of which feed directly on the larvae of pollinators (e.g. *Blastophaga*, *Ceratosolen*; Silvieus *et al.*, 2007; Hsu *et al.* in Harrison *et al.*, 2008; Tzeng *et al.*, 2008) and non-pollinators (e.g. *Philotrypesis*; Chen, 1998). Previous molecular phylogenetic studies suggested *Sycoscapter* have partially co-speciated with their hosts (Lopez-Vaamonde *et al.*, 2001). I found that only two *Sycoscapter* were associated within *F. triloba*, suggesting that they may reduce the pollinator population, because pollinator abundance was strongly negatively correlated with parasite presence (Herre, 1996). Tzeng *et al.* (2008) estimated that the reduction of the pollinator population by *Sycoscapter* was about 54%. In *F. formosana*, females *Sycoscapter* appear on male figs 1-6 weeks after pollination (Tzeng *et al.*, 2008). They lay eggs through the fig wall into fig ovules of different figs on one or more trees (Bean and Cook, 2001).

5.2.4 Effect of different habitats. My data showed that the effect of habitat disturbance on foundress was contradictory although disturbance did seem to consistently reduce seed production (Table 12, 13). Adult fig wasps have high ability to transport mass pollen over long-distance (much greater distances than the study sites, the farthest isolated fig trees was about 12 km from the nearby forest). Moreover, fig wasps have high host-finding ability, finding even isolated trees in the highly disturbed habitats. In addition, pollinators wasps may have the high pollinating ability in which a single foundress can be pollinated more than one figs, as reported on *F. hispida*, 16% of pollinated figs were found with no dead foundresses within the fig cavity, suggesting that the foundresses can and do re-emerge from the figs they have pollinated (Gibernau *et al.*, 1996; Pereira and Prado, 2006), whilst Moore *et al.* (2003) found that 68% of foundresses re-emerged from *F. montana* during their experiment. They also stated that the foundresses re-emergence because the oviposition sites are limited, and re-emergence rates were more common in dioecious than in monoecious fig species.

Even though observations of the dispersal of wasps are difficult to obtain, current knowledge of travel distances of fig wasps, particularly in monoecious species, is frequently over distances of more than 10 kilometers (Weiblen, 2002) that can be dispersed for long-distance over all my collection sites. Zavodna *et al.* (2005) suggested that habitat fragmentation may not affect pollinating fig wasp dispersal if conditions are favorable (e.g. strong wind) because pollinator populations apparently can rebound very quickly after local extinction when their host trees are present

(Bronstein and Hossaert-Mckey, 1995; Harrison, 2000). However, in *F. triloba* and *F. variegata* (both are ranked as rare locally and mainly are clustered only in primary forest; Maxwell and Elliott, 2001) the effect of forest fragmentation on foundress number was significant (Table 12). Few foundresses were found outside the primary forest, suggesting that the low densities, within-tree synchronicity and infrequent flowering of *F. trioba* and *F. variegata* require their pollinators to disperser over substantial distances. Therefore, in isolated fragments, the number of fig trees of *F. triloba* and *F. variegata* within the dispersal radius of pollinators most probably falls below the minimum critical size needed to support populations of the pollinator. Consequently, pollinators must have arrived from other places.

Herre (1999) reported that increased numbers of foundresses are associated with increases in seed production. However, in my results, one or two foundresses entered in single female fig of most species but seed set rates were relatively high, suggesting that individual wasps can carry sufficient pollens to pollinate flowers. For example, Ramirez (1969) reported that one pollinator wasp of *F. goldmanii* can pollinate at least 682 flowers. In confirmation of this, Patel and Hossaert-Mckey (2000) and Peng *et al.* (2005b) have shown that there were no significant differences in vacant ovary number per fig between various foundress pollinations. Anstett *et al.* (1996) also reported that seed set of *F. aurea* is limited by flower number and not by pollen, even in the case of a single foundress.

However, it seems, the foundresses number may be affect to the reproduction of the pollinator. Patel and Hossaert-Mckey (2000) found that mean pollinator offspring numbers were significantly lower for the one-foundress treatment than for the three- or eight- foundress treatment in *F. hispida*. Sex ratios of offspring also varied with the number of foundress per fig (Herre, 1985). In particularly, increased numbers of foundresses are associated with increases in male wasp proportion (Herre, 1999; Pereira and Prado, 2006). If the number of males is too small, no exit holes are bored and the female wasps remain entrapped inside the fig (Gali and Eisikowick, 1968). Molbo *et al.* (2004) and Zavodna *et al.* (2005) also reported that inbreeding levels are related to the number of foundresses, mating of pollinating wasps within a small number of foundress is more likely to be between siblings, whereas mating within many foundresses is likely to involve more nonsiblings. Therefore, increasing of foundresses number may reduce the risks of inbreeding level of fig wasps.

In planted plots, few seeds were recorded per fig (Table 13), even though the plot was not far from the primary forest (about 2 km). This implies that seed set rate may be lower with younger fig trees.

5.2.5 Implications for forest restoration. The mean seed number per fig during the rainy season, of most species, was higher than in other seasons (Table 14), suggesting that the rainy season is the optimum time for fig seed collection. Furthermore, collection of seeds from mature fig trees is better than from young trees because the figs contain more seeds.

The effects of habitat fragmentation on the numbers of foundresses and seeds of most selected *Ficus* species are not clear (Table 12, 13). This suggests that, *Ficus* spp. can be planted to restore forest, even on large isolated deforested sites, far away from natural forest, without worrying about their reproductive success, because pollinator wasps have a high ability to locate distant fig trees and carry-pollen to them.

5.3 *Ficus* propagation

5.3.1 Propagation from seed. All six *Ficus* species had germination percentages in excess of 35%, which is acceptable for nursery production of native trees for forest restoration purposes (Elliott *et al.*, 2002). As the early establishment of seedlings is the determinative phase in the growth cycle of *Ficus* (Galil, 1984). Suitable germination media should not contain forest soil, since most seedlings died of fungal infection, probably derived from soil pathogens including; *Penicillium* spp., *Fusarium* spp., *Aspergillus* spp., and *Rhizopus* spp. These fungi species were observed when seedlings were tested in a plant pathogen laboratory (pers. obs.). This is in agreement with Rahman *et al.* (2004) who reported that the excellent success of *Ficus* seedling production has been obtained from soil-free potting mix but well drained, good aeration and high water holding capacity because moisture availability is vital factor for fig seed germination and establishment (Galili and Meiri, 1981; Titus *et al.*, 1990; Urgessa, 2011). Lin *et al.* (2008) also highlighted forest soil was not a good substrate for long term survival of *Ficus* seedlings, whilst Herrera in Urgessa (2011) revealed that sand was the best medium for the germination of *F. vallischaude*. As described above, this result is also congruent with previous reports. Thus, the germination medium of sand and charred rice husk (1:1) is recommended for germinating *Ficus* seeds in nursery production.

Interactions between the germination medium composition and fungicide application on germination/survival rate might be explained by pH, since the combination of charred rice husk (pH 7.7-8.4) + fungicide (pH 8.2) had an alkaline-pH which is known to have a negative effect on germination rate (Goubitz *et al.*, 2003; Perez-Fernandez *et al.*, 2006). On the other hand, the combination of forest soil (pH 6.2) + fungicide (pH 8.2) was neutral, which is optimum for most seed germination. Unfortunately, a neutral pH is also optimum for growth of most the fungus species (http://en.wikipedia.org/wiki/soil_pH) that cause damping off diseases.

All fig seedlings performed well after placing in the high light intensity conditions, because most dioecious *Ficus* spp. are pioneer species that require full sunlight to grow (Laman, 1995; Thornton *et al.*, 2001). However, early *Ficus* seedling survival appears to be dependent on good moisture retention (Harrison *et al.*, 2003), so that continuous humidity is needed. However, most *Ficus* spp. trees respond negatively to over application of fertilizer (County, 2000). The addition of organic matter such as compost or a moderate application of 5-10-5 or 5-10-10 fertilizer is sufficient for the growth of *Ficus* spp. (Henley *et al.*, 1999). Particularly, phosphorus is considered one of the most important nutrients on growth of *Ficus* saplings (Attia *et al.*, 2004).

The production of planting stock of framework tree species for forest restoration projects requires simple techniques that are easily acquired by local communities and that maintenance of genetic diversity. *Ficus* spp. seeds are orthodox and easy to collect since they are available all year-round hence intensive phenology studies may not be needed. Therefore, production of planting stock of *Ficus* spp. from seeds in nurseries and planting out when they reach a plantable size by the optimum planting time is recommended for their use in broad-scale tropical forest restoration because these practices resulted in the highest growth rates and seedling survival in the nursery trials.

5.3.2 Propagation from cuttings. Producing *Ficus* spp. planting stock from cuttings was inefficient for all tested species. This agrees with the result of Danthu *et* *al.* (2002) who reported that most *Ficus* tree species of subgenus *Sycomorus* and *Ficus* had no capacity to propagate from cuttings. They also reported that the rooting capacity varied depending on the cutting material used, it decreased in the following order: long leafless hardwood, young nodal and apical cuttings, respectively. The poor growth and survival rates of planting stock derived from cuttings might also be explained by cutting from branches of mature trees which do not generally root well (Smits *et al.*, 1990; Kantarli, 1993). Longman and Wilson (1993) suggested that branches are unsuitable for cuttings because they have a different structure and growth hormones from main stems. Thus, after rooting, cuttings from branches grow into plants which may not grow normally, particularly developing reproductive parts rather than roots. However, in the case of dioecious *Ficus* species, vegetative propagation from cuttings might be useful to ensure a fairly even sex ratio among the planting stock. Vegetative propagation from cuttings may also be useful to select tree phenotypes with desirable features (i.e. female *Ficus* spp. trees which fruit when other foods are scarce, male *Ficus* spp. trees which fruit during the critical bottleneck for wasp dispersal). Further research on rejuvenation techniques of mature trees may help to increase rooting potential and survival rate (Hartmann *et al.*, 1990; Longman and Wilson, 1993; Kibbler *et al.*, 2004), but it seems expensive and requires intensive trained staff.

5.4 *Ficus* planting

5.4.1 Direct seeding. Since fig seeds are so small, they do not contain sufficient food reserves (endosperm) to support early seedling growth, which probably makes them unsuitable for direct seeding. Previous studies have shown that large or medium-sized seeds are most suitable for this technique (Manga and Sen, 1995; Doust *et al.*, 2006). Very high mortality rates after direct seeding of *Ficus* spp. trees have also been reported for *F. stupenda* planted in Borneo, of which only 1.3% remained alive at the end of 1 year (Laman, 1995). From the present study, most seedlings died of fungal infection (e.g. damping off diseases), probably derived from soil pathogens (pers. obs). Especially, *Aspergillus* spp. and *Fusarium* spp. are commonly known to damage fig saplings (Subbarao and Michailides, 1995; Doster and Michailides, 2007).

However, if the limiting factor of damping-off disease could be overcome, then direct seeding could become a very cost effective technique, because *Ficus* plants which survive the first rainy season grow rapidly (Fig. 26) and there are no nursery costs (Table 18).

5.4.2 Planting stock-raised in nursery from cuttings. Producing *Ficus* spp. planting stock from cuttings was inefficient for all tested species. Low percentage survival (15.1%, averaged across all species) and high cost were the most important reasons to reject this method for use in large-scale forest restoration projects, since it necessitates expensive re-planting. The poor growth and survival rates of planting stock derived from cuttings might be explained by cutting from branches of mature trees which do not generally root well (Smits *et al.*, 1990; Kantarli, 1993). In addition, the roots of cutting-grown plants are shallow, less well-branched, and less adept at nutrient and water uptake (Maynard and Bassuk, 1990). The roots of plants propagated from cuttings are also quite fragile and sensitive, and can be broken when placed directly into ground or during transportation (Dolgun and Tekintas, 2008).

Further field trials on the use of "truncheons" (i.e. large cuttings, ~2 m tall) which are commonly used for growing *F. glomerata*, *F. lutea*, *F. natalensis*, *F.*

pertusa, and *F. thoningii*, should be carried out since they can be established simply by placing them directly in the ground. Zahawi (2008) reported that after one year, survival of *F. pertusa* "truncheons" was 83%, with high establishment success and rapid growth. However, this technique seems to be suitable for small-scale restoration plantings.

5.4.3 Planting stock-raised in nursery from seed. Producing *Ficus* spp. planting stock from seeds performed well after transplanting in the high light intensity conditions of forest restoration plots. They also had resistant to insect attack. The recommended height of sapling for planting out for the framework species method is 30-60 cm (FORRU, 2006). The *Ficus* saplings, used in this experiment, were planted out when only about 20 cm tall. However this did not appear to affect their subsequent growth and survival. Therefore, *Ficus* seedlings can probably be planted out as soon as they have grown 20 cm or taller.

Two species established from seed achieved excellent survival rates (>70% after the 2nd rainy season; *F. oligodon* and *F. variegata*), while *F. auriculata*, *F. fulva*, *F. hispida* and *F. semicordata* had acceptable survival in field performance standards for framework species (>50%). All species also achieved acceptable or excellent height growth by the end of the second rainy season (>1.5 m, Elliott *et al*., 2003). Results of the study also revealed that the expense of planting stock-raised in nursery from seed is inexpensive, if most labor cost can be replaced with volunteers.

Moreover, *Ficus* spp. seeds are orthodox (Berg and Corner, 2005) and easy to collect since they are available all year-round hence intensive phenology studies may not be needed. Thus, this method can be applied in broad-scale restoration activities. Moreover, there were no differences in the establishment and growth performance of nursery-grown seedlings from seed among species studied. So, it is likely that the techniques described in this paper can be used for other dioecious *Ficus* tree species.