CHAPTER 2

LITERATURE REVIEWS

2.1 Deforestation in the tropics

Tropical deforestation has been a global conservation issue for several decades. Covering just 6% of the Earth's land surface, tropical forests are estimated to contain at least 50% of the Earth's total number of species (Erwin, 1988; Wilson, 1992). It is estimated that about two-thirds of all plant species on Earth (Montagnini and Jordan, 2005) or about 50,000 species of trees (Mora *et al*., 2011), grow in tropical forests. However, the area of natural tropical forests is still declining, the official figures indicate that between 1980 and 2005 A.D., the area of natural tropical forests worldwide declined from 19.1-19.7 to 17.7 million sq. km. (Grainger, 2008, from a review of FAO statistics); an average loss of about 0.37% per year. Estimates of total losses of tropical forest, since pre-industrial times, vary from 35 to 50% (Wright and Muller-Landau, 2006). At current rates of loss, Earth's last remnants of primary tropical forest will probably disappear sometime between 2100 and 2150 A.D. (adapted from Grainger, 2008).

The current main drivers of deforestation differ among the tropical continents. In Africa more than half (59%) of deforestation is carried out by families establishing small-scale farms, whereas in Latin America deforestation is mostly (47%) the result of industrial agriculture caused by global economic demand for agricultural products (particularly soybeans, bio-fuels and cattle ranching). In Asia, conversion of forest to small scale farms, and replacement of shifting agriculture with more intensive agriculture practices, account for 13% and 23% of deforestation respectively, whilst industrial agriculture, particularly oil palm and rubber plantation, account for 29% (FAO, 2009). According to 2005 report conducted by FAO, Vietnam has the second highest rate of deforestation of primary forests in the world second to only Nigeria.

Not only the loss of forests and their associated biodiversity is a serious issue in many tropical countries but also destruction of tropical forests and their replacement with agriculture is making a significant contribution to global climate change. Carbon dioxide, released when tropical forests are felled and burned, currently contributes about 15% towards the total carbon dioxide emitted into the atmosphere from human activities (Union of Concerned Scientist, 2011); the rest comes from burning fossil fuels. For several countries, like Brazil, Bolivia, Indonesia, Myanmar and Zambia, deforestation and degradation is their largest source of carbon dioxide emissions and just two of those countries, Brazil and Indonesia, account for almost half of global carbon dioxide emission from tropical deforestation (Boucher, 2008).

Tropical forests store about 17% of the total carbon contained in all of Earth's terrestrial vegetation. The pan-tropical average works out at about 240 tonnes of carbon stored per hectare of forest, split almost equally between the trees and the soil (IPCC, 2000). Forests in drier areas store less than the average, whilst tropical rain forests store much more. In contrast, the crop lands that often replace forest store, on average, only about 80 tonnes of carbon per hectare (almost all of it in the soil). So felling a hectare of tropical forest, and replacing it with agriculture, results in the emission of approximately 160 tonnes of carbon, whilst simultaneously reducing the global carbon sink, so that future carbon absorption is also reduced.

2.2 Summary of main forest restoration methods to restore degraded tropical forests.

2.2.1 Accelerated Natural Regeneration (ANR). This method has been used to restore forests on *Imperata* grassland in the Philippines for more than 30 years (Shono *et al.*, 2007). ANR is a simple and inexpensive technique, particularly to restore the large scale degraded areas. This method is appropriate on degraded sites which close to natural forest, with high densities of naturally established tree seedlings or saplings. However, the resulting forest from this method is mostly pioneer species, thus combination of ANR and tree planting (i.e. climax species) may be suitable to increase species diversity.

2.2.2 Maximum Diversity Plantings in Australia (Goosem and Tucker, 1995) and Japan-Malaysia (Miyawaki, 1993). This technique is very expensive, and requires high research and technical inputs, particularly in order to grow a wide range of tree species. However, this method has resulted in high species diversity and rapid forest recovery in some areas.

2.2.3 Nurse Crops or Foster Ecosystems in China (Mosseler *et al.*, 2005), Thailand (Norisada *et al.*, 2005), Puerto Rico (Parrotta, 1993) and Indonesia (Otsamo, 1998). This technique provides low biodiversity value, however it is suitable where sites are highly degraded (e.g. mining restoration). In several places, legumes have worked well as "nurse" trees to improve site conditions (soil organic matter, moisture-holding capacity).

2.2.4 Framework Species Method in Australia (Goosem and Tucker, 1995) and Thailand (Elliott *et al.*, 2003). The framework species method was developed as a practical way to restore degraded forest within the Queensland Wet Tropics World

Heritage Site, Australia (Goosem and Tucker, 1995; Tucker and Murphy, 1997; Lamb *et al.*, 1997; Tucker, 2000; Blakesley *et al.*, 2002; FORRU, 2006). This involves a single planting of 20-30 indigenous forest tree species (including both pioneers and climax species) that rapidly re-establish forest structure and ecosystem functioning.

2.2.4.1 The essential ecological characteristics of framework tree species:

1) Indigenous forest tree species.

2) Rapidly re-establish forest structure and ecological functioning when planted on deforested sites (e.g. high survival, rapid growth, dense, spreading crowns that shade out herbaceous weeds; flowering and fruiting at a young age which attract seed-dispersing wildlife etc.).

3) Drought resistant/fire resilient in seasonally dry areas.

4) Easy to propagate.

2.2.4.2 Problems of framework species method:

1) Lack of knowledge, very little research has been carried out on forest restoration using native species, primarily for biodiversity conservation (Blakesley *et al.*, 2002). For every species to be planted, information is required such as when to collect the seed, optimal storage and germination conditions, how to grow and where to plant the seedling, site preparation and after care (Elliott *et al.*, 1995).

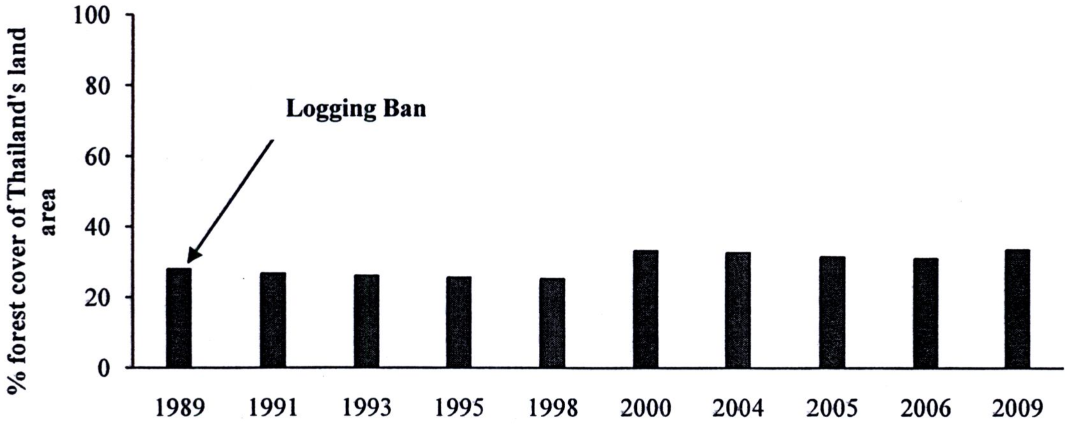
2) Seedling production and the design and management of mixed-species and plantations are complex (Hardwick, 1999).

3) High establishment and maintenance costs are needed especially during the first 2-3 years (Montagnini *et al.*, 1995).

4) The method works well in small areas but logistical problems must be solved before it can be scaled up (Elliott and Kuaraksa, 2008).

2.3 Deforestation and reforestation in Thailand

Like many tropical countries, Thailand faces a biodiversity crisis, as forests are cleared for development and agriculture. In Thailand, forest cover diminished from 53 to 28% between 1961 and 1988, with much of the loss in the teak forests of the north (Phothitai, 1992). Although, commercial logging in primary forest has been banned since 1989, the annual rate of deforestation remains at about 0.5% of remaining forest (19.30-25.28 percent of the country's area in 2000 A.D., FAO, 2001; FORRU, 2006). Due to tree planting has become popular all over Thailand in particular to support the reforestation project in commemoration of The Golden Royal Jubilee of Thailand monarch - His Majesty King Bhumibol Adulyadej. Therefore, between 2000 and 2009, forest cover was increased. At the present forest cover is estimated to be about 32% of land area (Fig. 1).



Source: Office of the Forest Land Management, Thailand 2011

Figure 1 Percent forest cover of the country's area after the commercial logging has been banned since 1989.

However, early tree planting efforts mostly involved establishing single-species plantations of exotic eucalypts or native pines, which were widely available from the Royal Forest Department (RFD) and the Forest Industry Organization (FIO) nurseries. Such plantations do little to conserve the watershed, biodiversity and fail to provide viable habitat for wildlife (Elliott and Kuaraksa, 2008).

In recent years, in Thailand there is much interest in the protection and restoration of the biodiversity in degraded forest lands. A recent report identified 8.7 million rai (3,498,483.86 Acres) of forestland in need of ecological restoration (by geographical information system; Panyanuwat *et al.*, 2008). Although, some restoration programs have been carried out using some native tree seedling species such as the Permanent Reforestation Project in Celebration of His Majesty the King by the Mae Fah Luang Foundation and SCB, the project has resulted in significant positive changes to both environment and the lives of local people in the project area (www.maefahluang.org, 2010). However, since seedling production for reforestation in Thailand is mainly undertaken by the Royal Forest Department nurseries (about 90 nurseries in all four main regions of the country), which produce a narrow range of indigenous forest tree species (Fig. 2). Therefore, unsurprisingly, when exotic (e.g. *Acacia mangium*, *Eucalyptus camaldulensis*, *Swietenia macrophylla* etc.) or native (e.g. *Dipterocarpus alatus*, *Pterocarpus macrocarpus*, *Tectona grandis* etc.) timber species continue to be favored for tree planting everywhere in Thailand. In this situation, new ways to produce planting stock of a wider range of indigenous forest tree species and to restore degraded forest ecosystems are both needed in order to successful forest restoration in Thailand.

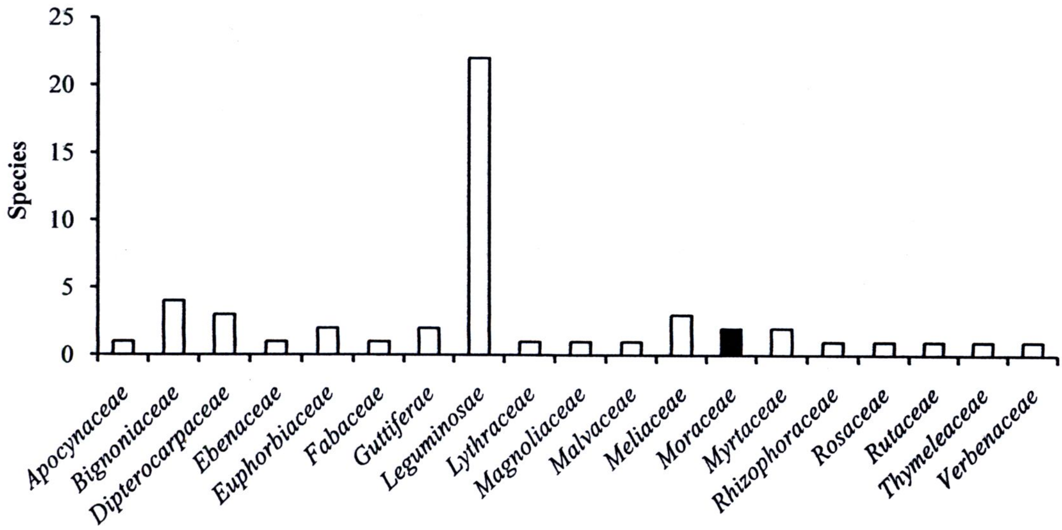


Figure 2 Seedling production reports of all RFD nurseries from 2006-2009 (www.forest.go.th/nursery).

2.4 The genus *Ficus*

Ficus comprises about 750 species of woody trees, woody climbers, shrubs, treelets, vines, epiphytes, and hemi-epiphytes in the family Moraceae, mainly tropical (Priyadarsanan, 2000; Berg and Corner, 2005; Berg *et al.*, 2011). Tropical Asian forests are particularly rich in *Ficus* species, with about 60% of known world species. Also, Southeast Asia is the centre of *Ficus* diversity (>350 species, Harrison, 2005). The genus *Ficus* is usually treated as a separate tribe within Moraceae, because of the unique inflorescence and wasp-dependent system of pollination (Jansen, 1979; Berg, 1990). The fig (technically a syconium) is an enclosed receptacle lined with unisexual flowers. In general, the number of flowers is related to the size of the fig (Berg, 1990). Most species the figs are borne in pairs in the axis of the leaves or on the twigs just behind the leaves. In others, figs are borne on trunks or branches (called as cauliflory). A few kinds of figs are borne on underground runners. The fruit type is an achene. The embryo is straight with cotyledons. The seeds contain endosperm, but in small amounts, although they can remain dormant for long period in dry and cool conditions (Berg and Corner, 2005).

Berg and Corner (2005) classified *Ficus* into 6 subgenera, 1) *Ficus,* 2) *Pharmacosycea*, 3) *Sycidium*, 4) *Synoecia*, 5) *Sycomorus* and 6) *Urostigma*. Two breeding systems occur among *Ficus* species which about half of the *Ficus* species worldwide are monoecious and half are (gyno) dioecious (Kerdelhue and Rasplus, 1996; Harrison *et al*., 2000; Greeff and Compton, 2002). Morphologically, *Ficus* are monoecious or gynodioecious according to the representation of the unisexual florets within the fig or syconium (Kjellberg *et al*., 1987; Weiblen, 2001).

2.4.1 Monoecious *Ficus*. In monoecious *Ficus* species, the figs contain both male and female flowers (without separate male and female trees). The female flowers are set out in three or more ovary layer and have styles of various lengths (Kerdelhue and Rasplus, 1996). Differing style lengths are important to separate the group of wasps (Weiblen *et al*., 2001). Generally, the deep-seated ovaries (on short pedicels) have long styles, while the shallow ovaries (on long pedicels) have short styles. When the female wasp enters the fig cavity, it lays eggs through the short-styles in the upper ovary layer and pollinates the deep-seated (with long-style flowers which out of reach for her ovipositor to lay an eggs, Galil and Eisikowitch, 1971). Armstrong and Disparti (1998) reported that the shallowest ovaries are mostly occupied by larva of the pollinator (i.e. *Ceratosolen* spp), the intermediate ovaries are mostly occupied by larva of non-pollinator which lay eggs from the outside (i.e. *Apocryptophagus, Sycophaga* spp.), and the deepest ovary layer produces mostly seeds. After pollination and oviposition the wasp dies in the fig. A wasp larva feeds on the galled tissue of its natal ovule. By the time the wasp offspring emerges from the galls in the fig cavity, the male flowers and seeds reach maturity. When escaping from the figs, the female wasps will bring pollen out, up to a receptive fig. Therefore, fig of monoecious *Ficus* will produce seeds, wasps, and pollens. Monoecious *Ficus* were proved to be associated with a significantly larger number of non-pollinating wasps than dioecious *Ficus* (Kerdelhue and Rasplus, 1996).

2.4.2 Dioecious *Ficus*. In dioecious *Ficus*, each *Ficus* species have separate male and female trees in the population, called gall and seed figs respectively (Kjellberg *et al.*, 1987). However, there is no external difference between male and female trees (Corner, 1952). Figs have two ovary positions, deep-seated ovaries with long styles in female figs (on female trees) and shallow ovaries with short styles in male figs (on male trees). Male trees bear "male" figs containing pollen-bearing male flowers (staminate florets) and short-style female flowers (short-styled pistillate florets). The ovaries of short-style female flowers often contain wasp larva if eggs were oviposited inside them. Therefore, male figs will produce pollens and wasps (including pollinator and non-pollinator). Female trees only bear “female” figs containing seed-bearing long-style female flowers and no male flowers. When the wasp enters the female fig, it can pollinate but is not able to lay any egg because the styles are too long for their ovipositors to reach the ovules. The wasps die without reproducing (Grafen and Godfray, 1991; Patel *et al.*, 1995). Therefore, female figs will produce only seeds.

The taxonomists believe that dioecious *Ficus* may have evolved from monoecious ancestral *Ficus* species (Berg, 1984; Kjellberg *et al.*, 1987; Berg, 1989;

Weiblen, 2001). Three hypotheses have been proposed for the evolution of dioecy including the role of seasonality (Kjellberg *et al.*, 1987), parasitic wasps (Kerdelhue and Rasplus, 1996) and the maintenance of pollinator populations in small groups of trees (Kameyama *et al.*, 1999).

2.5 The diversity of figs in Thailand

Throughout Thailand, the genus *Ficus* comprises 115 species, of which 108 species occur naturally and 7 species have been introduced: *Ficus benghalensis* L., *F. carica* L., *F. cyathistipula* Warburg, *F. elastica* Roxb., *F. lyrata* Warb., *F. natalensis* Hochst and *F. pumila* L. (Berg *et al.*, 2011). The majority of the native *Ficus* species inhabit lowland forests, whilst the genus is absent from mangrove forest (Chantarasuwan *et al.*, 2007).

Diversity is concentrated in the south where 60 species have been recorded, five of which are recent new addition *Ficus araneosa* King, *F. binnendijkii* (Miq.) Miq., *F. depressa* Blume, *F. dubia* Wall. ex King, and *F. beccarii* King (Chantarasuwan and Thong-Aree, 2006). Furthermore, among the collections of *Ficus* L. of Gardner and Sidisunthorn in Peninsular Thailand, several interesting specimens were found. Comparison of those specimens with Berg and Corner (2005), Kochummen (1978) and Ridley (1924) showed them to be the first records of *F. kerkhovenii* Valeton and *F. mollissima* Ridl. in Thailand and a new species, *F. thailandica* C.C. Berg & S. Gardner (Berg and Gardner, 2007). Twenty-two species were found in Kanchanaburi, western Thailand (Chantarasuwan *et al.*, 2007) which were classified into two groups i) moisture-specific group (i.e. *F. auriculata, F. callosa, F. fistulosa, F. racemosa*) and ii) non moisture-specific group (i.e. *F. hispida, F. semicordata, F. variegata, F.*

virens). Forty-seven species (both native and exotic species) were enumerated in the northeast of Thailand (Tanming and Chantaranothai, 2009). More than 30 species of *Ficus* are indigenous to northern Thailand (Gardner *et al.*, 2000; Maxwell and Elliott, 2001).

At present, molecular studies are popular for elucidating *Ficus* taxonomy (e.g. Promthep and Anantalabhochai, 2005; Sitthiphrom, 2006; Anuntalabhochai *et al.*, 2008; Pairuang, 2008; Ronsted *et al.,* 2008a). However, very little ecological research has been carried out on figs (Fig. 3) such as on the phenology (Poonswad *et al.*, 1998), seed dispersers (Sanitjan, 2002; Rakkien *et al.*, 2007; Suwannakerd and Aggimarangsee, 2007), fig-wasp interactions (Tarachai, 2008), fungal interactions (Wang *et al.*, 2008; Nandakwang *et al.*, 2008), chemical ecology (Soler *et al.*, 2011) and the use of figs for forest restoration (Elliott *et al.*, 2002, 2003; FORRU, 2006; Wangpakapattanawong and Elliott, 2008).

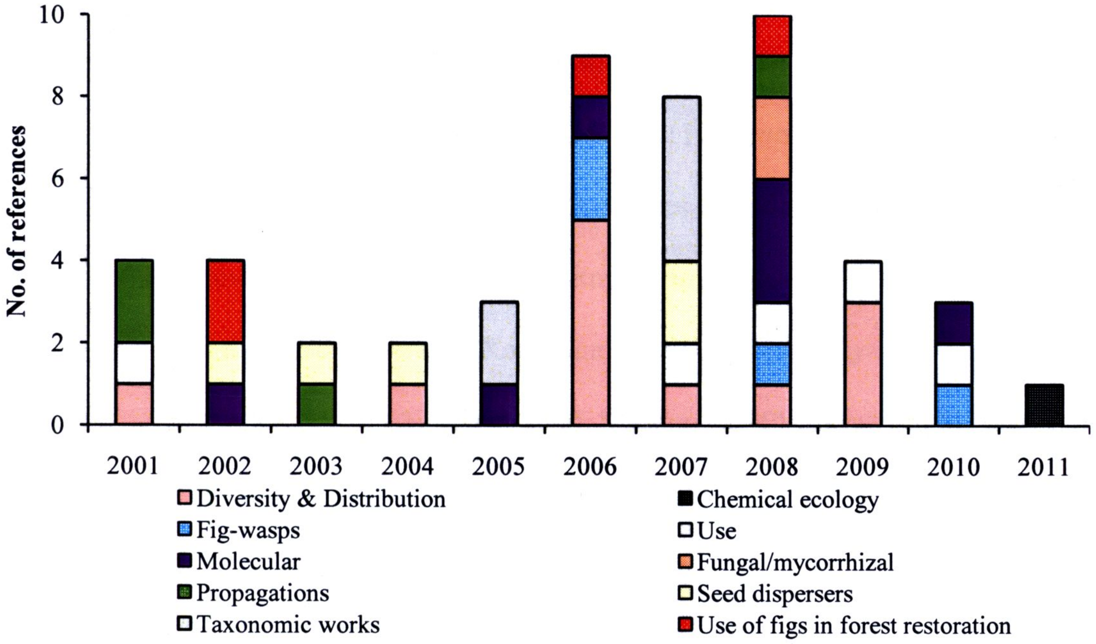


Figure 3 The type of study on *Ficus* species in Thailand (from 2001-present).

2.6 What species use figs?

Globally, over 1,200 vertebrate species, >10% of the world's bird species (18% of genera) and >6% of the world's mammals (14% of genera) have been recorded feeding on figs (Shanahan *et al.*, 2001b; Harrison *et al.*, 2008). Shanahan *et al.* (2001b) classified fig eating animals in three groups: i) *fig specialists* which are highly reliant in figs as a dietary resource year-round (e.g. hornbills, gibbons, monkey, binturongs, civets, fruit bats), in Thailand Suwannakerd and Aggimarangsee (2007) reported that 25% of the diet of White-handed gibbons (*Hylobates lar*) was of *Ficus* spp., ii) *the generalist fig-eaters* (e.g. bulbuls, pheasants, tree shrews) which appear to use figs as a supplement to diet of other fruits/animals, and iii) *casual fig-eaters* (e.g. gulls, kingfishers, motmots) which are generally not frugivorous and probably only eat figs opportunistically. Tapirs, deer, elephants, bears and wild pigs have all been observed eating figs (Mcconkey and Galetti, 1999; Sreekar *et al.*, 2010), however very little is known of the importance of figs to these animals or the role they play in *Ficus* dispersal.

In addition, Novotny and Basset (1998) found that 491 species of sap-sucking insects (Auchenorrhyncha, Hemiptera) were feed on 15 *Ficus* species in a lowland rain forest in Papua New Guinea figs. Other species including ants, dung beetles, snails, hermit crabs, fishes, and reptiles are known to consume fig fruits or seeds, many of which act as seed dispersers (Kaufmann *et al.*, 1991; Athreya, 1996; Laman, 1996; Davis and Sutton, 1997; Shanahan, 2000; Staddon, 2000). However, the groups of curassows, pheasants, pigtail macaque, chimpanzees and rodents are generally considered as seed predators of figs (Krefting and Roe, 1949; Corlett, 1998; Yumoto, 1999; Newton-Fisher, 1999). Parasitic nematodes (Martine *et al.*, 1973; Herre, 1993;

Pereira *et al.*, 2000; Harrison *et al.*, 2008), flies (Storey, 1975; Compton and Disney, 1991), lygaeid bugs (Slater, 1972), centipedes and mites (Pereira *et al.*, 2000), moths and weevils (Bronstein, 1988a), staphylinid beetles (Bronstein, 1988a; Figueiredo and Sazima, 1997), scale insects and pulp-feeders (Harrison *et al.*, 2008) are known to use figs. Insectivorous birds (e.g. swallows) and spiders make use of the fig-pollination system by feeding on mature fig-wasps (Figueiredo and Sazima, 1997; Pereira *et al.*, 2000). Figs also support a diverse community of fig-wasps (including pollinators and non-pollinators).

2.6.1 Seed dispersers of figs

Although water is reported to play a role in dispersal of some riverine *Ficus* species such as *F. cyathistipula, F. hispida* and *F. scabra* (Ridley, 1930; Berg and Wiebes, 1992; Horn, 1997), the majority of the *Ficus* species are dispersed by animal (both endo-zoochory and dys-zoochory). Normally, the diversity and widespread distribution of *Ficus* is reflected in the variety of animals that have been recorded feeding on figs. Kissling *et al.* (2007) reported that in Africa, frugivore diversity was correlated the diversity of fig species. In addition, it seems, larger fig-eaters are likely to disperse more fig seeds and disperse them greater distances than small fig-eaters. The majority of the *Ficus* seed dispersal guilds in tropical forests are;

2.6.1.1 Ants. In general, ants have been described as predators of fig wasps (Bronsteine, 1988a; Compton and Robertson, 1988; Thomas, 1988; Zachariades, 1994; Dejean *et al.*, 1997; Cushman *et al.*, 1998; Schatz and Hosseart-Mckey, 2003; Schatz *et al.*, 2006). Bronstein (1991) suggested that ants could be considered as in direct mutualists of figs and their pollinators, in order to reduce levels of parasitism of the tree's pollinators (Schatz *et al.*, 2006). However, ants were also found to have a role in fig seed dispersal (Kaufmann *et al.*, 1991; Compton *et al.*, 1996) but they are considered as secondary dispersal agents because they remove fig seeds which deposited in faeces (Roberts and Heithaus, 1986).

2.6.1.2 Birds. For 260 *Ficus* species (approximately 30% of described species), 990 bird species in 374 genera are known to eat figs (Shanahan *et al.*, 2001). In Borneo, up to 42% of bird species have been recorded feeding on figs (Shanahan, 2000). Most fig-eater birds are considered as true seed dispersers of *Ficus*. Compton *et al.* (1996) found that seed of *F. burtt-davyi* Hutch. defecated by the birds germinated more quickly than control seeds. Not only the frugivorous birds but also the insectivorous birds have been recorded feed on figs (Sreekar *et al.*, 2010). Among birds, fig-eating is most widespread in the parrot (Psittacidae) and pigeon (Columbidae) families. However, both are considered as seed predators rather than seed dispersers, as they digest all fig seeds ingested (Jansen, 1981; Pereira, 2006). Hornbills, leafbirds, bluebirds and barbets are also the specialist fig-eaters. Hornbills are capable of consuming large numbers of figs in a single feeding visit (i.e. consumed about 200 figs per sitting for Great hornbills or 27 figs per minute for Rhinoceros hornbill; Leighton, 1982) and often stay for a long time (approximately 3 h) in the fruiting fig tree (Shanahan, 2000). Lambert (1989) and Whitney *et al.* (1998) suggested that hornbills are important dispersers of *Ficus* species. Short feeding visits and defecation of viable seeds away from source trees make barbets are significant fig seed dispersers in Africa (Compton, 1996). In Borneo, India and Peninsular Malaysia, barbets are the most frequently observed fig-eaters (71±85% of its time foraging on figs), which not only they feed on canopy but also descend to lower forest strata (Ridley, 1930; Wells, 1982; Kannan, 1994; Grimmett and Inskipp, 1998;

Balasubramanian *et al.*, 1998). Bulbuls, woodpeckers, mousebirds, cuckoos, turacos, birds-of-paradise, thrushes, cracids, pheasants and many families of passerine birds are considered as the generalist fig-eaters, they are appear to use figs as a supplement to diets of other fruits. The members of bulbul family (62 confirmed fig-eating species in 16 genera) have been recorded feeding on 63 *Ficus* species. In terms of fig seed dispersal, bulbuls are important dispersers of small-fruited understorey *Ficus* trees that fail to attract larger frugivores. In general, bulbuls tend to make short feeding visits and fig seeds are defecated in a viable state (So, 1999; Shanahan, 2000). Corlett (1998) suggested that the bulbul family is an important agent of forest regeneration.

2.6.1.3 Fruit bats. *Ficus* species are known important diets of fruit bats (Hodgkison *et al.*, 2007). At the Anak Krakatau, Indonesia, Shilton (1999) reported that 90% of bat faeces contained *Ficus* seeds. Bats can eat figs at various heights (Peh and Chong, 2003), travel several km per night (Handley *et al.*, 1991) and deposit seeds over wide areas (Morrison, 1978; Kalko *et al.*, 1996). Therefore, fruit bats are of exceptional importance to seed dispersal and early rain forest regeneration (August, 1981; Shanahan *et al.*, 2001b).

2.6.1.4 Squirrels. Squirrels occur throughout the range of *Ficus* and are known to eat figs wherever they occur. Borges (1993) reported that during other fruits shortages in India, figs acted as important resources for Malabar giant squirrels. Squirrels can feed on figs both during the day and at night (flying squirrels). Not only on ripe figs but also some squirrels in Thailand (i.e. *Ratufa*, *Callosciurus* and *Tamiops*) were recorded eating unripe figs (Poonswad *et al.*, 1998). Therefore, squirrels are considered as both seed disperser and seed predator of *Ficus*.

2.6.2 Why are there so many fig-eaters?

2.6.2.1 *Ficus* is a large and widespread genus in the tropics (Corner, 1952; Jansen, 1979; Berg and Corner, 2005). *Ficus* spp. also exhibit more life-forms which can be attracted diverse groups of animals (Peh and Chong, 2003; Berg and Corner, 2005; Lomáscolo *et al.*, 2008).

2.6.2.2 Year-round production of figs at the population level, which is linked to their pollination biology, also makes *Ficus* a reliable food source for frugivorous animals year-round, especially during times of general fruit scarcity.

2.6.2.3 Large crop sizes and within-tree synchrony of fig ripening, thus many frugivore species can forage simultaneously, with a relaxation of competition (Lambert and Marshall, 1991).

2.6.2.4 High nutrient value per fig (Vellayon, 1981; Jordano, 1983; Herbst, 1986; Bronstein and Hoffmann, 1987; O'Brien *et al.*, 1998; Lambert, 1989; Rogers *et al.*, 1990; Borges, 1993; Conklin and Wrangham, 1994; Shanahan, 2000). Figs have high levels of minerals (Wendeln *et al.*, 2000) such as calcium which necessary to promote eggshell deposition and bone growth (O'Brien *et al.*, 1998). Figs are also rich in fiber (up to 27.3% dry weight), pulp water content (0.40 g water per fig) and calories (0.54 Kcal per fig, Jornado, 1983). Furthermore, figs are a potential source of animal protein in the form of larvae of fig-wasps and other insects (Vellayon, 1981; Kalina, 1988).

2.6.2.5 Much of the fig is edible and toxic compounds are generally absent (Jansen, 1979).

2.6.2.6 Figs are easy to handle and consume (Shanahan *et al.*, 2001b).

2.7 Importance and significance of figs

2.7.1 Barks. The bark of several species of *Ficus* is used for the preparation of string, rope, matting, paper and cloth (Brink *et al.*, 2003).

2.7.2 Extracted compounds. Various maladies are thought to be cured by the use of extract compounds of figs such as fevers, cholera, diabetes, diarrhea, dysentery, jaundice, mump, sterility, toothache, stomachache, leprosy, wounds, sores, vomiting diabetes and piles (Satyavati *et al.*, 1976; Rojo *et al.*, 1999; Kunwar and Busmann, 2006). The methanolic extract of stem bark and root of *F. racemosa* is comparable to that of paracetamol (standard drug) as an antipyretic (Chomchuen *et al.*, 2010). Extract compounds from the leaf and bark of *F. racemosa* were assayed for their toxicity against the early fourth-instar larvae of mosquito (Rahuman *et al.*, 2008). A commercial product, a proteolytic enzyme known as ficin, is also obtained from the latex of several species of *Ficus* (Condit, 1969).

2.7.3 Fruits. The fruits of *F. auriculata, F. elmeri*, *F. fistulosa*, *F. obpyramidata, F. pumila*, and *F. semicordata* are edible (Kunwar and Busmann, 2006), mainly are eaten by local people but none is delicious and widely consumed as *F. carica* (Berg and Corner, 2005; Harrison *et al.*, 2008).

2.7.4 Latexes. Fig-latex is used for rubber, as that of *F. elastica* (Indian Rubber tree), which was planted before the advent of *Hevea* (Tawan, 2000). Latex of *F. variegata* is used in the batik industry and gold leaf artwork (northern Thailand). Latex of some species is used as medicine such as to cure wounds and sores (Rojo *et al.*, 1999).

2.7.5 Leaves. Rough leaves of some species are used as sandpaper to scour wood and metal surface (Condit, 1969). Leaves of *F. auriculata*, *F. bengalensis*, *F.*

benjamina, F. cotinifolia, F. hispida, F. lacor, F. neriifolia, F. oligodon, F. religiosa, F. semicordata and *F. sycomorus* are used as cattle fodder (Condit, 1969; Amatya, 1992; Kunwar and Bussmann, 2006). In Thailand, young leaves and shoots of *F. lacor, F. oligodon* and *F. viren* are cooked or eaten raw (pers. obs.).

2.7.6 Ornamental plants. The beautiful foliage, good for shade and root systems, and easy to care after planted out in various habitats make *Ficus* trees are generally in favor. *Ficus microcarpa* and *F. benjamina* is the most popular indoor tree for homes and offices (www.ficustrees.info).

2.7.7 Roots. Roots of *F. stenocarpa* yield a strong and durable fiber which is used for fishing nets. Roots of *F. altissima* are used for cordage.

2.7.8 Special cultural and religious significant. *Ficus* is quite often associated with the culture, myth, religion and literature in many parts of the world (Priyadarsanan, 2000). The Common Fig (*F. carica*) tree is the first plant cited in the Bible. *Ficus thonningii* is a sacred tree in Nigeria, Africa. *Ficus sycomorus* as the tree of life in Egypt and its wood was used to make the inner coffin of the sarcophagus. In Oriental countries the fig is a symbol of fertility (Priyadarsanan, 2000). *Ficus benjamina, F. benghalensis, F. racemosa* and *F. religiosa* have special cultural and religious significant for both Hindus and Buddhist people, so they are unlikely to be felled (Xu *et al.*, 1996; Kunwar and Bussmann, 2006; Berg and Corner, 2005; FORRU, 2006).

2.7.9 Woods. In general, the wood of fig trees is soft and not durable (Condit, 1969). However, wood of many *Ficus* species are used for packing cases or burned for charcoal. In Bolivia, some free-standing *Ficus* trees are valuable for timber, which is used for furniture (Fredericksen *et al.*, 1999). Trunk of *F. rumphii* is used to make boats (Condit 1969).

2.8 *Ficus* phenology

Fig trees have complex reproductive phenologies (Spencer *et al.*, 1996). Galil and Eisikowitch (1968) divided the development of *F. sycomorus* (monoecious fig) into five phases: pre-female phase (all flowers are immature), female phase (receptive phase; female flowers are sexually mature and are pollinated by female wasps that enter the receptive syconia through the ostiole), inter-floral phase (developing phase; pollinated florets develop into seeds while parasitized florets form galls), male phase (ripening/releasing phases; male flowers are mature and liberate pollen) and post-floral phase (the syconium swells and ripens).

However, flowering asynchrony at the population-level, combined with flowering synchrony at the individual, is characteristic of figs (Jansen, 1979). This phenological pattern is necessary for the survival of their short-living, specialized Agaonid pollinators (Harrison, 2008; Jia *et al.*, 2008). Although within-tree synchrony is common but many cases of within-tree asynchrony have been documented, especially in dioecious figs (Bronstein and Patel, 1992; Corlett, 1993; Harrison *et al.*, 2008). Such within-crop asynchrony (receptive and releasing phases overlapping) was suggested as an adaptive strategy for fig trees to enable their pollinators to survive adverse conditions (Jia *et al.*, 2008). Bronstein (1989) also reported that the presence of overlapping receptive- and releasing-phases on the same tree reduces the size of *Ficus* populations necessary to guarantee pollinator persistence and is most potential benefit in small isolated populations, where pollinator arrivals may be limiting.

Owing to their numerical abundance, large crops and asynchronous fruiting within-population, *Ficus* can supply food for animals almost all the year. Fruiting peak in figs also coincides with some lean fruiting periods of non-fig species (David *et al.*, 2012). Thus, *Ficus* is often regarded as a keystone genus in tropical forests (Lambert and Marshall, 1991; Shanahan *et al.*, 2001b).

Seasonality in both fig and leaf production has often been noted in almost all published phenological studies (Corlett, 1984; Kjellberg *et al.*, 1987; Bronstein, 1989; Windsor *et al.*, 1989; Spencer *et al.*, 1996; Harrison *et al.*, 2000; Pereira *et al.*, 2007; David *et al.*, 2012). Syconium phenology often shows some correlation with climatic conditions, especially in non-equatorial *Ficus* species (Jansen, 1979; Patel, 1997). For example, fig flowering frequency decreased in dry and cold seasons (Jansen, 1979), fig development of *F. citrifolia* in cold season was longer than in other seasons (Pereira *et al.*, 2007), syconia production showed a strong correlation with rainfall (*F. variegata* in Australia, Spencer *et al.*, 1996) and with drought (*F. fulva* in Malaysia, Harrison *et al.*, 2000). In contrast, David *et al.* (2012) reported that ripe fig production was not correlated with climate in southern India.

The breeding system of a fig species can also influence reproductive phenology, especially in seasonal habitats (Spencer *et al.*, 1996). However, many authors have suggested that seasonal climatic variation is less problematic for dioecious figs than for monoecious figs (Valdeyron and Lloyd, 1979; Kjellberg *et al.*, 1987). In dioecious figs, female tress flower and fruit during conditions optimal for seed production and dispersal, whilst male trees produce figs more often than the females, to maintain the pollinator population (Spencer *et al.*, 1996).

Forest restoration for biodiversity conservation, watershed protection and carbon sequestration requires detailed knowledge of plant phenology (FORRU, 2006). This is especially so for forest restoration programs based on the 'framework tree species method' because propagation of a diverse crop of native forest tree species requires careful planning of seed collection and nursery work programs (FORRU, 2008). Furthermore, phenological data can be used to indicate the habitat preferences of tree species, provide information about pollination and seed dispersal mechanisms, and enable the identification of keystone tree species (Gilbert, 1980).

Therefore, knowledge of dioecious *Ficus* spp. phenology will increase understanding of their pollination and seed dispersal mechanisms, and will enable nursery work programs and planting techniques to be developed to improve forest restoration programs and provide constructive suggestions for the conservation of biodiversity in the tropics.

2.9 Fig wasps

Fig wasps are seed predator-pollinators (Harrison, 2006) and their interaction with *Ficus* species range from mutualism to parasitism (Weiblen *et al.*, 2001). All fig wasps are confined to figs as larvae, and their specialized diets are restricted to fig embryos, galled fig ovaries, fig seeds, or other fig wasp larvae (Boucek, 1988; Weiblen, 2002; Peng *et al.*, 2005; Pereira *et al.*, 2007). The fig insects can be classified into two categories, pollinators and non-pollinators (Priyadarsannan, 2000).

2.9.1 Pollinator wasps. Pollinators belong to the family Agaonidae (Chalcidoidea, Hymenoptera). Even though, the relationships between the major clades of Agaonidae remain largely unresolved, they can roughly be divided into two tribes; Agaonini and Blastophagini, based on characters of the female head (Wiebes, 1982). In contrast, Cruaud *et al.* (2009) proposed that the family should be divided into four subfamilies: Tetrapusiinae, Kradibiinae, Agaonidae and Blastophaginae, on the basis of molecular studies. There are twenty genera, of which eleven occur in the Malesian region; seven are confined in Africa and two are found in America (Wiebes, 1994; Berg and Corner, 2005). In general, each *Ficus* section is pollinated by its own genus of Agaonidae (Herre *et al.*, 1996). All of the pollinator fig-wasps are adapted to enter the syconial cavity through the bracts-guarded ostiole (Priyadarsanan, 2000). Indeed, the most reliable trait separating pollinators of monoecious and dioecious species is ovipositor length, which is always short in wasps associated with dioecious species and long in species associated with monoecious species (Weiblen, 2001).

In the interaction between figs and their pollinators, volatile substances produced by receptive figs are essential to attract the wasps to go in for the reproductive success of both fig and wasp (Bronstein, 1987; Ware *et al.*, 1993; Hossaert-McKey *et al.*, 1994; Gibernau *et al.*, 1997; Gibernau and Hossaert-McKey, 1998; Grison *et al.*, 1999; Grison-Pigé *et al.*, 2001; Song *et al.*, 2001). Several studies have shown that different species of *Ficus* emit clearly distinct chemical messages to attract only their specific pollinating wasp (Barker, 1985; Grison *et al.*, 1999; Hossaert-Mckey *et al.*, 2010). During the receptive phase of dioecious figs, male and female figs generally emit the same compounds (Grison-Pegé *et al.*, 2001; Chen *et al.*, 2009). However, during the dispersal phase, the sexes emit different volatiles (Borges *et al.*, 2008).

Among 40 or so fig species studied so far, at least 2 to 5 major compounds account for the majority of the total volatiles emitted by receptive figs (Chen *et al.*, 2009). For example, caryophyllene is the main compound which attracts *Vilisia compacta* (pollinators of *F. fulva*; Grison-Pigé *et al.*, 2002), geraniol attracts *Ceratosolen solmsi marchali* (pollinators of *F. hispida*) and linalool attracts *C. emarginatus* (pollinators of *F. auriculata*). *C. gravelyi* (pollinators of *F. semicordata*) is significantly attracted by 4-methylanisole, geraniol and terpineol (Chen *et al.*, 2004, 2009). Other major chemicals usually produced include as benzyl alcohol, farnesol, linalol oxide, cinnamic aldehyde, cinnamic alcohol, eugenol and vanillin (Gibernau *et al.*, 1997; Grison-Pigé *et al.*, 2001; Chen *et al.*, 2004). Therefore, the maintenance of the fig-fig wasp mutualism system is strongly dependent on the chemical orientation of pollinating fig wasps using fig volatiles (Chen *et al.*, 2004). In general, individual figs remain receptive for 2-3 weeks (Gibernau *et al.*, 1996), and about four days after pollination, the volatile emitted by receptive figs are absent as on *F. semicordata*, *F. racemosa* and *F. hispida* (Chen *et al.*, 2009). However, some *Ficus* species can prolong their receptivity and volatile production to wait for wasps when no wasps are available (Khadari *et al.*, 1995; Kameyana *et al.*, 1999).

To enter the fig, most female wasps use the third antennal segment which is usually dentiform. They press the antennae forward and use the "teeth" to lift the ostiolar scales. While on the way to the interior of the fig, they lose their wings and often also parts of the antennae. After the pollinators have entered a fig, oviposited (male fig) and pollinated (female fig), most die within the fig, although they sometimes enter more than one fig on the same plant (Moore *et al.*, 2003) such as with the common fig (*F. carica*), on which pollinators have been observed to oviposit in two different figs (Gibernau *et al.*, 1996). A wasp can lay (79)100 to 400, depending on the size/species of the insect (Berg, 1990; Compton, 1993). The preferred place for wasp egg deposition is mainly in flowers near the fig cavity (Jousselin *et al.*, 2001). Also, the number of eggs laid usually increases with number of foundresses (Moore *et al.*, 2003). Generally, ovipositing females lay one egg per female flower and they do this by inserting their ovipositor down the style (Jousselin *et al.*, 2001). An average of about 10 eggs is laid each hour by *Elisabethiella baijnathi*, the pollinator of *F. burtt-davyi* (Compton, 1993). Near the wasp egg, some drops of a fluid staining green with PAS-methylene blue are also deposited (Kjellberg *et al.*, 2005), the contents of which are presumably used to gall the ovaries (Compton *et al.*, 1994). Ovules that receive an egg develop into a gall, and the wasp larva feeds on the gall's inner tissue layers which present specialized cells for larval nutrition, rich in proteins and lipids (Verkerke, 1987, 1988; Pereira *et al.*, 2007).

As a typical hymenopteran, fig wasps have a haplodiploid sex determination system. Adult female wasps control their offspring's sex by regulating sperm access to eggs during oviposition, with diploid females (develop from fertilized eggs) and haploid males (develop from un-fertilised eggs; Charnov, 1982). If only a single female lays eggs in a fig, she produces an extremely female-biased sex ratio (only 5 to 10% of the offspring are males; West *et al.*, 2000) but if the wasp encounters other foundresses, it will produce a more male-biased sex ratio (Kjellberg *et al.*, 2005).

Inside the fig cavity, all fig-pollinating wasps share a similar life cycle (see more details below). Since wasps typically mate within their natal figs, siblings mating and local mate competition (competition between siblings for mates, LMC) are likely to occur (Zavodna *et al.*, 2007). Normally, fig wasps exhibit a very high degree of sexual dimorphism as a result of which different features between the two sexes of Agaonidae are presented in Table1.

Table 1 Different features of male and female pollinator wasps at the mature stages.

Feature	**Male wasp**	**Female wasp**	**Source**
Antennae	Poor-developed	Elaborate	Kjellberg *et al.* (2005)
Body	Concave	Smooth	Boucek (1988)
Color	Amber colored	Black	Kjellberg *et al.* (2005)
Eye	Blind	Well-developed	Ramirez (1991)
Head	Elongate	Flattened	Weiblen (2002)
Mount-parts	Strong, incisor-like	Weak, spade-like	Kjellberg *et al.* (2005)
Wings	Wingless	Winged	Boucek (1988)

Male wasp offspring emerge first and search for galls containing females. They use their antennae to test the right sex and species inside the galls (Murray, 1990). They gnaw a matting hole in the gall and, using their telescopic genitalia to mate with the female that lies entrapped within the gall (Kjellberg *et al.*, 2005; Song *et al.*, 2008). A single male can mate successively with 5 to 7 females. Each act of copulation takes about 4-6 seconds (Abdularahiman, 1986). At the end of the mating period, the males cut an exit hole out of the fig, through which the females, loaded with fresh pollen, exit the fig. Furthermore, some male fig pollinator species (e.g. *A. fimbriata* Waterston, a pollinator of *F. natalensis leprieuri* Miq.) show other behaviors, such as opening dehiscent anthers. Moreover, males of the section *Galoglychia*, after mating, grab the female by antennae, and pull her out into the cavity (Greeff *et al.*, 2003). Even though male morphology is adapted to move inside fig cavity, Kjellberg *et al.* (2005) supposed that males of some species may walk from one fig to another. In general, wasp larvae take 4-8 weeks to mature, depending on the species and weather conditions, but maturity always coincide with maturation of the fig's male flowers (Bronstein and Patel, 1992; Harrison and Rasplus, 2006). The freshly emerged females often exit via holes made by a male wasps and fly rapidly away in search of a new receptive fig. The wasps that pollinate figs can be active or passive pollinators.

2.9.2 Non-pollinating fig wasps (NPFWs). Up to now, the communities of non-pollinating fig wasps (NPFWs) remain little characterized and the real nature of their relationship with fig trees is still not clearly understood in most cases. Nevertheless, most *Ficus* species associate with a great diversity of non-pollinating wasps (Fellowes *et al.*, 1999). Non-pollinating wasps belong to the same Order Chalcidoidea as pollinators, and many of them belong to different families, mostly belonging to the Pteromalidae family (Rasplus *et al.*, 1998; Herre *et al.*, 2008). Most NPFW lineages are not closely related to the pollinators and have evolved convergent adaptations for syconium life (Cook and Rasplus, 2003). The absence of pollen pockets and the long ovipositors, with which to pierce the fig wall, distinguish NPFWs from pollinators (Silvieus *et al.*, 2007). In general, adult females of pollinating fig wasps are short-lived, whilst the longevity of some female NPFWs can extend to 2 months (Compton *et al.*, 1994). Thus, they can oviposit for a much longer time than pollinator wasps (Wang *et al.*, 2005). Proffit *et al.* (2007) demonstrated that NPFWs use volatile chemicals, produced by the fig, to locate their host, but they probably use other cues from the pollinator wasps (Compton *et al.*, 1994). They are also able to discriminate among volatile chemicals to recognize the appropriate stage of development for oviposition (Proffit *et al.*, 2007). Most of the non-pollinating wasps are externally ovipositing species, equipped with a long ovipositor to lay eggs from the outside, through the wall of the fig, but some are also internally ovipositing wasps, which enter into the fig through the ostiole (Weiblen, 2002; Cook and Rasplus, 2003).

NPFW include species with diverse larval biologies: gallers, inquilines (Kleptoparasites) and parasitoids (Kjellberg *et al.*, 2005). They can be classified according to the moment the females arrive on the fig to oviposit (Kerdehué *et al.*, 2000). Phytophagous gallers colonize figs at the same time or before the pollinating females (foundresses), they feed on proliferating nucellus and do not depend directly on fertilization of flowers by pollinators (Weiblen, 2002). Inquilines are also phytophagous, but they are not able to induce galls, thus they oviposit in already induced galls and in the process eliminate the galler larvae. Parasitoids feed directly on the gall larvae (Abdurahiman and Joseph, 1978) or by starving it by feeding on endosperm (Weiblen, 2002). Elias *et al.* (2008) predicted that the NPFWs that oviposit after fig pollination should be inquilines or parasitoids and their larvae must develop rapidly. The effect of NPFW on the fig-fig wasp mutualism differs according to their larval biology (Bronstein, 1992). However, several studies have shown that non-pollinating wasps have negative effects on the pollination system and mutualism of figs and their pollinators (Weiblen, 2002; Berg and Corner, 2005; Harrison and Rasplus, 2006) because they reduce the number of seed and pollinator wasps produced, by parasitizing pollinators or by competing with them for oviposition sites (Kerdelhué and Rasplus, 1996; Greeff and Compton, 2002; Perreira *et al.*, 2007).

However, several studies have shown that some of these wasp species may carry pollen and play a role in pollination of figs (Jousselin *et al.*, 2001; Cook and Lopez-Vaamonde, 2001; Cook and Rasplus, 2003). Some NPFW species (e.g. *Apocryptophagus* spp.) can prevent abortion of figs (Bronstein, 1991), which can potentially maintain vertebrate frugivore populations, especially when other fruits are in short supply. In *F. racemosa*, some of the non-pollinator species can develop independently in the figs without pollinators (Wang *et al.*, 2005). The males of many NPFWs are also capable of producing exit holes especially when the males of pollinator species are limited (Jansen, 1979; Compton *et al.*, 1994).

2.10 Pollination modes

Two major modes of fig pollination may be distinguished by differences in fig/wasp behavior and morphology: passive or active (Weiblen, 2002; Kjellberg *et al.*, 2005).

2.10.1 Passive pollination. Passive pollination is considered ancestral and in about one-third of *Ficus* species, pollination is passive (Kjellberg *et al.*, 2001). When pollination is passive, the pollinator does not show any pollen collection and deposition behavior (Jousselin and Kjellberg, 2001). Furthermore, they lack or have significantly smaller specialized structures on the meosterma (pollen pocket; Machado *et al.*, 2000). In passively pollinated fig species, pollen is abundant and their mature anthers tend to dehisce naturally; thereby wasps are generally completely dusted with the pollen (Machado *et al.*, 2000). In general, the pollen grains become trapped in abdomen, setae, wings and articulations (Galil and Eisikowick, 1968). Pollen can also sometimes be found in several other places of the body (e.g. between the mount parts or under the hypogidium; Ramirez and Malavasi, 1997). After leaving the fig, female wasps clean themselves, but some pollen is trapped between the abdominal pleura, as the gaster retracts on exposure to external air. When wasps enter a receptive fig, the gaster progressively swells in the moisture-saturated internal atmosphere. This enables progressive dispersal of pollen within the fig cavity (Galil and Neeman, 1977).

2.10.2 Active pollination. Active pollination is rare in nature, but in the case of *Ficus*, it occurs in about two-third of the species. In actively pollinated fig species, male flowers are small. Pollen is scarce and is not usually shed (Galil and Meiri, 1981). Wasps that actively pollinate show distinctive behaviors for collecting and depositing pollen (Herre *et al.*, 2008). Before leaving the natal fig, female wasps go to the anthers, pick some pollen with their forelegs and introduce it into specialized structures on the mesothorax, called pollen pockets (Kjellberg *et al.*, 2001). However, Newton and Lomo (1977) also suggested that the wasps may need a pollen load for maintaining balance and stability during flight. The number of pollen grains that can be carried in pollen pockets varied among *Ficus* species such as 1,000 pollens for *F. religiosa* (Galil and Snitzer-Pasternak, 1970) and 2,000 to 3,000 in *F. sycomorus* (Gali and Eisikowitch, 1968). Once the wasps have entered a receptive fig, each time they deposit an egg, and before withdrawing the ovipositor from the style, they pick some pollen with their forelegs and deposit it on the stigmas (Galil and Eisikowitch, 1974).

2.11 Dispersal of fig wasps

In the obligate mutualistic relationship between figs and their fig wasp pollinators, effective wasp dispersal is critical to the survival of both partners. Since the life span of female fig wasps is short (at most for a few hours to 2-3 days; Kjellberg *et al.*, 1988; Compton *et al.*, 1994; Figueiredo and Sazima, 1997; Yu *et al.*, 2006) and the crop development within fig trees is normally highly synchronized, wasps have only a short time to leave their natal tree and find a new tree bearing receptive figs in which to oviposit (Ware and Compton, 1994; Hossaert-Mckey *et al.*, 1994). Adult fig wasps are small, pregnant (about 2% of the pollinating fig wasps left the fig unmated; Godfray, 1988) and do not feed (Compton *et al.*, 1994). They are also weak fliers (recorded as <37 cm/sec or >1 km/h) and have no control over their flight direction, which depends on the wind (Compton, 1993; Harrison, 2003).

Therefore, the journey to find suitable figs is particularly hazardous to the wasps. It has been estimated that approximately less than one percent of fig pollinating wasps released from a natal tree survive during dispersal stage to find another receptive tree (Patel and Hossaert-Mckey, 2000). The influence of various environmental factors, such as wind speed, humidity and temperature, are major determinants of whether they are successful in locating receptive figs. Dunn *et al.* (2008) showed that the longevity of female wasps is positively correlated with moisture availability, whilst Wang *et al.* (2005) reported that the pollinator wasps can live longer during the cool season. Harrison (2000) also reported that the pollinators of dioecious figs are vulnerable to drought.

However, little is known about fig wasp flight patterns. Harrison (2003) found that fig wasps are very common above the canopy, whilst Zhang *et al.*, (2003, 2004) reported that the distribution patterns of fig wasp populations were all clumped in every season. Bronstein (1988a) considered that the mass, synchrony of arrival and departure of pollinators from fig trees probably make them less vulnerable to predation. Ware and Compton (1994) found that *E. baijnathi* (pollinator of *F. burtt-davyi*) prefers to leave their natal figs during the morning, when wind speeds and predators are both low, but during the winter they can delay until the afternoon. Whereas, *C. emarginatus* (pollinator of *F. auriculata*) prefers to disperse when the temperatures are 20-24°C and humidity is 85-93%, but it generally stopped hovering if the weather was windy and rainy (Peng *et al.*, 2003). Chemical volatiles, produced by figs when they are ready for pollination, are thought to be the means by which the wasps detect a suitable host. Once female wasps have detected the airborne volatiles (by using their antennae) from trees bearing receptive stage figs, they have landed into the canopy, where the low wind speeds and search for figs. Once the wasps arrive on a fig, they search for the ostiole and then attempt to crawl through it. However, they generally prefer entering figs which did not already contain a female wasp (Ware and Compton, 1994).

2.12 *Ficus* propagation and planting

Propagation and planting techniques of high commercial value *Ficus* species such as *Ficus benghalensis*, *F. benjamina*, *F. carica*, *F. elastica*, *F. microcarpa*, *F. pumila* and *F. religiosa* have long been extensively researched (e.g. Storey 1975; Condit, 1969; Henley *et al.*, 1999). However, very little work has been carried out on the vast majority of World's estimated 800 *Ficus* species. Due to lack of knowledge of the basic propagation and planting methods has limited their use, few *Ficus* species have been used in reforestation programs. For example, eight *Ficus* species, including *Ficus altissima*, *F. benjamina*, *F. callosa*, *F. glaberrima*, *F. hispida*, *F. racemosa*, *F. semicordata* and *F. subincisa*, are qualified as framework species for restoring forest ecosystems in northern Thailand (Elliott *et al*., 2003; FORRU, 2006). *Ficus pertusa* is commonly planted to restore abandoned tropical pastures in southern Costa Rica (Zahawi and Holl, 2009). *Ficus brachylepis*, *F. natalensis* and *F. dawei* help to promote regeneration in abandoned agriculture land of Uganda (Chapman and Chapman, 1999).

Ficus species may be propagated from seed, cuttings, layering, grafting and tissue culture (Chen, 1987; Munshi *et al*., 2004; Rahman *et al*., 2004; Dolgun and Tekintas, 2008; Mathew *et al*., 2011). With the exception of seeds and cuttings, these techniques are generally considered unsuitable for mass propagation, particularly in developing countries, due to high costs and the need for technical expertise (Longman and Wilson, 1993; Chapman and Chapman, 1999; Elster and Perdomo, 1999; Itoh *et al*., 2002; Mathew *et al*., 2011).

Most *Ficus* species are conventionally propagated by seeds (Rahman *et al*., 2004; Urgessa, 2011). However, germination and early seedling development of *Ficus* is slow and difficult, with damping off disease being a particular problem (Titus *et al*., 1990; FORRU, 2006). Growing *Ficus* from seeds also takes at least 18 months, which most are not ready for planting until the second planting season after germination (FORRU, 2006).

Propagation from cuttings is commonly used in several *Ficus* species, but it is slow and unreliable process (Khali *et al*., 1996; Rahman *et al*., 2004; Mathew *et al*., 2011). Most figs are generally propagated by hardwood cuttings (2-3 years of age, Hartman *et al*., 1990), but aerial rooting is often used for cuttings *Ficus* species of subgenus *Urostigma* (Danthu *et al.*, 2004). Root-promoting chemicals for cutting propagation of *Ficus* commonly contain Indole Butyric Acid (IBA). For example, the successful propagation of *F. roxberghii* was large sized cutting x IBA 100 ppm (Rana and Sood, 2011), whilst application of IBA 500 ppm substantially increased rooting percentage of *F. auriculata* and *F. glomerata* (Bhatt and Badoni, 1993). In addition, Idun *et al.* (2011) reported that teak sawdust + coconut coir (1:1) was the best medium for cutting propagation of *F. benjamina.*

Ficus trees thrive on a wide range of soils, even in rocky sites or without fertilization (Condit, 1947). Some species such as *F. deltoidea* and *F. oleifolia* are well adapted to nutrient-poor conditions (Berg and Corner, 2005). However, germination and early seedling survival of *Ficus* appears to be dependent on microsites with good moisture retention (Harrison *et al.*, 2003). Laman (1995) reported that low light level and water stress were critical factors limiting *Ficus* seedling growth in a Bornean rain forest canopy.

Direct seeding seems to be an alternative to tree planting as a way to accelerate succession on degraded areas with a minimum cost, because it reduces or eliminates the costs associated with propagating, raising, and planting seedlings (Lamb and Gilmour, 2003; Doust *et al.*, 2006; Cole *et al.*, 2011). However, a more systematic screening of potential species and their response to direct seeding under field conditions is required. Especially, in the case of *Ficus* spp., their use of direct seeding for forest restoration has not been tested.