CHAPTER 6

CONCLUSIONS

6.1 *Ficus* phenology

Asynchronous fig production at the population-level is a general feature of *Ficus* phenology which is necessary to ensure survival of their short lived-span pollinators. Year-round production of figs can potentially maintain vertebrate frugivore populations particularly during lean periods, when other fruits are in short supply (Compton, 1996). Thus, they are often regarded as a keystone group in tropical forests (Terborgh, 1986; Lambert and Marshall, 1991; Shanahan *et al.*, 2001b). In addition, *Ficus* spp. play a vital role of tropical forest restoration, in particular they help to maintain viable populations of seed-dispersers, which are vital for recovery of tree species richness.

Previous studies have considered that only monoecious hemi-epiphytic figs act as keystone species in the tropical forest ecosystems (e.g. Harrison *et al.*, 2003). However, the results of this study showed that most selected dioecious *Ficus* species also act as keystone species, in that they can supply food to wildlife, particularly at times of the year when other fruits may be scarce (Table 19). Herre (1996) also stated that the high photosynthetic rates and the continuous flowering year-round make fig trees useful for reducing carbon emissions and increasing sequestration. Especially, *Ficus* species have high ability to absorb carbon dioxide for producing their latex which is used as a defence mechanism against herbivore (Compton, 1996; Subbarao, 1996; Harrison, 2005).

The flowering cycle of female trees of most species appears to be adapted to the seasonal climate and may increase the probability of germination and seedling establishment. In contrast, male trees of most species reached a peak in wasp production to avoid the rainy season. This helps to increase the survival of the pollinators.

Consequently, the optimum time for fig seed collection of most species is during the late dry season to the early rainy season. As fig seeds of most species are available all year-round, intensive phenology studies and development of fig seed storage protocols may not be needed for the objectives of forest restoration projects.

In contrast at the level of individual trees, there was considerable variation in phenology evident among species. My findings showed that the patterns of within-male tree reproductive phenology can be divided into 3 groups: i) *F. hispida* and *F. semicordata* have completely within-tree asynchronous phenologies, whereby a single male tree maintained a continuous production of pollinators for 10 and 12 months, ii) *F. oligodon* and *F. triloba* have moderate degrees of within-tree reproductive asynchrony, and iii) the species with low degree of within-tree reproductive asynchrony (Appendix K).

Thus, the species with typical of within-tree reproductive asynchrony (receptive- and releasing-phase present simultaneously within an individual tree crown) would greatly decrease the number of trees necessary to sustain a wasp population. Whereas, species which exhibit high levels of crop synchrony within trees require larger populations of fig trees, than highly asynchronous species. If individual tree flowering is regular from year to year, the estimated minimum numbers of fig individuals, required to sustain pollinator wasps over the year, is presented in Figure

28. Not only can phenology explain the persistence of fig trees and their pollinators (Harrison and Shanahan, 2005), it may provide important information for conservation efforts, particularly to investigate the minimum key trees which are critical for year-round survival of local fig-wasp population, especially for low-density tree populations.

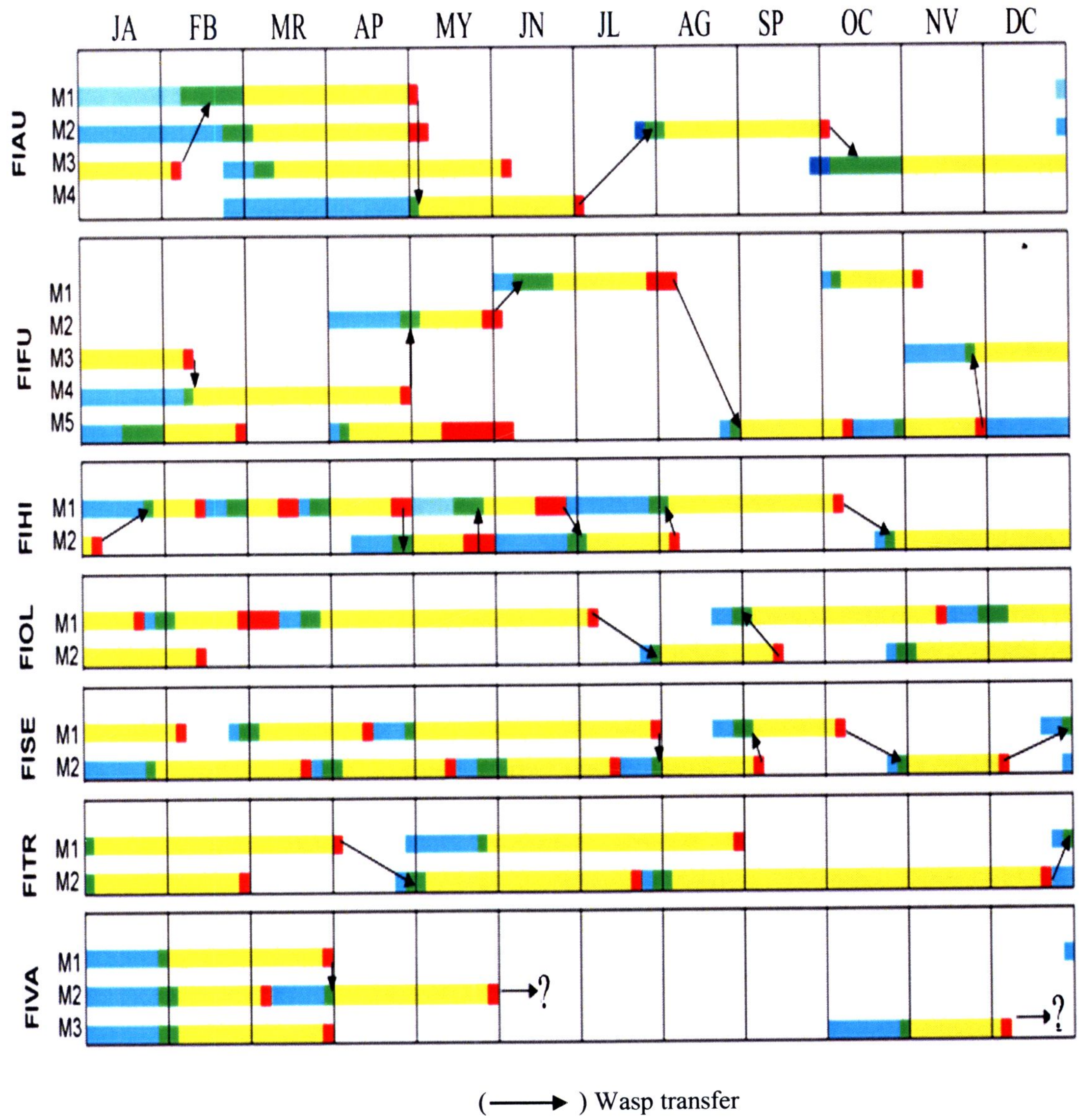

Figure 28 Model of crop distributions and minimum number of male trees (M) are necessary to sustain pollinator wasps over the year. Blue = Immature phase, green = Receptive phase, yellow = Developing phase and red = Releasing phases.

6.2 *Ficus* and their associated wasps

Thailand presents unique opportunities for studying figs and their associated wasps because it is the meeting ground of two fig flora/fig wasp faunas (Continental Asia and Sundaland). Despite a growing literature on fig wasps and their host plants (*Ficus* spp.) at the global level, studies in Thailand are in the primary phase and there remains much to investigate. Exploration of the fig wasp community ecology could help us better understand how these communities are structured. In particular, study of the community ecology of NPFWs may provide important information for forest restoration plans, in order to conserve introduce keystone species to rapidly facilitate biodiversity recover of tropical forests. Wang *et al.* (2005) showed that the effects of fragmentation has an obvious impact on the community structure of NPFWs, since most NPFWs are weak fliers, compared with the pollinators (Rasplus, pers. com.) and are mostly found in primary forest (Wang *et al.*, 2005). Thus, they may provide a useful index for monitoring forest recovery in forest restoration projects or to indicate the health of forest ecosystems. My findings also reveal many outstanding questions that still require investigation. For example, how is it possible for some NPFWs to reproduce in female figs? Direct observations and experiments on feeding capacities are necessary to clearly elucidate NPFW larval biologies and help understand better the impact they have on the fig-fig wasp mutualism. Additional studies are also needed on biogenic volatile organic compounds (BVOCs) that attract pollinators, NPFWs and seed dispersers, all of which have been little studied in Thailand.

Pollinator wasps can locate their host figs, even on isolated trees, in highly disturbed habitats and efficiently transport pollen to them over much longer distances than expected. Kobmoo *et al.* (2010) reported that *F. racemosa* is pollinated by a single population of a single agaonid wasp species, all over continental South-East Asia, indicating that each *Ficus* species supports large populations of their pollinators. Furthermore, pollinator populations can apparently rebound very quickly after local extirpation where their host trees are present (Bronstein and Hossaert-Mckey, 1995; Harrison, 2000). Fig trees play a leading role in mutualisms with their pollinators (Ma *et al.*, 2009). The stability of the pollinating wasp populations and pollination success ultimately depends on the fig tree population size. Forest restoration plans must maintain both partners and must tackle the issue of increasing the number of fig trees required to sustain the wasp population over the year-round.

6.3 *Ficus* propagation

Fig seed germination is high and synchronous. The seeds also have short dormancy (Fig. 16). Thus, pre-sowing seed treatments are not necessary. The low seed germination rate of *F. hispida*, maybe due to a thick mucilaginous coat (generally the mucilaginous structure is necessary to attract ants, which are considered as secondary seed dispersers; Kaufmann *et al.*, 1991) than seeds of other selected *Ficus* species. Sun-drying the seeds for several days may help to increase the germination rate, because sunlight breaks down the sticky seed coating which inhibits germination. This method also helps to prevent growth of fungi (FORRU, 2006).

However, Horn (1997) stated that optimum placement of fig seeds is more important than enhanced germination, because they have a low chance of establishing seedlings (Swagel *et al.*, 1997). Galil (1984) emphasized that the establishment of the very small seedlings is the determinative phase in the development cycle of figs. This is presumably the reason why figs and other Moraceae produce numerous seeds per fruiting episode increase the probability that at least a few of them will reach suitable germination micro-sites (Laman, 1996). Micro-site quality has been shown to be important for germination and seedling establishment of figs (Laman, 1995). Also, each *Ficus* species appears to have stringent micro-site requirements (Laman, 1995; Holbrook and Putz, 1996). The potential germination and establishment sites for *Ficus* require constantly moist (Galil, 1984; Swagel *et al.*, 1997), open place (Titus *et al.*, 1990) and bare soil (Ramirez, 1989). Swagel (1997) also suggested that the optimum temperature for fig seeds germinating is at room temperature (25-30°C).

Determining the conditions suitable for seed germination and seedling establishment in the natural habitat is very useful in improving nursery techniques. At the early stages, fig seedling establishment is very sensitive to soil pathogens (Moore, 1989; Titus *et al.*, 1990). Swagen *et al.* (1997) also suggested that germinating fig seeds directly in soil increase the risk of attack by soil pathogens. Thus, the potential substrate for germinating fig seeds in nursery should not contain soil. Fig seed germination requires sterilized local potting media such as humus from palm leaves (Swagel *et al.*, 1997), vermiculite (Storey, 1975) or mixtures of sand and charred rice husk (Kuaraksa and Elliott, 2011). The pH of media should be neutral or slightly acidic, whilst alkaline substrates are reported to have a negative effect on germination rate (Pérez-Fernández *et al.*, 2006). My findings showed that charred rice husk was highly alkaline. Soaking charred rice husk in water for 3-7 days is reported to neutralize the alkalinity before use (Promchot and Boonprakob, 2007).

Producing *Ficus* spp. planting stock from cuttings was difficult, expensive and inefficient for all tested species. This result agrees with Gautier (1996) who reported that both of the subgenus *Sycomorus* and *Ficus* have no cutting capacity. Thus, for large-scale forest restoration projects, vegetative propagation from cuttings is not recommended for use, particularly in the case of dioecious *Ficus* species. However, this method might work well in hemi-epiphytic *Ficus* species because the subgenus *Urostigma* is easily propagated by cuttings (Danthu *et al*., 2002; Blythe *et al*., 2004).

Palms are the most common support hosts for many *Ficus* species, in particular the hemi-epiphytic figs in the tropical dry forest (Swagel *et al*., 1997). Through Thailand, oil palms are widely planted in the south. Therefore, collect fig wildlings from oil palm plantation, to nurture in a nursery until they are ready for planting could be an alternative method of producing fig trees for supporting forest restoration in southern Thailand. This method may help to reduce propagation time, especially during the early stages of fig seedling development and also it may be of benefit to the oil palm plantation since plantation owners regard fig trees as parasites on their oil palm trees.

Because fig seedlings can be planted out when they are about 20 cm or taller, they exhibited high growth and survival rates after planting compared with other framework species. Thus, there is no need to stock *Ficus* seedlings for more than a year in the nursery. Since most fig tree species share similar reproductive and growth patterns, production schedule is grouped in Table 21.

Table 21 Production schedule for *Ficus* species in northern Thailand.

jl	ag	sp	oc	nv	dc	ja	fb	mr	ap	my	jn*
Collecting and Sowing		x	x	x	Pricking out[a]		x	Fertilizing[b]	x	Hardening	Planting

*Beginning of rainy season; [a]After the 2nd pair of true leaves has expanded (about 1-2 cm tall), [b]10 granules of a slow release fertilizer (14-14-14) per seedling, x = grow on.

Table 22 Summary of the selected *Ficus* species classification (Based on Elliott *et al.* 2003).

Ficus species	Ease of propagation[a]	Survival[b]	Growth[c]	Crown Width[d]	Weed suppression[e]	Fire resilience[b,*]	Overall classification
F. auriculata	A	A	A	M	A	E	A
F. fulva	A	A	A	M	E	-	A
F. hispida	M	A	A	M	E	A	A
F. oligodon	M	E	A	M	E	E	A
F. semicordata	A	E	E	M	E	-	A
F. variegata	A	E	E	M	E	-	A

Note: Field performance based on 17 months after planting.

[a] Germination percentage in the nursery; E=excellent (>75%); A=acceptable (50-75%); M=marginal (25-50%); R=rejected (<25%).

[b] E= >70%; A=50-69.9%; M=45-49.9%; U= <45%.

[c] E= >2 m; A=1.5=1.99 m, M= 1.25-1.49 m; U= <1.25 m.

[d] E= >1.8 m; A=1.5-1.79 m; M=1.0-1.5 m; U= <1.0 m.

[e] E= >1; A=0.5-1.0; M=0.4-0.49, U= <0.40.

[*] Resilience to fire exhibited by a subsample of trees planted in 2007 (34 months old at the time of the fire). The mean number of coppics (6 months after forest fire occurred in year 3 plot 2007) was 3.2±2.2 (*N*=11), 6.8±1.9 (*N*=10) and 6±1.9 (*N*=15) for *F. auriculata*, *F. hispida* and *F. oligodon*, respectively; (-) = No data.

Table 23 Parameter values may affected on the abundance of the selected *Ficus* species in Doi Suthep - Pui National Park.

Species	Trees density[a]	Sex Balance[b]	Distribution[c]	Time of main seed-crop produced[d]	Pollinators stability[e]	Non-pollinators associated[f]	Ability to sustain their pollinator[g]	Overall score
F. auriculta	1	0	0	0	1	1	1	4
F. fulva	1	1	1	0	1	1	1	6
F. hispida	0	0	0	0	0	0	0	0
F. oligodon	0	0	0	0	1	0	1	2
F. semicordata	0	0	0	0	0	0	0	0
F. triloba	1	0	1	1	0	0	1	4
F. variegata	1	1	1	0	1	0	1	5

[a]0 = high density, 1 = low density.

[b]0 = balance, 1 = unbalance.

[c]0 = wide, 1= narrow; [d]0 = suitable (beginning rainy season), 1 = unsuitable (late rainy season).

[e]0 = year-round dispersal, 1 = critical bottleneck for wasp dispersal.

[f]0 = low proportion within a single fig, 1 = high proportion within a single fig.

[g]0 = high asynchronous fig production within-tree, 1 = low asynchronous fig production within-tree.

6.4 *Ficus* planting

All the selected dioecious *Ficus* tree species in this study are highly suitable as framework species for forest restoration projects (Table 22). Most dioecious *Ficus* species reveal a spectrum of pioneer ecologies (Harrison and Shanahan, 2005) such as fast-growing, tolerant of most soils (even in rocky sites), drought and lights conditions (Herre, 1996; Swagel *et al.*, 1997), insect-resistance (Compton, 1996; Subbarao, 1996; FORRU, 2006) and fire-resilient (Table 22), all of which make them suitable for growing in highly degraded habitats (Harrison and Shanahan, 2005).

Dioecious *Ficus* species also play a significant role in forest succession in the tropics (Shanahan *et al.*, 2001a). Especially, in regenerating tropical forests, dioecious *Ficus* species are an exceptionally important resource for attracting a diversity of frugivores that can disperse seeds of other plant species, influencing plant community composition, and rates of succession (Compton, 1996). Further research is needed to compare biodiversity recovery between planted plots with high density of *Ficus* species and those with a more even composition of other framework species.

Most *Ficus* tree species are light-demanding and their establishment is restricted when growing under the other trees crowns (Swagel *et al.*, 1997). Therefore, when inter-planting *Ficus* with other framework species, it is better to plant *Ficus* seedlings nearby slower-growing climax framework tree species (e.g. *Aphanamixis* spp., *Castanopsis* spp.) because they can act as the nurse plant of the climax framework tree species in early establishment stage, in particular to provide shade and to suppress weed growth.

The hemi-epiphytic *Ficus* species are not recommended for use in forest restoration because they will probably establish naturally once the forest has reached a more advanced stage of recovery, especially since many of the pioneer framework tree species recommended by FORRU (e.g. *Melia*, *Tectona* and *Eugenia*) are the preferred host trees of strangler figs (Galil, 1984).

6.5 Implications for management and conservation the rare figs

Although many factors may affect the abundance of *Ficus* species (Table 23), it seems that, phenology is of critical important. Thus, understanding the reproductive ecology of *Ficus* spp. has important implications for management and conservation. The phenology of female trees of *F. triloba* is unfavorable for seed germination and seedling establishment, since the trees produced the main seed crop at the end of the rainy season. To maintain the population of *F. triloba* in the national park, seedlings must be produced from seed in a restoration tree nursery and planted out when they are an acceptable quality by the optimal planting time. Since most species which showed a bottleneck for wasp dispersal are ranked as rare in the park, a shortage of pollinators may also affect *Ficus* reproduction/abundance. Especially, the large gaps between flowering male trees of *F. variegata* (about 4 months, Fig. 28) that are unbridgeable by the pollinators may lead to local extirpation of their pollinator wasps. To maintain pollinator populations of *Ficus* species which have critical bottlenecks for wasp dispersal, it is especially important to increase the number of male trees, which are critical for year-round survival of local fig-wasp population (i.e. fruiting in the rainy season, the whole set of key trees in Fig. 28).

In general, for large-scale planting, raised-nursery *Ficus* seedlings from seeds is recommended as it produced the best results (both in terms of field performance and cost effectiveness). However, to maintain pollinator populations of rare *Ficus* spp.

with critical bottle-necks for wasp dispersal, vegetative techniques (e.g. cutting, grafting and truncheon) might be useful to ensure an even sex ratio. It might also be a way to produce a range of individuals with complementary phenological patterns (because each individual tree has its own reproductive phenology rhythm; Kjellberg and Maurice, 1989) and thus eliminate seasonal bottlenecks in wasp reproduction. Particularly, further field trials on the use large vegetative stakes (by placing them directly in the ground) from male fig trees, which fruit during the critical bottleneck for wasp dispersal may help to shorten time required to sustain a local pollinator population. Generally, fig saplings growing from seeds take 5-7 years to initiate their first figs (FORRU, 2006) whereas cuttings or grafts from the branches of mature trees can be reduced to timing to first fig production to 1-3 years (Storey, 1975). Furthermore, planting stock derived from branches of mature trees may provide food resource/perch site to attract seed dispersing wildlife in early-successional stage when other framework species have no fruits. Zahawi and Augspurger (2006) reported that the animal-dispersed seed rain is enhanced beneath planted 2-m tall-*Ficus* stakes, which can then play a role similar to remnant vegetation. Optimal planting sites for all rare *Ficus* species are in degraded areas of mixed forest, because their natural distribution is commonly found to that zone.

6.6 Implications for other uses of figs

Not only are figs trees important to forest restoration but also they can be incorporated into agro-forestry systems (Gautier, 1996; Rana and Sood, 2011). The characteristics of figs which could make them as candidate species in agro-forestry systems are:

1. *Ficus* species are edible (e.g. *F. oligodon*, *F. semicordata*).

2. The litter from fig trees can be used for maintenance of soil fertility and for making the soil fertile again (Ramirez, 1989; Tegegne, 2008).

3. The complex root systems of figs are not only necessary to control of soil erosion but it usually is associated with diverse mycorrhizal fungi. Silman and Krisel (2006) stated that *Ficus* is keystone species for soil microbial community structure. Therefore, the symbiotic relationship with diverse soil microbial may also help the other economic species to grow and to resist the pathogenic fungi.

4. Fig trees can act as nurse-tree and as live-fences (Gautier, 1996). They also are shade-providers to light-sensitive species as in the systems of "fig-coffee-banana" in Africa (Ipulet, 2007).

5. They have high ability to attract a wide range of pollinating and seed-dispersing animals which provides benefits to other economic trees, in particular for increasing reproductive success for fruit production (Novotny *et al.*, 2005; Eshiamwata *et al.*, 2006).

6.7 Overall conclusion

The phenology study from this research has helped to consolidate the position of *Ficus* spp. trees as "keystone species" in tropical forest ecosystems. Fig trees are also the "controlling partner" in fig-wasp mutualisms. Therefore, the conservation of *Ficus* populations contributes to the conservation of many species of tropical animals and plants. Not only are *Ficus* tree species most suitable for promoting biodiversity conservation, they also yield several useful products such as traditional medicines, edible fruits, fuel-wood, fodder for domestic animals etc. The deep and complex root systems of figs provide them with an ability to control soil erosion like no other group of tree species, especially in highland restoration projects on steep slopes, or in the rehabilitation of open caste mines.

In addition, figs exhibit a relatively high capacity to absorb water which will be useful in flood prevention (Patino *et al.*, 1994). Several *Ficus* species also have high ability for use in the phytoremediation of metals in polluted terrestrial environments (Yeo and Tan, 2011). Therefore, *Ficus* species have high value in terms of environmental services. All tested *Ficus* tree species acted as excellent framework species, thus they should be grown and planted in broad-scale restoration activities.