REPRODUCTIVE ECOLOGY AND PROPAGATION OF FIG TREES (*FICUS* SPP.) AS FRAMEWORK TREES FOR FOREST RESTORATION

CHERDSAK KUARAKSA

DOCTOR OF PHILOSOPHY

IN ENVIRONMENTAL SCIENCE

THE GRADUATE SCHOOL

CHIANG MAI UNIVERSITY

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Thesis Title	Reproductive Ecology and Propagation of Fig Trees (*Ficus* spp.) as Framework Trees for Forest Restoration
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ABSTRACT

Fig (*Ficus* spp.) trees have been promoted as framework species for tropical forest restoration, because they are considered to be keystone species. This thesis presents on a study of the reproductive ecology, propagation and planting techniques for seven Asian dioecious *Ficus* species, which will enable their inclusion in forest restoration plantings. Study consisted of *Ficus auriculata*, *F. fulva*, *F. hispida*, *F. oligodon*, *F. semicordata*, *F. triloba* and *F. variegata*.

At the population-level, most species produced figs all year round, but fig abundance varied seasonally. Maximum production of ripe figs by female trees of most species occurred in the rainy season (May-August, except for *F. triloba*), whilst the main fig crop of male trees peaked 1-3 months before female trees. Four species *F. auriculata*, *F. fulva*, *F. oligodon* and *F. variegata* had critical bottleneck periods for wasp survival, especially during the rainy season, when the wasp-producing figs of male trees were least abundant. At the level of individual trees, considerable variation in phenology was evident among species. Only *F. hispida* and *F. semicordata* had completely within-tree asynchronous phenologies (receptive- and releasing/ripening-phases present simultaneously within individual tree crowns).

Most pollinators and non-pollinators found in this study were specific to single host fig species. However, *F. hispida* was pollinated by two pollinator species, whilst *F. auriculata* and *F. oligodon* shared the same pollinator. The effects of habitat fragmentation on the numbers of foundresses and seeds of most selected *Ficus* species was unclear, because pollinator wasps were highly efficient at locating their host *Ficus* spp., even isolated trees, in highly disturbed habitats and transported pollen to them over much longer distances than anticipated.

The most efficient method of producing *Ficus* spp. planting stock for forest restoration projects was from seed. Propagation from cuttings was much less successful. Seedlings produced from seed had the highest rates of growth and survival both in the nursery and in field trials. In field trials, use of planting stock from seed was also more cost-effective than direct seeding and vegetative propagation.

The study generated scientifically-based recommendations that will be useful for development of efficient forest restoration programs that maintain keystone resources in tropical forest ecosystems such as i) optimum time/place for seed collection, and optimum planting sites for each species ii) recommendations on the propagation and planting of dioecious fig species, and iii) forest restoration plans to sustain the obligate ecological relationships between fig-trees and their pollinators.

Most tested *Ficus* tree species acted as excellent framework species, thus they should be grown and planted in broad-scale restoration activities across the Asia-Pacific region.

ชื่อเรื่องวิทยานิพนธ์	นิเวศวิทยาการสืบพันธุ์และการขยายพันธุ์ไม้ยืนต้นในสกุล มะเดื่อ ไทร (*Ficus* spp.) เพื่อเป็นพรรณไม้โครงสร้างสำหรับการฟื้นฟูป่า	
ผู้เขียน	นายเชิดศักดิ์ เกื้อรักษ์	
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	ดร. มาร์ติน ออสเสท แมกกี้	อาจารย์ที่ปรึกษาร่วม
	ดร. สุทธาธร ไชยเรืองศรี	อาจารย์ที่ปรึกษาร่วม

บทคัดย่อ

ไม้ในกลุ่มมะเดื่อ ไทร ได้รับการส่งเสริมเป็นพรรณไม้โครงสร้างสำหรับปลูกเพื่อฟื้นฟูสภาพป่าในเขตร้อน เนื่องด้วยมีความสำคัญในระบบนิเวศโดยเฉพาะในแง่ของการเป็นแหล่งอาหารสำหรับสัตว์ป่า วิทยานิพนธ์นี้ได้เสนอผลการศึกษาทางด้านนิเวศวิทยาการสืบพันธุ์ การขยายพันธุ์และกรรมวิธีการปลูก ในมะเดื่อแบบแยกเพศแยกต้นจำนวน 7 ชนิด เพื่อประโยชน์ในการนำไปใช้ในโครงการฟื้นฟูป่าประกอบด้วย มะเดื่อใบใหญ่ ไทรใบขน มะเดื่อปล้อง มะเดื่อเกลี้ยง มะเดื่อปล้องหิน มะเดื่อขนทองและมะเดื่อผูก

ในระดับประชากรมะเดื่อเกือบทุกชนิดติดผลตลอดปีแต่ปริมาณมากน้อยขึ้นอยู่กับฤดูกาล ต้นเพศเมียส่วนใหญ่ให้ผลผลิตในช่วงฤดูฝน ขณะที่พัฒนาการของช่อดอกในต้นเพศผู้ส่วนใหญ่เกิดในช่วงหน้าแล้งก่อนหน้าต้นเพศเมียประมาณ 1-3 เดือน เนื่องด้วยมีต้นเพศผู้ของมะเดื่อใบใหญ่ ไทรใบขน มะเดื่อเกลี้ยงและมะเดื่อผูกติดผลในปริมาณน้อยในช่วงฤดูฝนทำให้การกระจายตัวของตัวผสมเกสรอาจถูกจำกัด เมื่อพิจารณาระดับภายในต้นพบว่ารูปแบบพัฒนาการของผลมีความแตกต่างกันอย่างชัดเจนในมะเดื่อแต่ละชนิดแต่ส่วนใหญ่เป็นไปโดยพร้อมเพรียง มีเฉพาะมะเดื่อ

ปล้องและมะเดื่อปล้องหินที่พัฒนาการของผลภายในต้นเดียวกันมีหลากหลายระยะในช่วงเวลาเดียวกัน

ความสัมพันธ์ระหว่างมะเดื่อกับแตนมะเดื่อส่วนใหญ่เป็นแบบเฉพาะเจาะจงคือมีแตนเพียงหนึ่งชนิดที่ทำหน้าที่เป็นแมลงพาหะถ่ายเรณู อย่างไรก็ดีพบแตนผสมเกสร 2 ชนิดในมะเดื่อปล้องในขณะที่มะเดื่อใบใหญ่และมะเดื่อเกลี้ยงใช้แตนผสมเกสรชนิดเดียวกัน นอกจากนี้เราพบว่าแตนผสมเกสรมีศักยภาพสูงในการผสมเกสรและค้นหาต้นมะเดื่อเพื่อวางไข่ไม่ว่าต้นมะเดื่อนั้นจะอยู่ห่างไกลจากต้นอื่นหรืออยู่ในสภาพสิ่งแวดล้อมที่โดนรบกวนจากกิจกรรมของมนุษย์

วิธีที่เหมาะสมในการขยายพันธุ์มะเดื่อเพื่อใช้ปลูกฟื้นฟูสภาพป่าคือการเพาะจากเมล็ดเพราะต้นกล้ามีอัตราการเจริญเติบโตและอัตราการรอดตายสูงทั้งในเรือนเพาะชำและแปลงทดลอง นอกจากนี้การเพาะจากเมล็ดยังเป็นวิธีที่สะดวก ง่ายและประหยัดเมื่อเปรียบเทียบกับกรรมวิธีอื่น

ผลที่ได้จากการศึกษาไม่เพียงแต่ทำให้เราทราบถึงช่วงเวลาในการเก็บเมล็ด การขยายพันธุ์ เทคนิควิธีและสถานที่ที่เหมาะสมในการปลูกมะเดื่อแต่ละชนิด องค์ความรู้ที่ได้ยังสามารถนำไปประกอบใช้วางแผนการจัดการในโครงการฟื้นฟูป่าเพื่ออนุรักษ์ไว้ทั้งมะเดื่อและแตนมะเดื่อที่มีบทบาทสำคัญต่อระบบนิเวศ

มะเดื่อที่ศึกษาส่วนใหญ่มีคุณสมบัติเป็นพรรณไม้โครงสร้างที่ดีสมควรนำไปใช้อย่างแพร่หลายในโครงการฟื้นฟูป่า

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ABBREVIATIONS

ANR	Accelerated Natural Regeneration
AFTSC	ASEAN Forest Tree Seed Centre; Muak-Lek, Saraburi, Thailand
BA	Bare Branches, Leaf Fall
BB/DF	Degraded Teak and Bamboo + Deciduous Forest
CBGP	Centre de Biologie et de Gestion des Populations, Montpellier, France
CRGR	Relative Canopy Width Growth Rate
DA	Disturbed Areas
DBH	Diameter at Breast Height
DOF	Deciduous Dipterocarp - Oak Forest
DSNP	Doi Suthep - Pui National Park
DVP	Developing Phase
EGF	Primary Evergreen Forest
EG/PINE	Evergreen Forest with Pine
FAO	Food and Agriculture Organization
FIAU	*Ficus auriculata* Lour.
FIFU	*Ficus fulva* Reinw. ex Blume
FIHI	*Ficus hispida* L.f.
FIO	Forest Industry Organization
FIOL	*Ficus oligodon* Miquel

FISE	*Ficus semicordata* Buch.-Ham. ex Sm.
FITR	*Ficus triloba* Buch.-Ham. ex Voigt
FIVA	*Ficus variegata* Blume
FORRU-CMU	Forest Restoration Research Unit of Chiang Mai University
FS	Fig Size
HMDS	Hexamethyldisilazene
HRGR	Relative Height Growth Rate
IPCC	Intergovernmental Panel on Climate Change
IBA	Indole Butyric Acid
IMP	Immature Phase
LMC	Local Mate Competition
ML	Mature Leaves
MLD	Median Length of Dormancy
NPFWs	Non Pollinating Fig Wasps
PAS	Periodic Acid-Schiff Stain
RA	Monthly Mean Rainfall
RCD	Root Collar Diameter
RCP	Receptive Phase
RFD	Royal Forest Department
RGR	Relative Growth Rate
RLP	Releasing Phase (male trees)
RPP	Ripening Phase (female trees)
RRGR	Relative Root Collar Diameter Growth Rate
SCB	Siam Commercial Bank

SE	Seed Number
SG	Secondary Growth
SL	Senescence Leaves
TE	Monthly Mean Temperature
YL	Young Leaves

CHAPTER 1

INTRODUCTION

Principle and rationale

Destruction of tropical forests continues to be a major threat to global biodiversity and also contributes significantly to global climate change. Forest restoration could be a significant part of the solution, if efficient techniques can be developed and socio-political conditions allow them to be practiced. Many tropical countries have recently started incentive programs to restore tropical forest lands, particularly for carbon sequestration and biodiversity conservation. However, the effectiveness of such restoration projects depends on the development of simple but effective methods to grow, plant, and take care of the many tree species that comprise tropical forest ecosystems. Restoration ecology is still a young and developing science, and tropical forest ecosystems are complex, with different sites requiring different restoration techniques. Several methods have been developed to restore degraded tropical forest lands such as maximum diversity plantings (Miyawaki, 1993), nurse crops or foster ecosystems (Parrotta, 1993), staggered planting of primary forest species (Knowles and Parrotta, 1995) and scattered tree planting (Lamb and Gilmour, 2003). Most approaches involve planting of tree seedlings. However, conventional reforestation methods involving planting of tree seedlings are costly, high labor and research input required (Engel and Parrota, 2001; Erskine, 2002; Lamb *et al*., 2005; Shono *et al*., 2007; Birch *et al*., 2010).

Like many tropical countries, tree planting has become popular all over Thailand in particular as a response to mitigate global climate change. However, many tree planting projects fail, due to the planting of inappropriate species, and inadequate planting techniques and post-planting maintenance regimes (Elliott and Kuaraksa, 2008), particularly when using forest native tree species, about which little is known (Blakesley *et al*., 2002). Since 1994, the Forest Restoration Research Unit of Chiang Mai University's Biology department (FORRU-CMU) has been developing methods to restore forest ecosystems to deforested sites within protected areas, for biodiversity conservation and environmental protection in northern, Thailand. FORRU-CMU scientists successfully developed accelerated natural regeneration (ANR) techniques by adapting the so-called "the framework species method" to restore evergreen forest (above 1000 m elevation) in northern Thailand. Biodiversity recovery was achieved and the tree species composition of restored plots approached that of the original primary forest more rapidly than would occur by natural regeneration. Planting 29 framework tree species resulted in more than 70 non-planted tree species re-colonizing the plots within 8 years (Sinhaseni, 2008) and bird species richness rose from 30, before planting, to more than 80, within 6 years (Toktang, 2005). This project not only carried out useful technical research on the science of restoration ecology, but on social factors that lead to successful project implementation. Education and outreach transferred the knowledge gained to various target groups such as school children, villagers, foresters and conservationists, both from Thailand and neighboring countries (FORRU, 2006; Elliott and Kuaraksa, 2008). However, two remaining challenges include i) how can these concepts and methods be scaled up and applied to larger areas or different degraded forest types and ii) lack of basic knowledge of each native tree species needed to support the framework tree species method.

In addition to well-known groups such as nitrogen-fixing species Legumes and oaks/chestnuts (Fagaceae), fig trees (*Ficus* spp., Moraceae) have been promoted as framework species for forest restoration (Goosem and Tucker, 1995; FORRU, 1998, 2006). Elliott *et al*. (1997) recommended that about 20% of planted seedlings should be *Ficus* spp.

1.1 The important characteristics that make fig trees as candidate framework species for forest restoration include:

1.1.1 Figs are considered as keystone species in tropical forests ecosystems because the can sustain frugivorous animal species and community through periods of resource scarcity (Howe, 1977; Jansen, 1979; Leighton and Leighton, 1983; Terborgh, 1986; Lambert and Marshall, 1991; Shanahan *et al*., 2001b; Bleher *et al*., 2003; Harrison *et al*., 2008).

1.1.2 Figs have highly mutualistic relationships with diverse groups of animals (Compton and Disney, 1991; Herre, 1996; Novotny and Basset, 1998; Kerdelhue *et al*., 2000; Harrison *et al*., 2008).

1.1.3 Figs play an important role in supporting high biodiversity in the tropical forest ecosystems, particularly in regenerating forest ecosystems or in facilitating regeneration of disturbed habitats (Shanahan *et al*., 2001a; Ronsted *et al*., 2008b; Muhanguzi and Ipulet, 2011).

1.1.4 Figs have high value for Non-Timber Forest Product (Thomen, 1939; Condit, 1969; Berg and Corner, 2005).

1.1.5 Figs are fast-growing, high survival and growth performance when planted out in degraded areas (Jansen, 1979; FORRU, 2006) or under the harshest of conditions (i.e. forest fire, drought, salt and acid soil, and heavy polluted area (Condit, 1969; Morton, 1987; Riffle, 1998; Dazhi, *et al*., 2003). Figs also are resistant to wind, herbivores and pathogen (Jansen, 1979; Harrison *et al*., 2000; FORRU, 2006).

1.1.6 Figs produce dense systems of tough roots which prevent soil erosion (FORRU, 2006).

1.1.7 Figs are important shade-donor species, especially in deciduous forest habitats (Rao, 1963 in Condit, 1969). They also are excellent weed suppressor when planting out in degraded habitats (FORRU, 2006).

In Thailand, deforestation has reduced large forest tracts to tiny isolated fragments, each of which is incapable of supporting viable populations of plant and animal species (FORRU, 2006). As keystone species such as *Ficus* species start to disappear, their extinction could have a devastating effect on biological diversity of tropical forest ecosystems (Terborgh, 1986; Nason *et al*., 1998) because fig trees are important in maintaining diversity particularly in tropical and subtropical forests (Jansen, 1979; Cook and West 2006; Harrison, 2006; Dunn *et al*., 2008).

Nevertheless, currently the use of *Ficus* spp. trees in forest restoration programs is limited due to lack of knowledge about their basic ecology, phenology, propagation and planting techniques. Moreover, most studies of *Ficus* spp. reproductive ecology and their use in forest restoration program have been conducted on monoecious species rather than on dioecious ones (Yu *et al*., 2006). Therefore, the investigation of scientific knowledge of dioecious *Ficus* tree species is necessary to enable inclusion of them in forest restoration programs and provide constructive suggestions for the conservation of keystone resources in tropical forest ecosystems. Not only scientific knowledge of fig tree species is necessary for successful restoration by using the framework tree species method, to maintain biodiversity in tropical forest ecosystems, but also basic knowledge of dioecious figs is important to plan and design adequate strategies for conservation and management, before *Ficus* spp. become extirpated from the local habitat.

1.2 Why study dioecious figs?

1.2.1 Most research on *Ficus* in the past was focused on monoecious rather than dioecious *Ficus* spp (Corlett, 1993; Patel, 1996; Harrison *et al*., 2000; Yu *et al*., 2006). Therefore, very little literature is available on dioecious figs (i.e. ecology, propagation and planting techniques) to enable inclusion of them in forest restoration programs.

1.2.2 Dioecious fig species are probably relatively more important in facilitating the regenerative process than monoecious species because most (dioecious fig species) are considered as pioneer species (Shanahan *et al*., 2001b).

1.2.3 For forest restoration plans, management of dioecious figs is more complex than for in monoecious figs because they have two sexes (Montagnini and Jordan, 2005).

1.2.4 Most dioecious *Ficus* trees species in Doi Suthep-Pui National Park are at high risk of extirpation (15 of 19 dioecious *Ficus* species are ranked as rare; Maxwell and Elliott, 2001).

1.3 Research objectives

1.3.1 To develop a better understanding of the reproductive ecology (including phenological patterns and interactions with their wasps) of the target dioecious *Ficus* species.

1.3.2 To facilitate the use of *Ficus* spp as keystone framework species in forest restoration programs by developing optimum propagation and planting techniques.

1.4 In order to achieve the aim, the observations were designed into four main parts including:

1.4.1 *Ficus* phenology

Specific questions were:

1.4.1.1 Are dioecious *Ficus* spp. keystone species which maintain biodiversity on Doi Suthep-Pui National Park?

1.4.1.2 Is fig/leaf development related to climate?

1.4.1.3 Is the phenological behavior of each species related in its abundance?

1.4.1.4 When is the optimum time for seed collection of each species?

1.4.1.5 Where is the optimum planting site for each species?

1.4.1.6 How can forest restoration projects be designed to conserve rare *Ficus* spp.?

1.4.1.7 Does phenological study help to separate two closely related species (*F. auriculata* and *F. oligodon*)?

1.4.2 *Ficus* and their associated wasps

Specific questions were:

1.4.2.1 How many species of fig-wasp (including pollinators and non-pollinators) associate with the selected *Ficus* species?

1.4.2.2 Does habitat fragmentation affect foundress and seed numbers (per fig)?

1.4.2.3 Does seasonality affect seeds number per fig?

1.4.3 *Ficus* propagation

Specific questions were:

1.4.3.1 What is the suitable propagation method for producing planting stock of *Ficus* in nursery to support forest restoration projects?

1.4.3.2 What are the optimal treatments (medium composition and fungicide application) to maximize germination and prevent damping off diseases on young *Ficus* seedlings?

1.4.3.3 What are the optimal methods of cutting propagation (cutting position and application of rooting hormone) to maximize rooting ability of *Ficus*?

1.4.3.4 Do light intensity conditions and fertilizer application accelerate *Ficus* seedling growth and make them ready for planting (about 30-60 cm tall) within a year in nursery?

1.4.4 *Ficus* planting

Specific question was:

1.4.4.1 What is the optimum method (both in terms of field performance and cost effectiveness) for establishing *Ficus* spp. tree under field conditions, which can be applied to broad-scale restoration activities?

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).

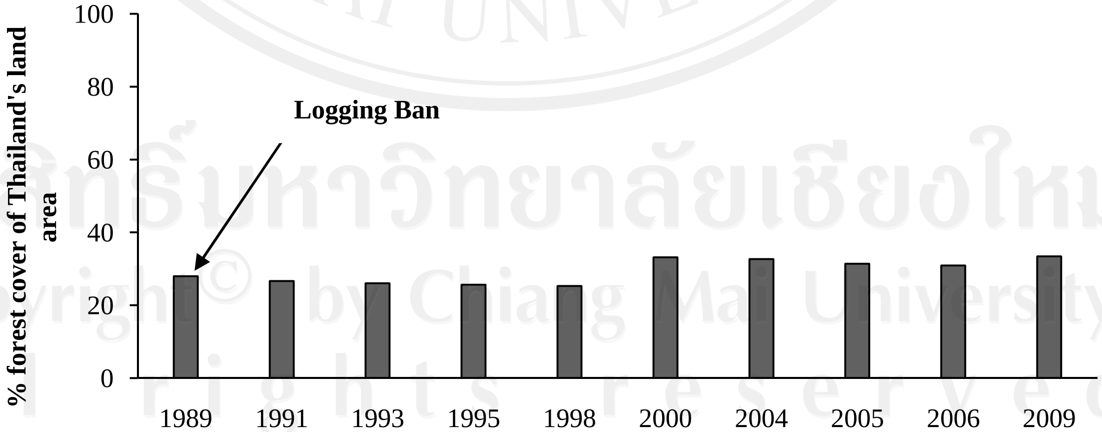
2) Seedling production and the design and management of mixed-species and plantations are complex (Hardwick, 1999).

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.

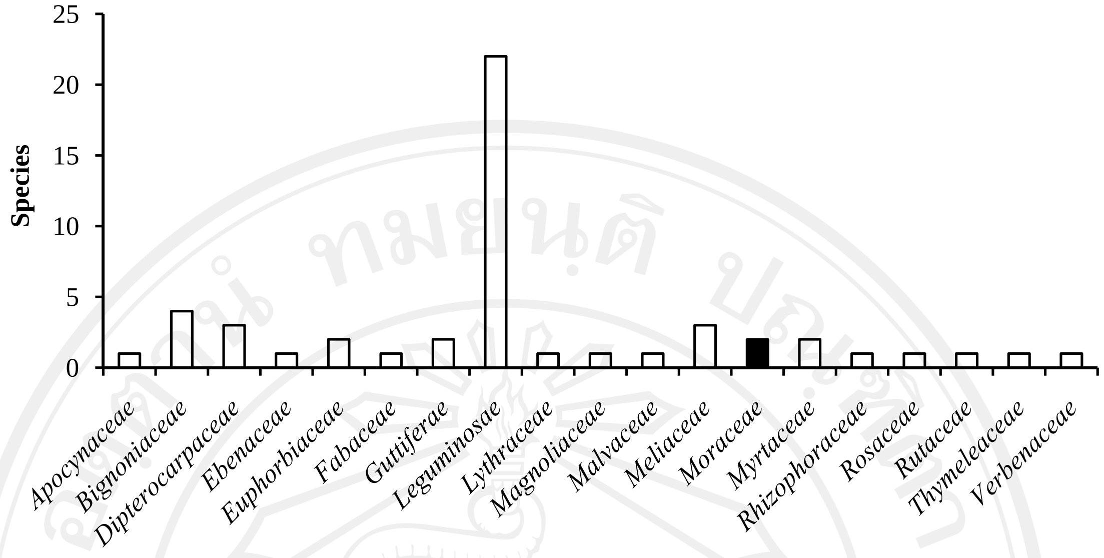


Figure 2 Seedling production reports of all RFD nurseries from 2006-2009 (www.forest.go.th/nursery).

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).

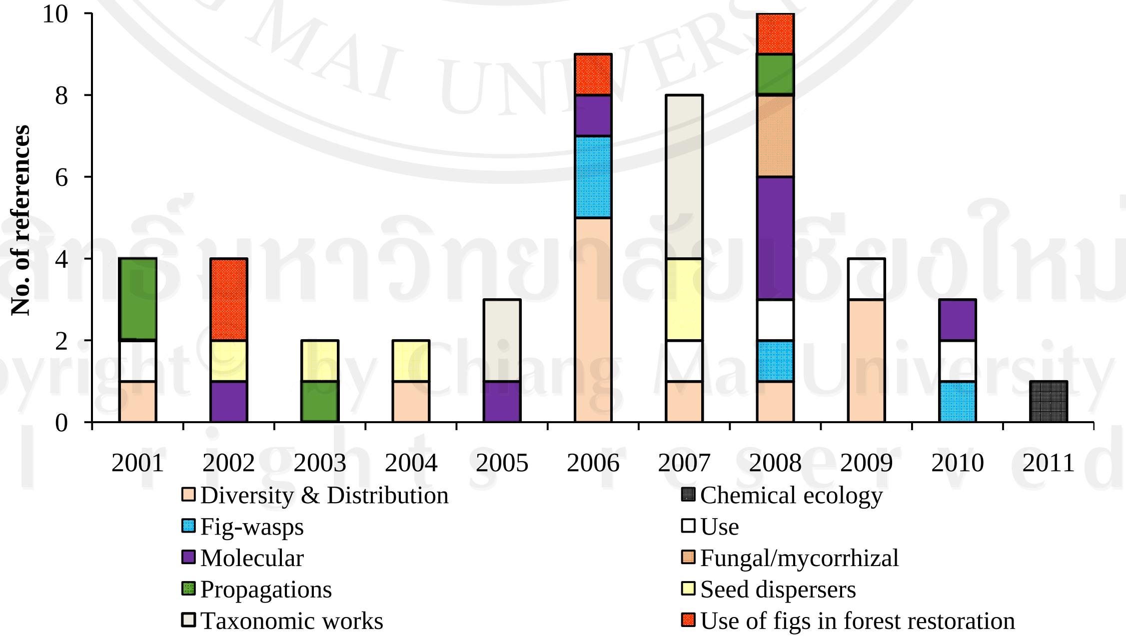


Figure 3 The type of study on *Ficus* species in Thailand (from 2001-present).

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.

CHAPTER 3

METHODOLOGY

3.1 Study site

This research was conducted in Doi Suthep-Pui National Park, (18º51´N latitude and 98º54´E longitude), Chiang Mai, Northern Thailand. The park supports three forest types: deciduous dipterocarp-oak forest from sea level to *c.* 800 m., mixed forest (evergreen + deciduous) from *c.* 800 to 1,200 m. and hill evergreen forest above 1,200 to the summit at 1,685 m. (Maxwell and Elliott, 2001). The area has a monsoonal climate with pronounced dry and wet seasons. The wet season lasts from May to October and the dry season from November to April. The dry season is subdivided into the cool-dry season (November to January) and the hot-dry season (February to April; Fig. 4).

Ficus spp. trees were propagated in the research nursery of the Forest Restoration Research Unit (FORRU-CMU) at 1,050 m elevation, in the south of the park, north-west of Chiang Mai City, Northern Thailand (18°51´N latitude and 98°54´E longitude). Experiment plots were established in a degraded watershed, in the north of the park (18°52´N latitude and 98°51´E longitude) at 1,150 m above sea level. The plots had been cleared of forest approximately 30 years ago, to provide land for cultivation of cabbages, corn, potatoes etc. Before tree planting, the plots were dominated by herbaceous weeds such as *Pteridium aquilinum* (L.) Kuhn, *Bidens pilosa* L. var *minor* (Bl.) Sherf and grasses e.g. *Phragmites vallatoria* (Pluk. ex L.)

Veldk, *Imperata cylindrical* (L.) P. Beauv var. major (Nees) C. E. Hubb. ex Hubb and Vaugh (pers. obs).

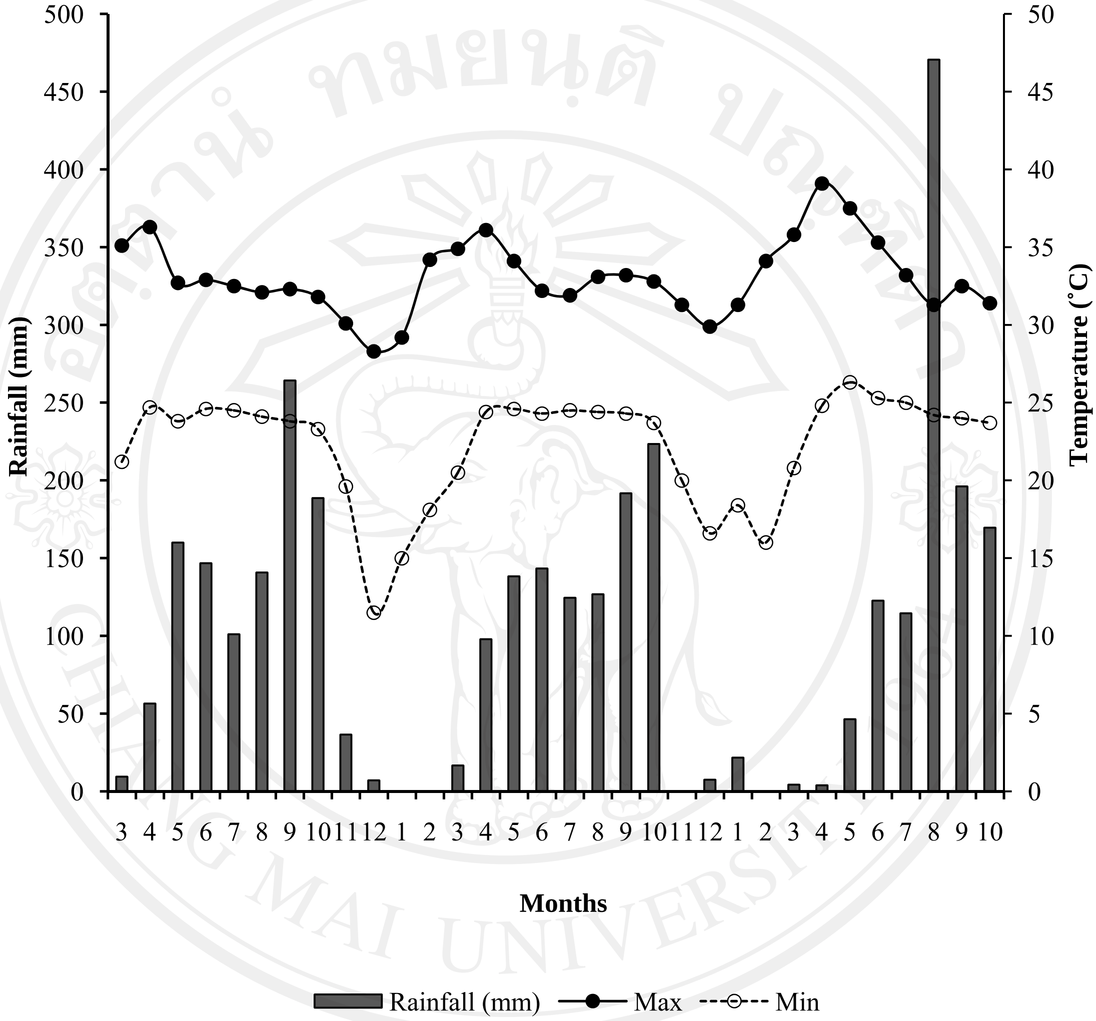


Figure 4 Average monthly rainfall (mm), maximum and minimum temperature (˚C) at the Northern Meteorological Center, about 3 km. from the National Park (from March 2008 - October 2010).

3.2 Study species

3.2.1 ***Ficus auriculata*** Lour. (subgenus *Sycomorus*, section *Sycomorus*, subsection *Neomorphe*). *Ficus auriculata* is a medium-sized tree, up to 20 m tall, becoming shortly buttressed. Young leaves are red, becoming green when mature. Figs grow on spurs that extend from the trunk, main branches (cauliflorous form) and sometimes from the crown roots (stoloniflorous form). The fig is reddish or purple at maturity. The female figs and young leaves are edible. This species grows in mixed deciduous and evergreen forests, often near streams, on various substrates (Berg *et al*., 2011). Figs production commences from the 5th year after planting (FORRU, unpubl. data, 2004).

3.2.2 *Ficus oligodon* Miquel (subgenus *Sycomorus*, section *Sycomorus*, subsection *Neomorphe*). The morphology of *F. oligodon* and *F. auriculata* is very similar. While the two species are confused in the latest taxonomic revision (Berg *et al*., 2011), they are readily recognizable in the field. In our research nursery (FORRU-CMU), external characters of leaf shape/size (*F. auriculata*: broad leaves and *F. oligodon*: narrower often toothed leaves), and the color of petiole of young seedlings or saplings (*F. auriculata*: greenish and *F. oligodon*: reddish) are used to separate *F. auriculata* from *F. oligodon*. *Ficus oligodon* is a spreading tree, which grows in all forest types in Doi Suthep-Pui National Park (under the name of *F. fistulosa* Reinw. ex. Bl. var *fistulosa* in Maxwell and Elliott, 2001). Figs are borne singly or in small clusters from tubercles on the trunk and a larger branch. The female figs and young leaves are edible, and it is also an excellent host tree for Lac insects (*Laccifer lacca* Kerr., per. obs.). They produced figs from the 6th year after planting and are very attractive to seed-dispersing birds (FORRU, 2006).

3.2.3 *Ficus variegata* Blume (subgenus *Sycomorus*, section *Sycomorus*, subsection *Neomorphe*). *Ficus variegata* is a pioneer, large-sized tree (up to 40 m tall) with prominent buttresses. The bark is smooth, pale pinkish brown (the tree is sometimes named the red stem-fig). Leaves are thin, heart-shaped and have a toothed edge. The figs grow in dense clusters on the trunk and main branches. The fig is pink to red (or sometimes green) at maturity. It is mostly found in evergreen forest throughout the country, often near streams (Berg *et al*., 2011). However, some individuals are found in relatively open forest as isolated trees (per. obs.).

3.2.4 *Ficus hispida* L.f. (subgenus *Sycomorus*, section *Sycocarpus*). *Ficus hispida* is a small or moderate-sized tree. Leaves are very rough and generally opposite. Through Thailand, the rough leaves are used to clean off mucilage from eels before cooking. Figs are axillary, cauliflorous and flagelliflorous. Figs are yellowish when ripe. This species grows in all forest types throughout the country, but it is most common in secondary growth, in drier climates, at low altitudes. All parts of this plant can be used in tradition medicine for the treatment of various ailments, for example, their stems have been utilized for the treatment of human breast cancer (Pratumvinit *et al*., 2009). In forest restoration projects, this species has been ranked as an excellent framework species (Elliott *et al*., 2003). Planted saplings produced figs within 3 years after planting and showed excellent weed suppressing capabilities and fire resilience (FORRU, 2006).

3.2.5 *Ficus semicordata* Buch.-Ham. ex Sm. (subgenus *Sycomorus*, section *Hemicardia*). *Ficus semicordata* is a tree with wide-spreading branches, brown hairs on leafy twigs, leaf and syconium. Leaves are alternate, prominently asymmetric especially at the base, and the mature leaves are rough and scurfy. This species is cauliflorous. The leafless fig-bearing branches develop at the base of the trunk and often become stolon-like, trailing across the forest floor. At some distance from the trunk such branches may start to grow upwards and become leafy, establishing satellite trees. Externally the figs are red-brown at maturity. This species grows in all forest types, but mainly in disturbed areas and secondary growth forest. The female figs are edible and sweet. In forest restoration projects, this species is easy to propagate from seeds (Kuarak *et al*., 2000). Planted saplings grow very rapidly and figs are produced prolifically from the 3rd year after planting (FORRU, 2006).

3.2.6 ***Ficus fulva*** Reinw. ex Blume (subgenus *Ficus*, section *Eriosycea*, subsection *Eriosycea*). *Ficus fulva* is a small tree, growing in the understory of mixed evergreen-deciduous forest. Whereas, in Malaysia, *F. fulva* is very common on small ridges, sifting cultivation and large landslide gaps in the primary forest (Harrison *et al*., 2000). It forms almost pure stand with wide spreading branches and dense foliage. Twigs, leaves and figs have short white (silky hairs) bristles. The figs are axillary on the twigs, in pairs below the leaves on previous season's growth. The interior is scarlet and yellow to orange at maturity. The main seed dispersers of *F. fulva* are bulbuls (e.g. *Pycnonotus goiavier* Scopoli) and fruit bats (Harrison *et al*., 2000).

3.2.7 ***Ficus triloba*** Buch.-Ham. ex Voigt (subgenus *Ficus*, section *Eriosycea*, subsection *Eriosycea*). *Ficus triloba* is a tree with stiff brown hairs on various parts. The leaves are borne in spiral and are often subpalmately 3-5-7-lobed. The figs are axillary, sessile, and may present lateral bracts. At maturity, it is yellow to red-brown. *Ficus triloba* was found only the forest understory of primary mixed evergreen-deciduous forest in the park, whilst Berg *et al*. (2011) reported that it can also be found in deciduous dipterocarp forest. In restoration plots, saplings produced figs within 5 years after planting (per. obs). More details of the seven selected dioecious *Ficus* species are presented in Table 2 and Appendix A.

Table 2 Overview of distribution, habitat and abundance of the seven selected dioecious *Ficus* species.

***Ficus* Species** [a]	**Distribution Range** [b] (Country)	**Habitat** [c]	**Elevation** [d] (m)	**Abundance Rank** [e]
F. auriculata	Bhutan, Cambodia, China, India, Laos, Myanmar, Nepal, Pakistan, Thailand, Vietnam	streams in dof, egf, eg/pine	891-1,319	rare
F. fulva	Brunei, China, India, Indonesia, Malaysia, Myanmar, Thailand, Vietnam	da, sg in egf	923-1,100	rare
F. hispida	Australia, Bhutan, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Sri Lanka, Thailand, Timor, Vietnam	da in bb/df, sg	326 -1,351	medium
F. oligodon	Bhutan, China, India, Malaysia, Myanmar, Nepal, Thailand, Vietnam	da, open bb/df, mxf, egf, sg	605-1,336	medium
F. semicordata	Bhutan, China, India, Malaysia, Myanmar, Nepal, Thailand, Vietnam	sg, da in bb/df, egf, eg/pine	418-1,531	medium

Table 2 (continued)

***Ficus* Species** [a]	**Distribution Range** [b] (Country)	**Habitat** [c]	**Elevation** [d] (m)	**Abundance Rank** [e]
F. triloba	Bangladesh, Bhutan, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Vietnam	da, sg in egf	1050-1300	rare
F. variegata	Australia, Cambodia, China, India, Indonesia, Japan, Laos, Malaysia, Myanmar, Philippines, Thailand, Vietnam	egf	899-1343	rare

[a] All selected *Ficus* species were dioecious; free-standing.

[b] Source: Flora of China (Zhekun and Gilert, 2003); Flora Malesiana (Berg and Corner, 2005); Flora of Thailand (Berg *et al*., 2011).

[c] Source: Maxwell and Elliott (2001); dof = deciduous dipterocarp-oak forest, egf = primary evergreen forest, eg/pine = evergreen forest with pine, da = disturbed areas, sg = secondary growth, bb/df = degraded teak & bamboo + deciduous forest.

[d] Altitude range (m) of the parent/donor trees were found along the seed/cutting collection trails of Doi Suthep-Pui National Park.

[e] Species abundance in the park is ranked by Maxwell and Elliott (2001); *F. fulva* is a synonym of *F. hirta* Vahl var. *roxburghii* (Miq.) and *F. oligodon* is a synonym of *F. fistulosa* Reinw. ex Bl. var. *fistulosa.*

3.3 Methods

3.3.1 *Ficus* phenology. Two transect lines were established to study the phenology of these species, traversing every forest type found in the National Park (from 320 to 1,685 m. elevation). Trail A (yellow line) ran across the park from east to west, whilst trail B (red line) ran from north to south (Fig. 5).

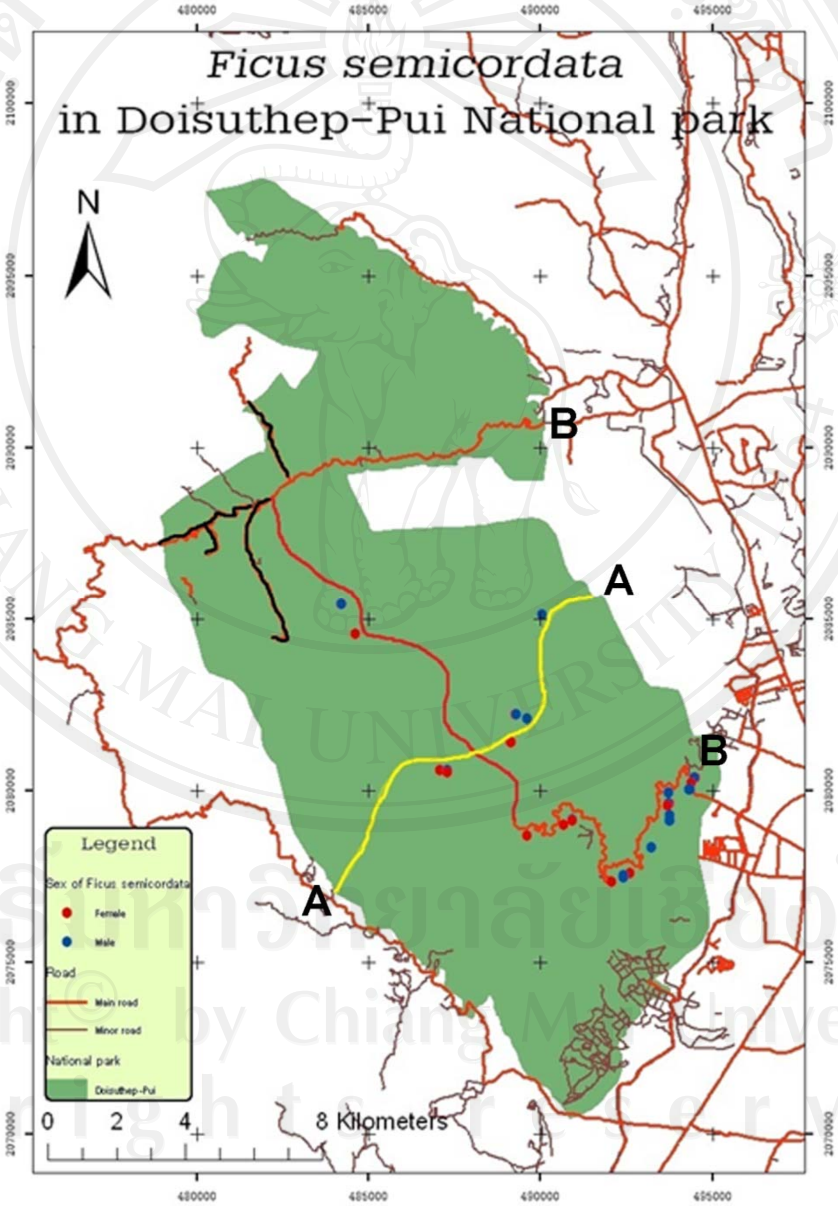
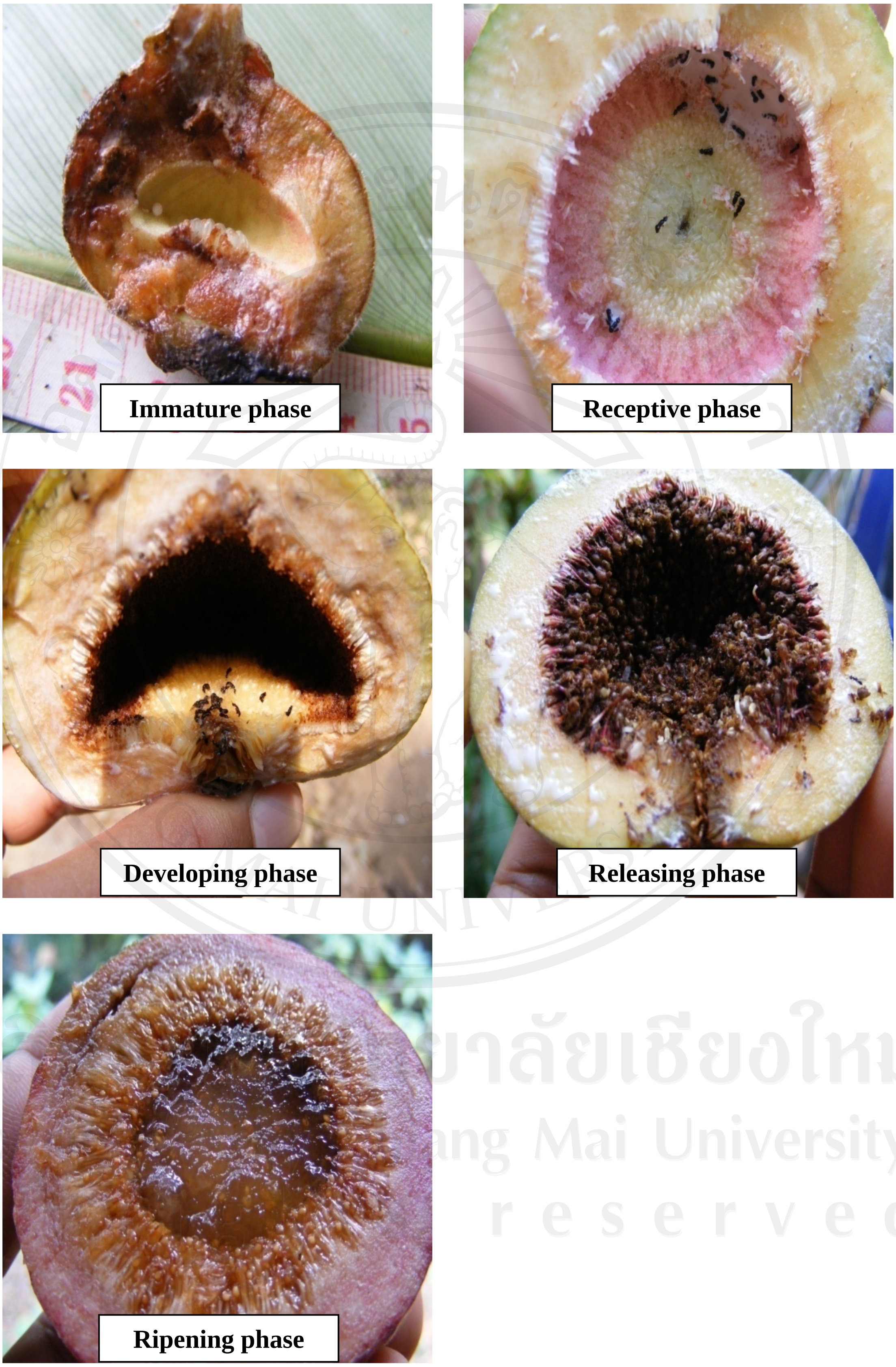


Figure 5 Map of the main part of Doi Suthep-Pui National Park and two phenology trails (A and B) along the park.

All mature individuals of the selected *Ficus* species (dbh >10 cm), within 20 m to the left and right of the transect lines, were selected for monitoring, tagged and their position recorded by GPS. Selected fig trees were observed monthly from March 2008 to February 2009. They were scanned with binoculars and scored for different pheno-phases of figs and leaves, using the crown density method (Koelmeyer, 1959). This method uses a linear scale of 0-4; with 4 representing the maximum intensity of figs or leaves. Values of 3, 2, and 1 represent three quarters, half and one quarter of the maximum intensity respectively. A value of 0.5 was used to indicate the presence of small amounts of figs and leaves below one-quarter of the maximum intensity.

Since the habits of the seven selected *Ficus* tree species were different (figs in leaf-axils, stem-figs and earth-figs), the abundance of figs was assessed in relation to the density of fig-bearing spurs or stolons on each tree. The scoring system for the developmental phases of the figs was modified from Galil and Eisikowich (1968) and Koelmeyer (1959) by splitting the developmental cycle into four pheno-phases (Fig. 6) and by using a linear scale of 0-5 (with 5 representing the maximum intensity of figs).

However, for leaf phenology, the original crown density method (using scores ranging from 0 to 4) was followed (Table 3). During each census, samples of 10-20 figs from each tree were collected for dissection and determining the stage of development. Figs at the receptive and ripening phases of both sexes were measured with a calipers and the number of seeds/wasps inside were also counted.



Immature phase

Receptive phase

Developing phase

Releasing phase

Ripening phase

Figure 6 Stages of fig development of *Ficus oligodon*.

Table 3 The scoring system on figging and leafing phenology.

Fig Index [a]	**Leaf Index** [b]
NON-Phase = No figs on each tree	BA = Bare branches, leaf fall
IMP-Phase = Immature phase	YL = Young leaves
RCP-Phase = Receptive phase	ML = Mature leaves
DVP-Phase= Developing phase	SL = Senescence leaves
RPP/RLP-Phase = Ripening phase (female trees) / Releasing phase (male trees)	

[a] The sums of fig index have to be equal 5.

[b] The sums of leaf index have to be equal 4.

3.3.2 Fig wasp collection. The fig wasp community was studied on seven dioecious *Ficus* species in Doi Suthep-Pui National Park, northern Thailand, from March 2008 to February 2009. Male figs of all selected *Ficus* species were collected and cut into halves during the early releasing phase, when figs still had no exit holes (10 figs from each of five trees). The figs were stored at room temperature (ca. 25-30˚C) in glass jars covered with fine nylon cloth, to allow the fig wasps to emerge. All emerging wasps were collected and preserved in 70% alcohol, and then dried in the laboratory of Centre de Biologie et de Gestion des Populations (CBGP), Montpellier, France by using hexamethyldisilazene (HMDS) method.

HMDS method

1. Fig wasp specimens were removed from 70% alcohol and soaked in 96% alcohol (in a microporous basket) twice (30 minutes per time).

2. They were then put into absolute alcohol (100%) twice (30 minutes per time). The purpose of these two baths was to totally dehydrate the insects.

3. They were soaked again in Hexamethyldisilazane (HMDS) twice (30 minutes per time).

4. Finally, specimens were put in an incandescent lamp. The drying time depended on the temperature: at 25˚C = 8 hours, at 45˚C = 4 hours and at 60˚C (under a lamp) about 1 hour.

Later, the specimens were ready for mounting and photography. During the mounting process, the dried wasps were glued onto the side of a card (including ovipositor), wings were removed above and then the wasps were put flat under a microscope for detailed study. The specimens were photographed with digital camera (LEICA Z16 APOA) using the Cartograph program. Identifications were made using available keys (Wiebes, 1994) with the help of J. Y. Rasplus of the Centre de Biologie et de Gestion des Populations (CBGP), Montpellier, France, and by comparison with reference collections from China held by J.Y. Rasplus.

3.3.3 Seed/foundress collection. During each census of the phenology study (12 times from March 2008 to February 2009), samples of 10-20 figs from each tree along the two transect lines, traversing different habitats (Table 4) were used to investigate the stability of fig tree and fig-wasp populations. All seeds/wasps were counted in each fig at the ripening phase. To investigate the number of foundresses, figs were dissected in early DVP-phase, when foundressess are still intact and easy to find. Figs were cut into four pieces, and the heads of foundresses counted from each fig. Figs at the receptive and ripening phases of both sexes were measured with calipers.

Table 4 The three sampling sites were selected on basis of the distribution of fig trees and the degree of human disturbance.

Sampling sites	**Site description**
Primary forest	Fig trees are still in groups (>10 trees per sq. km). The area is generally well conserved with >90% of the area covered by forests.
Restoration plot	The Ban Mae Sa Mai plot, located at the north end of DSNP, approximately 2 km from primary forest. The surrounding area is mainly fragmented by crop fields. *Ficus* spp. were planted from 1999 to the present by FORRU, averaging about 2-10 fig trees per sq. km.
Highly disturbed	Outside the conservation areas, difficult to find the other fig trees within 1 sq. km (1 trees per sq. km). The areas were highly disturbed by people and infrastructure (e.g. campus, farm, urban).

3.3.4 *Ficus* propagation. All seeds and cuttings were collected from trees beside dirt tracks which run through natural or disturbed forest ecosystems of the park.

3.3.4.1 Propagation from seed. Mature, ripe figs of the six selected *Ficus* spp. were collected from 10 or more individual trees of each species. Fruits were removed directly from the plant, rather than harvested from the ground, principally to reduce the risk of diseases-infection (FORRU, 2006). Figs were opened and the seeds scraped out with a spoon. The pulp was sieved through a mosquito net in water, so that viable seeds passed through the mosquito net and sank. Seeds were spread out on paper and left to dry for 1-2 days being sown into modular plastic trays, by placing them on the surface of the germination medium, uncovered. The effects of varying the composition of the germination medium, and applying fungicide and fertilizer were tested. The 3 media tested were i) forest soil only ii) a 1:1 mixture of sand and soil and iii) a 1:1 mixture of sand and charcoalized rice husk. The two fungicide treatments were i) Orthocide® 50 "Captan" applied first to the soil surface when seeds were sown and again 1 month afterwards and ii) no fungicide treatment. The two fertilizer treatments were i) 1 granule of Osmocote 14:14:14 per seedling module, every three months after germination and ii) no fertilizer treatment. The experimental design was randomized complete block design with three replications of each of the 12-treatment combinations with 100 seeds for each replicate (Table 5). Seeds were watered by hand using a fine spray bottle. Germination and survival were monitored weekly, and the experiment ended 30 days after the final germination event was recorded.

Table 5 Experimental design on seed germination trials.

Treatments	**Description**
T1	soil + no fungicide + no fertilizer (control)
T2	soil + no fungicide + fertilizer
T3	soil + fungicide + no fertilizer
T4	soil + fungicide + fertilizer
T5	soil and sand (1:1) + no fungicide + no fertilizer

Table 5 (continued).

Treatments	**Description**
T6	soil and sand (1:1) + no fungicide + fertilizer
T7	soil and sand (1:1) + fungicide + no fertilizer
T8	soil and sand (1:1) + fungicide + fertilizer
T9	sand and charcoalized rice husk (1:1) + no fungicide + no fertilizer
T10	sand and charcoalized rice husk (1:1) + no fungicide + fertilizer
T11	sand and charcoalized rice husk (1:1) + fungicide + no fertilizer
T12	sand and charcoalized rice husk (1:1) + fungicide + fertilizer

3.3.4.2 Propagation from cuttings. A low-cost technique was used for cutting experiments, developed at the ASEAN Forest Tree Seed Centre; Muak-Lek, Thailand (AFTSC), using closed plastic bags to retain high humidity, a so-called a non-mist propagation system (Kantarli, 1993). Cuttings were collected from both sexes of the six selected adult *Ficus* spp. tree species. Lateral branches were cut and mature and hardened branches selected. Each cutting was 4 nodes long (about 10-20 cm in length, depending on species), basal cuts at least 0.5 cm below a node, with only one leaf attached, and the leaf on each cutting was cut in half. The cuttings were put in a plastic bag and placed in a refrigerator (5°C) overnight to seal the wound and prevent bacterial infection. The basal ends of the cuttings were dipped in rooting powder hormone (Seradix; IBA≠3; 4-(Indol-3-yl) butyric acid). Cuttings were planted to half of their length (2 nodes) into black plastic bags (5 x 13 cm) filled with sand and charcoalized rice husk (1:1). The small plastic bags were then placed in larger plastic bags (60 x 90 cm; with one liter of water added), sprayed with water until the medium was saturated. Plastic bags were closed firmly to prevent moisture loss and kept under 70% shade. After that, the plastic bags were opened weekly, for 5-10 minutes, to allow some moisture out, dead or yellowing leaves were removed. Plants were watered only when the soil surface dried or if there was no evidence of condensation on the inside of the plastic bag. Time to emergence of first shoot, root and survival was observed weekly. Once mature leaves had expanded, seedlings from both techniques were pricked out and potted into new containers (black plastic bags, 6.5 x 22 cm) using a medium of soil, peanut husk and coconut husk (2:1:1). Cutting experiments were conducted to assess the effects of cutting from 3 different positions of harvested branches (terminal shoot, middle and lower) and two rooting hormone treatments (rooting powder hormone; Seradix # 3; treated/not treated). A randomized complete block design was used for all treatments (Table 6), with three replications for each species. Each replicate consisted of 36 cuttings.

Table 6 Experimental design on cutting trials.

Treatments	**Description**
T1	upper + without rooting hormone
T2	upper + with rooting hormone
T3	middle + without rooting hormone
T4	middle + with rooting hormone
T5	lower + without rooting hormone
T6	lower + with rooting hormone

3.3.4.3 Seedling growth trials. Seedlings from both propagation types were tested the effects of light intensity and frequency of fertilizer application. A randomized complete block design was used with three replications of 4-treament combinations with 30 seedlings for each replicate (Table 7). Seedling growth (root collar diameter, height, canopy width and health) and survival rate were monitored monthly.

Table 7 Experimental design on seedling growth trials.

Treatments	Description
T1	full sun light + slow-release fertilizer, applied every 3 months
T2	full sun light + slow-release fertilizer, applied every 2 months
T3	under 70% of shade net + slow-release fertilizer, applied every 3 months
T4	under 70% of shade net + slow-release fertilizer, applied every 2 months

3.3.5 *Ficus* plantings. Three different methods were tested for establishing *Ficus* spp. trees i) direct seeding; ii) planting stock from cuttings; and iii) planting stock from seed. Three replicated blocks (each approximately 30 x 30 m) were established to compare the field performance of the three planting stock types of six *Ficus* species in disturbed habitats. Plots were prepared by weeding with hand tools about one week before planting. In each block, different planting stock types of the six *Ficus* species (30 individuals per block for each of the two planting stock types, and 60 units of *Ficus* seeds for direct seeding; one unit = 1 bamboo tube with 100 seeds) were planted randomly (except for direct seeding where seeds were sown in rows in order to find them easily when monitoring), with a mean distance between plants of 1.5 meters. Fifty grams of fertilizer (NPK 15-15-15) was applied in a ring around each tree (but not for direct seeds). After planting out, plots were weeded and additional dose of fertilizer applied at 6 week intervals, during the rainy season for the first two years after planting. The planted trees were monitored for field performance (survival and growth rates) 3 times; i) immediately post planting ii) at the end of the first rainy season and iii) at the end of the second rainy season. Measurements included height (root-collar to highest meristem measured by measuring pole); root collar diameter (measured with Vernier calipers; canopy width (at widest point using a tape measure) and the health of the trees was scored on a scale of 0 (dead) to 3 (perfect health).

For direct seeding, seeds were sown on the surface of the soil but protected inside bamboo tubes 8 x 10 cm (half of the bamboo tubes were stuck in soil), in order to prevent seed movement due to wind and rain. Each tube contained about 100 seeds but was counted as one unit irrespective of how many seeds germinated. Germination was monitored at weekly intervals for 3 months. After expansion of the second true leaf pairs, seedlings were monitored for field performance, using the standard silvicultural and monitoring methods as for the other planting stock types.

3.4 Data analysis

3.4.1 *Ficus* phenology. Separate analyses were carried out for male and female trees of each species. A monthly percentage of each reproductive phase and each leaf index were calculated. Fig crop duration was determined as the time from the appearance of the first fig to the disappearance of all the figs from an individual tree.

The mean duration and frequency of crops for individual trees and at the population-level were then calculated. The prevalence of asynchrony of fig production was also calculated as the % of individuals in each species population which bore both receptive and releasing phase figs within their crowns, averaged across the whole study period. Correlation analysis (Pearson's Correlation) was performed for receptive (RCP) phase versus ripe or wasp releasing (RPP/RLP) phase of female and male tree; monthly rainfall versus leaf/fig initiation; monthly temperature versus leaf/fig initiation; and leaf flushing versus fig initiation. All tests were carried out at $P \leq 0.05$ significance level using SPSS (version 17.0). Mean diameters of figs at each developmental stage and mean number of seeds/wasps per fig were calculated from all the censuses. Also, external and internal traits of each developmental stage (color, odor, non-pollinator, wasp-predator, seed-disperser etc.) were recorded.

3.4.2 Figs and their associated wasps. *T*-tests were used to explore differences between the two sexes. ANOVA (LSD) was used to explore differences in seed production and foundress numbers among different habitats and seasonality.

3.4.3 *Ficus* propagations/plantings. Data were subjected to analysis of variance (ANOVA, MANOVA), *T*-test and least significant difference (LSD) or Scheffe test (where needed) at $P=0.05$ significance level. The median length of dormancy (MLD) was calculated from the germination times of all seeds which germinated. Overall success of germination/cutting trials was defined as the probability of germination/shooting multiplied by the probability of early seedling survival, converted to a percentage, i.e. the number of seedlings that could be potted from sowing 100 seeds or make 100 cuttings. The relative growth rates (RGR) were calculated using the formula:

$$RGR= ([\ln (G2) – \ln (G1)] / (T2-T1)) \times 365 \times 100$$

where G1 and G2 are the growth parameters (root collar diameter, height and canopy width) at the beginning (T1) and end (T2) of the sampling period (FORRU, 2008).

3.4.4 Cost evaluation. Cost per plant of each planting stock type was calculated for each stage of the process throughout the study period (1.5 years for direct-seeded and 2.5 years for both nursery-grown plants). Operational costs and labor requirements for activities from seedling production in the nursery to post-planting maintenance were recorded. These included all materials and labor costs associated with seed/cutting collection, planting stock production, transportation, site preparation, plantation establishment and maintenance. We used a rate of US$ 6.53 per day (8 hr) to calculate labor expenses.

CHAPTER 4

RESULTS

4.1 Distribution in the park

Ficus hispida, *F. oligodon* and *F. semicordata* were found in all forest types throughout the park. *Ficus hispida* and *F. semicordata* trees were both most common in deciduous forest (<800 m above sea level), whilst *F. oligodon* was common in mixed forest (800-1,200 m above sea level). *Ficus auriculata* and *F. variegata* were found at elevations >800 m above the sea level, mainly in mixed forest. *Ficus fulva* and *F. triloba* were restricted to mixed forest (Fig. 7). The numbers of male and female trees of most species found along the phenology trails were similar, except for *F. fulva* and *F. variegata* (Table 8).

4.2 *Ficus* phenology

4.2.1 General phenology. The peak period of leaf fall for most species generally coincided with the cool-dry period, and was usually negatively correlated with rainfall and temperature (Table 9). There was no difference in leafing pattern between male and female trees of *F. auriculata*, *F. hispida*, *F. oligodon*, and *F. semicordata*. However, *F. fulva*, *F. triloba* and *F. variegata* showed gender differences in leafing phenology (Figs. 9-15; b, d). The gender differences were not homogenous among these three species.

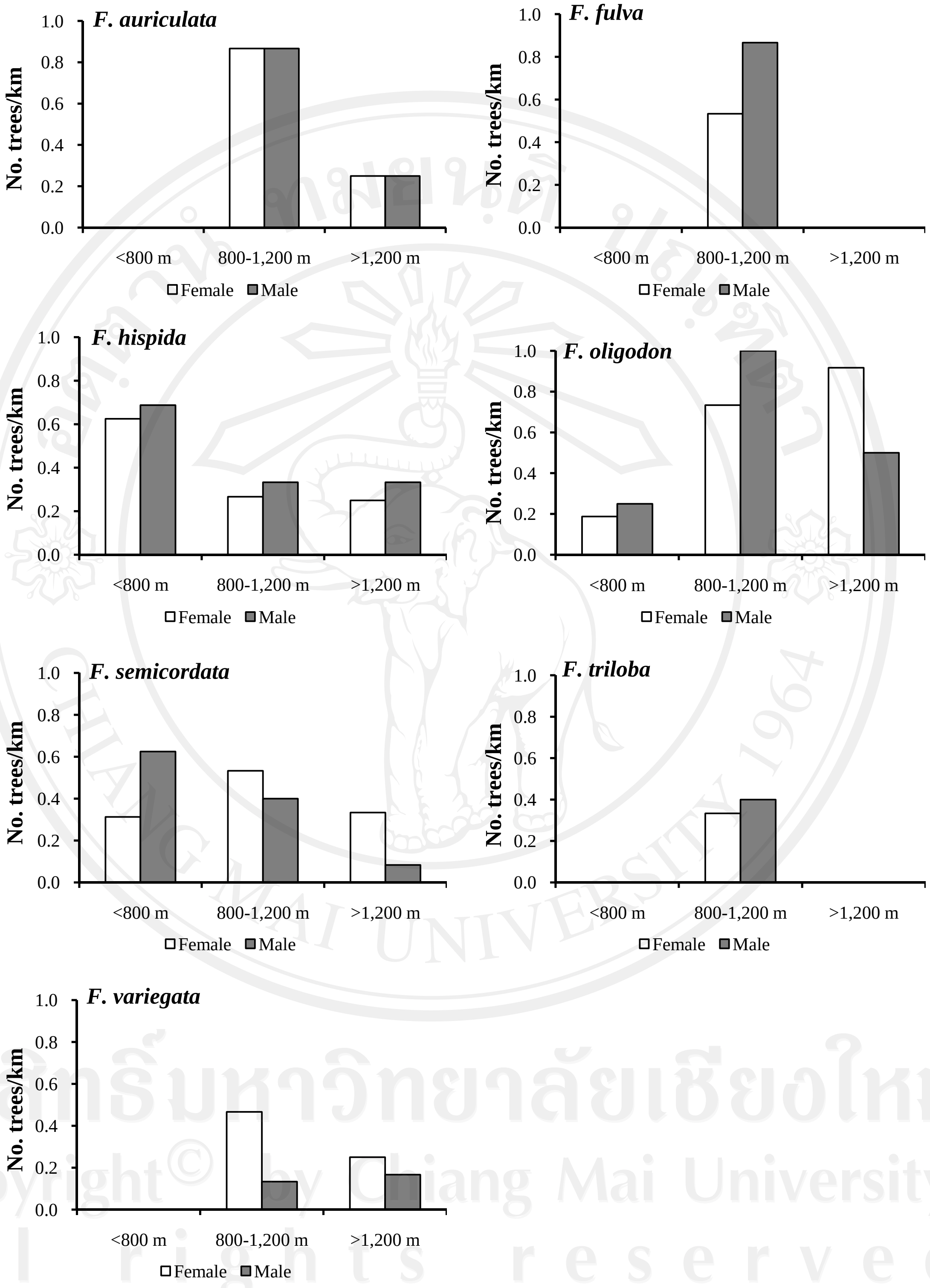
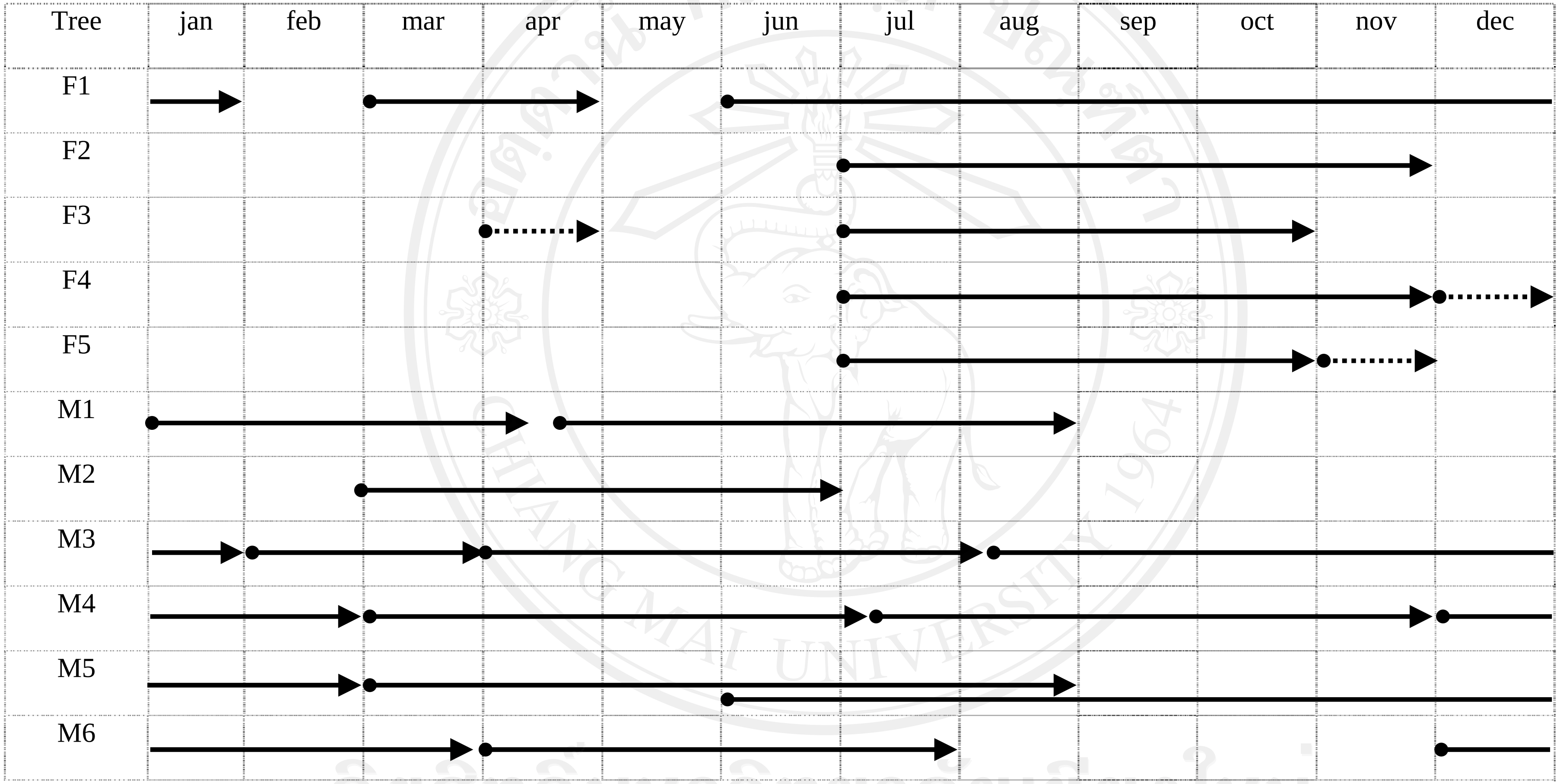


Figure 7 Number of trees per kilometer of phenology trail in each elevation type (<800 m above sea level=16 kilometers, 800-1,200 m above sea level=15 kilometers and >1,200 m above sea level=12 kilometers).

At the population-level, all species bore fig crops several times throughout the year but fig abundance varied seasonally (Figs. 9-15; a, c). For most species, fig developmental phases were not correlated with climatic conditions. However, it seems that, male trees were more sensitive to weather parameters than females (Table 9). At the population-level, receptive phase figs of most species (particularly of female trees) were produced throughout the year, but peaks in receptive phase figs occurred at different times between the sexes. At the receptive phase, female figs of most species were bigger than male figs, whilst at the mature stage the female figs of all species were smaller than male figs (*T*-test, N=50, P<0.05; Table 8). Female trees of most species produced fig crops more frequently than male trees (except for *F. oligodon*, *F. triloba* and *F. variegata*) and the duration of crop development was longer than that of male trees (except for *F. auriculata* and *F. triloba*). The number of seeds of most species was positively correlated with fig size (Table 9). At the individual-level, individual trees of all species had their own rhythm of reproductive phenology (Fig. 8).

For most species, the production of seeds (female trees) and wasps (male trees) varied between seasons. Also, the timing of peak fig production, at the population-level, differed between sexes. Male trees of most species produced their main fig crops mainly in the dry season, about 1-3 months before the peaks in fig production of female trees (depending on species). Seed production of most species peaked at the beginning of rainy season (except for *F. triloba*). A correlation between fig crop initiation and new leaf flushing was more common for female trees rather than for male trees.



F=Female tree, M=Male tree; ●⟶ Completed crop (the periods between fig initiation - ripening), ●┈▶ Abortion crop

Figure 8 An example of fig production rhythms of *F. triloba* at the individual-level.

Table 8 Details of selected trees were found along the phenology trails and sexual specialization of the study figs in Doi Suthep-Pui National Park, northern, Thailand (Mean ± SD).

Species	Sex [1]	Elevation (m)	GBH [2] (cm)	Crop duration (months)	Asynchronous fig production [3] (%)	No. of seeds/wasps (per fig)	Fig size at RCP [4] (mm)	Fig size at RPP/RLP [4] (mm)	Crop abortion (%)
F. auriculata	F=16	891-1,319	78.1±35.6	3.3±1.2	30.6	5,969±4,287	48.0 x 46.3^{a}	66.2 x 53.7^{b}	0.0
	M=16	895-1,299	83.5±29.8	4.7±1.2	5.6	301±96	54.2 x 43.2^{a}	86.0 x 65.6^{a}	4.8
F. fulva	F=8	923-1,014	48.0±29.0	3.9±2	12.5	858±311	13.0 x 16.0^{a}	17.7 x 19.2^{b}	5.0
	M=13	989-1,100	49.0±17.9	2.5±0.8	17.2	67±12	12.0 x 11.8^{b}	20.3 x 20.0^{a}	0.0
F. hispida	F=17	326-1,351	55.5±14.2	2.9±1.2	41.4	1,140±486	17.2 x 14.0^{a}	28.5 x 25.4^{a}	0.0
	M=20	330-1,268	63.1±14.8	2.9±0.9	41.5	155±7	17.7 x 15.0^{a}	29.3 x 23.7^{a}	0.0
F. oligodon	F=25	616-1,293	69.2±23.3	5.1±1.9	10.5	8,692±4,244	37.4 x 31.3^{a}	61.0 x 53.1^{b}	2.7
	M=25	605-1,336	83.3±27.7	4.1±1.4	20.6	1,400±7	36.5 x 30.2^{a}	70.7 x 61.1^{a}	2.5
F. semicordata	F=17	418-1,531	68.7±25.5	3.3±1.2	57.8	712±413	9.7 x 8.3^{a}	23.4 x 19.3^{b}	0.0
	M=17	420-1,401	65.4±18.6	3.1±1.1	29.9	163±50	7.0 x 7.0^{b}	32.2 x 24.7^{a}	0.0

Table 8 (continued)

Species	Sex [1]	Elevation (m)	GBH [2] (cm)	Crop duration (months)	Asynchronous fig production [3] (%)	No. of seeds/wasps (per fig)	Fig size at RCP [4] (mm)	Fig size at RPP/RLP [4] (mm)	Crop abortion (%)
F. triloba	F=5	994-1,172	40.4±14.7	3.4±2.4	3.4	2,755±783	27.0 x 28.0^{b}	30.5 x 35.8^{b}	33.3
	M=6	1,000-1200	60.0±35.1	4.8±1.8	15.4	515±30	28.6 x 35.2^{a}	40.1 x 46.1^{a}	0.0
F. variegata	F=10	899-1,343	212.9±95.4	6.4±2.5	3.4	1,825±978	23.0 x 22.0^{a}	32.6 x 28.7^{b}	0.0
	M=4	1,084-1,205	163.5±2.1	3.4±0.5	6.3	187±15	18.2 x 17.1^{b}	41.5 x 33.5^{a}	0.0

[1] Sex: F = Female trees and M = Male trees.

[2] GBH = Girth at breast height (1.3 m from the ground).

[3] Asynchronous fig production is the mean percentage of total trees observed (of each species) which bore both releasing and receptive figs simultaneously, averaged across the total study period.

[4] Developmental phases; RCP = Receptive phase; RPP = Ripening phase; and RLP = Releasing phase (width x length).

Different letters denote significant differences between sexes according to a *T*-test at a significant level of *P*<0.05.

Table 9 Results of Pearson's correlation test between weather conditions (monthly average rainfall and temperature) with leaf and reproductive phenologies of seven selected fig species. RA=Monthly mean rainfall, TE=Monthly mean temperature; SL=Senescence leaf, BA=Bare area, leaf fall, YL=Young leaf; IMP=Immature phase, RPP=Ripening phase, RLP=Releasing phase, RCP=Receptive phase; FS=Fig size (width x length), SE=Seed number; vs=versus.

Correlations [a]	*F. auriculata*		*F. fulva*		*F. hispida*		*F. oligodon*		*F. semicordata*		*F. triloba*		*F. variegata*	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M
RA vs SL	-0.6*	-0.6*	ns	ns	-0.6*	-0.6*	ns	ns	-0.6*	-0.6*	ns	-0.6*	ns	ns
RA vs BA	ns	ns	ns	-0.5*	ns	-0.6*	ns	-0.5*	-0.6*	ns	ns	ns	ns	ns
RA vs YL	ns	ns	-0.7**	ns	ns	ns	-0.6*	-0.6*	ns	ns	0.6*	ns	ns	ns
TE vs SL	-0.7**	-0.7**	ns	-0.5*	ns	-0.6*	-0.9**	-0.9**	ns	-0.6*	ns	-0.6*	-0.8**	-0.8**
TE vs BA	ns	ns	-0.7**	-0.7*	ns	ns	-0.9**	-0.9**	ns	ns	ns	ns	-0.8**	-0.8**
TE vs YL	ns	ns	ns	ns	ns	ns	ns	ns	0.5*	0.6*	ns	0.5*	ns	ns
RA vs IMP	ns	-0.6*	ns	-0.6*	ns	-0.7**	-0.7**	ns	ns	ns	ns	ns	ns	ns
RA vs RPP	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
TE vs IMP	ns	-0.7**	ns	ns	ns	ns	ns	-0.9**	0.5*	ns	ns	ns	ns	-0.7**
TE vs RPP	ns	ns	0.7*	ns	ns	0.6*	ns	ns	ns	0.6*	ns	ns	ns	ns
IMP vs YL	ns	ns	0.6*	ns	ns	ns	0.9**	ns	ns	ns	ns	ns	0.6*	ns
RLP vs RCP	0.6*	ns	ns	ns	0.8**	ns	0.6*	ns	ns	ns	ns	ns	ns	ns
FS vs SE	ns	-	ns	-	0.8*	-	0.7**	-	0.8**	-	ns	-	0.5**	-

*$P<0.05$, **$P<0.01$, ns = non significant ($P>0.05$); [a] Correlations between weather conditions, leaf phenology and syconia phenology.

4.2.2 Phenology of each species

4.2.2.1 *Ficus auriculata*. *Ficus auriculata* trees were semi-deciduous (dropping leaves at least 50% canopy fullness). Leafing patterns did not differ between male and female trees (Fig. 9b, d). Generally, most trees changed their leaves once per year but the trees were never leafless. However, some individual trees shed leaves all year round but in small amounts, particularly trees located far from streams or moist areas. Leaf senescence and leaf fall occurred during the mid-dry season (January to February) and leaf flushing occurred in March. Leaf senescence was significantly and negatively correlated with rainfall and temperature (Table 9).

At the individual-level, male figs bore up to 3 (mean 1.6) crops a year, female trees up to 10 (mean 2.9). Some female trees bore figs all year round but not male trees. Fig crop duration on female trees was shorter than on male trees (Table 8). Peak ripe fig production on female and male trees occurred in July and April, respectively (Fig. 9a, c). Abortion of young figs occurred only on male trees (about 4.8% of total crops), mainly for crops produced in rainy season.

Within-trees, asynchronous fig production (releasing and receptive figs present simultaneously within an individual tree crown) was common on female trees but was rare on male trees (Table 8). Fig initiation of male trees was negatively correlated with average monthly temperature and rainfall. Peak pollen and wasp production (RLP) coincided with peak female receptivity (Table 9).

4.2.2.2 *Ficus oligodon*. *Ficus oligodon* trees were semi-deciduous, but the trees were never leafless (maximum leaf drop about 60% of the canopy area in December-

January). Both sexes renewed leaves in small quantities all year round. Leafing patterns were the same for male and female trees (Fig. 10b, d). At the population-level both sexes changed their leaves in small amounts all year round but rarely from April to July. At the individual-level, most trees produced their new leaves 1-2 times per year (less than 20% of trees observed produced new leaves nearly year-round). Leaf senescence occurred from August to February, peaking from November to January. Leaf fall mainly occurred from December to January, and new leaf production was highest in February. Leaf flushing was positively and significantly correlated with fig crop initiation for female trees. Also, rainfall and temperature conditions were negatively correlated with leafing phenology of both sexes (Table 9).

At the individual-level, male trees bore up to 4 (mean 2) crops a year; female trees up to 5 (mean 1.5), and some trees of both sexes bore figs all year round. Crop duration of female trees was longer than that of male trees (Table 8). Fig production peaked in March for male trees and in May for female trees (Fig. 10a, c). Abortion of young figs occurred in the small amount of both sexes (2.7% and 2.5% for female and male trees respectively) mainly in crops produced in the rainy season (from July to August).

Within-tree, asynchronous fig production was more common on male trees rather than on female trees (Table 8). Fig initiation on male trees was negatively correlated with average monthly temperature, but for female trees, it was negatively correlated with average monthly rainfall (Table 9). Also, fig initiation of female trees was positively correlated with leaf flushing. Pollen and wasp production (RLP) were also positively correlated with female receptivity (Table 9).

4.2.2.3 *Ficus variegata*. Leafing phenology differed between the sexes (Fig. 11b, d). Female trees were deciduous while most male trees (3 out of 4 male trees observed) were semi-deciduous (i.e. leaf exchange in small amounts over a prolonged period). Females started to drop their leaves from the mid-rainy season to the dry season (August to March), but leaf exchange on male trees occurred later, mainly starting in the dry season (October-March). However, peaks of leaf senescence, leaf fall and new leaf flushing occurred in November (to December), January and February, respectively for both sexes. Leaf flushing was positive correlated with the fig initiation of female trees but was not correlated with new crops of male trees. Also, leafing phenology of both sexes of *F. variegata* was affected by average monthly temperature, rather than by rainfall (Table 9).

Most of the study trees did not produce figs (61% of all trees observed), although all individuals were apparently mature (mean GBH >100 cm), therefore sex could not be determined for non-fruiting trees. For those that could be sexed, at the population-level, only female trees produced figs all year round. Male trees produced figs for only 4 months of the year (from December to March). At the individual-level, both sexes bore 2 crops a year (mean crop number, 1.3 and 1.1 for male and female trees, respectively), and some individual female trees bore figs all year round. Crop duration of female trees was longer than that of male trees (Table 8). Peak ripe fig production of male and female trees occurred in March and May, respectively (Figure 11a, c).

Within-trees of both sexes, fig production were synchronous (Table 8). Also, fig initiation of female trees coincided with new leaf flushing (Table 9).

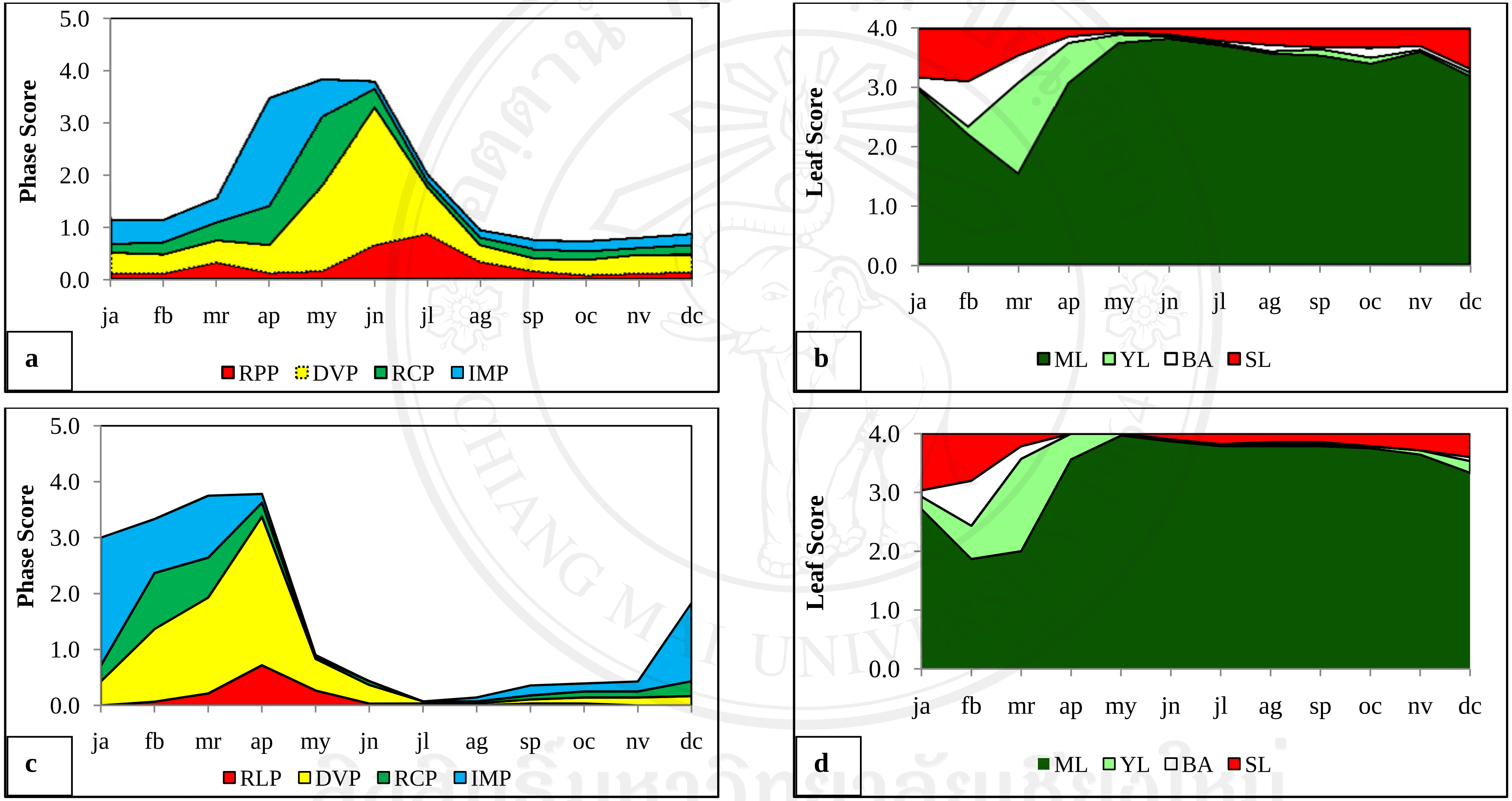


Figure 9 Leaf and fig production rhythms of *Ficus auriculata* at the population-level; female trees (a) reproductive phenology and (b) leafing phenology, male trees (c) reproductive phenology and (d) leafing phenology.

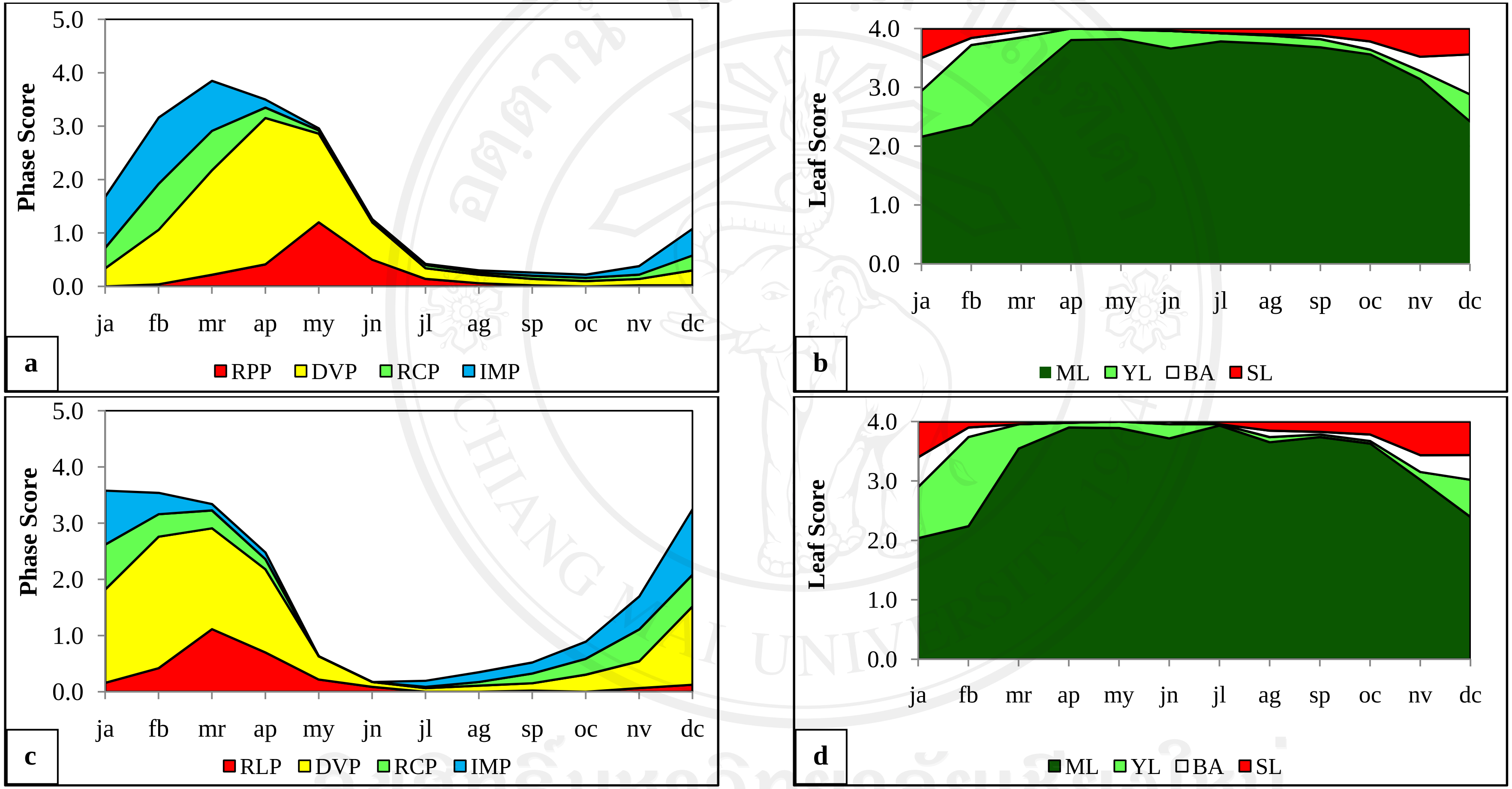


Figure 10 Leaf and fig production rhythms of *Ficus oligodon* at the population-level; female trees (a) reproductive phenology and (b) leafing phenology, male trees (c) reproductive phenology and (d) leafing phenology.

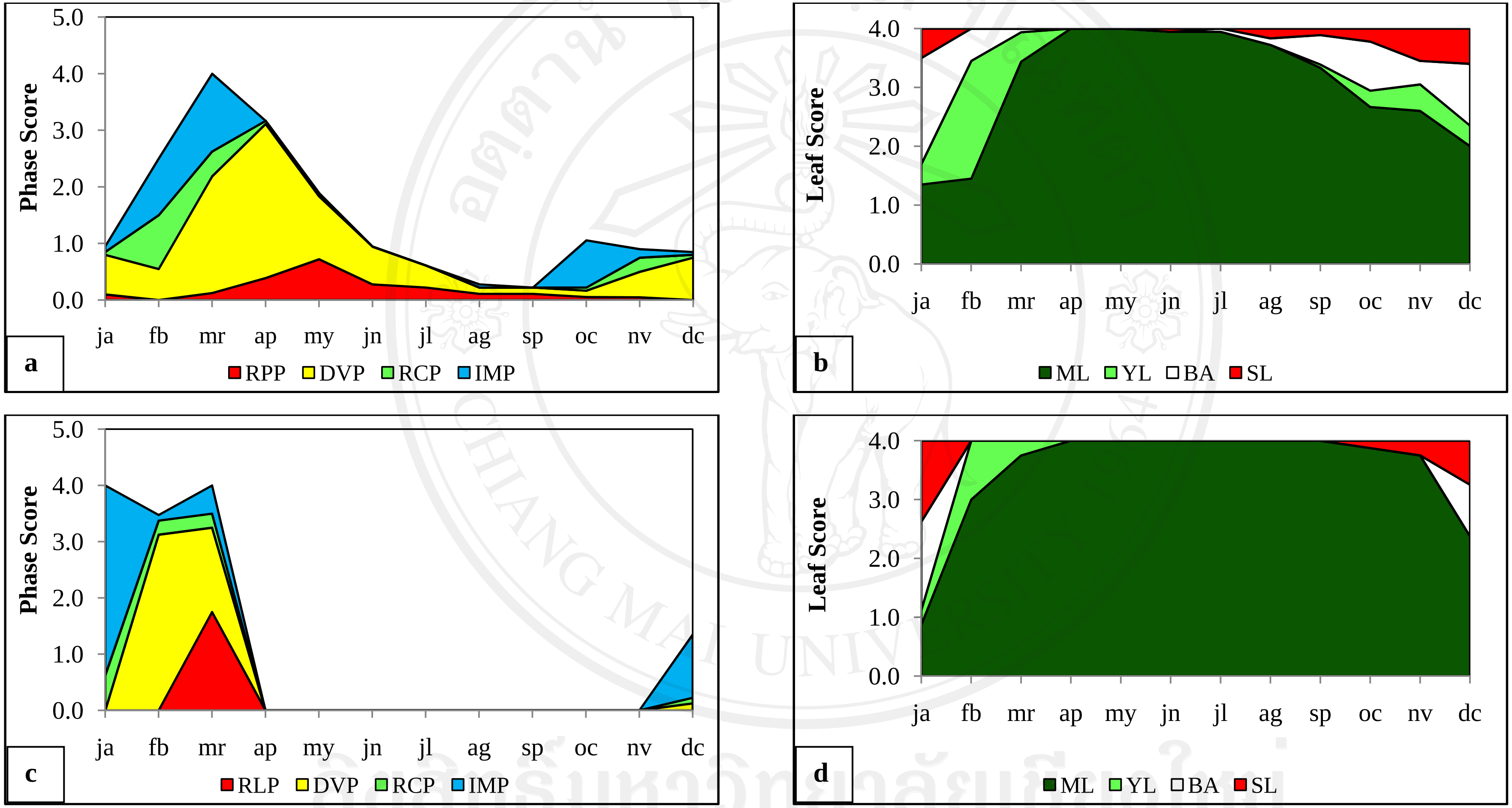


Figure 11 Leaf and fig production rhythms of *Ficus variegata* at the population-level; female trees (a) reproductive phenology and (b) leafing phenology, male trees (c) reproductive phenology and (d) leafing phenology.

4.2.2.4 ***Ficus hispida***. Most trees of both sexes (>80% of tree observed) were evergreen, but leaf changing in small amounts occurred at irregular intervals throughout the year (<10% canopy fullness), especially in the dry season (October to May). There were no differences in leafing pattern between the sexes (Fig. 12b, d). Leaf senescence and leaf fall peaked in the dry season (January to April), and leaf flushing peaked in May. Leafing phenology of male tree was more sensitive to climatic conditions (average monthly temperature and rainfall) than that of female tree (Table 9).

At the individual-level, male figs bore up to 8 (mean 5.1) crops a year; female trees up to 12 (mean 5.4). There were no differences in crop duration between female and male trees (Table 8). Wasp and seed production of *F. hispida* occurred year-round but both peaked in May (Fig. 12a, c). Within-tree, asynchronous fig production was fairly common on both sexes. Most trees initiated new figs, whilst some immature figs of the previous crop were still on the tree, and some trees were never without figs throughout the observation period. Fig initiation on male trees was negatively correlated with average monthly rainfall. Pollen and wasp production (RLP) were positively correlated with female receptivity (Table 9).

4.2.2.5 ***Ficus semicordata*****.** *Ficus semicordata* was evergreen. Leaf exchange occurred in small amounts throughout the year. Leafing patterns did not differ between male and female trees (Fig. 13b, d). Some new leaves were produced in all months of the year. Leaf senescence and leaf fall was maximal in February, while maximum new leaf production began in May. New leaf flushing was positively correlated with rising temperature and leaf senescence of both sexes was negatively correlated with rainfall (Table 9).

At the individual-level, male figs bore up to 8 (mean 4.3) crops a year; female trees up to 7 (mean 4.8), and most individual trees of both sexes bore figs all year round. Crop duration of females and males was similar (Table 8). At the population-level, wasp and seed production of *F. semicordata* peaked in July for male trees and in August for female trees (Figure 13a, c). Within-tree, asynchronous fig production was fairly common on both sexes. Most trees started producing new figs while some immature figs of the previous crop were still on the tree, however, asynchronous fig production within female trees was higher than that of male trees (Table 8). Average monthly temperature was positively correlated with fig initiation of female trees and fig ripening of male trees (Table 9).

4.2.2.6 *Ficus fulva*. *Ficus fulva* was deciduous. Both sexes shed all their leaves and expanded new ones within a few weeks. However, leafing patterns of female and male trees were different. Most female trees exchanged their leaves twice per year (from August to January, and from April to May), the highest peaks of leaf senescence, leaf fall and leaf flushing were in November, December and January respectively (Fig. 14b). New leaf production was positively correlated with fig initiation (Table 9). On the other hand, most male trees exchanged their leaves only once per year, the peak of leaf changing generally occurred 3 months after that of female trees. The highest peaks of leaf senescence, leaf fall, and leaf flushing were in February, March and April respectively (Fig. 14d). Temperature was negatively correlated with leaf fall of both sexes (Table 9).

At the individual-level, male figs bore up to 5 (mean 1.9) crops a year; female trees up to 4 (mean 2.4), and some trees (of both sexes) bore figs all year round. Crop duration of female trees was longer than that of male trees (Table 8). Ripe fig production peaked in February and May, for male and female trees respectively (Fig. 14a, c). Abortion of young figs occurred only on female trees (about 5% of total crops), mainly in crops produced at the beginning of the cool dry season (October). Within-tree, asynchronous fig production was rare on both sexes (Table 8). Also, fig initiation of female trees was positively correlated with new leaf flushing (Table 9).

4.2.2.7 *Ficus triloba*. The leafing pattern differed between the sexes of *F. triloba* (Fig. 15b, d). Female trees were semi-deciduous but male trees were deciduous. Leaf senescence and leaf fall of female trees mainly occurred in the dry season (not all leaves) peaking in February and May respectively with leaf flushing peaking in June. Male trees changed their leaves all year round. Most male trees dropped all their old leaves twice per year, with leaf exchange peaking 1 month earlier (January to February) than that of female trees. Leaf senescence and leaf fall peaked in February whilst leaf flushing peaked in April-May. The leafing pattern of male trees was more sensitive to climatic conditions than that of female trees. Leaf flushing of female trees was positively correlated with rainfall and for males it was positively correlated with average monthly temperature (Table 9).

At the individual-level, male figs bore up to 3 (mean 2.2) crops a year; female trees up to 2 (mean 1.8). Some individual male trees bore figs all year round but not so for female trees. Crop duration of female trees was shorter than that of male trees. Abortion of young figs on female trees was high (33.3%; Table 8), especially in crops produced during the dry season. Peak fig production of female and male trees was evident (July for male trees and October for female trees; Figure 15a, c). Within-tree, asynchronous fig production of both sexes was rare, and was mainly seen on male trees rather than on female trees (Table 8).

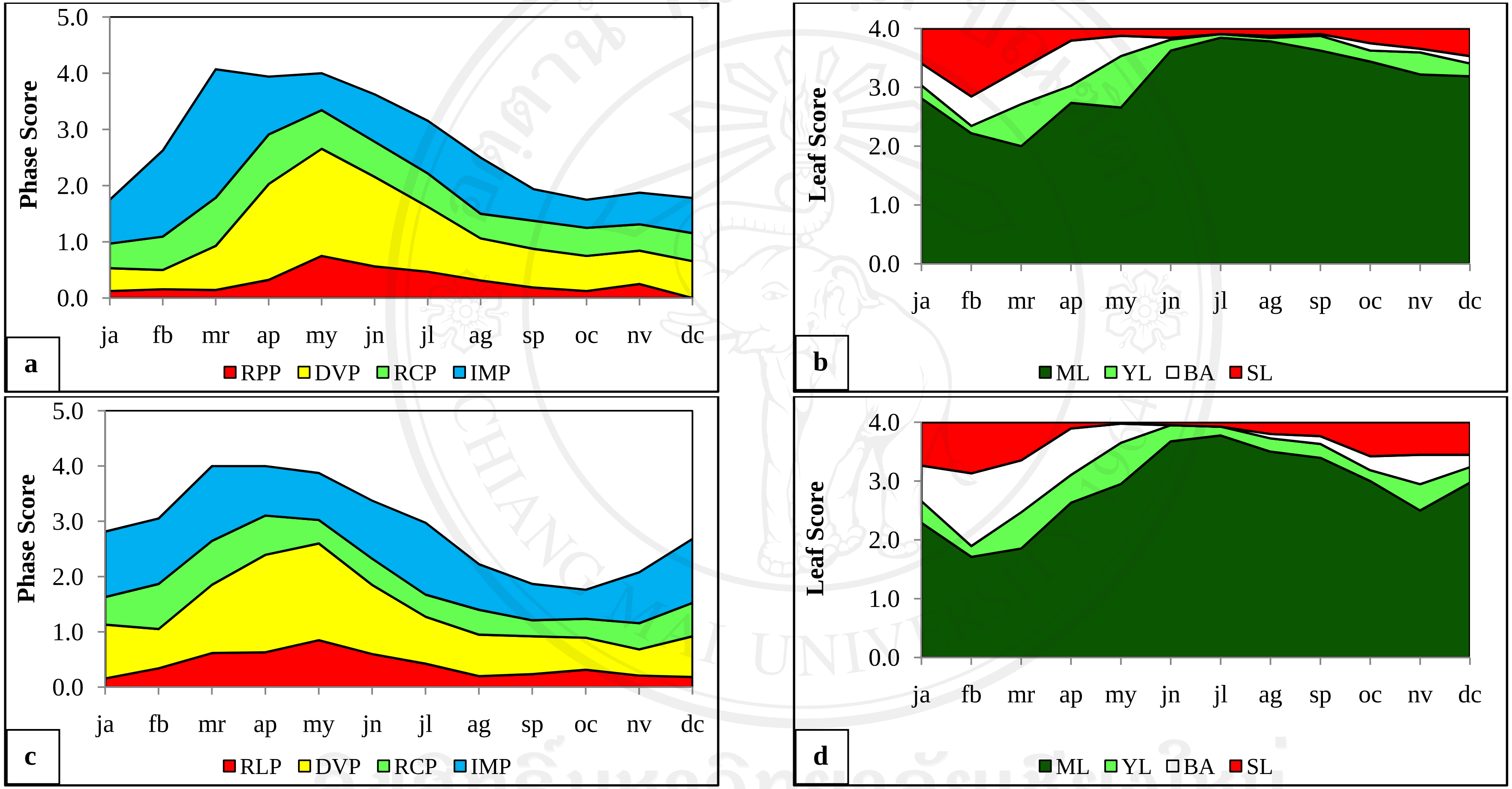


Figure 12 Leaf and fig production rhythms of *Ficus hispida* at the population-level; female trees (a) reproductive phenology and (b) leafing phenology, male trees (c) reproductive phenology and (d) leafing phenology.

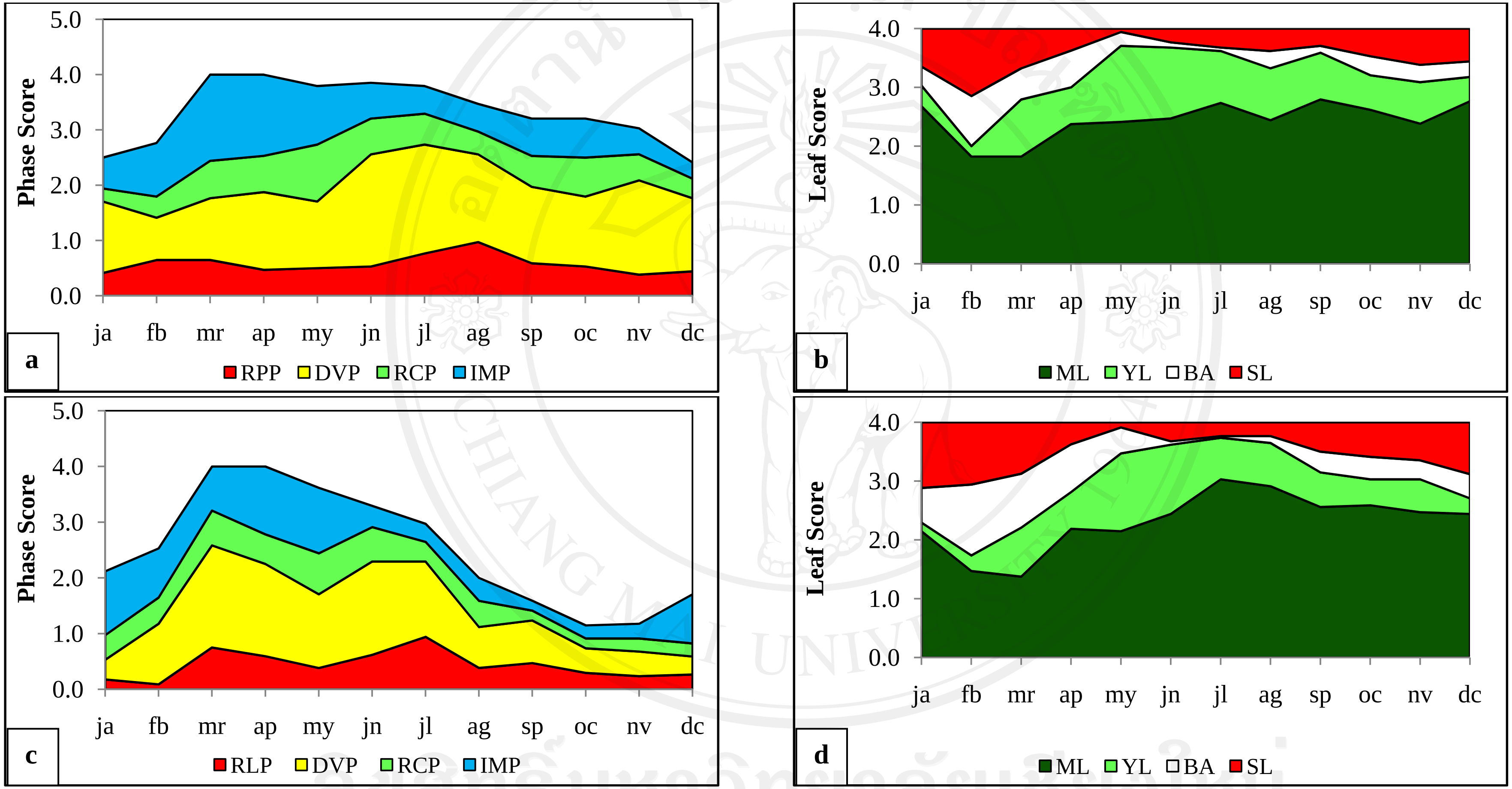


Figure 13 Leaf and fig production rhythms of *Ficus semicordata* at the population-level; female trees (a) reproductive phenology and (b) leafing phenology, male trees (c) reproductive phenology and (d) leafing phenology.

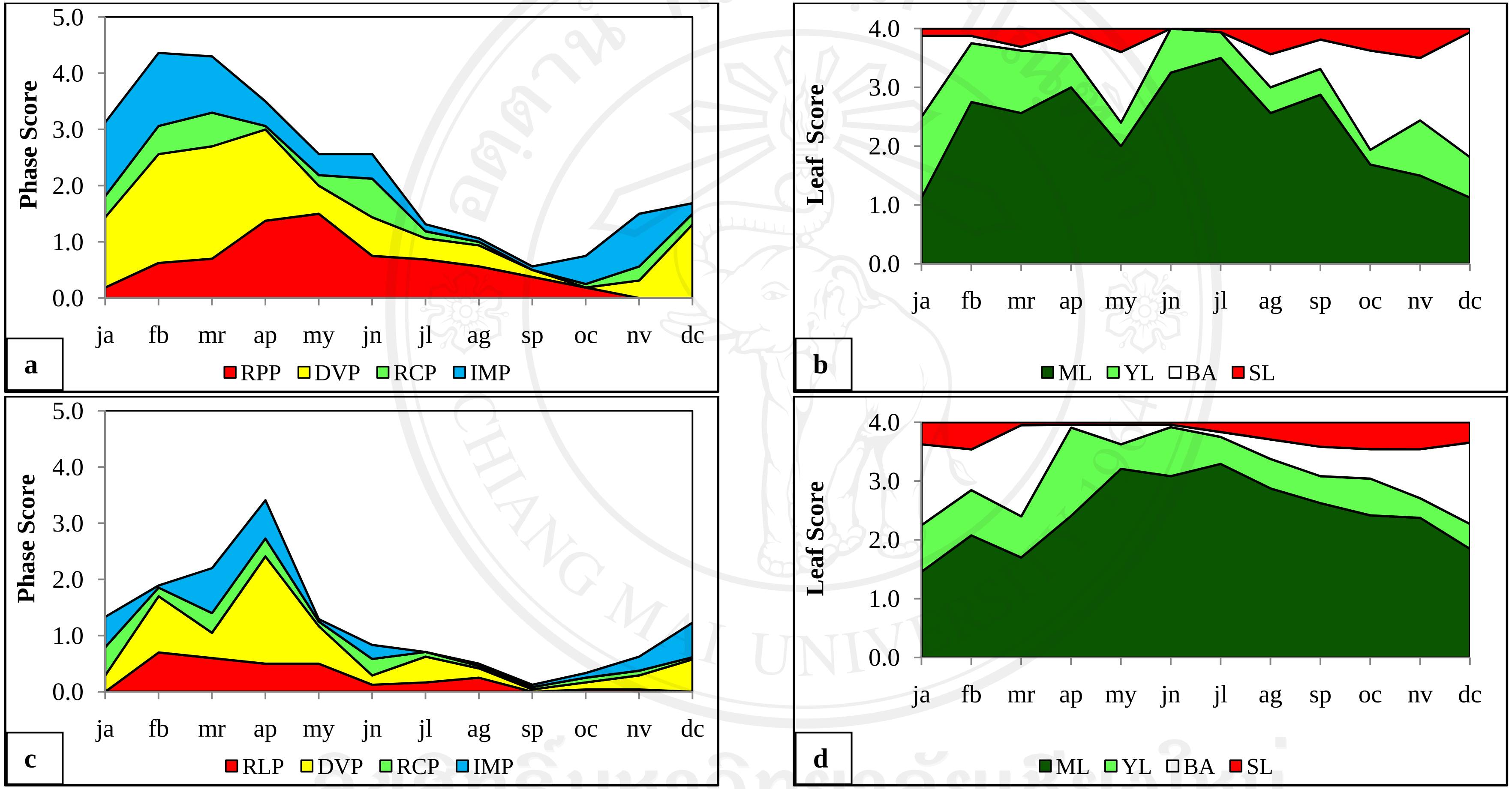


Figure 14 Leaf and fig production rhythms of *Ficus fulva* at the population-level; female trees (a) reproductive phenology and (b) leafing phenology, male trees (c) reproductive phenology and (d) leafing phenology.

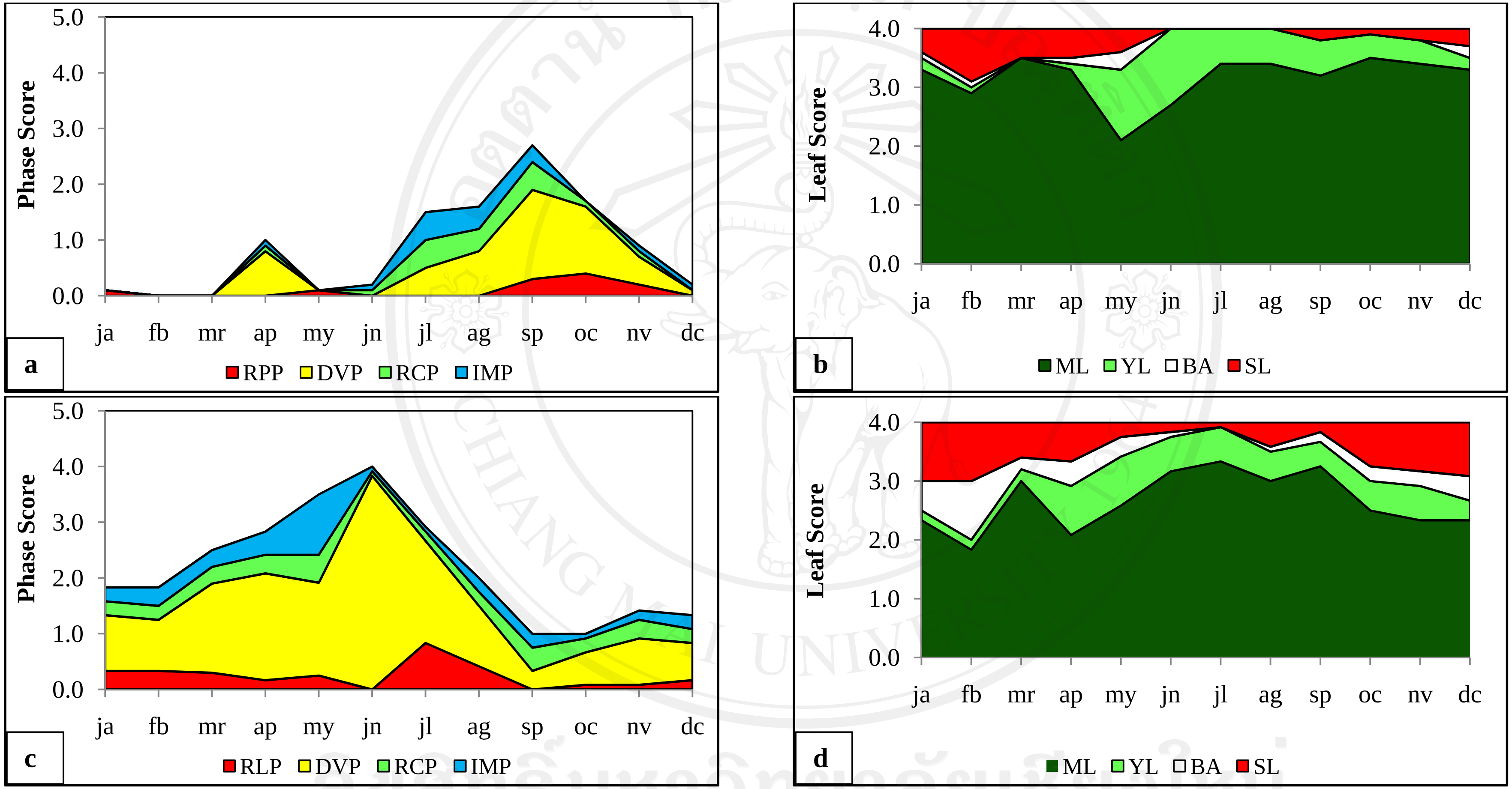


Figure 15 Leaf and fig production rhythms of *Ficus triloba* at the population-level; female trees (a) reproductive phenology and (b) leafing phenology, male trees (c) reproductive phenology and (d) leafing phenology.

4.3 *Ficus* and their associated wasps

4.3.1 General. At receptivity, fig sizes of the selected *Ficus* species varied between sexes. Female figs were larger than males. The number of foundresses per fig varied among *Ficus* species, but exhibited a positive correlation with fig size. Small figs tended to host fewer foundresses than larger ones. For example, in *F. fulva* and *F. semicordata*, the number of foundresses in one fig varied from 1 to 4, whilst in the biggest fig, *F. auriculata* the number of foundresses reached up to 227. For *F. fulva*, *F. semicordata*, *F. triloba* and *F. variegata*, more than 40% of all samples were entered by a single foundress. There was usually no significant difference in foundress number between female and male figs of most species (except for *F. auriculata*, *F. hispida* and *F. variegata*; Table 10). The female fig cavity of most species filled with a jelly-like substance during ripening, except for female figs of *F. hispida*, which dried at fig maturity. At fig maturity, the diameter of male figs was obviously larger than that of female figs (Table 10). However, female figs of all species produced more seeds than male figs produced pollinators (Table 13). Although, the mean number of seeds per fig varied seasonally, seed production of most species in the rainy season was higher than in other seasons (Table 14). Only female figs of *F. oligodon* produced non-pollinating wasps, even through the numbers were few.

In male figs of the seven selected *Ficus* species, 30 species of 7 genera of fig wasp were found. In all species, males were wingless. Two genera of pollinators found consisted of *Ceratosolen* and *Vilisia*. *Ficus fulva*, *F. semicordata*, *F. triloba* and *F. variegata* had specific pollinators, whilst *F. auriculata* and *F. oligodon* shared the same species of *C. emarginatus* as the pollinator, and *F. hispida* had two species as pollinator (Table 11).

The non-pollinating wasp community varied among *Ficus* species but did not depend on the size of fig. On average, there were between three and four NPFWs per host, ranging from 2 (*F. fulva* and *F. triloba*) to 6 (*F. oligodon* and *F. semicordata*). *Philotrypesis*, *Platyneura* and *Sycoscapter* were the dominant groups in most studied figs, whilst *Apocrypta* spp. were rarely recorded (Table 11).

The number of emerging pollinators, averaged per fig, varied from 28 (*F. auriculata*) to 1,400 (*F. oligodon*). The percentage of pollinators in a single fig was higher than that of non-pollinators in most figs (except for *F. auriculata* and *F. fulva*, Table 10). Pollinators accounted for 91% of total fig wasps in *F. oligodon*, 87.9% in *F. triloba*, 87.6% in *F. hispida*, 84.8% in *F. semicordata* and *F. variegata*. However, in *F. fulva* and *F. auriculata* the pollinators accounted for only 48.5% and 9.5% of the total fig wasps.

In general, in dioecious *Ficus* species, fig wasps were mostly found only in male figs but *Platyneura* sp. reproduced in both female and male figs of *F. oligodon*, although *Platyneura* sp. was found on a female *F. oligodon* in only crop in rainy season (June to August).

4.3.2 Effect of fragmentation. Habitat disturbance had contradictory effects on the number of foundresses among *Ficus* species (Table 12) but had a consistent and highly significant effect on seed production. Disturbance significantly reduced seed production (Table 13).

Table 10 Sexual specialization of the selected *Ficus* species in different phases.

Species	Sex	Fig Size (W x L mm)		Mean foundreses per fig	No. of associated fig-wasps per fig		
		RCP	RPP/RLP	(Mean ± SE)	Pollinators	Non-pollinators	Fig wasp ratio (pollinator/non-pollinator)
FIAU	F	48.0 x 46.3^{a}	66.2 x 53.7^{b}	12.3± 2.7^{b}	-	-	-
	M	54.2 x 43.2^{a}	86.0 x 65.6^{a}	58.7± 14.4^{a}	28.5±7.8	272.5±96.9	1 : 9.6
FIFU	F	13.0 x 16.0^{a}	17.7 x 19.2^{b}	1.8± 0.6^{a}	-	-	-
	M	12.0 x 11.8^{b}	20.3 x 20.0^{a}	2.0± 0.4^{a}	66.9±12.0	70.9±9.4	1 : 1.1
FIHI	F	17.2 x 14.0^{a}	28.5 x 25.4^{a}	7.5± 0.9^{a}	-	-	-
	M	17.7 x 15.0^{a}	29.3 x 23.7^{a}	4.1± 0.5^{b}	154.5±7.1	21.9±5.3	1 : 0.1
FIOL	F	37.4 x 31.3^{a}	61.0 x 53.1^{b}	9.0± 3.3^{a}	-	-	-
	M	36.5 x 30.2^{a}	70.7 x 61.1^{a}	13.9± 5.3^{a}	1,400.0±41.7	139.0±30.7	1 : 0.1
FISE	F	9.7 x 8.3^{a}	23.4 x 19.3^{b}	1.9± 0.3^{a}	-	-	-
	M	7.0 x 7.0^{b}	32.2 x 24.7^{a}	2.2± 0.5^{a}	163.1±49.7	29.3±2.9	1 : 0.2
FITR	F	27.0 x 28.0^{b}	30.5 x 35.8^{b}	5.0± 2.5^{a}	-	-	-
	M	28.6 x 35.2^{a}	40.1 x 46.1^{a}	2.6±1.5^{a}	515.0±30.1	71.0±5.0	1 : 0.1
FIVA	F	23.0 x 22.0^{a}	32.6 x 28.7^{b}	4.7± 0.6^{a}	-	-	-
	M	18.2 x 17.1^{b}	41.5 x 33.5^{a}	3.3± 0.3^{b}	186.5±15.3	33.5±10.6	1 : 0.2

FIAU = *F. auriculata*, FIFU = *F. fulva*, FIHI = *F. hispida*, FIOL = *F. oligodon*, FISE = *F. semicordata*, FITR = *F. triloba*, FIVA = *F. variegata*

F = female; M = male; RCP = Receptive phase; RPP = Ripening phase; RLP = Releasing phase; (-) = No wasp in female fig.

Different superscript letters (within a column) denote significant differences between sexes according to a *T*-test at a significant level of P<0.05.

Table 11 Fig wasps reared from seven *Ficus* species in Doi Suthep-Pui National Park, during March 2008 - February 2009.

Species	Families/sub-families of fig wasps [a]	Associated fig wasps	Pollination mode
F. auriculata	Agaonidae (*Agaoninae*)	*Ceratosolen emarginatus* Mayr	Pollinator
	Pteromalidae (*Sycoryctinae*)	*Philotrypesis longicaudata* Mayr	Non-pollinator
	Pteromalidae (*Sycoryctinae*)	*Philotrypesis* sp.	Non-pollinator
	Agaonidae (*Sycophaginae*)	*Platyneura* sp.	Non-pollinator
F. fulva	Agaonidae (*Agaoninae*)	*Valisia compacta* Wiebes	Pollinator
	Pteromalidae (*Sycoryctinae*)	*Philotrypesis* sp.	Non-pollinator
	Pteromalidae (*Sycoryctinae*)	*Sycoscapter* sp.	Non-pollinator
F. hispida	Agaonidae (*Agaoninae*)	*Ceratosolen solmsi marchali* Mayr	Pollinator
	Agaonidae (*Agaoninae*)	*Ceratosolen solmsi* Mayr	Pollinator
	Pteromalidae (*Sycoryctinae*)	*Apocrypta bakeri* Joseph	Non-pollinator
	Pteromalidae (*Sycoryctinae*)	*Philotrypesis pilosa* Mayr	Non-pollinator
	Pteromalidae (*Sycoryctinae*)	*Philotrypesis* sp.	Non-pollinator
F. oligodon	Agaonidae (*Agaoninae*)	*Ceratosolen emarginatus* Mayr	Pollinator
	Pteromalidae (*Sycoryctinae*)	*Philotrypesis longicaudata* Mayr	Non-pollinator
	Pteromalidae (*Sycoryctinae*)	*Philotrypesis* sp1	Non-pollinator
	Agaonidae (*Sycophaginae*)	*Platyneura* sp1	Non-pollinator
	Agaonidae (*Sycophaginae*)	*Platyneura* sp 2	Non-pollinator
	Pteromalidae (*Sycoryctinae*)	*Sycoscapter roxberghi*	Non-pollinator

Table 11 (continued).

Species	Families/sub-families of fig wasps [a]	Associated fig wasps	Pollination mode
F. semicordata	Agaonidae (*Agaoninae*)	*Ceratosolen gravelyi* Grandi	Pollinator
	Pteromalidae (*Sycoryctinae*)	*Apocrypta* sp.	Non-pollinator
	Pteromalidae (*Sycoryctinae*)	*Philotrypesis dunia* Joseph	Non-pollinator
	Pteromalidae (*Sycoryctinae*)	*Philotrypesis* sp1	Non-pollinator
	Agaonidae (*Sycophaginae*)	*Platyneura cunia*	Non-pollinator
	Agaonidae (*Sycophaginae*)	*Platyneura* sp1	Non-pollinator
	Pteromalidae (*Sycoryctinae*)	*Sycoscapter trifemmensis*	Non-pollinator
F. triloba	Agaonidae (*Agaoninae*)	*Vilisia esquirolianae* Chen & Chou	Pollinator
	Pteromalidae (*Sycoryctinae*)	*Sycoscapter* sp1	Non-pollinator
	Pteromalidae (*Sycoryctinae*)	*Sycoscapter* sp2	Non-pollinator
F. variegata	Agaonidae (*Agaoninae*)	*Ceratosolen appendiculatus* Mayr	Pollinator
	Pteromalidae (*Sycoryctinae*)	*Philotrypesis bimaculata* Mayr	Non-pollinator
	Agaonidae (*Sycophaginae*)	*Platyneura spinitarsus*	Non-pollinator
	Pteromalidae (*Sycoryctinae*)	*Sycoscapter patellaris* Mayr	Non-pollinator

[a] Taxonomy based on Boucek (1988) and Rasplus *et al.* (1998).

Table 12 The mean number of foundresses per fig was collected from the different collection sites (Mean ± SD).

Species	**No. of foundreses per fig**			
	Primary forest	Highly disturbed habitat	Planted plot	*P* -Value
F. auriculata	24.3 ± 5.9^{a} (*N*=56)	30.2 ± 8.5^{a} (*N*=33)	24.0 ± 3.0^{a} (*N*=20)	0.699, ANOVA
F. fulva	1.9 ± 1.1 (*N*=19)	-	-	-
F. hispida	2.5 ± 0.5^{a} (*N*=20)	5.7 ± 0.5^{a} (*N*=45)	6.3 ± 3.1^{a} (*N*=30)	0.475, ANOVA
F. oligodon	11.1 ± 2.6 (*N*=19)	-	-	-
F. semicordata	2.3 ± 0.5^{a} (*N*=60)	2.0 ± 0.6^{a} (*N*=30)	2.0 ± 0.3^{a} (*N*= 40)	0.531, ANOVA
F. triloba	11.5 ± 1.5^{a} (*N*=20)	1.6 ± 0.4^{b} (*N*=50)	1.3 ± 0.3^{b} (*N*=40)	$P<0.05$, ANOVA
F. variegata	4.7 ± 0.4^{a} (*N*=33)	1.8 ± 0.3^{b} (*N*=26)	-	$P<0.05$, *T*-Test

Values in a row with different superscript letters are significantly different according to *T*-test or *LSD*-test at $P<0.05$.

(-) = No sample collected.

Table 13 Mean seeds per fig by different sample sites.

Species		**Seeds per fig**			
	Proportion of wasps / seeds produced in single syconium	Primary forest Mean ± SD	Highly disturbed habitat Mean ± SD	Planted forest Mean ± SD	*P* -Value
FIAU	1 : 32	9,685 ± 1,560^{a} (*N*=17)	4,812 ± 3,689^{ab} (*N*=17)	2,801 ± 45^{b} (*N*=12)	0.016, ANOVA
FIFU	1 : 6	858 ± 312 (*N*=24)	-	-	-
FIHI	1 : 8	1,337 ± 528^{a} (*N*=32)	1,015 ± 403^{ab} (*N*=37)	812 ± 340^{b} (*N*=25)	0.005, ANOVA
FIOL	1 : 6	8,859 ± 4,115 (*N*=50)	-	-	-
FISE	1 : 4	781 ± 379^{b} (*N*=56)	1,213 ± 471^{a} (*N*=37)	713 ± 414^{b} (*N*=42)	0.000, ANOVA
FITR	1 : 5	2,755 ± 784 (*N*=35)	-	-	-
FIVA	1 : 11	2,342 ± 209^{a} (*N*=29)	1,552 ± 152^{b} (*N*=36)	-	0.03, *T*-Test

FIAU= *F. auriculata*, FIFU= *F. fulva*, FIHI= *F. hispida*, FIOL= *F. oligodon*, FISE= *F. semicoradata*, FITR= *F. triloba*, FIVA= *F. variegata*

Values in a row with different superscript letters are significantly different according to *T*-test or *LSD*-test at *P*<0.05.

(-) = No sample collected.

Table 14 Seasonal effects on seed production (per fig).

Species	**No. of seeds per fig** (Mean ± SE)			*P*- value
	Rainy Season (June-September)	Cool-dry Season (October-January)	Dry Season (February-May)	
F. auriculata	10,759 ± 2,873^{a} (*N*=40)	5,798 ± 1,506^{b} (*N*=27)	5,028 ± 805^{b} (*N*=30)	*P*<0.05
F. fulva	-	-	858 ± 31 (*N*=24)	-
F. hispida	921 ± 107^{a} (*N*=41)	1,026 ± 260^{a} (*N*=50)	1,192 ± 65^{a} (*N*=58)	*P*=0.20
F. oligodon	8,063 ± 444^{a} (*N*=40)	-	8,883 ± 657^{a} (*N*=44)	*P*=0.712
F. semicordata	951 ± 116^{a} (*N*=32)	613 ± 66^{b} (*N*=30)	693 ± 68^{ab} (*N*=43)	*P*< 0.05
F. triloba	2,742 ± 221^{a} (*N*=33)	2,838 ± 686^{a} (*N*=20)	-	*P*=0.88
F. variegata	2,302 ± 36^{a} (*N*=23)	789 ± 135^{b} (*N*=29)	2,288 ± 881^{a} (*N*=32)	*P*<0.05

Similar superscript letters in the same row indicate means, which are not significantly different.

(-) = No sample collected.

4.4 *Ficus* propagation

4.4.1 Propagation from seed. Seeds of all species began to germinate within 3-4 weeks after sowing and completed germination within 7-8 weeks (Fig. 16). Germination was epigeal and the first true leaves were opposite. Median length of dormancy (MLD) ranged from 19 to 23 days, but was not significantly different among treatments and species. Germination percentages for each species, averaged across all treatments ranged from 36 to 73 %. Statistical analysis divided the species into three germination classes: i) those with high germination: *F. variegata* (73%), *F. fulva* (70%) and *F. auriculata* (68%) and ii) those with moderate germination: *F. semicordata* (51%) and *F. oligodon* (47%), and those with low germination *F. hispida* (36%) ($P<0.05$, Table 15).

For all species, the germination medium of forest soil alone resulted in the highest germination percentage (63%), followed by 61% for sand/forest soil and 48% for sand/charred rice husk ($P<0.05$, Fig. 17A). In contrast, after germination, the survival rate of young fig seedlings of all species was significantly higher (67%) in sand/charred rice husk than in both of the other media ($P<0.05$, Fig. 17B). Fungicide application tended to decrease germination and survival rates ($P=0.055$, $N=216$ and $P=0.044$, $N=209$, respectively, Fig. 17C-D), whilst fertilizer application reduced only the survival rate of young seedlings ($P=0.001$, $N=209$; Fig. 17E-F).

Interactions between media and fungicide application also had a significant effect on germination and survival rates for all species at $P<0.01$ level (Fig. 18). Maximum overall success of the germination treatments (proportion germinated x proportion survival), averaged across all species, was T9 ($P<0.05$, $N=18$; sand and charcoalized rice husk + no fungicide + no fertilizer; Fig. 19).

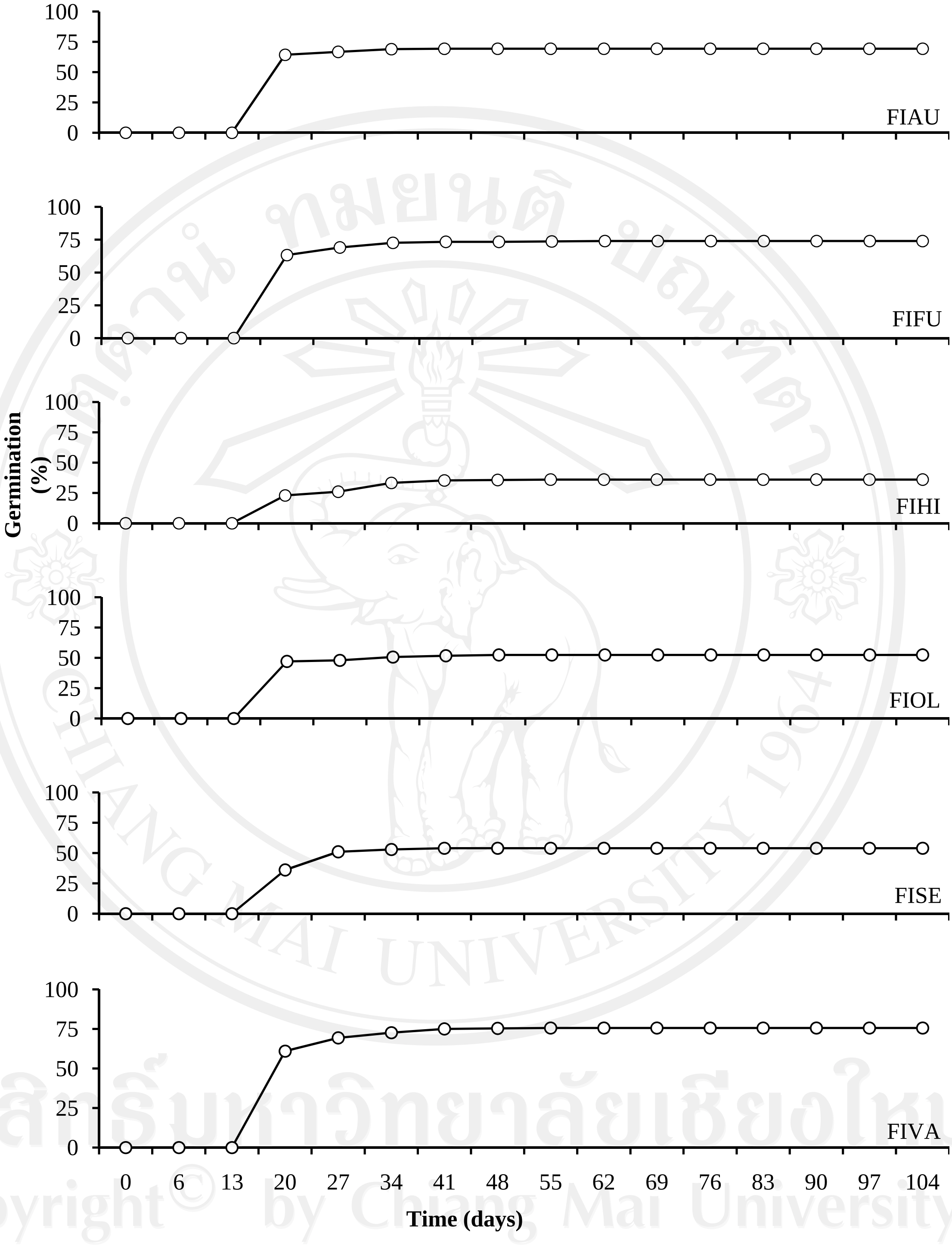


Figure 16 Fig seed germination from control treatment (T1) of each species in the nursery trials (FIAU = *F. auriculata*, FIFU = *F. fulva*, FIHI = *F. hispida*, FIOL = *F. oligodon*, FISE = *F. semicordata* and FIVA = *F. variegata*).

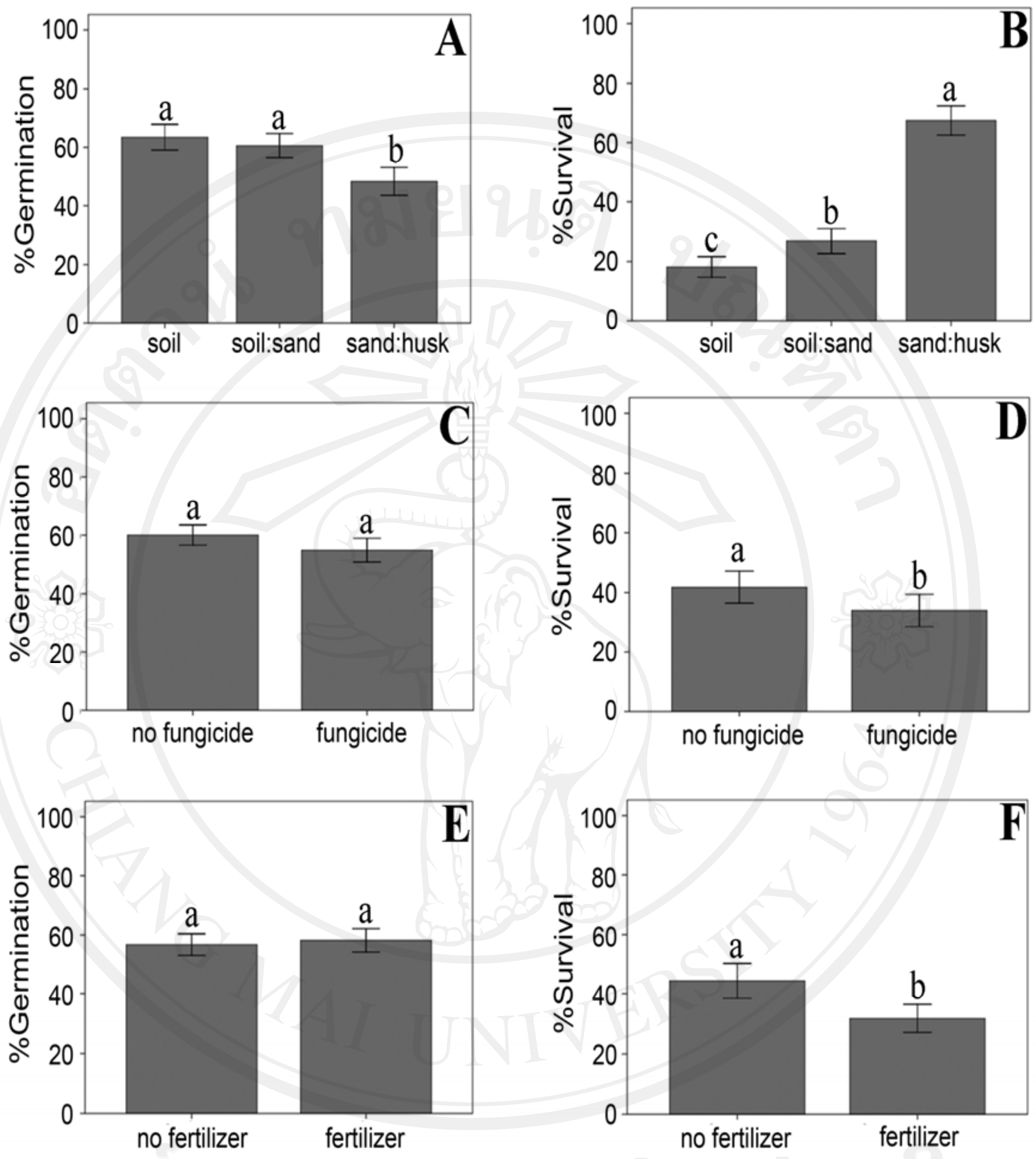
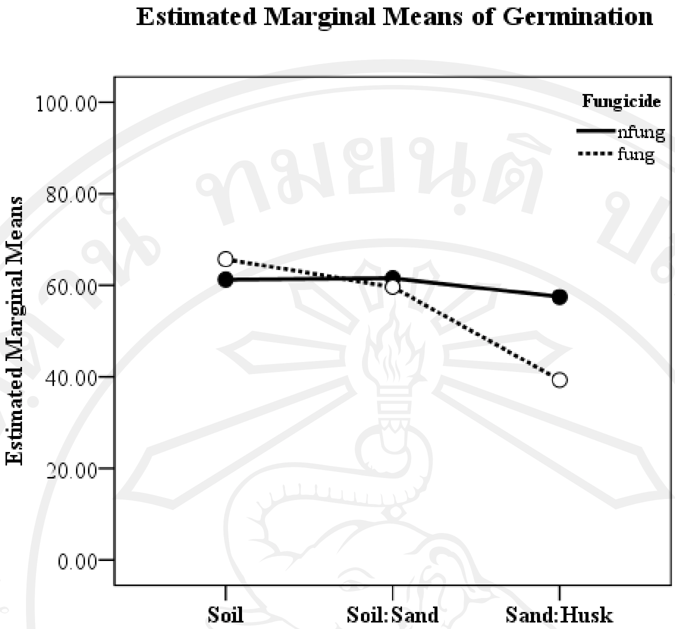


Figure 17 Seed germination trials, averaged across all species. A-B = effect of the germination medium compositions on germination and survival rates, C-D = effect of the fungicide applications on germination and survival rates, and E-F = effect of the fertilizer applications on germination and survival rates. Letters above bars indicate significant differences (*P*<0.05).



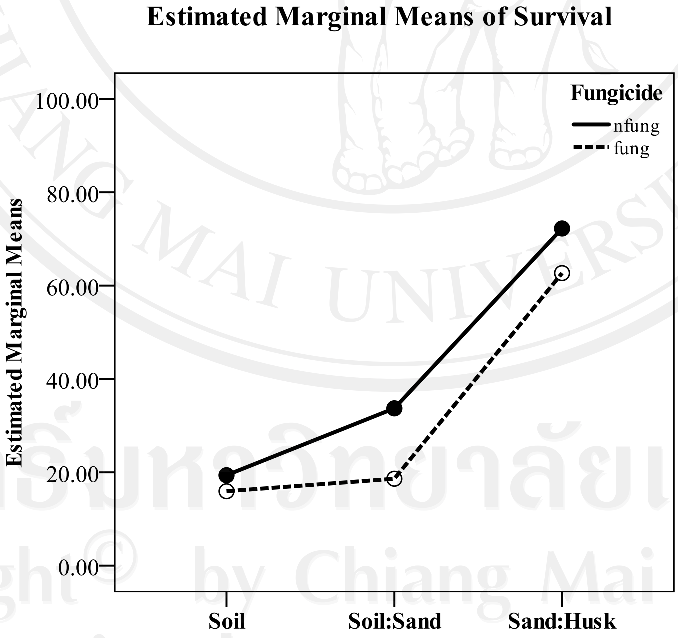


Figure 18 Interactions between the germination medium composition and fungicide application on germination and survival rate, averaged across all species. nfung = no fungicide, fung = fungicide applied.

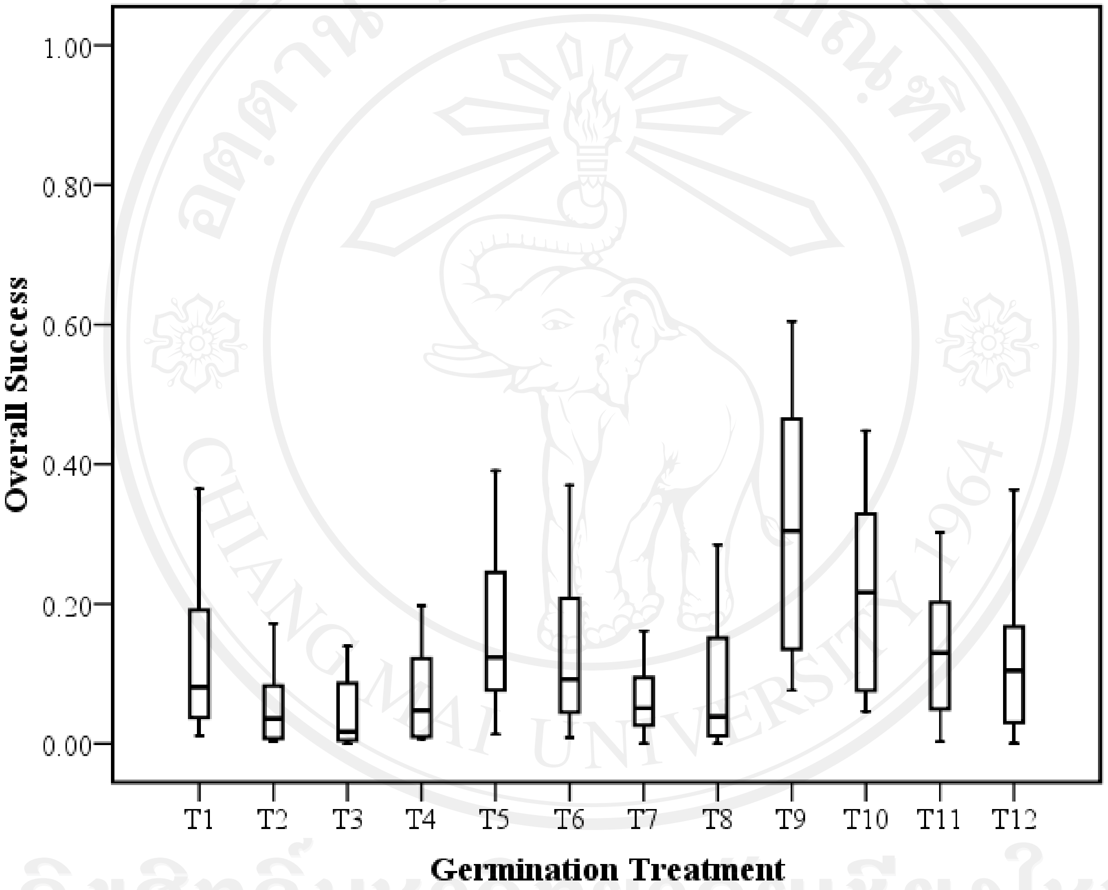


Figure 19 Overall successes (proportion germinated x proportion survival) of the germination treatments by transplanting time, averaged across all species.

Table 15 Results of germination and seedling growth trials on *Ficus* spp. Seeds of all species of all treatments were sown on 17-August-2008, seedlings were pricked out on 31-January-2009.

Species		Seed germination trials			Seedling growth of the most effective treatment (T1= full sun light + 10 granules of fertilizer every 3 months)						
		Averaged across all treatments			1 month after pricking out		4 month after pricking out				
	Seed collection (Month)	MLD (days)	Germination (%)	Survival (%)	RCD (mm)	Height (cm)	RCD (mm)	Height (cm)	RRGR (%year^{-1})	RHGR (%year^{-1})	Survival (%)
FIAU	July	21±3	68±12^{a}	48±25	1.7±0.2	2.1±0.2	6.6±0.3	22.7±2.5	558.1	966.0	81±11
FIFU	July	20±3	70±14^{a}	29±25	1±0.0	1.1±0.1	5.9±1	23.1±11.2	719.8	1,222.0	45±10
FIHI	May	23±2	36±7^{c}	34±28	1±0.0	1.2±0.3	5.1±0.3	23.8±1.1	660.7	1,211.5	78±22
FIOL	June	19±2	47±7^{bc}	40±29	1.3±0.1	2±0.2	6.2±0.4	17.1±4.8	633.6	876.7	73±19
FISE	July	20±2	51±9^{b}	32±31	1.1±0.2	1.5±0.1	5.6±0.6	28.3±6.5	650.3	1,182.4	72±18
FIVA	July	19±3	73±15^{a}	40±20	1.2±0.1	1.8±0.3	6.3±0.2	26.5±3.5	661.4	1,083.8	82±14

Mean ± SD; Variables: MLD = Median length day; RCD = Root collar diameter; RRGR = Relative growth rate for root collar diameter, RHGR = Relative growth rate for height. Different superscript letters (in the same column) indicates statistical differences among species (*P*- value<0.05).

Table 16 Details of seedlings propagated by cutting at the first planting season (6 months after removing from the propagator), averaged across all treatments.

Species	Cutting Date	Transplanting Date	Shooting (%)	Rooting (%)	Survival by transplanting time (%)	Mean diameter (mm)	Mean height (cm)	Mean canopy (cm)	RRGR (%year^{-1})	RHGR (%year^{-1})	RCGR (%year^{-1})	Survival by planting time (%)
FIAU	27-Sep-08	10-Nov-08	75±5^{a}	19±4^{ab}	53±4^{a}	12±2	21±2	30±5	42.4	88	113.1	23
FIFU	25-Sep-08	12-Nov-08	20±4^{b}	3±1^{c}	7±2^{c}	8±2	17±2	27±5	106.9	69.2	110.9	17
FIHI	17-Sep-08	10-Nov-08	63±7^{a}	20±5^{a}	47±7^{ab}	10±1	18±2	30±4	94.5	88.4	202.8	33
FIOL	19-Sep-08	10-Nov-08	67±9^{a}	16±4^{ab}	48±7^{ab}	9±2	16±2	26±5	123.3	54.9	171.0	27
FISE	18-Sep-08	12-Nov-08	75±5^{a}	20±2^{a}	39±5^{ab}	8±1	16±2	18±4	89.0	66.0	111.5	17
FIVA	27-Sep-08	11-Nov-08	53±8^{a}	6±2^{ab}	28±5^{b}	12±1	17±2	23±4	68.6	81	156.9	20

Mean ± SD; Variables: RRGR = Relative growth rate for root collar diameter (mm), RHGR = Relative growth rate for height (cm) and RCGR = Relative growth rate for canopy width (cm). Different superscript letters (in the same column) indicates statistical differences among species (*P*-value<0.05).

At time of pricking out (after expansion of the second true leaf pairs) seedlings were tiny; only 1.1 to 2.1 cm tall. However, subsequent seedling growth rate of all species was very high, especially for seedlings in full sunlight with 10 granules of slow release fertilizer (Osmocote) applied every 3 months (T1, Fig. 20). However, it did not differ significantly among species (Fig. 21A-C). By planting time, seedlings had mostly grown taller than 20 cm (>800% year^{-1} height relative growth rate, >500% year^{-1} root collar diameter relative growth rate) and seedlings of all species remained in good health throughout their growth in the nursery (Fig. 21D). Seedling survival rates of most species were also very high (>70% survival; except for *F. fulva*; Table 15). However, the mean overall success (proportion germinated x proportion survival) of all species was fairly low. *Ficus variegata* had the highest mean overall success compared with all other species (SD 0.03, *P*<0.05, Fig. 22).

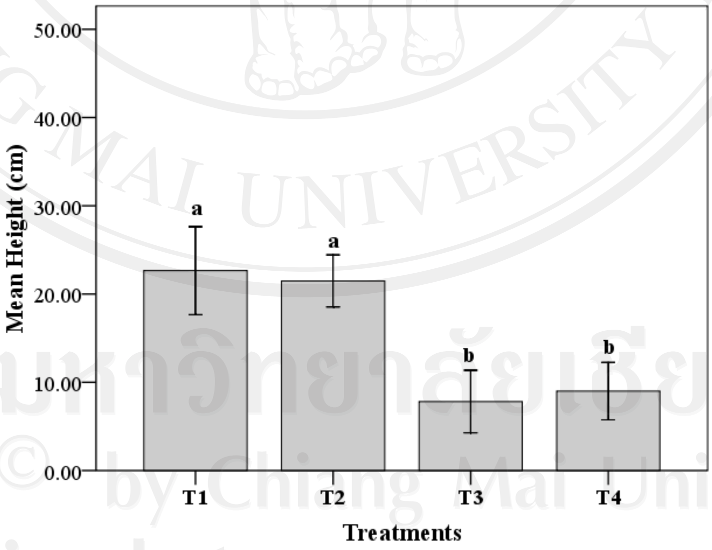


Figure 20 Seedling growth trials, averaged across all species by planting time. Different letters above the bars indicate significant differences among treatments (*p*<0.05).

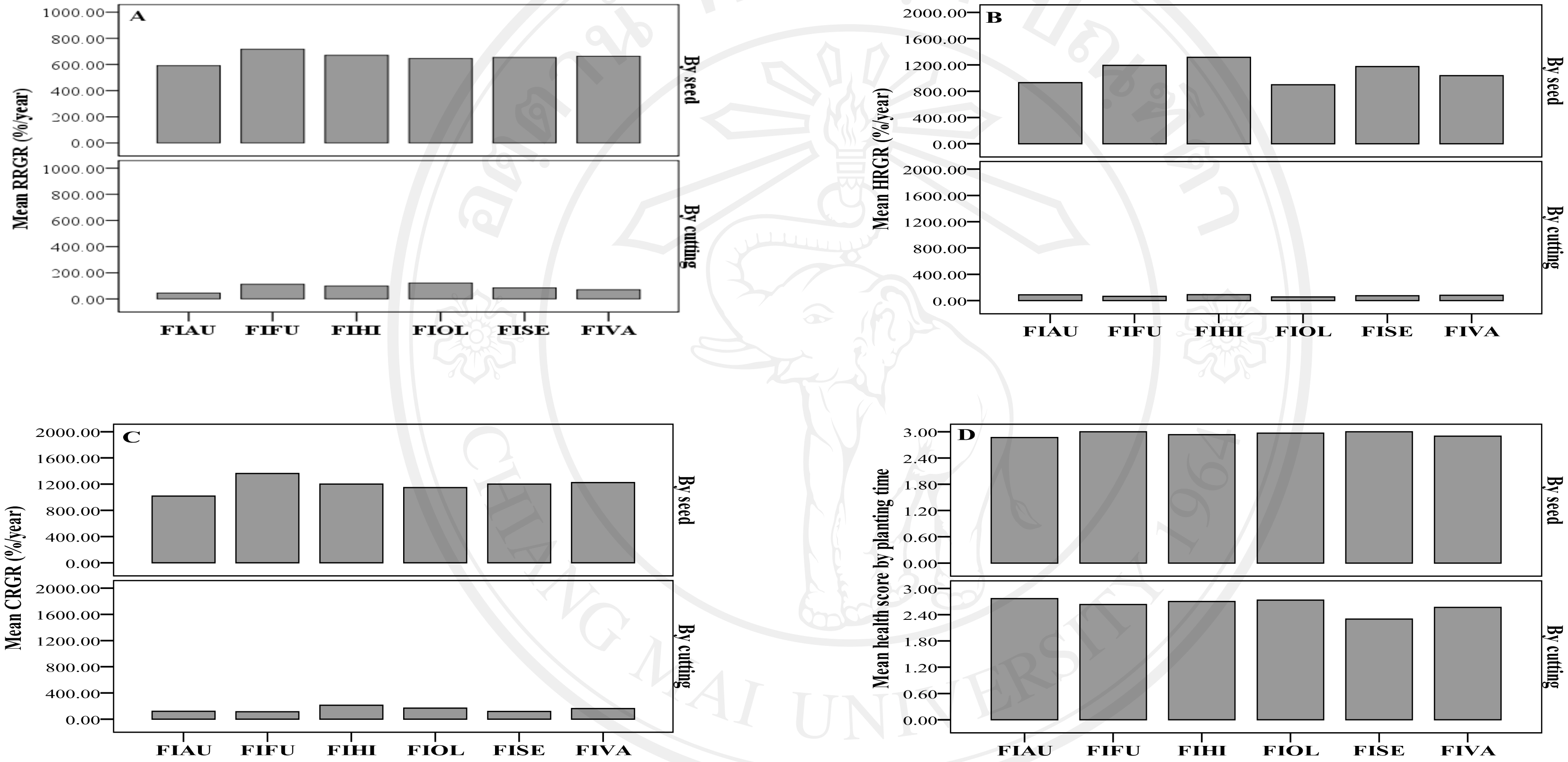


Figure 21 Mean relative growth rates and mean health scores of the most effective treatment by species for each propagation types after 1 year in the nursery. RRGR = relative root collar diameter growth rate (mm), HRGR = relative height growth rate (cm) and CRGR = relative canopy width growth rate (cm).

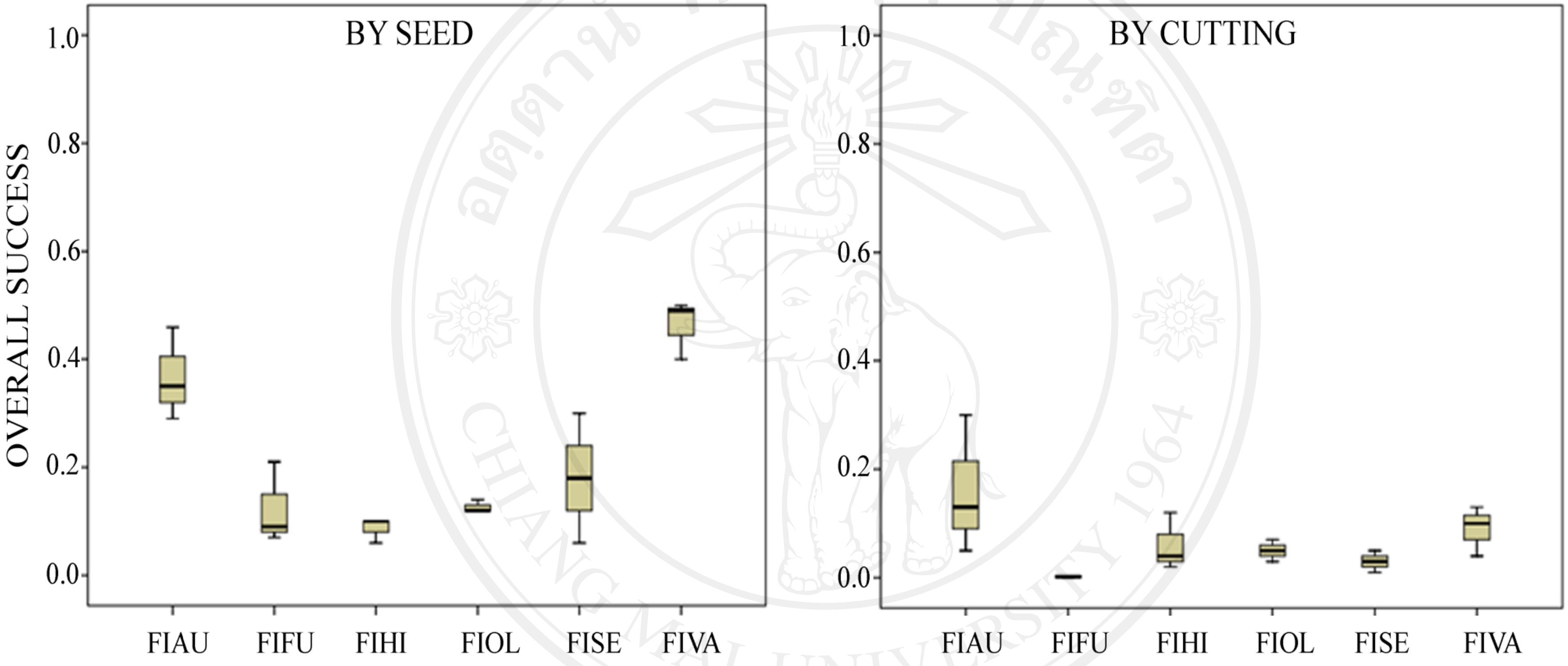


Figure 22 Overall successes (proportion germinated/rooted x proportion survival) of each species by planting time. FIAU = *Ficus auriculata*, FIFU = *Ficus fulva*, FIHI = *Ficus hispida*, FIOL = *Ficus oligodon*, FISE = *Ficus semicordata* and FIVA = *Ficus variegata*.

4.4.2 Propagation from cuttings. All species developed new shoots 2-4 weeks after being placed in the propagation bags, and most cuttings produced new roots about a week after above ground growth initiated. Averaging across all species, the mean shooting/rooting percentage was 59%. Shooting/rooting ability also varied significantly among species (ANOVA, *P*<0.05, Table 16). The older parts of the cuttings sprouted new leaves and roots easier than the younger parts (Fig. 23A-B) and they exhibited high survival rates after shooting/rooting (Fig. 23C). Rooting hormone affected rooting ability of all species (*P*<0.05, Fig. 23D). However, there were no interaction effects between cutting position and hormone application (*P*=0.738 for shooting and *P*=0.132 for rooting).

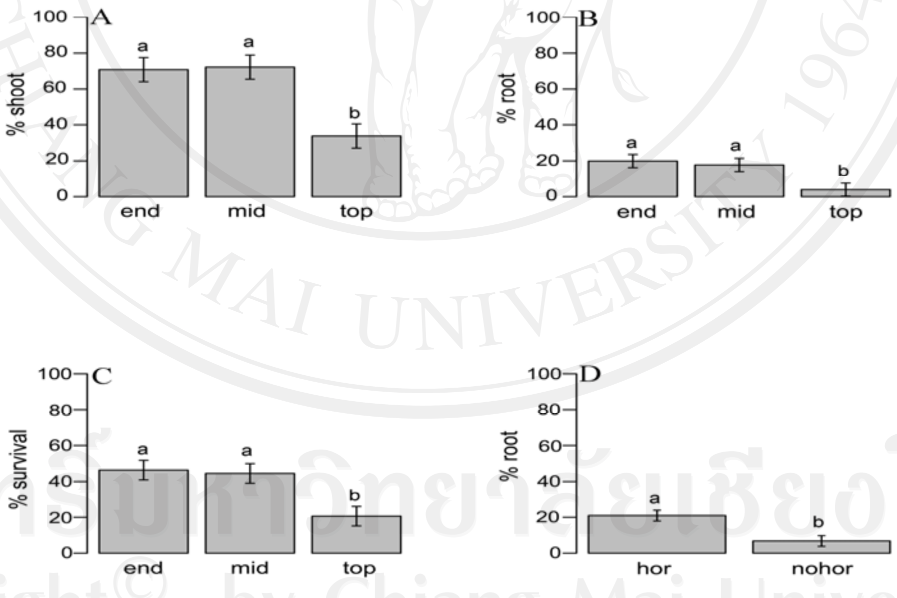


Figure 23 Cutting trials, averaged across all species. (A-C) effect of the cutting positions on percent shooting, rooting and survival, (D) effect of the rooting hormone applications on percent rooting; top = terminal shoot (upper part), mid = middle part, end = lower part; hor = with rooting hormone, nohor = without rooting hormone.

Within 7-8 weeks, cuttings of all species were ready for removal from the enclosed plastic bags (mature leaves produced). Averaging across all species, treatment which resulted in maximum survival rates and production of seedlings ready for transplantation was T6 (lower + rooting hormone; $P<0.05$, $N=18$; Fig. 24).

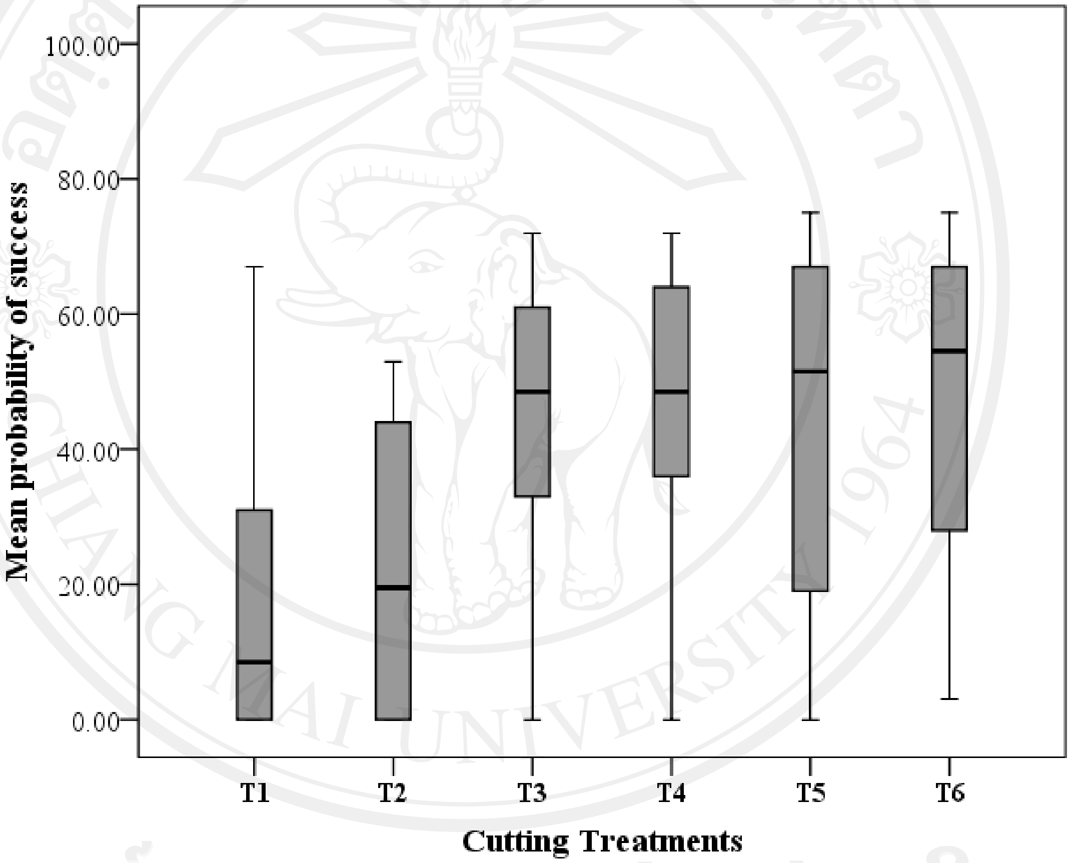


Figure 24 Overall successes (proportion shooted x proportion survival) of each treatment by transplanting time. T1 = upper + without rooting hormone, T2 = upper + with rooting hormone, T3 = middle + without rooting hormone, T4 = middle + with rooting hormone, T5 = lower + without rooting hormone and T6 = lower + with rooting hormone.

However, after the cuttings were removed from the enclosed plastic bags and replanted in a new container, their growth and survival rates were fairly low (<33% survival and RHGR <100 % year^{-1}). By the first planting time, the mean height for individual species ranged from 16 cm for *F. oligodon* and *F. semicordata* to 21 cm for *F. auriculata* (Table 16). *Ficus fulva* had, significantly, the lowest mean overall success, compared with all other species (*P*<0.05, Fig. 22).

4.4.3 Propagation type comparison. During the first 12 months period in the nursery, averaged across all species, the relative growth rate of seedlings (656.7±40.6% year^{-1} for root collar diameter, 1,091.8±164.2% year^{-1} for height and 1,192.0±111.4% year^{-1} for canopy width) was higher than that of rooted cuttings (88.6±8.3% year^{-1} for root collar diameter, 75.6±13.3% year^{-1} for height and 149.1±9.6% year^{-1} for canopy width). Stock plants derived from seed also showed higher success rates than that of stock plants derived from cuttings (0.22 and 0.07 respectively, *T*-Test, *P*<0.05). However, by planting time, seedling size varied among propagation types. Seedlings derived from seed were significantly taller and had higher mean health scores compared with stock plants derived from cuttings (23.0±4.9 cm and 17.7±2 cm for height, 2.9±0.1 and 2.6±0.2 for health score, respectively, *T*-Test, *P*<0.05). Conversely, seedlings propagated from cuttings showed significantly higher mean root collar diameter than that of seedlings propagated from seed (10.1±2 mm and 5.9±0.4 mm respectively, *T*-Test, *P*<0.05). However, there were no significant differences in mean canopy width among the propagation types (29.3±2.1 cm for stock plants derived from seed and 26.3±4.8 cm for stock plants derived from cuttings, *T*-Test, *P*=0.19).

4.5 *Ficus* plantings

4.5.1 Direct seeding. Seed germination in the field ranged from 47.2±8.1% (*F. hispida*) to 73.9±2.8% (*F. auriculata*), the median length of dormancy (MLD) ranged from 20 days (*F. oligodon*) to 28 days (*F. variegata*), but the differences among species were not statistically significant (*P*=0.27 for germination and *P*=0.06 for MLD; Fig. 25).

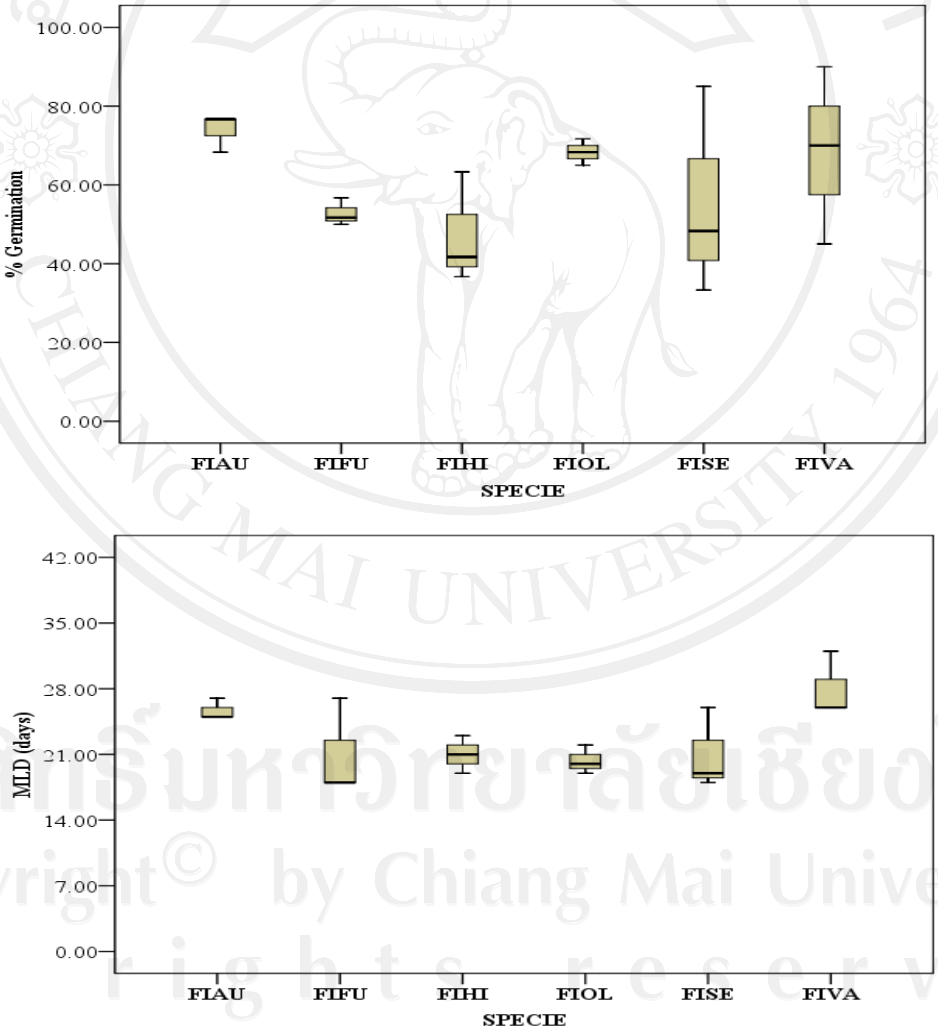


Figure 25 Mean germination and median length of dormancy (MLD) of the direct seeding trials.

However, seedling survival after germination of all species was very low. The highest mortality for all species occurred during the first rainy season (>90% mortality by one month after germination) due to damping-off diseases. Overall mortality rate of most species was 100% during the first dry season, except for *F. hispida* of which only 1.7% (SD 0.3) of seeds planted remained alive at the end of 2nd rainy season (Fig. 26D). Relative growth rates (%RGR year^{-1}) of *F. hispida* saplings that survived the period December 2009 to October 2010 are presented in Fig. 26A-C.

4.5.2 Planting stock-raised in nursery from cuttings. After planting out in disturbed areas, 67% of plants propagated from cuttings died within 7 months (averaged across all species). At the end of the second rainy season, mean survival of saplings across all species was 15.1% (SD 3.5). The mean values for individual species ranged from 0% for *F. fulva* to 36.7% for *F. hispida*, differences among species in relation to survival rate (ANOVA, $P<0.05$, Fig. 26D). The relative growth rate of seedlings propagate from cuttings was also fairly slow, with differences among species statistically significant for mean RRGR and HRGR ($P<0.05$, Fig. 26A-B). *Ficus auriculata* had the highest mean height (77.6 cm), followed by *F. variegata* (69.6 cm) and *F. oligodon* (51.6 cm); significantly taller compared with the other species (ANOVA, $P<0.05$). Whilst, *F. variegata* had, significantly, the highest mean root collar diameter (23.3 mm) and mean canopy width (98.1 cm) compared with all other species (ANOVA, $P<0.05$, Table 17).

4.5.3 Planting stock-raised in nursery from seed. The trees were approximately 20 cm tall when planted (averaged across all species) but they mostly grew taller than 1.5 m after 1.5 years with *F. semicordata* and *F. variegata* reaching 2 m (Table 17). From May 2009 to October 2010, *F. fulva* achieve the highest growth rate (RRGR=141.2±11.3% year^{-1} and HRGR=183.1±12.3% year^{-1}), whilst *F. semicordata* had the highest CRGR (115.6±7.2% year^{-1}). However, differences in relative growth rates among species were not statistically significant (Fig. 26A-C). At the end of the second rainy season, *F. variegata* had the highest mean root collar diameter and mean height (37.8 mm and 264.6 cm respectively), whilst *F. semicordata* had the highest mean canopy width (141.4 cm), however analysis of variance showed no significant differences among the species means (ANOVA, *P*=0.59 for root collar diameter, *P*=0.08 for height and *P*=0.55 for canopy width). Survival after two rainy seasons averaged 68.1% (SD 5.7) across all species. The mean values for individual species ranged from 63.3% for *F. semicordata* to 78.3% for *F. variegata*. Overall, there were no statistically significant differences for survival among species (Fig. 26D).

4.5.4 Planting stock type comparison. By the end of the second rainy season (1.5 years after planting), averaging across the species, nursery-grown saplings from seeds performed significantly better than other planting stock types. They had, significantly, the highest survival rate (68.1%), highest relative growth rate (126.8±14.1% RRGR year^{-1}, 162.2±16.7% HRGR year^{-1} and 105.3±9.8% CRGR year^{-1}) and the largest seedling size (31.6±4.1 mm for root collar diameter, 199.3±45.1 cm for height and 122.9±13.3 cm for canopy width).

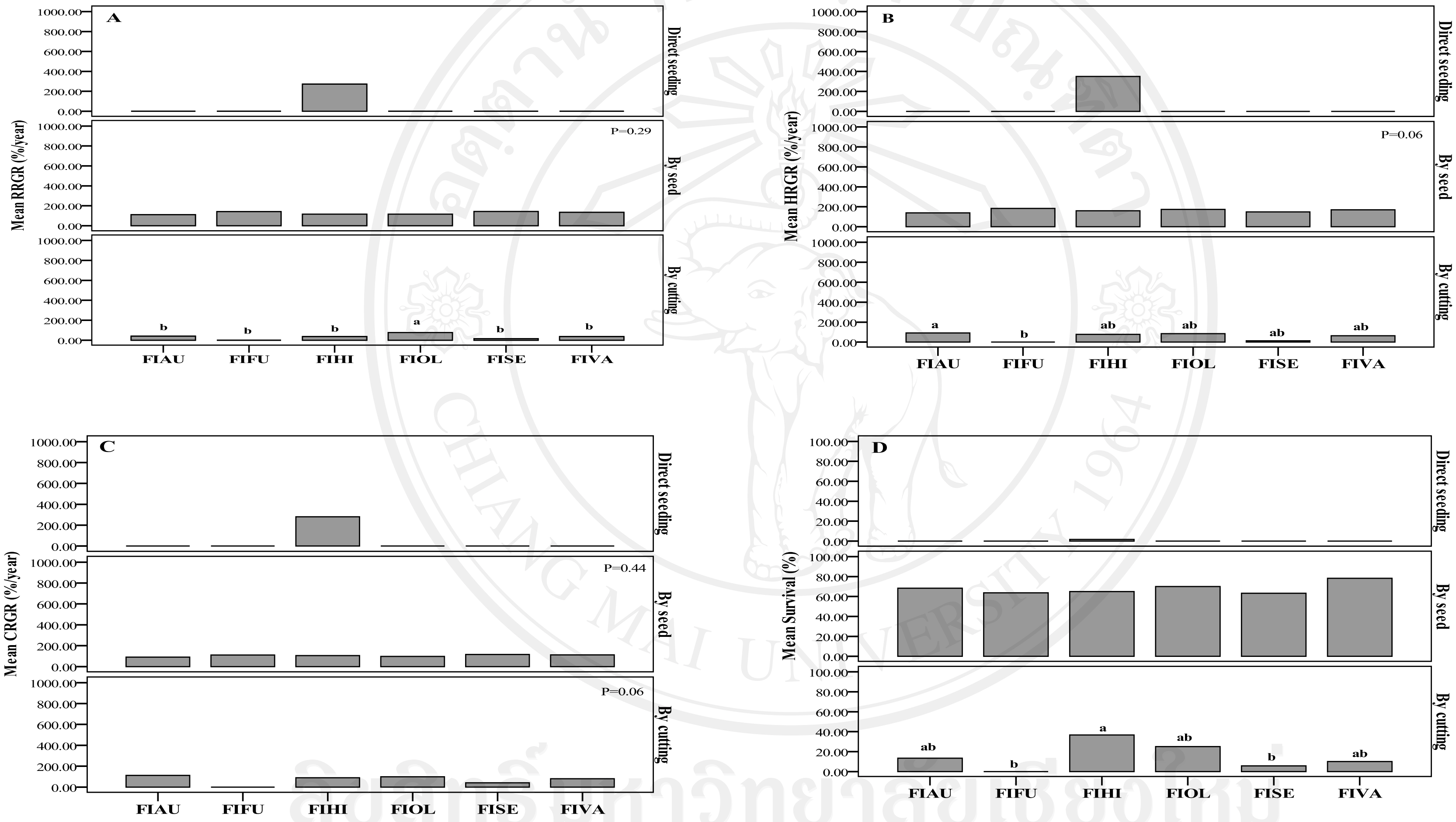


Figure 26 Mean relative growth rate and mean survival by species for each planting stock types after 1.5 years of planting out in disturbed habitats. Different letters above the bars indicate significant differences among species ($P<0.05$).

Table 17 Seedling growth comparison between the planting stock types for each species, which attained at the end of the second rainy season (1.5 years after planting out); RCD = Root collar diameter; Mean ± SD; (-) = All seedlings were dead.

Species	Direct seeding	Planting stock from seed	Planting stock from cuttings
Ficus auriculata			
RCD (mm)	-	31.7±2.8^{a}	21.1±1.0^{b}
Height (cm)	-	162.4±17.6^{a}	77.6±5.4^{b}
Canopy width (cm)	-	119.1± 4.0^{a}	93.7±2.9^{a}
Health	-	2.3±0.2^{a}	2.8±0.3^{a}
Ficus fulva			
RCD (mm)	-	30.5±6.0	-
Height (cm)	-	196.1±42.2	-
Canopy width (cm)	-	121.2±35.3	-
Health	-	3.0±0.0	-
Ficus hispida			
RCD (mm)	35.5±13.4^{a}	26.3±8.7^{a}	18.6±2.0^{a}
Height (cm)	188.5±54.4^{a}	154.8±61.3^{ab}	50.1±2.8^{b}
Canopy width (cm)	141.0±84.6^{a}	108.2±27.6^{a}	73.1±2.2^{a}
Health	3.0±0.0^{a}	2.6±0.3^{a}	2.8±0.1^{a}

Table 17 (continued).

Species	**Direct seeding**	**Planting stock from seed**	**Planting stock from cuttings**
Ficus oligodon			
RCD (mm)	-	28.8±5.9^{a}	16.9±1.7^{b}
Height (cm)	-	174.6±33.8^{a}	51.6±12.3^{b}
Canopy width (cm)	-	111.4±23.4^{a}	75.6±15.5^{a}
Health	-	2.7±0.1^{a}	2.7±0.3^{a}
Ficus semicordata			
RCD (mm)	-	34.3±12.0^{a}	12.0±6.9^{b}
Height (cm)	-	243.3±70.0^{a}	29.2±16.7^{b}
Canopy width (cm)	-	141.4±27.0^{a}	68.7±39.3^{b}
Health	-	2.8±0.2^{a}	2.7±0.3^{a}
Ficus variegata			
RCD (mm)	-	37.8±9.7^{a}	23.3±0.4^{a}
Height (cm)	-	264.6±49.8^{a}	69.6±9.1^{b}
Canopy width (cm)	-	136.0±23.3^{a}	98.0±3.2^{a}
Health	-	2.8±0.1^{a}	2.5±0.7^{a}

Values in a row with different letters are significantly different among planting stock types according to *T*-test or *LSD*-test (where needed) at $P < 0.05$.

4.5.5 Cost comparison. Based on our calculations, the cost per plant of each planting stock types are presented in Table 18 (see Appendix J for more details). The major cost of all planting stock types was for labor which account for 79.5%, 70.5% and 77.1% of total costs (for direct seeding, planting stock-raised in nursery from seed and cutting, respectively). If the survival rates are 100 percent, direct seeding was the cheapest technique, but when we took mortality rate into account, planting stock-raised in the nursery from seed was the most cost-effective, compared with the other two techniques.

Table 18 Establishment and maintenance costs (per plant).

Items	**Planting Stock Type**		
	Direct Seeding	Planting stock-raised in nursery from seed	Planting stock-raised in nursery from cutting
Nursery materials [a]	0	\$0.03	\$0.04
Labor cost in nursery [b]	0	\$0.14	\$0.40
Field materials [c]	\$0.09	\$0.20	\$0.20
Labor cost in field [d]	\$0.35	\$0.41	\$0.41
Total cost (100% survival)	\$0.44	\$0.78	\$1.05
Establishment cost [e] (per plant established)	**\$25.88**	**\$1.14**	**\$6.95**

[a] Nursery materials include containers, media, fertilizer and rooting hormone; [b] Labor for seed/cutting collection, seed/cutting preparation, seed sowing/cutting, potting, watering, fertilizing, weeding and grading. During the period of study, manual labor cost average \$6.53 per day (8 hr); 1 US\$=30.65 Thai baht; [c] Field materials include bamboo stakes, bamboo tubes, fertilizers and gasoline; [d] Labor for seeds/seedling transferring, planting, weeding and fertilizing; [e] Based on survival rates at the end of the 2nd rainy season were 1.7% for direct seeding (averaging only for *F. hispida*), 68.1% for seed and 15.1 for cutting (averaging across all species).

Source: Kuaraksa and Elliott (2011).

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).

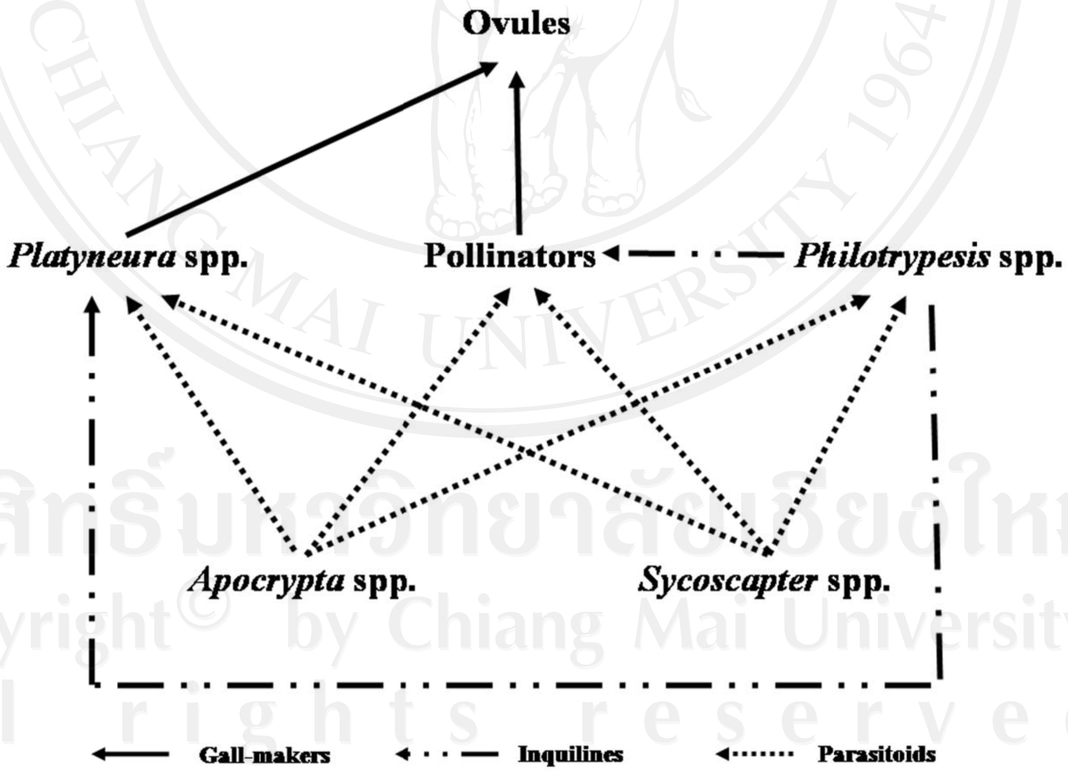


Figure 27 Relationship summarizing of the fig wasps associated with the *Ficus* species studied, in the Doi Suthep-Pui National Park, Thailand.

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, becaud 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.

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).

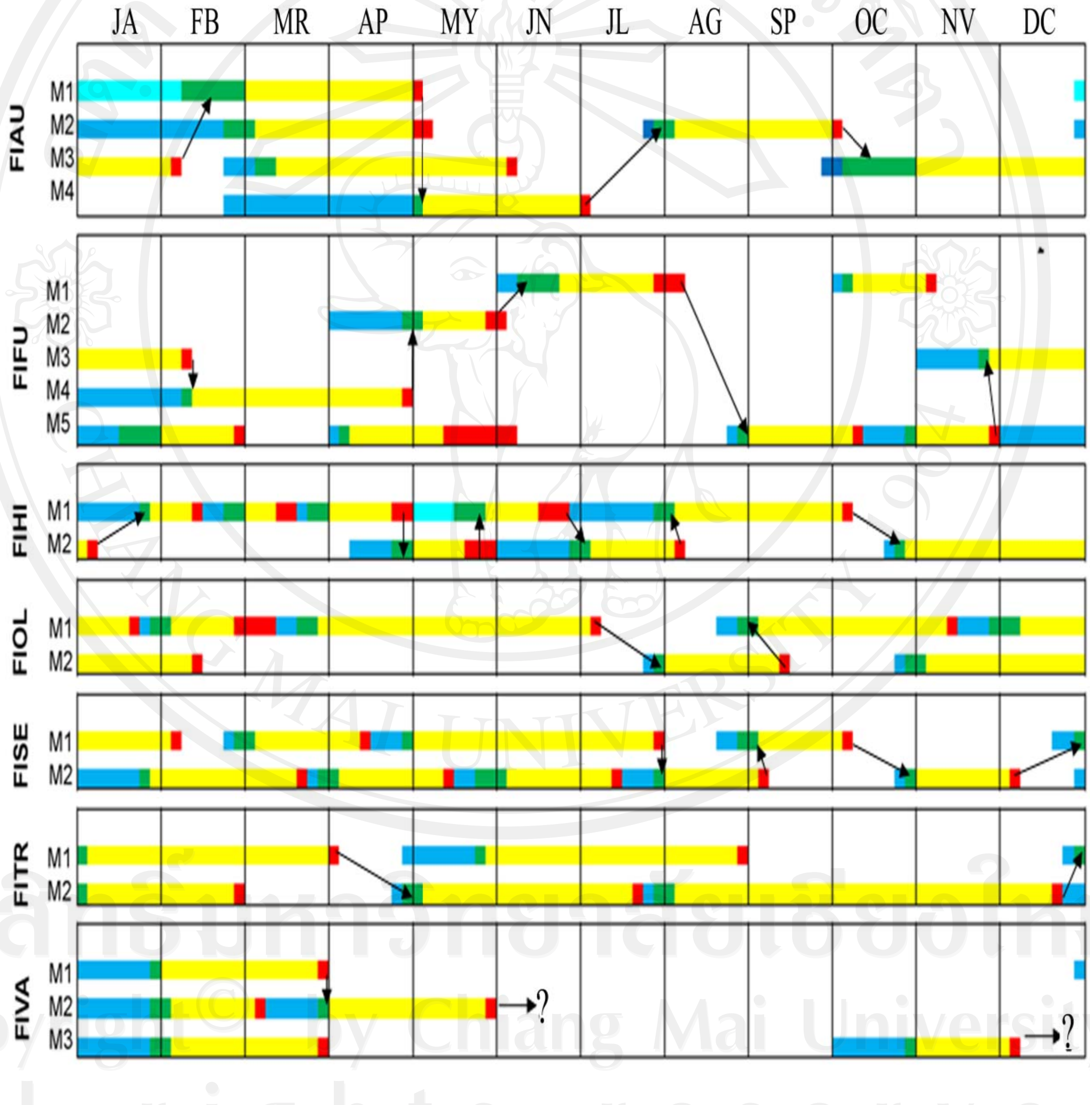
The flowering cycle of female trees of most species appears to be adapted to the seasonal climate and may increase the probability of germination and seedling establishment. In contrast, male trees of most species reached a peak in wasp production to avoid the rainy season. This helps to increase the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



(⟶) Wasp transfer

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.

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APPENDICES

APPENDIX A

THE ILLUSTRATIONS OF THE SEVEN SELECTED DIOECIOUS *FICUS* SPECIES

Ficus auriculata Lour.

Ficus oligodon Miquel

Ficus variegata Blume

Ficus hispida L.f.

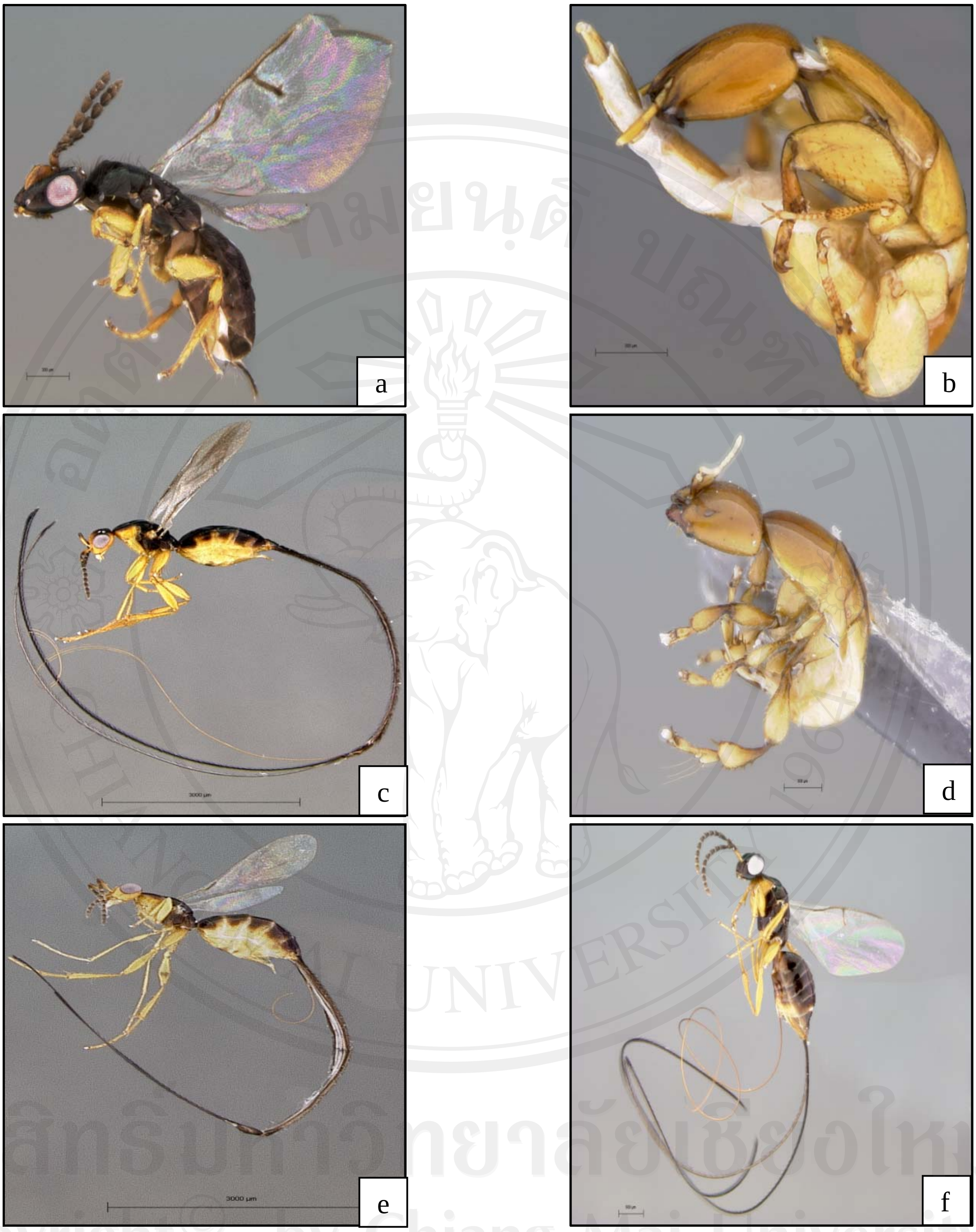
Ficus semicordata Buch.-Ham. ex Sm.

Ficus fulva Reinw. ex Blume

Ficus triloba Buch.-Ham. ex Voigt

APPENDIX B

THE ILLUSTRATIONS OF THE FIG WASPS DEVELOPING IN FIGS OF *FICUS AURICULATA* IN DOI SUTHEP-PUI NATIONAL PARK, NORTHERN, THAILAND



(a) female *Ceratosolen emarginatus*, (b) male *Ceratosolen emarginatus*, (c) female *Philotrypesis longicaudata*, (d) male *Philotrypesis longicaudata*, (e) *Philotrypesis* sp. and (f) *Platyneura* sp.

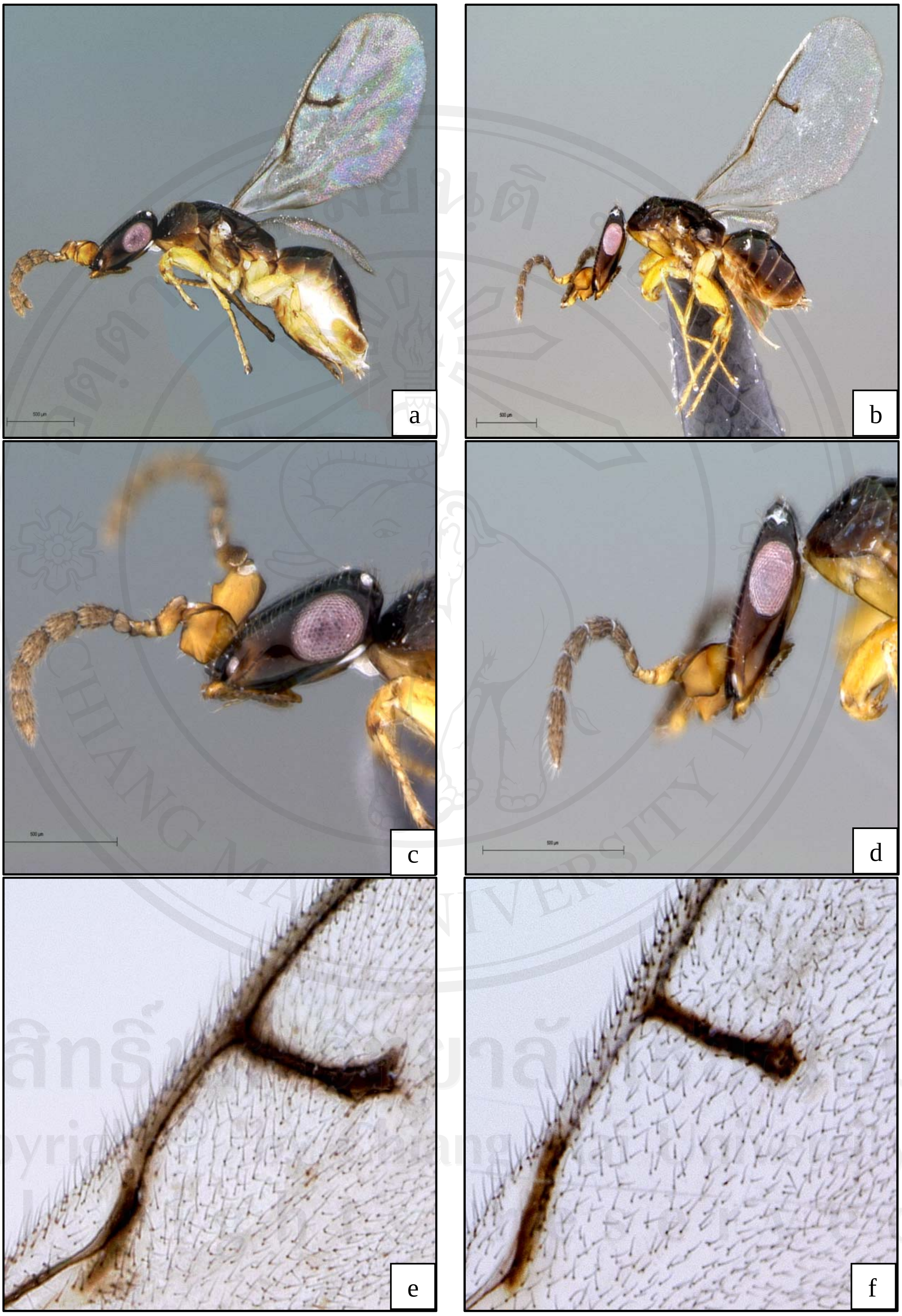
APPENDIX C

THE ILLUSTRATIONS OF THE FIG WASPS DEVELOPING IN FIGS OF *FICUS FULVA* IN DOI SUTHEP-PUI NATIONAL PARK, NORTHERN, THAILAND

(a) female *Valisia compacta*, (b) male *Valisia compacta*, (c) female *Philotrypesis* sp., (d) male *Philotrypesis* sp., (e) female *Sycoscapter* sp. and (f) male *Sycoscapter* sp.

APPENDIX D

THE ILLUSTRATIONS OF THE FIG WASPS DEVELOPING IN FIGS OF *FICUS HISPIDA* IN DOI SUTHEP-PUI NATIONAL PARK, NORTHERN, THAILAND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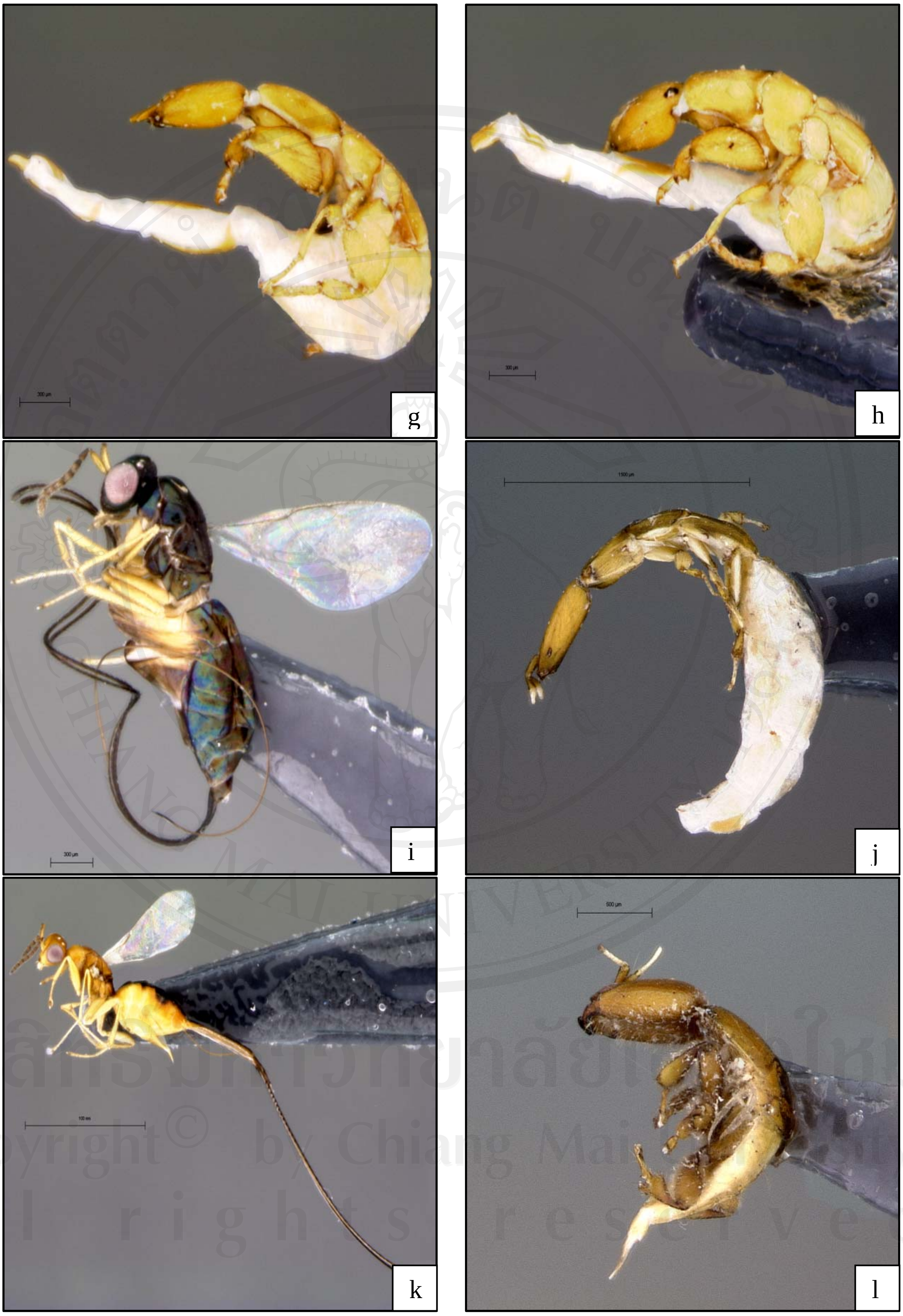
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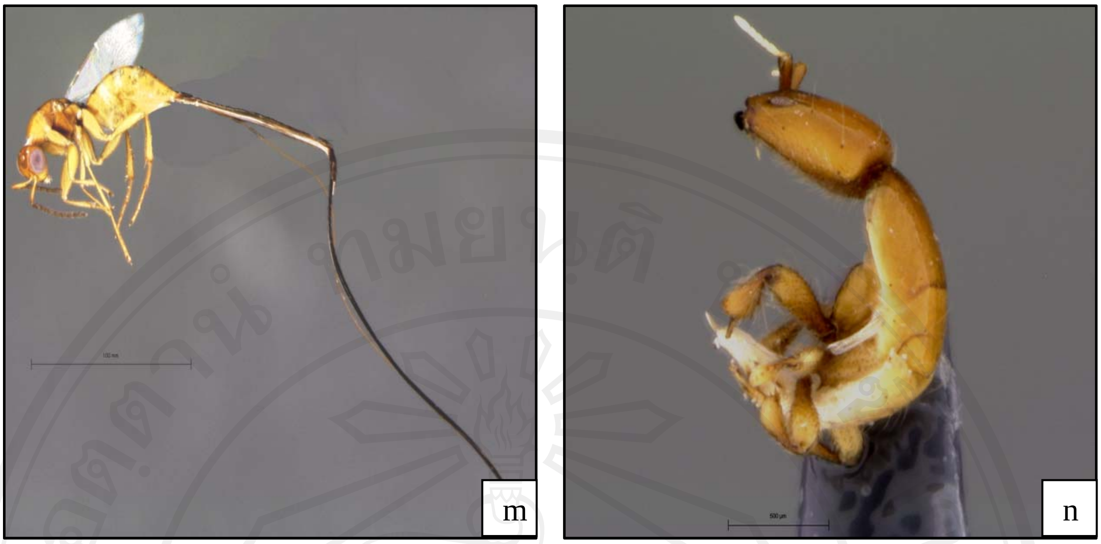
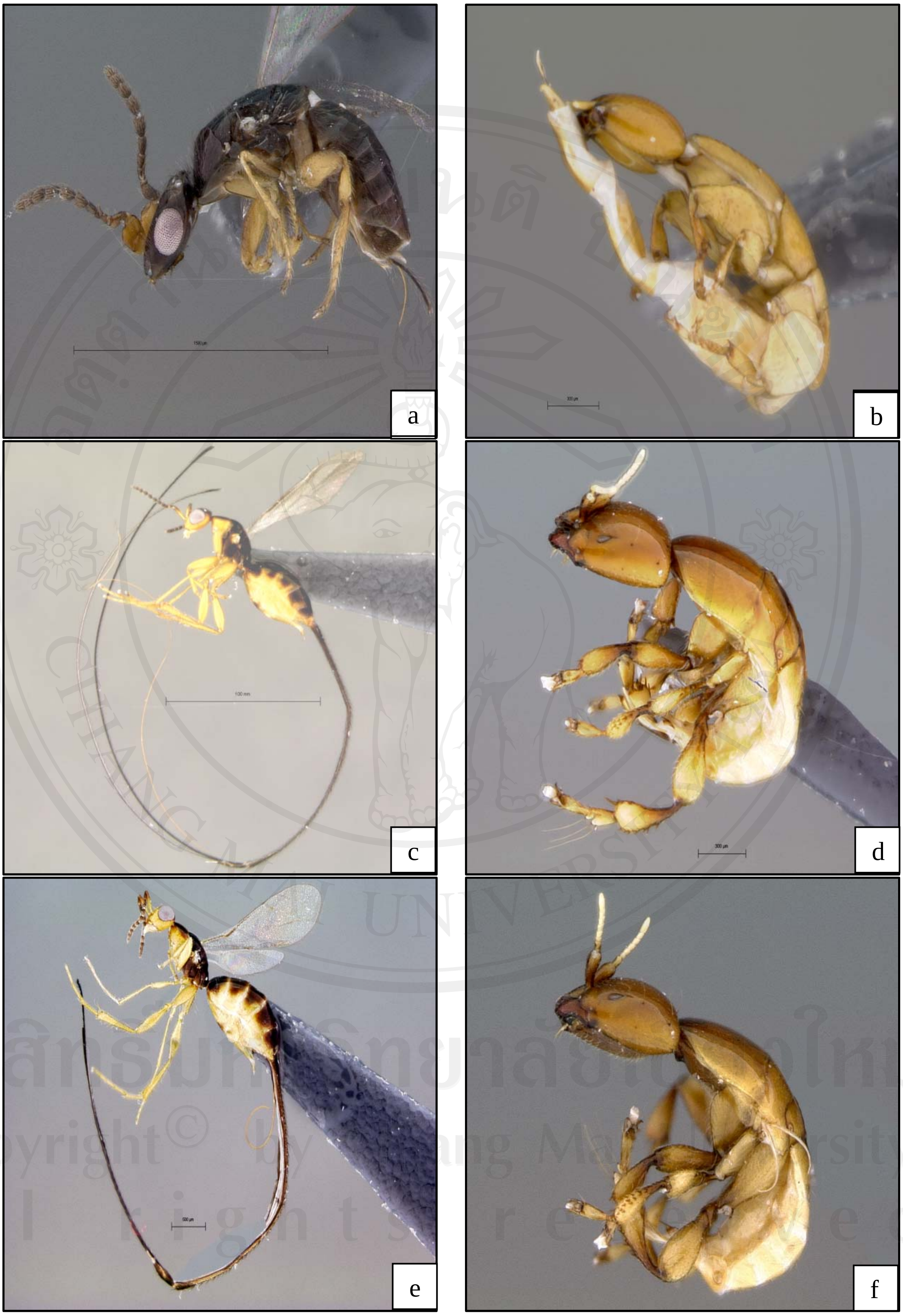


(a) female *Ceratosolen solmsi marchali*, (b) female *Ceratosolen solmsi*, (c) head of *Ceratosolen solmsi marchali*, (d) head of *Ceratosolen solmsi*, (e) venation of *Ceratosolen solmsi marchali*, (f) venation of *Ceratosolen solmsi*, (g) male *Ceratosolen solmsi marchali*, (h) male *Ceratosolen solmsi*, (i) female *Apocrypta bakeri*, (j) male *Apocrypta bakeri*, (k) female *Philotrypesis pilosa*, (l) male *Philotrypesis pilosa*, (m) female *Philotrypesis* sp. and (n) male *Philotrypesis* sp.

APPENDIX E

THE ILLUSTRATIONS OF THE FIG WASPS DEVELOPING IN FIGS OF *FICUS OLIGODON* IN DOI SUTHEP-PUI NATIONAL PARK, NORTHERN, THAILAND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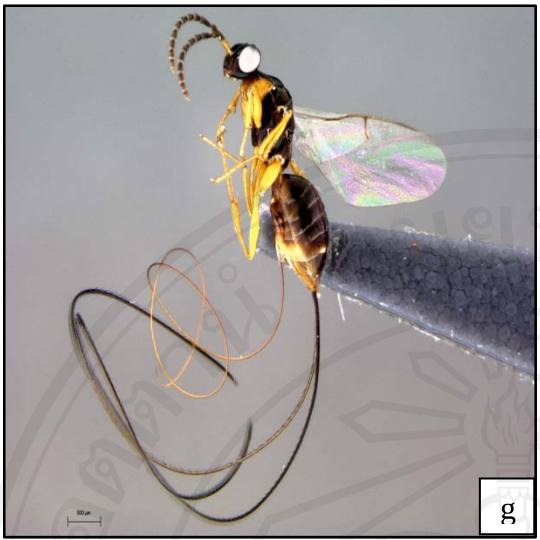
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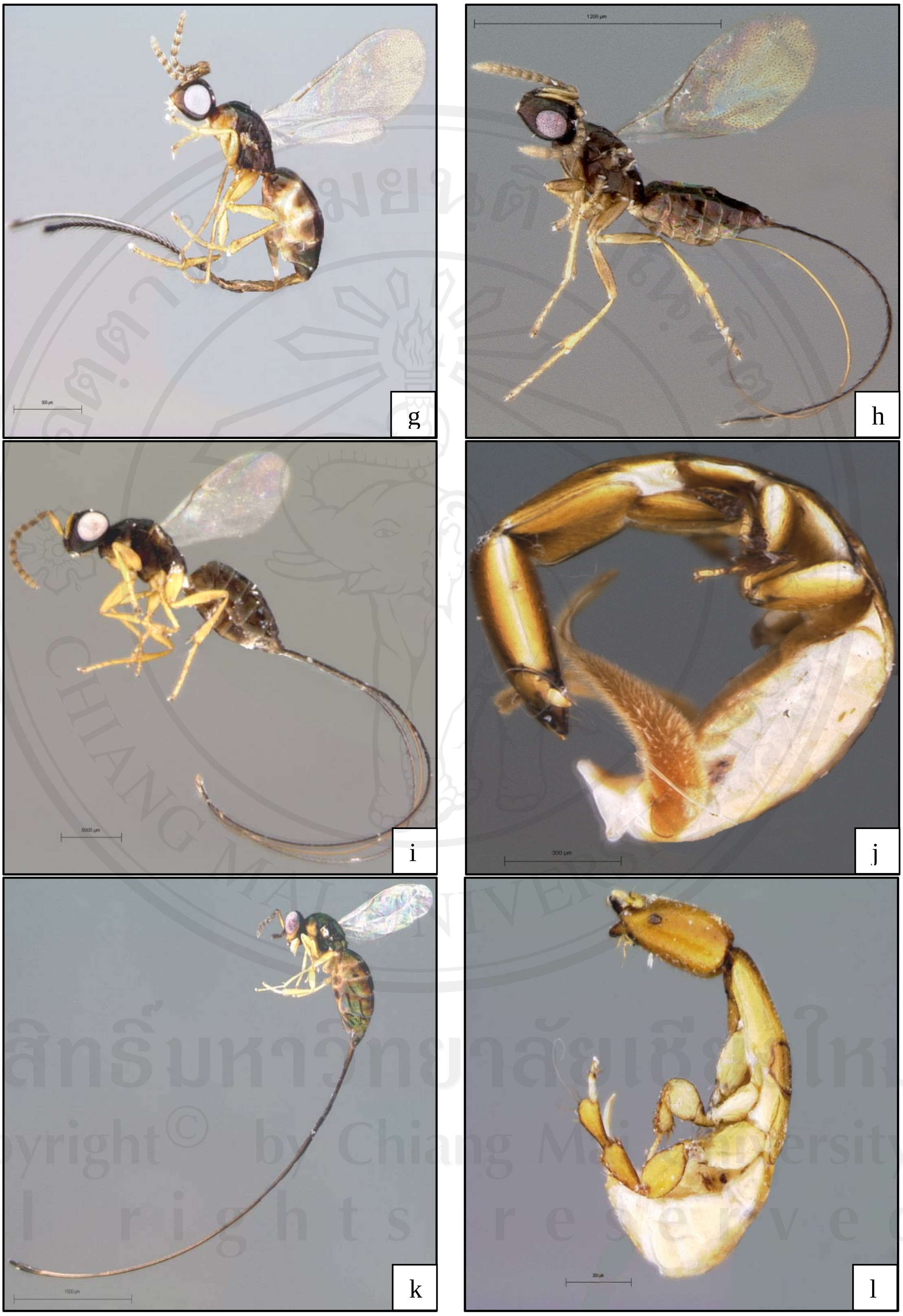
(a) female *Ceratosolen emarginatus*, (b) male *Ceratosolen emarginatus*, (c) female *Philotrypesis longicaudata*, (d) male *Philotrypesis longicaudata*, (e) female *Philotrypesis* sp1, (f) male *Philotrypesis* sp1, (g) female *Platyneura* sp1, (h) male *Platyneura* sp1, (i) female *Platyneura* sp2, (j) male *Platyneura* sp2, (k) female *Sycoscapter roxberghi*, (l) male *Sycoscapter roxberghi* and (m) *Platyneura* which oviposited on the female figs of *F. oligodon* and produced viable offspring.

APPENDIX F

THE ILLUSTRATIONS OF THE FIG WASPS DEVELOPING IN FIGS OF *FICUS SEMICORDATA* IN DOI SUTHEP-PUI NATIONAL PARK, NORTHERN, THAILAND

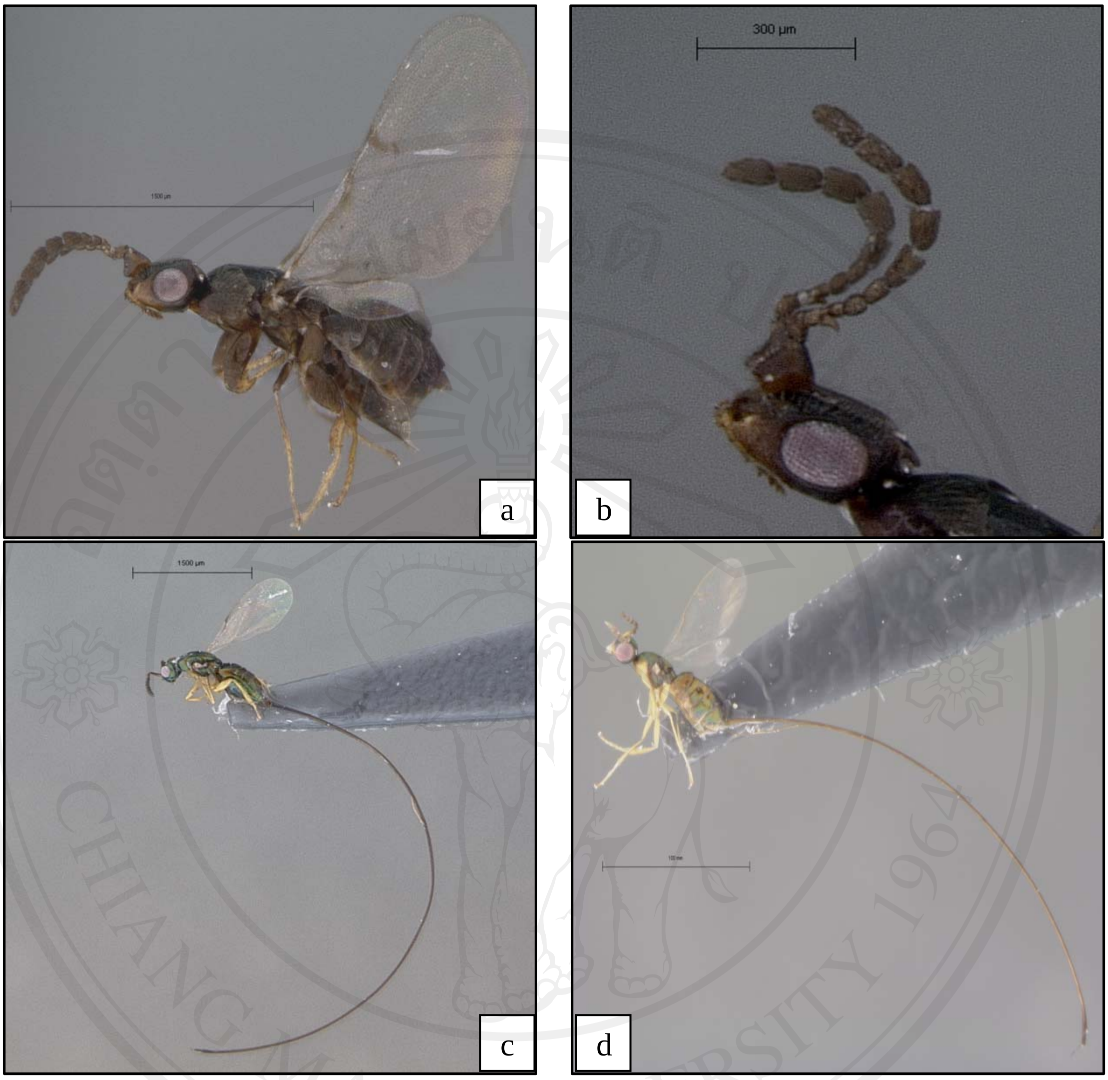
(a) female *Ceratosolen gravelyi*, (b) male *Ceratosolen gravelyi*, (c) female *Apocrypta* sp., (d) male *Apocrypta* sp., (e) female *Philotrypesis dunia*, (f) male *Philotrypesis dunia*.



(g) *Philotrypesis* sp1, (h) *Platyneura* sp1, (i) female *Platyneura cunia*, (j) male *Platyneura cunia*, (k) female *Sycoscapter trifemmensis* and (l) male *Sycoscapter trifemmensis*.

APPENDIX G

THE ILLUSTRATIONS OF THE FIG WASPS DEVELOPING IN FIGS OF *FICUS TRILOBA* IN DOI SUTHEP-PUI NATIONAL PARK, NORTHERN, THAILAND



(a) *Vilisia esquirolianae*, (b) head of *Vilisia esquirolianae*, (c) *Sycoscapter* sp1 and (d) *Sycoscapter* sp2.

APPENDIX H

THE ILLUSTRATIONS OF THE FIG WASPS DEVELOPING IN FIGS OF *FICUS VARIEGATA* IN DOI SUTHEP-PUI NATIONAL PARK, NORTHERN, THAILAND

(a) *Ceratosolen appendiculatus*, (b) *Philotrypesis bimaculata*, (c) *Platyneura spinitarsus* and (d) *Sycoscapter patellaris*.

APPENDIX I

LARVA ECOLOGY OF NON-POLLINATING FIG WASPS FROM THE PREVIOUS STUDIES

Genus	Larval ecology
Apocrypta	1) Parasitoid of pollinator (Abdurahiman and Joseph, 1979; Abdurahiman, 1986; Kerdelhué and Rasplus, 1996; Murray, 1990; Kerdelhué *et al*., 2000; Weiblen *et al*., 2001; Xu *et al*., 2003; Proffit *et al*., 2007; Wang and Zheng, 2008; Peng *et al*., 2005; Sun *et al*., 2008). 2) Parasitoid of *Apocryptophagus* (Godfray, 1988; Weiblen *et al*., 2001; Weiblen, 2002). 3) Parasitoid of *Philotrypesis* (Compton *et al*., 1994; Peng *et al*., 2005). 4) Parasitoid of *Platyneura* (Ulenberg, 1985; Silvieus *et al*., 2007; Sun *et al*., 2008). 5) Inquiline (Galil and Eisikowich, 1968; Pereira *et al*., 2007). 6) Seed predator (Jansen, 1979).
Philotrypesis	1) Inquiline (Baijnath and Ramcharun, 1988; Compton *et al*., 1988; Peng *et al*., 2005; Shi *et al*., 2006; Proffit *et al*., 2007; Pereira *et al*., 2007; Zhai *et al*., 2008; Harrison *et al*., 2008). 2) Cleptoparasite (Abdurahiman, 1986; Cook and Rasplus, 2003). 3) Parasitoid (Abdurahiman, 1986; Godfray, 1988; Compton *et al*., 1994; Murray, 1990; Joseph, 1958 in Jiang *et al*., 2006; Weiblen *et al*., 2001; Silvieus *et al*., 2007).

Genus	**Larval ecology**
Platynuera	1) Gall-maker (Shi *et al*., 2006; Proffit *et al*., 2007; Silvieus *et al*., 2007; Sun *et al*., 2008; Kuaraksa, per. obs., 2009). 2) Parasitoid (Xu *et al*., 2003; Elias *et al*., 2008). 3) Seed predator (Compton *et al*., 1991).
Sycoscapter	1) Inquiline (Shi *et al*., 2006). 2) Parasitoid (Godfray, 1988; Boucek, 1993; Compton *et al*., 1994; Laman and Weiblen, 1998; Weiblen *et al*., 2001; Cook & Lopez-Vaamonde, 2001; Silvieus *et al*., 2007; Tzeng *et al*., 2008). 3) Phytophagous kleptoparasites (Boucek, 1993 in Lopez-Vaamonde *et al*., 2001).

APPENDIX J

ESTABLISHMENT AND MAINTENANCE COSTS OF THREE PLANTING STOCK TYPES WERE RECORDED THROUGHOUT THE STUDY PERIOD (BAHT PER PLANT)

Items	Direct Seeding	Planting stock-raised in nursery from seed	Planting stock-raised in nursery from cutting	Note
Materials				
Germination tray	-	0.09	-	104 holes/20 baht/2 times used
Black plastic bags 2”x5”	-	-	0.13	333 bags/kg/45 baht
Black plastic bags 2.5”x9”	-	0.19	0.19	236 bags/kg/45 baht
Clear plastic bags	-	-	0.25	3 baht/bag, 1 bag contain 12 cuttings
Forest soil	-	0.21	0.21	362.12 cm^{3}x 0.00059 baht
Peanut husk	-	0.13	0.13	181.06 cm^{3} x 0.0007 baht
Coconut husk	-	0.1	0.1	181.06 cm^{3} x 0.0006 baht
Sand	-	0.03*	0.1**	* 47.73 cm^{3} x 0.0008; ** 128.755 cm^{3} x 0.0008 baht
Charred rice husk	-	0.02*	0.07**	* 47.73 cm^{3} x 0.0006 bath; ** 128.755 cm^{3} x 0.006 baht
Osmocote	-	0.04*	0.08**	* 0.3 g, 150 baht/kg, 1 time; ** 0.3 g, 150 baht/kg, 2 times
Rooting hormone	-	-	0.07	1,200 cuttings/80 baht
Bamboo stake	0.25	0.25	0.25	200 stakes/50 baht
Bamboo tube	0.06	-	-	50 tubes/ 3 baht

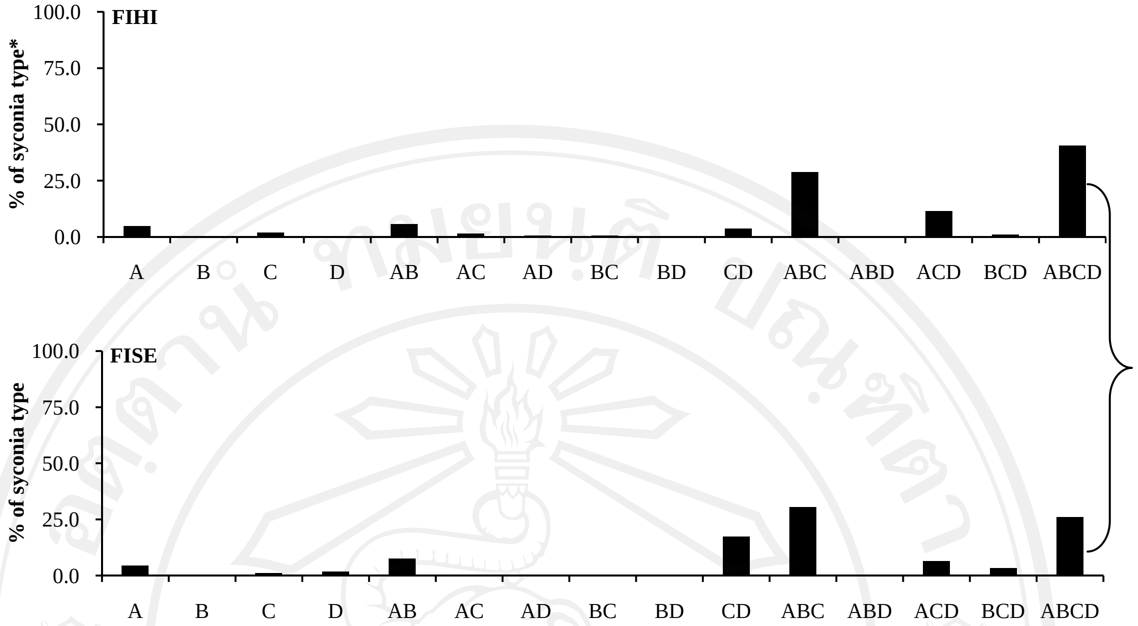
Items	Direct Seeding	Planting stock-raised in nursery from seed	Planting stock-raised in nursery from cutting	Note
Materials				
Rabbit fertilizer	2.4*	5.6**	5.6**	* 50 kg/800 baht/1,000 seedlings, 3 times; ** 7 times
Gasoline	-	0.33	0.33	1,500 seedlings/500 baht
Labor				
Seed collection	0.008	0.008	-	3,000 seeds/hour
Seed preparation	0.016	0.016	-	3,000 seeds/ 2 hours
Seed sowing	1.48*	0.075**	-	* 540 holes/4 persons/4 hours; ** 100 seeds/ 1.5 hours
Cutting collection	-	-	0.25	100 cuttings/ hour/ person
Cutting preparation	-	-	0.33	300 cuttings/4 hours/person
Cutting action	-	-	0.54	216 cuttings/ 4 persons/ 4 hours
Bamboo tube preparing	0.2	-	-	1,000 tubes/ 8 hours/ person
Watering (before potting)	-	1.73	-	10,400 seeds/ 2 hours/ 2 times per day x 180 days
Watering (in propagator)	-	-	7.4	8 times/ 216 cuttings/ 2 persons/ 4 hours
Potting	-	0.4*	0.66**	* 500 seedlings/ 8 hours/ person; ** 300 seedling

Items	Direct Seeding	Planting stock-raised in nursery from seed	Planting stock-raised in nursery from cutting	Note
Labor				
Fertilizing (in nursery)	-	0.06*	0.125**	* 400 seedlings/ hour/ 1 time; ** 2 times
Watering (after potting)	-	1.875*	2.625**	* 2,000 seedlings/ hour/150 days; ** 210 days
Weeding (in nursery)	-	0.2	0.2	500 seedlings/ 4 hours/ person
Grading	-	0.05	0.05	500 seedlings/ hour/ person
Seedling transferring	-	0.8	0.8	1,500 seedlings/ 6 persons/ 4 hours
Driver	-	0.06	0.06	1, 500 seedlings/ 4 hours/ person
Planting	-	2	2	500 seedlings/ 4 hours/ 5 persons
Weeding (after planting)	8.4	8.4	8.4	500 seedlings/ 3 persons/ 8 hours/ 7 times
Fertilizing (after planting)	0.6*	1.4**	1.4**	* 500 seedlings/ 4 hours/ person/ 3 times; ** 7 times

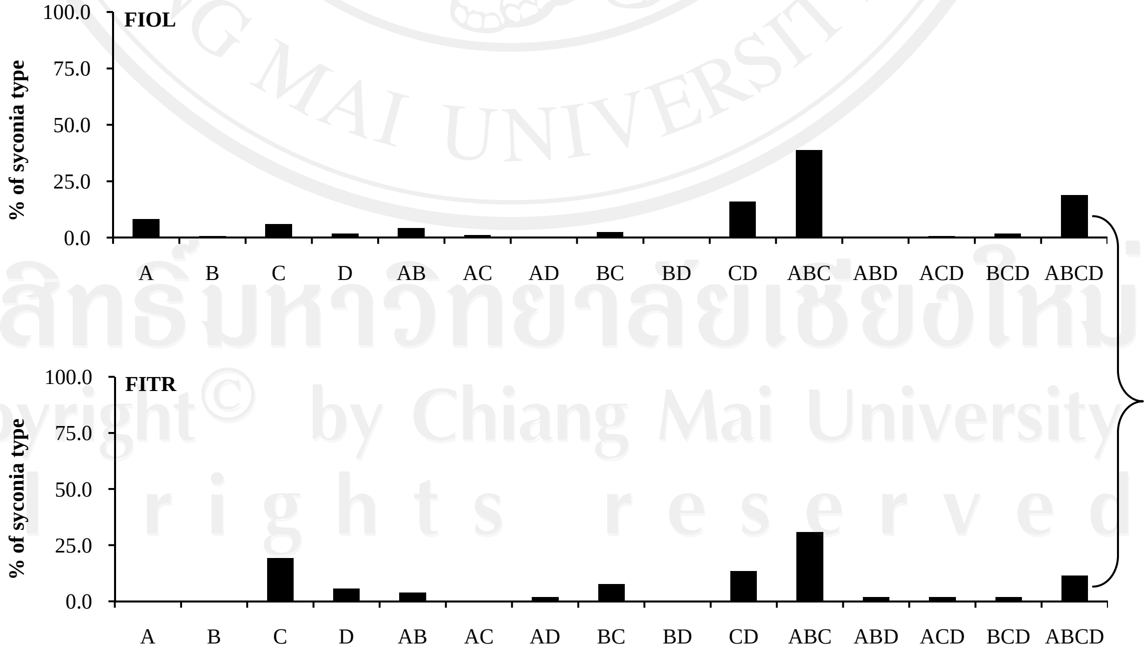
During the period of study, manual cost average 200 baht per day (8 hours).

APPENDIX K

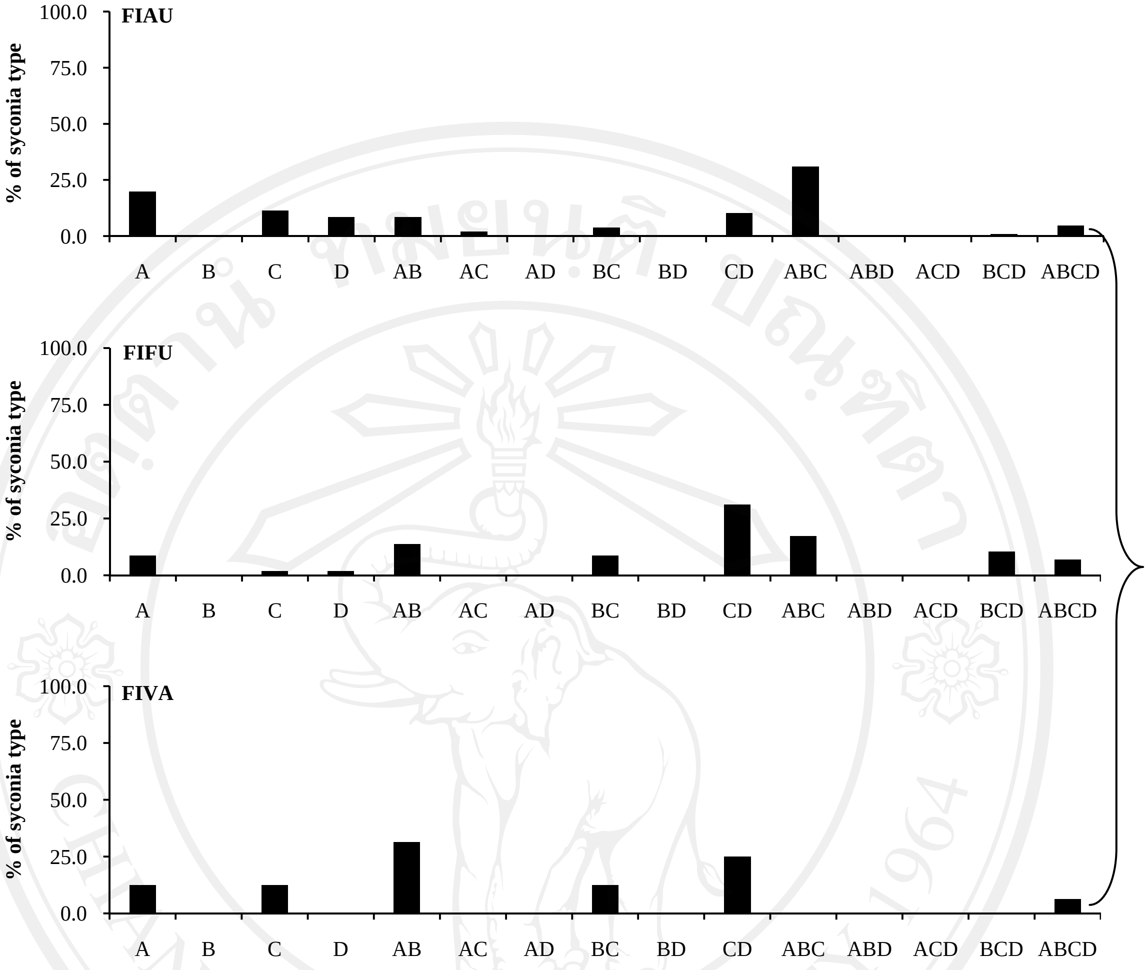
TYPE OF SYCONIA DEVELOPMENTS WITHIN MALE TREES OF SEVEN SELECTED FIG SPECIES



1. Species with high degree of within-tree reproductive asynchrony; A, B, C and D represent syconia in the immature-, receptive-, developing- and releasing-phases, respectively. *= % of individuals of the type in total individual observed.



2. Species with moderate degree of within-tree reproductive asynchrony.



3. Species with low degree of within-tree reproductive asynchrony.

CURRICULUM VITAE

Name	Mr. Cherdsak Kuaraksa
Date of birth	January 10, 1974
Education background	
High School Certificate	Phatthalung School, 1993
B.Sc. (Agriculture)	Department of Agricultural Extension, Faculty of Agriculture, Chiang Mai University, Chiang Mai, Thailand, 50200, 1997
M.Sc. (Biology)	Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai, Thailand 50200, 2002
Work experience	
1997-1998	Researcher Assistant, Chiang Dao Wildlife Sanctuary, Chiang Mai, Royal Forestry Department, Thailand
1998-2002	Researcher, Forest Restoration Research Unit, Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai, Thailand, 50200
2002-2007	Research Manager, Forest Restoration Research Unit, Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai, Thailand 50200

Training course

2001	Propagation of forest tree species, ASEAN-CANADA Forest Tree Seed Centre Project, Muak-Lek, Saraburi, Thailand
2005	Tree Nursery Management, Eden Project, Cornwall, U.K.
2009	Plant-pollinator mutualisms, Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier, France

Fields of speciation

1. Forest restoration
2. Tropical plant ecology
3. Plant propagation, Agroforestry

Publications

Blakesley, D., Anusarnsunthorn, V., Kerby, J., Navakitbumrung, P., **Kuaraksa, C**., Zangkum, S., Hardwick, K. and Elliott, S. 2000. Nursery technology and tree species selection for restoring forest biodiversity in northern Thailand. In: Elliott, S., Kerby, J., Blakesley, D., Hardwick, K., Woods, K. and Anusarnsunthorn, V. (eds.), *Forest restoration for wildlife conservation*. Chiang Mai University, Thailand, pp. 207-222.

Blakesley, D., Elliott, S., **Kuaraksa, C**., Navakitbumrung, P., Zangkum, S. and Anusarnsunthorn, V. 2002. Propagating framework tree species to restore seasonally dry tropical forest: implications of seasonal seed dispersal and dormancy. *Forest Ecology and Management*, 164: 31-38.

Elliott, S. and **Kuaraksa, C**. 2008. Producing framework tree species for restoring forest ecosystems in Northern Thailand. *Small-scale Forestry*, 7(3-4): 403-415.

Elliott, S., Navakitbumrung, P., Zangkum, S., **Kuaraksa, C**., Kerby, J., Blakesley, D. and Anusarnsunthorn, V. 1999. Effects of fertilizer on the performance of six native tree species, planted to accelerate the recovery of biodiversity in a degraded upland watershed. In “Research reports on Biodiversity in Thailand”, published by the Biodiversity Research and Training Program (BRT), Bangkok.

Elliott, S., Navakitbumrung, P., Zangkum, S., **Kuaraksa, C**., Kerby, J., Blakesley, D. and Anusarnsunthorn, V. 2000. Performance of six native tree species, planted to restore degraded forestland in northern Thailand and their response to fertilizer. In: Elliott, S., Kerby, J., Blakesley, D., Hardwick, K., Woods, K. and Anusarnsunthorn, V. (eds.), *Forest restoration for wildlife conservation*. Chiang Mai University, Thailand, pp. 244-255.

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Scholarships

2000	Thailand's Biodiversity Research and Training Program (BRT); “Factors affecting growth of wildlings in the forest and nurturing methods in nursery”.

2007	International Foundation for Science (IFS); “Propagation and field trials of threatened tree species for conservation in northern Thailand”.
2008	The Royal Golden Jubilee Ph.D. Program, Thailand Research Fund.

Presentations

14-16 September 2005	Oral presentation on ‘How to plant a tropical forest’. The Rainforest Gathering Conference, 14-16 September 2005, Eden Project, Cornwall, U.K.
21-23 March 2007	Oral presentation on ‘Seedling production for forest restoration’. Royal Forestry Department Annual Conference, Chiang Mai Empress, Thailand.
1-3 April 2010	Oral presentation on ‘Reproductive ecology and propagation of fig trees (*Ficus* spp.) as framework trees for forest restoration’. RGJ-Ph.D. Congress XI, Jomtein Palm Beach Hotel and Resort, Pattaya, Chonburi, Thailand.
19-23 July 2010	Oral presentation on ‘The use of fig trees (*Ficus* spp.) in forest restoration plantings’. The 2010 International Meeting of the Association for Tropical Biology and Conservation. Sanur-Denpasar, Bali, Indonesia.