

## Phenology of *Ficus racemosa* in Xishuangbanna, Southwest China<sup>1</sup>

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### ABSTRACT

Leaf and fig phenology (including leafing, flowering, and fruiting) and syconium growth of *Ficus racemosa* were studied in Xishuangbanna, China. Leaf fall and flushing of *F. racemosa* occurred twice yearly: in mid-dry season (December to March) and mid-rainy season (July to September). The adult leaf stage of the first leaf production was remarkably longer than that of the second. *F. racemosa* bears syconia throughout the year, producing 4.76 crops annually. Asynchronous fig production was observed at a population level. Fig production was independent of leafing. Fig production peaks were not evident, but fluctuation was clear. Diameter growth rates of syconium were normally higher in early developmental stages than in later stages, and reached a peak coinciding with the female flower phase. The mean  $\pm$  SD of syconium diameter of the female flower phase was  $2.19 \pm 0.36$  cm, and reached  $3.67 \pm 0.73$  cm of the male flower phase. Syconium diameter and receptacle cavity quickly enlarged at the female and male flower phases. Monthly diameter increment of the syconium was primarily affected by average monthly temperature, rather than rainfall or relative humidity.

*Key words:* fig trees; leaf fall; southern Yunnan; syconium.

SEASONAL RHYTHM IS A BASIC CHARACTERISTIC OF LIFE (Zhu & Wan 1975). The study of plant phenology provides knowledge about the patterns of plant growth and development as well as the effects of the environment and selective pressures on flowering and fruiting behavior. The flowering of certain plants signals agronomic time (Richards *et al.* 1996), and changing phenology may also indicate climate change (Penuelas & Filella 2001, Fitter & Fitter 2002). Detailed investigations on plant growth and development can improve our understanding of the strong effects of environmental factors on life-forms in nature.

In contrast to temperate regions, seasonal changes in the tropics are less evident. As a result, individuals of the same plant species are often less synchronous in reproductive and leaf phenology (Richards *et al.* 1996). Asynchronous reproduction and leaf turnover occur in most figs (*Ficus* species), which bear fruit year-round (Galil & Eisikowitch 1968b, Milton *et al.* 1982, Milton 1991, Patel 1997). Figs are therefore very important resources for frugivores when other foods are in short supply, and continuous fruiting may be a mechanism that maintains biodiversity in tropical rain forests (Janzen 1979, Lambert & Marshall 1991, Xu 1994, Nason *et al.* 1998).

Figs have an obligate mutualistic relationship with their species-specific pollinating wasps (Galil & Eisikowitch 1968b, 1971; Ramirez 1969; Wiebes 1979; Herre 1987, 1989; Bronstein 1988, 1999; Patel 1996, 1997; Anstett *et al.* 1997; Ma *et al.* 1997; Herre *et al.* 1999; Kerdelhue & Rasplus 2000; Cook & Lopez-Vaamonde 2001; Hossaert-McKey & Bronstein 2001; Weiblen 2002), and therefore have special phenological characteristics in both monoecious and dioecious species (Galil & Eisikowitch 1968b; Kjellberg & Maurice 1989; Bronstein *et al.* 1990; Khadari *et al.* 1995; Patel 1996, 1997; Kerdelhue *et al.* 2000; Patel & Hossaert-McKey 2000). Fig development is divided into pre-female flower, female flower,

interfloral, male flower, and postfloral phases (Galil & Eisikowitch 1968a). Fig wasps emerge from gall flowers of figs at the male flower phase followed by pollination by the female fig wasps searching for figs in the female flower phase for oviposition (Janzen 1979, Weiblen 2002).

*Ficus racemosa* L. is a common species in Xishuangbanna, with a wide distribution in Southeast Asia (Wu 1995). The species exists in almost all tropical rain forest types in Xishuangbanna. *F. racemosa* is the only Asiatic species belonging to the monoecious section of the subgenus *Sycomorus*, as most *Sycomorus* species occur in Africa (Galil & Eisikowitch 1968a). *Ficus racemosa* is also the only fig species in Xishuangbanna with a leafless phase. *Ficus racemosa* is a large-sized tree species, reaching 25–40 m in height and 60–120 cm in DBH. Owing to a high seed germination rate, large amount of fruit production, fast growth, spreading crowns, and great dimensions, *F. racemosa* is a dominant species in the riverside rain forests of Xishuangbanna. *Ficus racemosa* are also excellent host trees for lac insects. The species is well preserved by local Dai people in accordance with their Buddhist religious traditions (Xu *et al.* 1996). *Ficus racemosa* is a monoecious species, and unisexual flowers develop inside one syconium, with male flowers and female flowers maturing asynchronously. Pollination of *F. racemosa* can only succeed through its fig wasp (Chalcidoidea, Agaonidae, *Ceratosolen fusciceps* Mayr 1885), and the pollinating wasp depends on the fig for habitat to lay eggs and complete their life cycle. Because of this obligate mutual relationship, it may be necessary for *F. racemosa* to regulate its phenology and syconium growth to fit the life cycle of its pollinating wasp, as discovered in other “fig–fig wasp” mutualisms (Herre 1989, Kjellberg & Maurice 1989, Patel 1996, Kerdelhue *et al.* 2000, Patel & Hossaert-McKey 2000, Song *et al.* 2001, Yang *et al.* 2002). However, little is known about the basic ecology and life history of this fig species.

In this paper, we ask the following questions: (1) What are the patterns of leaf and reproductive phenology of *F. racemosa* in Xishuangbanna, and is there a correlation between fruit production

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and leaf-changing as in other species (Routhier & Lapointe 2002)?; (2) What is the growth pattern of syconium in *F. racemosa*, and what is the syconium diameter when pollinators enter the receptacle through the ostioles, and wasps emerge from the syconium?; and (3) Does the fig–fig wasp system respond to local seasonal change? Understanding these questions may contribute to our understanding of the propagation (Richards *et al.* 1996, West *et al.* 2000, 2001; Otero-Arnaiz & Oyama 2001), plant–insect interactions (Corlett 1987, Kjellberg & Maurice 1989, Windsor *et al.* 1989), coevolution, and effects of climate change (Gunster 1994, Morellato & Leitao-Filho 1996, Corlett & Lafrankie 1998, Harrison 2000, 2001) on the fig–fig wasp mutualism, and perhaps provide constructive suggestions for the conservation of biodiversity in the tropics.

## METHODS

Xishuangbanna has a typical tropical monsoon climate which is alternately dominated by a warm–wet air mass off the Indian Ocean during the summer and a continental air mass of subtropical Asia during the winter. This weather pattern results in an annual rainy (May to October) and dry (November to April) seasons (Zhang 1963, Cao *et al.* 2006). Field investigations were conducted in the vicinity of the town of Menglun (21°41'N, 101°25'E), in northern Mengla County. Study sites were covered with fragmented riverside rain forest characterized by *Bombax malabarica*, *F. racemosa*, and several species of bamboo (Cao & Zhang 1997, Zhu *et al.* 2006).

**LEAFING AND FIG PRODUCTION.**—Leafing and fig production (including flowering and fruiting) of six large mature individuals of *F. racemosa* were monitored every 5 d from January 2000 to January 2002, and the same phenological characteristics of an additional 14 trees were recorded from January 2001 to January 2002. For fig production we followed the procedures suggested by Galil and Eisikowitch (1968a) and divided the developmental period into five phases (Table 2). Thirty syconia of each tree were collected for dissecting and determining the stages of development. Leafing and fig production were determined by scores according to the rules stated in Figure 1.

**SYCONIUM GROWTH PATTERN.**—Sixty syconia of each of the six trees were collected at regular 10-d intervals from January 2000 to March 2001. Size parameters were measured for 30 syconia from each collection. For external size, two vertical diameters and one axial length of a syconium were measured with a caliper. The syconium was then split into quarters through the pole, and four measurements of the thickness of flank-fig-wall were taken. Thickness of the fig wall near the ostiole was also measured. The remaining 30 syconia were used to determine dry weight after oven-drying at 120°C. The fig sizes suitable for pollination and pollinator emergence, syconia internal and external color, and the pollinator associated with each syconium were also investigated. In the period from 3 March to 13 May 2000, the thickness of the female flower layer and bract layer along the axial line of syconium were also surveyed. Meteorological data

including air temperature, relative humidity, and rainfall were obtained from Xishuangbanna Tropical Rainforest Ecosystem Station near the study site.

## RESULTS

**LEAFING AND FIG PRODUCTION.**—Based on the visual observation of 20 individuals of *F. racemosa*, leaf fall and flushing occurred twice a year: once during the mid-dry season (December to March) and again during the mid-rainy season (July to September). The green adult leaf stage of the first leaf production was much longer than that of the second (Table 1).

*Ficus racemosa* bore fruit crops several times throughout the year. For trees 1 through 6, the number of crop-bearing times in 25 mo were 8, 11, 9, 12, 10.2, and 10.5, respectively (Fig. 1). Thus, *F. racemosa* usually bears crops 4.76 times a year. Fig production asynchrony in the population was obvious. Fig production seems to act independent of leafing. Peak fruit production was not evident; however, fluctuations were clear. Generally, a relatively small production episode followed a mass-production episode and eventual decline. Syconia production curves varied among trees of different ages. Young trees produced smaller crop sizes than middle-aged trees. The middle-aged trees usually bore the largest amount of syconia, while the very old trees had a lower production. Abortion of young syconia occurred on several occasions, including tree 1 in the middle of June 2001, tree 4 in the first 10 d of March 2000, and tree 6 in the last 10 d of November 2000, and again over the last 10 d of May 2001.

*Ficus racemosa* had normal syconium development while individuals were in leafless stages. For instance, tree 1 in the first 10-d period of December 2001, and tree 6 in the first half of January 2001 and the second half of December 2001. In addition, some trees started producing new syconia while some immature syconia of the previous crop were still on the tree.

**SYCONIUM DEVELOPMENT.**—According to Galil and Eisikowitch (1968a), the development of syconia is divided into five phases: phase A (pre-female), phase B (female), phase C (interfloral), phase D (male), and phase E (postfloral). The duration of each phase in *F. racemosa* was identified by dissecting the syconia and identifying the characteristics of the syconium and pollinating wasps. Developing phases of syconium were considerably longer in the foggy–cool season (Table 2).

Diameter and axial length growth of syconia were highly correlated ( $r = 0.98$ ,  $N = 5762$ ) and were in a very strong synchronous rhythm. The values of diameter and axial length of syconium were almost equal, and the average diameter/length of axial ( $D/L$ ) ratio was  $1.07 \pm 0.10$  ( $N = 5762$ ).

Syconium diameter increment was highly variable during different developmental phases and seasons. Syconium diameter increase was higher in early developmental phases (including phase A, phase B, and early phase C) than in later phases, and reached a peak around phase B, the female flower phase (Fig. 2). The average ( $\pm$ SD) diameter of syconium at the female flower phase when

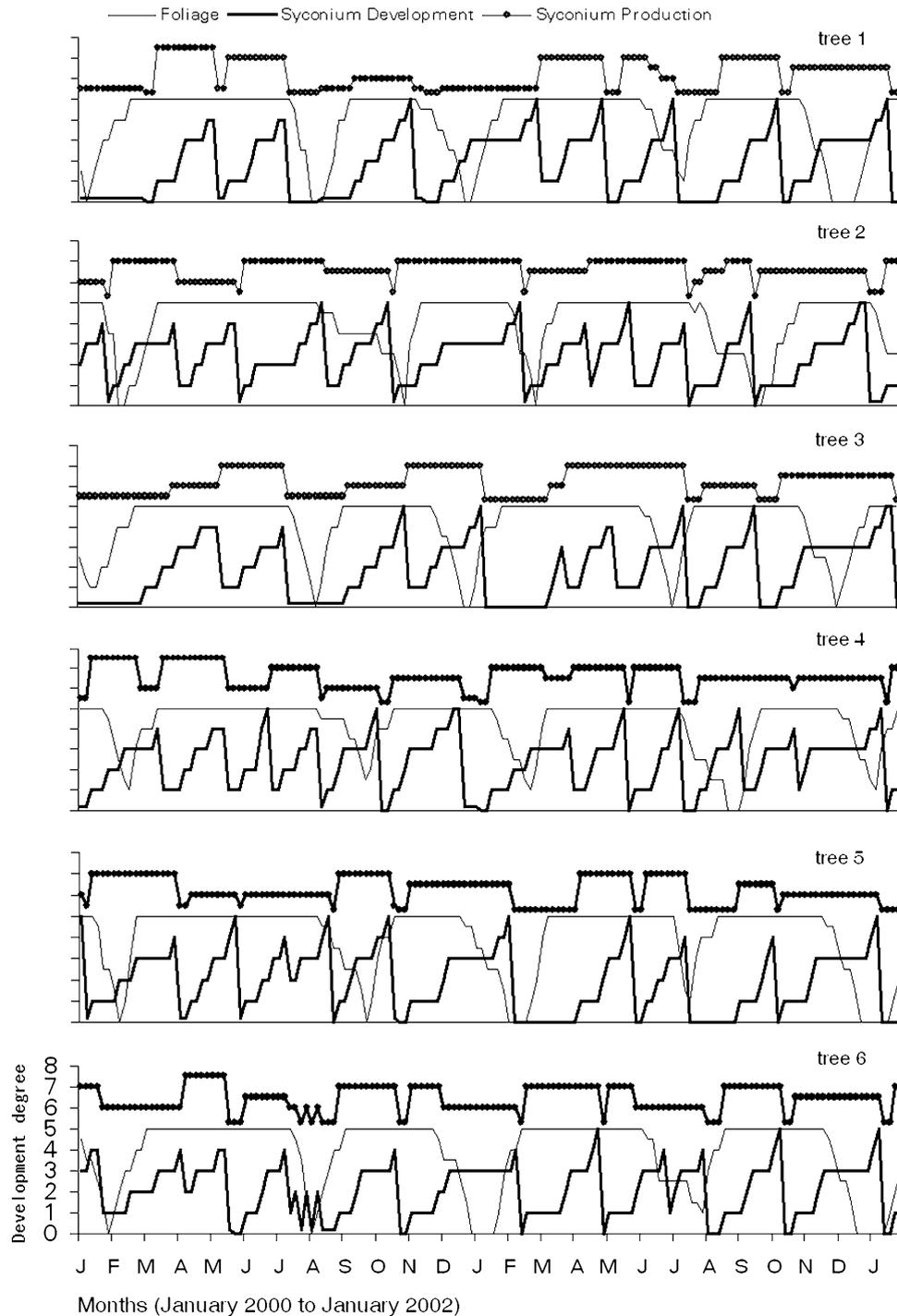


FIGURE 1. Leaf and fig production rhythms of *Ficus racemosa*. Development phase scoring: leafless = 0, bud-break = 1, leaf-bud opened = 2, beginning of leaf expansion = 3, peak leaf expansion = 4, leaf matured = 5, leaf yellow = 4.5, beginning of leaf fall = 3.5, peak of leaf fall = 2.5, end of leaf fall = 1.5; no syconia on the tree = 0, a few syconia = 0.2, pre-female phase = 1, female phase = 2, interfloral phase = 3, male phase = 4, postfloral phase = 5; no syconia production = 5.3, very few production = 5.5, a few production = 6, not so much production = 6.5, much production = 7, very much production = 7.5.

pollinating wasps enter the syconia was  $2.19 \pm 0.36$  cm ( $N = 246$ ). The diameter of syconium at the female flower phase during the dry-warm season was the largest, and differed from the foggy-cool or rainy season significantly. However, the diameter of syconium

at the male flower phase when fig wasps emerge was smallest in the dry-warm season, followed by the rainy and foggy-cool seasons (Fig. 3). Mean  $\pm$  SD of syconium diameter when fig wasps emerged from the syconia was  $3.67 \pm 0.73$  cm ( $N = 647$ ).

TABLE 1. Duration of leaf-changing stages of *Ficus racemosa* ( $d$ ; Mean  $\pm$  SD),  $N = 28$  plants.

	Leaf-bud flushing	Leaf expanding	Mature leaf	Color changing	Leaffall	Leafless
First cohort (December to March)	7.7 $\pm$ 4.8	13.0 $\pm$ 7.1	132.0 $\pm$ 30.1	7.5 $\pm$ 3.5	19.0 $\pm$ 11.0	6.0 $\pm$ 7.9
Second cohort (July to September)	5.1 $\pm$ 2.0	13.0 $\pm$ 6.0	76.0 $\pm$ 25.0	8.4 $\pm$ 6.7	13.0 $\pm$ 18.0	9.2 $\pm$ 9.1

INCREMENT OF THE FIG WALL THICKNESS.—Because it is impossible to preserve a fig while measuring its wall thickness (that requires cutting the syconium), we tested whether syconium diameter might be used to predict the wall thickness. Thus, two significant regression equations were calculated: a linear function expression for the flank-fig-wall (equation (1);  $R^2 = 0.88$ ), and an exponential expression for the fig wall near the ostiole (equation (2);  $R^2 = 0.80$ ; Fig. 4).

$$T_f = 0.1436D + 0.0329 \quad (1)$$

$$T_o = 0.1646D^{0.8278} \quad (2)$$

Here,  $T_f$  is the thickness of flank-fig-wall,  $T_o$  is the thickness of fig wall near the ostiole, and  $D$  is the diameter of fig syconium ( $D < 6.18$ ).

DRY WEIGHT ACCUMULATION OF SYCONIUM.—Dry weight of syconium includes two elements: the dry weight of the inflorescence

TABLE 2. Duration and characteristics of syconium developing phases of *Ficus racemosa*.

Syconium developing phase	Sequence of events	External appearances and internal characteristics	Duration (d)		
			Dry-warm season ( $N = 12$ )	Rainy season ( $N = 14$ )	foggy-cool season ( $N = 6$ )
Phase A (pre-female)	Newly formed syconia swell rapidly, female flowers develop, male flowers remain in anlage	Syconia are small ( $D < 2.19$ cm) and delicate green, with tightly closed ostiolar bracts. In the early stage, the syconium cavity is nearly full of bracts, later, it enlarges, and stigma color changes from pistachio to pink	23.17 $\pm$ 11.39	17.93 $\pm$ 5.17	19.50 $\pm$ 5.50
Phase B (female)	Female flowers within individual syconia are receptive to pollen. Pollinator wasps enter syconia, lay eggs, and complete pollination, and then die in the syconia	Syconia are bright green, small white spots can be seen on the surface, ostioles are relatively loose, syconia are odoriferous. Stigmas inside the receptacle become white	5.11 $\pm$ 1.01	2.23 $\pm$ 0.00	8.69 $\pm$ 3.13
Phase C (interfloral)	Each wasp larva feeds on the contents of one ovule, and seeds develop in syconia. Male flowers develop quickly into the visual form	Syconia become bottle green, with beige spots on the surface. In the middle of this phase, watery fluid is produced in the cavity of syconia then disappears. At the later stage of this phase, syconia become yellow	28.58 $\pm$ 6.05	21.86 $\pm$ 4.31	44.67 $\pm$ 17.34
Phase D (male)	Mature offspring of fig wasps emerge and mate within the natal syconium. Simultaneously, male flowers mature, producing pollen. Female pollinating wasps collect pollen from the newly mature anthers and exit the syconium from the hole chewed by male wasps and search for other receptive syconia to lay eggs	Syconia become rose-red and somewhat soft, the cavities of them are dry. Inside the cavities, there are fig pollinating wasps and some other species of parasitic wasps	2.36 $\pm$ 0.00	1.58 $\pm$ 0.00	5.21 $\pm$ 0.82
Phase E (postfloral)	Seeds in the syconia mature, the syconia become soft and fleshy and attractive to dispersers	Syconia become amaranth, eventually abscise from trees, many species of birds, mammals, ants, butterflies, and other animals eat them	5.20 $\pm$ 0.94	4.11 $\pm$ 0.03	7.03 $\pm$ 1.98

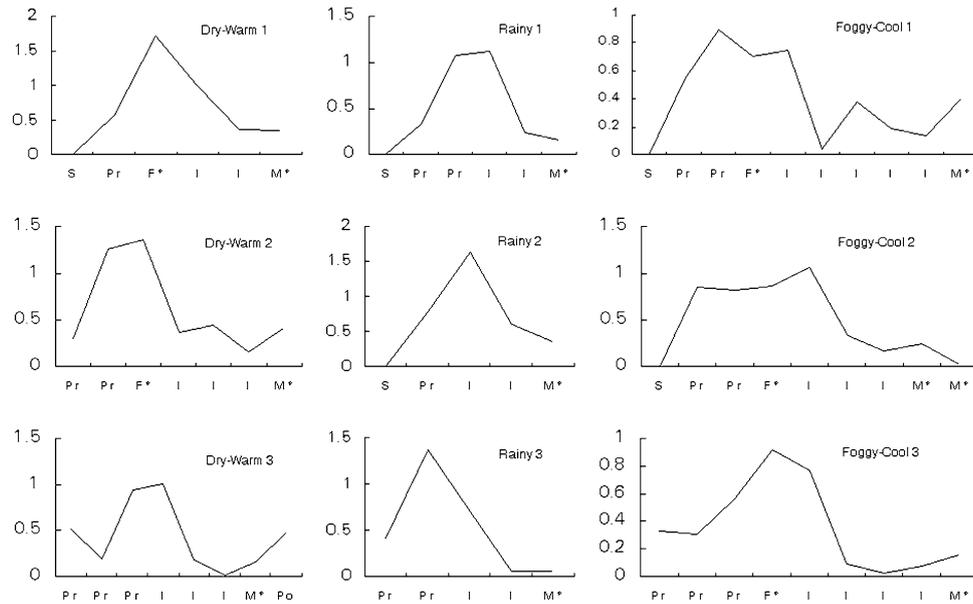


FIGURE 2. Diameter growth rates (cm/10 d,  $N = 30$ ) of syconia of three randomly sampled trees in different seasons. Here, S is the starting of syconia initiation, Pr is pre-female, F\* is female, I is inter floral, M\* is male, and Po is postfloral phase.

and the dry weight of the wasps within. Dry weight (g) of *F. racemosa* syconium showed a significant exponential relationship with diameter (Fig. 5):

$$W_d = 0.1037 D^{2.4386} \quad (3)$$

where  $W_d$  is the dry weight of a syconium, and  $D$  is the diameter of a syconium ( $R^2 = 0.89$ ;  $D < 5$ ).

Furthermore, correlation analysis indicated that temperature is the major environmental factor associated with syconium growth. The correlation coefficients of average monthly diameter increase with average monthly temperature, average monthly air relative

humidity, and monthly amount of rainfall were 0.73, 0.36, and 0.61 ( $N = 15$ ), respectively.

## DISCUSSION

Compared with *Ficus variegata* and most other tropical *Ficus* tree species (Windsor *et al.* 1989, Richards *et al.* 1996, Spencer *et al.* 1996), *F. racemosa* in Xishuangbanna produces two cohorts of leaves per year rather than one, and renews leaves continuously by alternation. Two mechanisms may explain the observed pattern in leaf

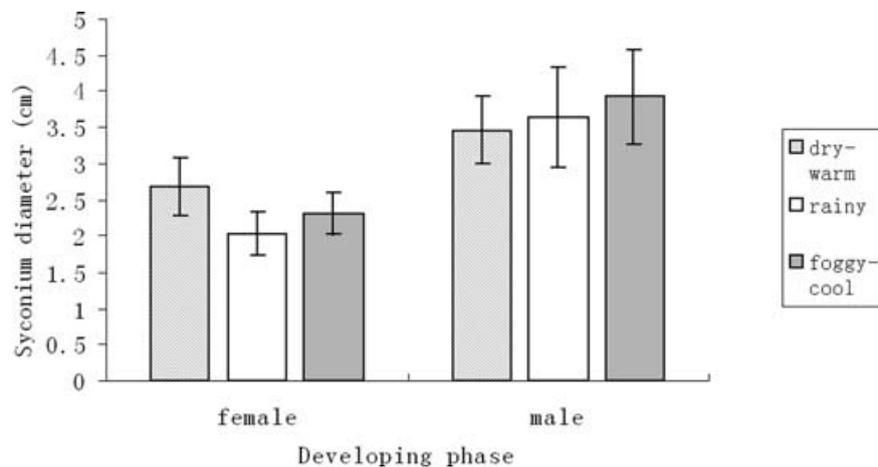


FIGURE 3. Syconia diameter (mean  $\pm$  SD;  $N = 110$ ) at female and male phases in dry-warm, rainy, and foggy-cool seasons.

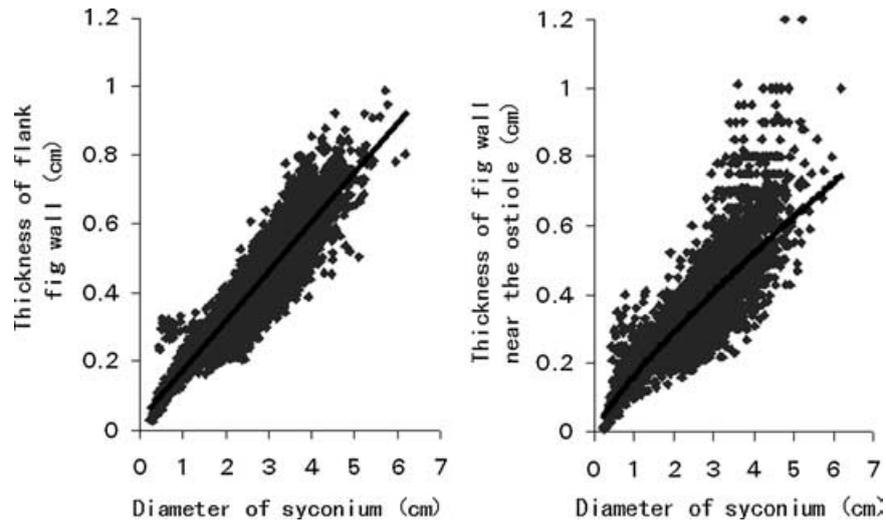


FIGURE 4. The linear regression of fig wall thickness to diameter ( $N = 5762$ ).

phenology. First, intracrown fruiting synchrony might be necessary for monoecious figs such as *F. racemosa* to avoid inbreeding depression. Coinciding with patterns of reproductive phenology, regular leaf replacement may have evolved in order to supply sufficient photosynthetic materials for reproductive structures. Second, leaf phenology of this fig species could be an adaptation to local climate as Xishuangbanna is in the northernmost region of tropical Southeast Asia, and there is a marked dry season. It is still unclear,

however, why *F. racemosa* turns over leaves in the middle of the rainy season in Xishuangbanna. Future studies are needed to determine the principle drivers of leaf phenology. Despite the general leaf phenology of *F. racemosa*, an individual display may reflect microhabitat characteristics and age of the tree.

The unique flowering pattern in *F. racemosa* of dichogamy within one syconium and asynchrony at the population level has been described as a common feature in monoecious figs (Galil & Eisikowitch 1968b, Bronstein 1988, Bronstein *et al.* 1990). The evolutionary significance of this trait is mainly to avoid self-fertilization. However, the selective force in the reproductive success of this kind of fig species is the availability of receptive syconia within a distance that pollinating wasps are capable of flying. Thus, a number of individuals are needed within a local fig population in order to maintain the pollinator population (Bronstein *et al.* 1990). If not, young syconia abortion and local wasp extinction are both inevitable (Kjellberg & Maurice 1989). Fluctuations in syconia production for *F. racemosa* indicated that the possibility of successful pollination may limit fig crop size.

*F. racemosa* provides food and habitat for the many species of birds, mammals, and insects that were observed around trees when syconia matured (Yang *et al.* 1997). As a keystone resource in tropical rain forests, figs, particularly the species with high fruit production such as *F. racemosa*, *F. sycomorus*, and *F. hispida*, contribute to the maintenance of biodiversity in tropical rain forest systems by supplying abundant foods to frugivores, soil animals, and microbes, thus strengthening the food web in the forest ecosystem (Kimura *et al.* 2001, Shanahan *et al.* 2001).

The pattern of syconium diameter increment indicated that the syconium growth process of *F. racemosa* has a close relationship with parasitic wasps (and its pollinator), because the increase rate was remarkably higher in phase A than phase C when wasps had already invaded the syconia. This was likely the result of resource competition between wasps and the inflorescence itself. A great number

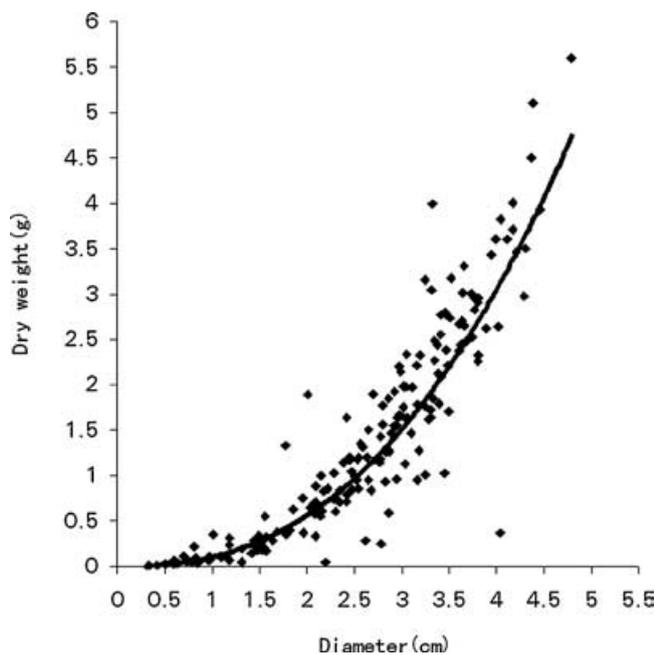


FIGURE 5. Dry weight accumulation of a syconium in the gradient of diameter increasing ( $N = 186$ ).

of wasp larvae (usually several hundred to over one thousand) need large amounts of nutrients for their development.

Thickness of the fig walls might be important for wasps. In the period of phase B (female flower phase), several species of nonpollinating wasps attempt to oviposit through the fig wall. Thus the thickness of the fig wall may be a limiting factor to the reproduction of other parasitic wasps. At phase D (male flower phase), emergence channels must be excavated by male wasps in order to allow the female wasps to exit. Therefore, fig wall thickness could be a limiting factor to the wasp exiting process too.

The corresponding enlargement of syconium diameter and receptacle cavity indicates that the fig–fig wasp interaction is highly evolved. Along the development process of a syconium, two peaks of diameter increase were observed around the critical time for the fig–fig wasp interaction, phase B, plant pollination and wasp oviposition, and phase D, where insects mate and pollen is dispersed by the female wasps. A relatively large cavity at phase B may increase the female fitness of the fig and pollinating wasp. A large cavity at phase D may enhance the male fitness of the fig through more active and sufficient pollen collection by female pollinating wasps, and also offers adequate space for wasps to mate, increasing fecundity.

Due to the short life cycles of fig wasps, and short growth cycle of syconium, the fig–fig wasp symbiosis is an excellent model for studies in ecology and climate change. Yearly change in the phenology of *F. racemosa* may shed light on the effects of climate change on the mutualism of fig and fig pollinating wasp.

The duration of a syconium growth cycle of *F. racemosa* was much longer in the foggy–cool season (winter) than in the rainy season (summer) in Xishuangbanna (Table 2). The key developing stage in fig–fig wasp symbiosis is phase B, when the two partners interact. There were several long phase B periods distributed throughout the year. The limiting factor in the dry–warm season might be high temperatures that restrict the flying and other activity of wasps. In the rainy season, downpour may be the main limiting factor, and in the foggy–cool season, population size of fig may pass through a bottleneck. Climate change trends predicted for the transitional tropical region are more seasonally restricted rainfall, prolonged dry season, and higher rainfall intensity. These changes in climate trends could potentially exacerbate the limiting factors to the reproductive success of the figs and fig pollinating wasps, especially at phase B. Climatic changes and local bottlenecks in syconium and pollinating wasp production could threaten the stability of the mutualism (Patel 1996, Corlett & Lafrankie 1998, Harrison 2000, 2001). However, the capability of adjustment and adaptation of figs and fig wasps may be underestimated. Does the mutualism between figs and fig wasps have enough flexibility to adapt the climate change in the future? Although climate change may threaten the fig–fig wasp mutualism, human disturbance to natural ecosystems may be more problematic. Further studies on the detailed life history of fig pollinating wasps, including chemical ecology, physiology, and molecular-level phylogeny, could greatly improve the understanding of the coevolutionary mechanism of figs and their pollinating wasps, and prompt the better conservation of natural ecosystems.

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## LITERATURE CITED

- ANSTETT, M. C., M. HOSSAERT-MCKEY, AND F. KJELLBERG. 1997. Figs and fig pollinators: Evolutionary conflicts in a coevolved mutualism. *Trends Ecol. Evol.* 12: 94–99.
- BRONSTEIN, J. L. 1988. Limits to fruit production in a monoecious fig: Consequences and obligate mutualism. *Ecology* 69: 207–214.
- BRONSTEIN, J. L. 1999. Natural history of *Anidarnes bicolor* (Hymenoptera: Agaonidae), a galler of the florida strangling fig (*Ficus aurea*). *Florida Entomologist* 82: 454–461.
- , P. H. GOUYOU, C. GLIDDON, F. KJELIBERG, AND G. MICHLOUD. 1990. The ecological consequences of flowering asynchrony in monoecious figs: A simulation study. *Ecology* 71: 2145–2156.
- CAO, M., AND J. H. ZHANG. 1997. Tree species diversity of tropical forest vegetation in Xishuangbanna, SW China. *Biodiv. Conserv.* 6: 995–1006.
- , X. ZOU, M. WARREN, AND H. ZHU. 2006. Tropical forests of Xishuangbanna, China. *Biotropica* 38: 306–309.
- COOK, J. M., AND C. LOPEZ-VAAMONDE. 2001. Fig biology: Turning over new leaves. *Trends Ecol. Evol.* 16: 11–13.
- CORLETT, R. T. 1987. The phenology of *Ficus fistulosa* in Singapore. *Biotropica* 19: 122–124.
- , AND J. V. LAFRANKIE JR. 1998. Potential impacts of climate change on tropical Asian forests through an influence on phenology. *Climatic change* 39: 439–453.
- FITTER, A. H., AND R. S. R. FITTER. 2002. Rapid changes in flowering time in British plants. *Science* 296: 1689–1691.
- GALIL, J., AND D. EISIKOWITZ. 1968a. On the pollination ecology of *Ficus sycamorus* in east Africa. *Ecology* 49: 259–269.
- , AND ———. 1968b. Flowering cycles and fruit types of *Ficus sycamorus* in Israel. *New Phytol.* 67: 745–758.
- , AND ———. 1971. Studies on mutualistic symbiosis between syconia and sycophilous wasps in monoecious figs. *New Phytol.* 70: 773–787.
- GUNSTER, A. 1994. Phenological niches of coexisting serotinous plants in the Mamib Desert. *J. Trop. Ecol.* 10: 531–544.
- HARRISON, R. D. 2000. Repercussions of El Niño: Drought causes extinction and the breakdown of mutualism in Borneo. *Proc. R. Soc. Series B* 267: 911–915.
- . 2001. Drought and the consequences of El Niño in Borneo: A case study of figs. *Popul. Ecol.* 43: 63–76.
- HOSSAERT-MCKEY, M., AND J. L. BRONSTEIN. 2001. Self-pollination and its costs in a monoecious fig (*Ficus aurea*, Moraceae) in a highly seasonal subtropical environment. *Am. J. Bot.* 88: 685–692.
- HERRE, E. A. 1987. Optimality, plasticity and selective regime in fig wasp sex ratio. *Nature* 329: 627–629.
- . 1989. Coevolution of reproductive characteristics in 12 species of New World figs and their pollinator wasps. *Experientia* 45: 637–647.
- , N. KNOWLTON, U. G. MUELLER, AND S. A. REHNER. 1999. The evolution of mutualisms: Exploring the paths between conflict and cooperation. *Trends Ecol. Evol.* 14: 49–53.

- JANZEN, D. H. 1979. How to be a fig? *Ann. Rev. Ecol. System.* 10: 13–51.
- KERDELHUE, C., AND J. Y. RASPLUS. 1996. Non-pollinating Afrotropical fig wasps affect the fig–pollinator mutualism in *Ficus* within the subgenus *Sycomorus*. *Oikos* 75: 3–14.
- , J. P. ROSSI, AND J. Y. RASPLUS. 2000. Comparative community ecology studies on Old World figs and fig wasps. *Ecology* 81: 2832–2849.
- KHADARI, B., M. GIBERNAU, M. C. ANSTETT, F. KJELLBERG, AND M. HOSAERT-MCKEY. 1995. When figs wait for pollinators: The length of fig receptivity. *Am. J. Bot.* 82: 992–999.
- KIMURA, K., T. YUMOTO, AND K. KIKUZAWA. 2001. Fruiting phenology of fleshy-fruited plants and seasonal dynamics of frugivorous birds in four vegetation zones on Mt. Kinabalu, Borneo. *J. Trop. Ecol.* 17: 833–858.
- KJELLBERG, F., AND S. MAURICE. 1989. Seasonality in the reproductive phenology of *Ficus*: Its evolution and consequences. *Experientia* 45: 653–660.
- LAMBERT, F. R., AND A. G. MARSHALL. 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *J. Ecol.* 79: 793–809.
- MA, W. L., Y. CHEN, AND H. Q. LI. 1997. A summarize of the study on fig trees and their pollinators. *Acta Ecol. Sin.* 17: 209–215.
- MILTON, K., D. M. WINDSON, D. W. MORRISON, AND M. A. ESTRIBI. 1982. Fruiting phenologies of two neotropical *Ficus* species. *Ecology* 63: 752–762.
- MILTON, K. 1991. Leaf change and fruit production in six neotropical Moraceae species. *J. Ecol.* 79: 1–26.
- MORELLATO, P. C., AND H. F. LEITAO-FILHO. 1996. Reproductive phenology of climbers in a southeastern Brazilian Forest. *Biotropica* 28: 180–191.
- NASON, J. D., E. A. HERRE, AND J. L. HAMRICK. 1998. The breeding structure of a tropical keystone species. *Nature* 391: 685–687.
- OTERO-ARNAIZ, A., AND K. OYAMA. 2001. Reproductive phenology, seed-set and pollination in *Chamaedorea alternans*, an understory dioecious palm in a rain forest in Mexico. *J. Trop. Ecol.* 17: 745–754.
- PATEL, A. 1996. Variation in a mutualism: Phenology and the maintenance of gynodioecy in two Indian fig species. *J. Ecol.* 84: 667–680.
- . 1997. Phenological patterns of *Ficus* in relation to other forest trees in southern India. *J. Trop. Ecol.* 13: 681–695.
- , AND M. HOSAERT-MCKEY. 2000. Components of reproductive success in two dioecious fig species, *Ficus exasperata* and *Ficus hispida*. *Ecology* 81: 2850–2866.
- PENUELAS, J., AND I. FILELLA. 2001. Responses to a warming world. *Science* 294: 793–795.
- RAMIREZ, W. B. 1969. Fig wasps: Mechanism of pollen transfer. *Science* 163: 580–581.
- RICHARDS, P. W., R. P. D. WALSH, I. C. BAILLIE, AND P. GREIG-SMITH. 1996. *The Tropical Rain Forest—an ecological study*, 2nd edition, p. 574. Cambridge University Press, Cambridge, England.
- ROUTHIER, M. C., AND L. LAPOINTE. 2002. Impact of tree leaf phenology on growth rates and reproduction in the spring flowering species *Trillium erectum* (Liliaceae). *Am. J. Bot.* 89: 500–505.
- SHANAHAN, M., S. G. COMPTON, S. SO, AND R. T. CORLETT. 2001. Fig-eating by vertebrate frugivores: A global review. *Biol. Rev.* 76: 529–572.
- SONG, Q. S., D. R. YANG, G. M. ZHANG, AND C. R. YANG. 2001. Volatiles from *Ficus hispida* and their attractiveness to fig wasps. *J. Chem. Ecol.* 27: 1929–1942.
- SPENCER, H., G. D. WEIBLEN, AND B. FLICK. 1996. Phenology of *Ficus variegata* in a seasonal wet tropical forest at Cape Tribulation, Australia. *J. Biogeogr.* 23: 467–475.
- WEIBLEN, G. D. 2002. How to be a fig wasp. *Annu. Rev. Entomol.* 47: 299–330.
- WEST, S. A., E. A. HERRE, AND B. C. SHELDON. 2000. The benefits of allocating sex. *Science* 290: 288–291.
- , M. G. MURRAY, C. A. MACHADO, A. S. GRIFFIN, AND E. A. HERRE. 2001. Testing Hamilton's rule with competition between relatives. *Nature* 409: 510–513.
- WIEBES, J. T. 1979. Co-evolution of figs and their insect pollinators. *Annu. Rev. Ecol. Syst.* 10: 1–12.
- WINDSOR, D. M., D. W. MORRISON, M. A. ESTRIBI, AND B. DE LEON. 1989. Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Inland, Panama. *Experientia* 45: 647–653.
- WU, Z. Y. 1995. *Flora Yunnanica* (Tomus 6), p. 910. Science Press, Beijing, China.
- XU, Z. F. 1994. Figs—a keystone resources in the tropical rain forest ecosystems of South Yunnan. *Chin. Biodiversity* 2: 21–23.
- , H. M. LIU, G. Q. CHEN, AND J. Y. CUI. 1996. Ethnobotanical culture of fig trees in Xishuangbanna. *J. Plant Resour. Environ.* 5: 48–52.
- YANG, D. R., C. D. LI, AND B. YANG. 1997. Studies on animal structure and biodiversity on *Ficus* in the tropical rain forest of Xishuangbanna, China. *Zool. Res.* 18: 189–196.
- , Y. Q. PENG, Q. S. SONG, G. M. ZHANG, R. W. WANG, T. Z. ZHAO, AND Q. Y. WANG. 2002. Pollination biology of *Ficus hispida* in the tropical rainforest of Xishuangbanna, China. *Acta Bot. Sin.* 44: 519–526.
- ZHANG, K. Y. 1963. An analysis on characteristics and forming factors of climate in the south part of Yunnan. *Acta Meteorol. Sin.* 33: 210–230.
- ZHU, H., M. CAO, AND H. HU. 2006. Geological history, flora and vegetation of Xishuangbanna, Southern Yunnan. *Biotropica* 38: 310–317.
- ZHU, K. Z., AND M. W. WAN. 1975. Phenology, p. 131. Science Press, Beijing, China.