![Springer logo]

Variation in reproductive output of *Ficus superba* despite aseasonal reproduction

Chow Khoon Yeo · Hugh Tiang Wah Tan

Abstract Studies of *Ficus* reproductive phenology have focused on documenting its seasonality and dependence on meteorological factors. While there have been reports that duration of receptivity of syconia can be prolonged in response to pollinator limitation, the effect of pollination rate on the duration of phenological phases over a year has not been examined. Percentage of unpollinated syconia, number of foundresses per pollinated syconium, duration of receptivity, frequency of single-sex broods, crop size, frequency of parasitisation, persistence of ripe syconia, and mass abscission were recorded for *Ficus superba* at the crop level. Percentage of unpollinated syconia is significantly negatively correlated with the number of foundresses per syconium, and positively correlated with the duration of receptivity, and the persistence of ripe syconia. Despite the absence of sesonality in reproduction, the occurrences of receptive syconia and ripe syconia showed unimodal and bimodal peaks, respectively, owing to prolongment of these phases. This is attributable to meteorological factors, which are

hypothesized to influence pollinator dispersal, or population dynamics, and thus pollination rate. This highlights the overlooked significance of pollinator, and possibly frugivore phenology in accounting for *Ficus* reproduction, and suggests that while reproduction may be aseasonal, reproductive potential may not be. Furthermore, crop size was shown to affect the number of foundresses per syconium, duration of receptivity, and persistence of ripe syconia. Possible adaptive value of producing crops of different sizes is discussed.

Keywords Crop size · Fig phenology · Pollination rate · Reproduction · Seasonality

C. K. Yeo (✉) · H. T. W. Tan
Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, 117543 Singapore, Singapore
e-mail: cveyck@nus.edu.sg

H. T. W. Tan
e-mail: hughtan@nus.edu.sg

Introduction

The genus *Ficus* has been identified as a keystone plant resource in Africa, Southeast Asia, and the Neotropics for its aseasonal fruit production, required for the year-round survival of a wide range of vertebrate frugivores (Leighton and Leighton 1983; Terborgh 1986; Lambert and Marshall 1991; Tweheyo and Lye 2003). Milton (1991), in a study of fruit and leaf production phenology of Moraceae genera, including *Ficus*, added that this family may also be important for supporting animals that feed on the leaves in the Neotropics. However, Shanahan et al. (2001) viewed

🌱 Springer

the assertion as not convincingly tested, while Chapman et al. (2005) questioned the importance of *Ficus* as a fall back resource for frugivores.

As a keystone resource, the reproductive phenology of *Ficus* has a special relevance for conservation, and ecosystem integrity. Janzen (1979a) realized that the host-specificity, short lifespan of the pollinator, and usually high intra-tree figging synchrony of *Ficus* individuals, requires well-staggered overlapping reproduction of the *Ficus* individuals to sustain the species-specific Agaonidae pollinators. The successful persistence of this mutualism is indirectly crucial for frugivorous and folivorous animal species dependent on *Ficus*. Bronstein and Hossaert-McKey (1995) and Harrison (2000) have documented local extinction of pollinators brought about by a hurricane and an El Niño-linked drought, respectively. However, it is unclear what this will portend for the mutualism in an imminent global-scale climate change (IPCC 2007).

The true magnitude of the impact may depend on the importance of both exceptional supra-annual meteorological events (e.g., El Niño Southern Oscillation) and regular interannual variation, the nature of cues for the timing of phenology, pre-adaptation to extreme conditions, fragmentation of habitats, the mobility and territory size of the mutualists etc. These factors have been variously discussed by Borchert (1998), Fenner (1998), and Corlett and Lafrankie (1998) in the general context of plant communities.

In this case, the timing and interactions between the obligate mutualists could be more critical, and the phenology of the mutualists may be interdependent and feedback on each other. However, *Ficus* reproductive phenological studies are not helpful in clarifying matters. Many have focused on immediate meteorological explanations (e.g., Milton et al. 1982; Bronstein 1989; Milton 1991; Bronstein and Patel 1992; Smith and Bronstein 1996; Zhang et al. 2006; Pereira et al. 2007), while few also studied supra-annual events (e.g., Bronstein and Hossaert-McKey 1995; Harrison 2000). But they do not examine how meteorology could affect the phenology through pollinator–plant interaction, even though other studies have shown that the duration of receptivity could be extended in the absence of pollinators (Bronstein 1988; Khadari et al. 1995; Ansett et al. 1996a).

Yang et al. (2000, 2005) have reported seasonal variation in pollinator foundress number, seed yield,

pollinator progeny yield, and empty galls in Xishuangbanna, Yunnan, China. But no study has yet shown pollination rate affecting plant reproductive phenology. The aim of the present study on *Ficus superba* is to see if pollination rate is correlated with variation in reproductive phenology in the context of an equable climate, not disturbed by any supra-annual event. If the two are shown to be correlated to meteorological factors, a causal relation between meteorology, pollination rate, and phenology could be demonstrated, showing that the plant–pollinator interaction is responsive to more subtle environmental cues than expected. Should this be the case, it would have to be factored in when extrapolating possible effect of climate and environmental changes on the long-term survival of both parties of the mutualism.

Methods

Species studied

Ficus superba (Miq.) Miq. (subgenus *Urostigma*, section *Urostigma*, subsection *Urostigma*) occurs in exposed coastal habitats in Singapore in highly aggregated groups (C.K. Yeo, pers. obs.). It is a monoecious, deciduous species found in coastal and monsoon forests, ranging from Thailand through Java, the Lesser Sunda Islands, Borneo (Anambas and Natuna Islands), Sulawesi and Moluccas (Ceram) (Berg and Corner 2005). In the course of this study, plants were found predominantly as hemiepiphytes (stranglers), and lithophytes in human-modified environments, but only as lithophytes on Singapore's offshore islands with intact beach vegetation. Larger plants can become free standing reaching heights of up to 30 m with trunk diameter at breast height (dbh) of up to 3.6 m (C.K. Yeo, pers. obs.). Reproduction is generally synchronous within each plant, producing non-overlapping crops (C.K. Yeo, pers. obs.), bearing ramiflorous syconia on curved branches ca. 1 cm long (Berg and Corner 2005). The pollinator for the species is *Platyscapa corneri* Wiebes (Wiebes 1994). *Camarothorax* sp. and *Apocrytophagus* sp. were the most common non-pollinating phytophagous chalcid wasps, accounting for almost all the non-pollinator wasps observed (C.K. Yeo, pers. obs.).

Study site and climate

Singapore lies approximately 137 km north of the equator, with the Singapore Island centered at latitudes 1° 19′N and longitude 104° 01′E (Foo 2002). With a total land area of 604.2 km², it consists of Singapore Island and 63 offshore islands (Foo 2002). Mean daily temperature ranges from 25.5°C in December and January, to 27.3°C in May and June, varying only about 1.8°C over the year (Chia and Foong 1991). Northeast Monsoon occurs from December to March, and Southwest Monsoon from June to September (Foo 2002). There is no distinct dry period, with annual rainfall averaging at 2,345 mm, and monthly rainfall most abundant from November to January, and least in July (Foo 2002). Mean daily sunshine hour is highest in February, March and July, and lowest in November and December, while day length varies little over the year from 12.1 to 12.2 h (Chia and Foong 1991). Lowest mean daytime relative humidity occurs in February at 76.0%, and highest occurs in December at 82.5%, while maximum daily relative humidity approaches 100% throughout the year (Chia and Foong 1991). Total monthly dry days, monthly mean relative humidity, total monthly sunshine hour, total monthly rainfall, monthly mean daily evaporation rate, monthly mean, minimum, and maximum temperatures obtained from Changi Meteorological Station (Meteorological Division, National Environmental Agency, Singapore), from January 2003 to December 2004, are plotted in Fig 1. It shows no distinctive seasonal pattern.

Reproductive phenological study

Phenological data were obtained from weekly observation of 28 plants from the 28 September 2003 to 6 March 2005, inclusive (526 days; 75 weeks). Twenty-three of the plants were from insular localities: nine sampled from Pulau Sajahat, and 13 from St. John's Island. The remaining plants were from three accessible locations on Singapore Islands, all within 5 km of the coast: four from Bedok, one from Nanyang Technological University, and one from Singapore Botanic Gardens (Fig. 2). The maximum distance between localities was 37.6 km, while most plants were within 1 km of the nearest neighbor. Twenty plants reproduced during the observation period, thus the remaining eight were classified as

juveniles. The duration of the maximum overlap in observations between all 20 plants, lasting a contiguous 58 weeks (19 October 2003 to 27 November 2004), was used to estimate population level reproductive phenological parameters.

The reproductive stage of each plant was scored from at least ten collected syconia per observation, whenever possible. The developmental stages were named according to Galil and Eisikowitch (1968), in the following developmental phase sequence: A (prefloral), B (with receptive female flowers), C (interfloral, pollinated and oviposited by pollinator), D (male flower efflorescence, wasp eclosion), E (syconia consumed by frugivores). The initial observation (initiation) of each phase, as well as the duration for which the phase was observed (occurrence) were noted.

It has been observed that sparse ripe syconia could persist on plants for up to 13 weeks in low numbers, unable to attract frugivores (C.K. Yeo, pers. obs.), probably owing to a direct relation between crop size and frugivory (Korine et al. 2000). Therefore, a Phase E ≥ 10% is added to designate a Phase E stage with at least 10% of ripe crop intact, to better reflect a period of effective seed dispersal. For comparison, vegetative leaf change phenology was also noted for all 28 plants, with a leaf change event marked by a loss of at least 90% of leaves followed by a flush of new leaves.

Seasonality of phenology

To test for the aseasonality of reproduction, phenological data were analyzed as circular data. Fifty-two continuous weeks of phenological data were chosen for analysis, with Week 1 starting on November 30 2003. Each week, the number of individuals exhibiting a given reproductive stage of interest was noted. A week's observation was treated as a vector in a 1/52 sector of a circle, whose length corresponded to the number of individuals at a given phenological stage. The peak occurrence of a stage in the year could then be estimated from the angle of the resultant vector (ϕ). The test statistic, $z = nr^2$, was calculated from the total number of events observed (n) and the mean magnitude (r) of the resultant vector, following Batschelet (1981). Rayleigh's Test was used to detect significant unimodal or bimodal departures from random distribution.

◢ Springer
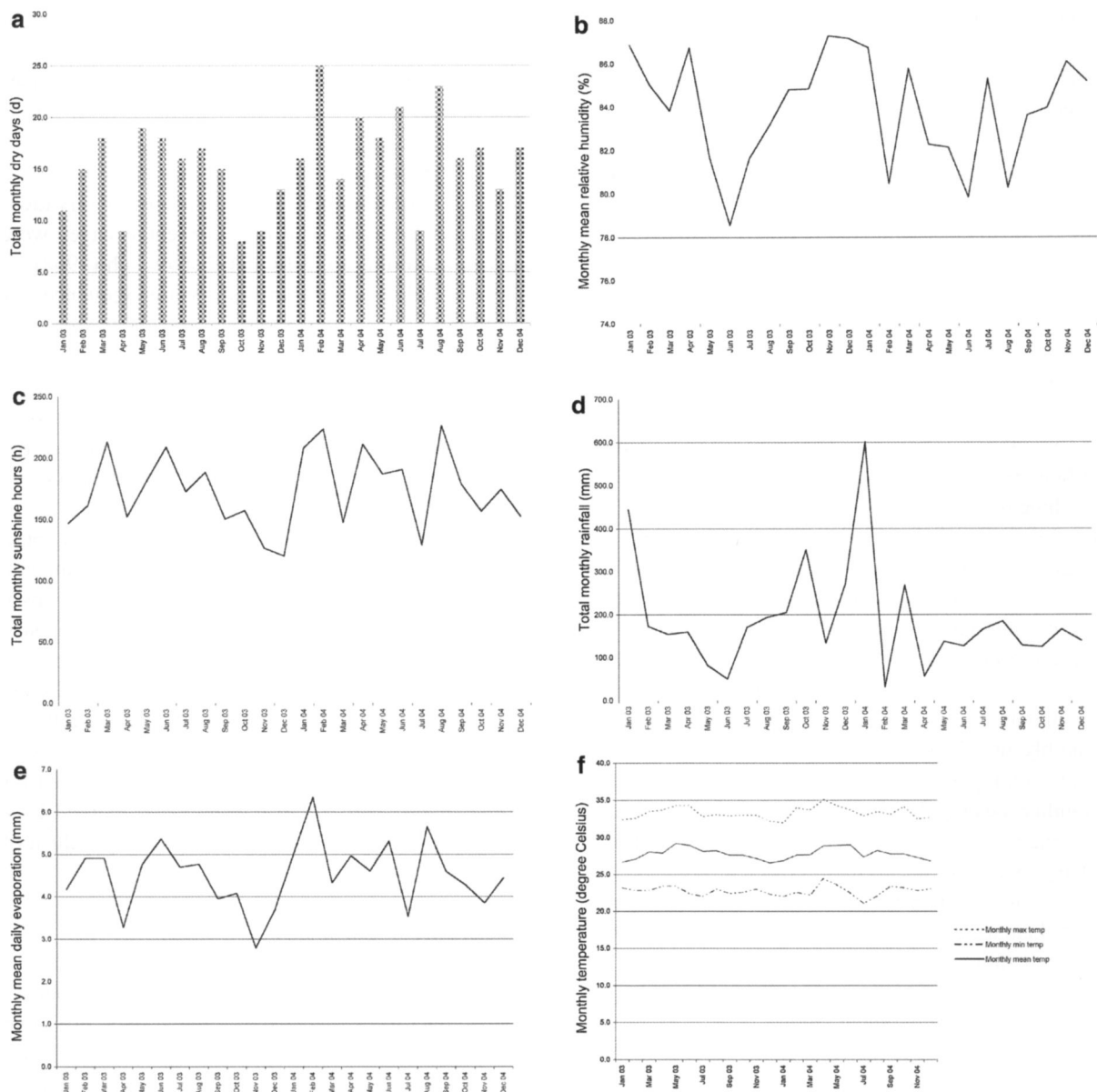
Fig. 1 Plots of **a** Total monthly dry days, **b** Monthly mean relative humidity, **c** Total monthly sunshine hour, **d** Total monthly rainfall, **e** Monthly mean daily evaporation, and **f** Monthly mean, maximum, and minimum air temperatures obtained from Changi Meteorological Station (Meteorological Division, National Environmental Agency, Singapore), from January 2003 to December 2004

Crop study

Syconia were collected over the entire duration of individual crops (reproductive events), each considered to start from the point of syconium initiation (Phase A). The reproductive events were classified as either big or small. A small event is defined as one that initiated syconia fewer than 10% of full capacity of production. From repeated earlier observations made of a number of syconia-bearing curved branches chosen on easily observable parts of crowns, the maximum numbers of syconia they bore were

Fig. 2 Locations for *F. superba* plants used in the phenological study

noted. Thus, the percentage of capacity realized could be estimated from the number of syconia produced by these reference branches. Failure and success of events were also noted, with failure defined as an event not culminating in Phases D or E. Abscission of more than 90% of any crop was noted as near-failures, if not devoid of Phase D or E syconia.

The number of pollinator foundresses trapped in each pollinated syconium past-Phase B was noted, and the mean number of pollinator foundresses per syconium calculated for each reproductive event. The percentage of syconia unvisited past receptive Phase B (termed "failed female syconia"), duration of Phases B, E ≥ 10% and E, percentages of syconia with all male or female pollinator broods, percentages of syconia with entire broods failing to eclose or disperse, and percentages of syconia with parasitic wasps, *Camarothorax* sp. or *Apocrytophagus* sp., were noted. Unpollinated past-Phase B syconia, although usually abscised, were often observed to be retained on a plant for a number of weeks or more rarely an entire reproductive event. They are easily identified from the senescent synstigmata and female flowers. Identification of the wasps was done using Boucek (1988) and Wiebes (1994). Rank correlation tests were used to test relation of crop quality characteristics to percentage of failed female syconia, mean number of foundresses per syconium, and

duration of Phase B of each event. Their dependence on crop size was determined using Kruskal-Wallis tests, while Fisher's Exact Tests were used to determine if there was any relationship between crop size and failure or near-failure of reproductive events. Rank correlation and Kruskal-Wallis tests were performed using CoStat Version 6.310 (CoHort Software, U.S.A.).

Effect of meteorological variables on phenology

Weekly meteorological data of mean evaporation rate, mean, maximum and minimum temperatures, mean relative humidity, mean sunshine hours, total rainfall, and number of dry days were obtained from Changi Meteorological Station (Meteorological Division, National Environmental Agency, Singapore). The meteorological station was chosen for its coastal location, so that its data may be more representative of conditions experienced by the plants, even though Chia and Foong (1991) believed that the coastal influence on climate is negligible for Singapore. Rank correlation tests were performed, using CoStat Version 6.310 (CoHort Software, U.S.A.), with leaf change, start of reproduction (initiation of Phase A), and the occurrences and initiation of Phases B and E, against each meteorological variable preceding them by up to 8 weeks.

Springer

Results

Reproductive phenology

Each reproductive plant on average initiated reproduction 4.03 ± 1.75 times a year. The average duration of reproduction, from Phase A to Phase E, lasted 7.66 ± 3.33 weeks, and the average duration between the initiation of reproduction averaged 11.61 ± 7.39 weeks. Leaf change was observed in 24 plants, and each plant on average underwent 1.22 ± 0.11 leaf changes a year.

The initiation of reproduction and phases appears to be random or aseasonal, but the occurrences of Phases B and E $\geq$ 10% show unimodal, and occurrence of Phase E shows bimodal departures. The peaks are attributed to longer duration of the phases rather than clustered initiation. See Fig. 3 for monthly mean durations of Phases B, E $\geq$ 10%, and E. Big events, small events and the sum of failures and near-failures also appear to be random, while significant departure is noted for leaf change. The alternative hypothesis for its bimodal distribution could not be rejected. See Table 1 for details.

In all, 86 reproductive events were observed in their completion (from Phases A to the end) within the 58 weeks. Of these 22 were small events. Fisher's Exact Tests were performed to determine if the small events were more prone to produce failures (three of the small, and two of the big events) or failures plus near-failures (four of the small, and six of the big events), compared to big events. The results failed to reject the null hypotheses of no difference in their
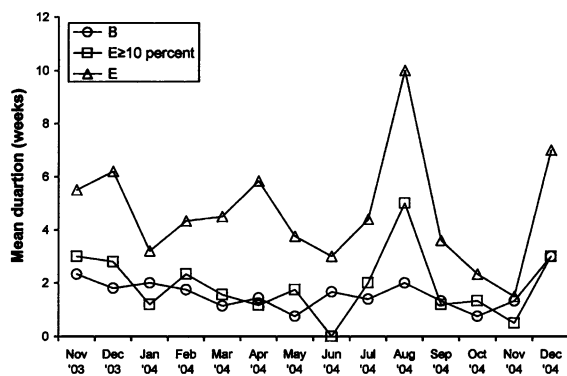
numbers of failures ($P = 0.103$), or near-failures plus failures ($P = 0.227$).

Crop characteristics

Detailed notes on the syconia were recorded for 50 of the 86 complete events observed. Percentage of failed female syconia is significantly positively correlated to percentages of syconia with all female broods (Spearman $r = 0.437$, $P = 0.05$), with broods failing to eclose (Spearman $r = 0.447$, $P = 0.03$), duration of Phase E (Spearman $r = 0.476$, $P = 0.03$), and negatively to mean number of pollinator foundresses per syconium (Spearman $r = -0.510$, $P < 0.005$). Mean number of foundresses per syconium is significantly positively correlated to percentages of syconia with broods that failed to eclose (Spearman $r = 0.503$, $P < 0.01$), and with all male broods (Spearman $r = 0.458$, $P = 0.03$). Duration of Phase B is significantly positively correlated to percentage of failed female syconia (Spearman $r = 0.676$, $P < 0. 005$), percentages of syconia with broods that failed to eclose (Spearman $r = 0.528$, $P < 0.005$), and with all male broods (Spearman $r = 0.520$, $P < 0.005$), durations of Phases E $\geq$ 10% (Spearman $r = 0.430$, $P = 0.005$) and E (Spearman $r = 0.520$, $P < 0.005$). Furthermore, duration of Phase B was also found to be correlated significantly with the duration of other subsequent developmental phases, such as Phases C (Spearman $r = 0.364$, $P = 0.02$) and D (Spearman $r = 0.356$, $P = 0.03$).

We wanted to see if the percentage of failed female syconia, mean number of foundresses per syconium, and durations of Phases B, E $\geq$ 10%, and E could be related to size of crop. Kruskal-Wallis tests showed that small events have higher mean number of foundresses per syconium ($H = 6.05$, $P = 0.04$), shorter Phases B ($H = 12.88$, $P = 0.01$), and E ($H = 8.22$, $P = 0.01$). Besides shorter Phase E $\geq$ 10% ($H = 4.67$), small events also have lower percentages of failed female syconia ($H = 2.05$), syconia with single-sex broods ($H = 0.595$ for all male, $H < 0.001$ for all female), and pollinators failing to eclose or disperse ($H = 0.081$, and $H = 1.31$, respectively), and higher percentages of syconia with two species of non-pollinating wasps, *Camarothorax* sp. ($H = 0.223$) and *Apocrytophagus* sp. ($H = 1.62$), but they are non-significant. All *P*-values reported above have been amended with Bonferroni corrections.

Fig. 3 Monthly mean duration of Phases B, E $\geq$ 10%, and E

Table 1 Results of Rayleigh's Test for uniform distribution

Phases	Alternative hypothetical distribution	Peak(s)	Test Statistic (z)	P
Start of reproductive events	Unimodal	18 Jan 2004	1.690	>0.1
Initiation of B	Unimodal	1 Feb 2004	2.805	>0.05
B	Unimodal	1 Feb 2004	6.617	<0.01
Initiation of E	Unimodal	28 Mar 2004	1.167	>0.1
E ≥ 10%	Unimodal	29 Feb 2004	4.405	<0.02
E	Bimodal	11 Jan 2004, 11 Jul 2004	3.913	<0.02
Leaf change	Bimodal	21 Dec 2003, 20 Jun 2004	3.032	<0.05
Big events	Unimodal	1 Feb 2004	1.902	>0.05
Small events	Bimodal	21 Dec 2003, 20 Jun 2004	2.509	>0.05
Failures plus near-failures	Unimodal	14 Mar 2004	2.717	>0.05

"Unimodal" and "bimodal" refer to the alternative hypotheses of unimodal or bimodal peaks in phases being tested using Rayleigh's Test. In cases where both alternative hypotheses are rejected, only the result with a smaller P-value is tabulated

Relationship between weather and phenology

While leaf change shows significant correlation to total sunshine hours, total rainfall, and number of dry days, there are only non-significant correlations between meteorological variables and the initiation of syconia. However, there are significant correlations between maximum temperature, minimum temperature, mean temperature, relative humidity and total rainfall, and occurrences of reproductive Phases B and E (see Table 2 for details). There is a 4 to 5-week lag for Phase B, and an 8-week lag for Phase E. The relationships between meteorological factors and Phase E mirror those with Phase B, probably due to the developmental relation between the two phases. This agrees with the correlation between occurrences of Phase B and Phase E with a 4- (Spearman $r = 0.491$, $P < 0.001$) to 5-week lag (Spearman $r = 0.498$, $P < 0.001$). The lag is probably reflective of the duration of intervening development. The strongest positive correlation is found between Phase B and mean humidity, and strongest negative correlation, between Phase B and mean temperature.

Discussion

Dependence of reproductive output on duration on pollination rate

The initiation of syconium production in *F. superba* appears to be random or aseasonal, and does not show dependence on meteorological factors. Aseasonality could be an adaptive feature, as Kjellberg and Maurice (1989) and Anstett et al. (1995, 1997) have demonstrated with simulations that the number of plants needed to support the pollinator increases with seasonality of reproduction. This contrasts with leaf change, which shows departure from randomness and correlation with meteorological variables. This affirms that the plants are able to perceive meteorological cues despite the equable climate, and more importantly, it is supportive of the view that reproductive and vegetative phenology may to differing degrees be internally controlled and externally influenced (Borchert 1983).

Despite the randomness of reproductive events, the occurrences of Phases B, E ≥ 10%, and Phase E showed peaks. Variable availability of pollinator is suspected to be the cause of the discrepancy, as earlier studies have shown that the duration of Phase B could be extended by 2–3 weeks in the absence of pollinators (Bronstein 1988, Khadari et al. 1995, Ansett et al. 1996a), while receptive syconia were observed to persist non-senescent for up to 4 weeks in *F. superba* (C.K. Yeo, pers. obs.). The hypothesis appears to be borne out by the positive correlation between the percentage of failed female syconia (inverse of pollination rate) and duration of Phase B, and the negative correlation between the former and mean number of pollinator foundresses per syconium (pollination intensity).

There are also significant correlations between the duration of Phase B and all subsequent phases within

Table 2 Spearman r correlation coefficients between initiation of reproduction, occurrences of leaf change, Phases B and E and various weekly meteorological variables

Week before	Meteorological variables	Mean evaporation (mm)	Maximum temperature (°C)	Minimum temperature (°C)	Mean temperature (°C)	Mean relative humidity (%)	Total sunshine hours (h)	Total rainfall (mm)	Number of dry days (d)
0	Leaf change	0.080	0.198	0.173	0.039	0.176	0.056	0.061	0.034
	Start of reproductive phase	-0.018	0.195	0.180	-0.088	0.193	-0.058	0.048	0.023
	Phase B	0.005	-0.036	-0.062	-0.285*	0.131	-0.007	-0.030	0.022
	Phase E	0.042	0.052	0.150	-0.049	0.185	0.062	-0.117	0.004
1	Leaf change	0.174	0.158	0.237	0.125	0.048	0.235	-0.035	0.172
	Start of reproductive phase	0.081	0.219	0.145	0.066	0.034	0.128	-0.168	0.112
	Phase B	0.175	-0.085	0.126	-0.071	-0.024	0.085	-0.187	0.187
	Phase E	0.174	0.059	0.034	0.082	0.089	0.158	0.0082	0.083
2	Leaf change	0.346*	0.076	0.232	0.075	-0.021	0.383***	0.014	0.279*
	Start of reproductive phase	0.164	0.102	0.210	0.082	-0.016	0.167	-0.118	0.248
	Phase B	0.240	-0.076	0.247	-0.036	-0.033	0.288*	-0.247	0.308
	Phase E	-0.075	0.061	-0.032	-0.126	0.220	-0.089	0.202	0.059
3	Leaf change	0.167	-0.058	-0.033	-0.022	0.104	0.168	0.055	0.134
	Start of reproductive phase	0.086	0.064	0.160	0.015	0.099	0.119	0.079	0.161
	Phase B	-0.024	-0.295	-0.079	-0.261	0.250	0.083	0.170	-0.017
	Phase E	0.007	-0.087	-0.141	-0.233	0.195	-0.058	0.144	0.044
4	Leaf change	0.098	-0.069	0.007	-0.016	0.142	0.054	0.124	0.099
	Start of reproductive phase	0.103	0.007	0.037	0.003	0.149	0.229	0.096	0.050
	Phase B	-0.231	-0.357**	-0.229	-0.383****	0.438***	-0.168	0.317*	-0.216
	Phase E	0.230	-0.036	-0.056	-0.094	-0.082	0.117	-0.041	0.202
5	Leaf change	0.130	-0.111	-0.163	-0.076	0.210	0.072	0.387***	0.050
	Start of reproductive phase	0.047	-0.152	0.011	-0.098	0.137	0.001	0.026	0.089
	Phase B	-0.148	-0.210	-0.275*	-0.356**	0.357**	-0.135	0.264	-0.182
	Phase E	0.218	0.060	0.292*	-0.029	-0.105	0.189	-0.179	0.262
6	Leaf change	0.145	-0.191	0.048	-0.116	0.156	0.036	0.076	0.183
	Start of reproductive phase	0.104	-0.002	-0.131	-0.078	0.105	-0.020	0.066	0.095
	Phase B	-0.0.31	-0.272*	0.167	0.304*	0.241	-0.135	0.182	-0.054
	Phase E	0.072	-0.176	0.195	-0.072	0.079	0.133	-0.216	0.119

Table 2 continued

Week before	Meteorological variables	Mean evaporation (mm)	Maximum temperature (°C)	Minimum temperature (°C)	Mean temperature (°C)	Mean relative humidity (%)	Total sunshine hours (h)	Total rainfall (mm)	Number of dry days (d)
7	Leaf change	0.222	-0.153	-0.081	-0.015	0.085	0.176	0.274*	0.197
	Start of reproductive phase	0.071	-0.187	-0.104	-0.152	0.127	-0.019	0.109	0.062
	Phase B	0.029	-0.170	0.008	-0.232	0.143	-0.054	0.103	-0.040
	Phase E	0.028	-0.239	-0.018	-0.140	0.118	0.020	-0.141	0.135
8	Leaf change	0.106	-0.241	0.077	-0.015	0.105	0.175	0.203	0.131
	Start of reproductive phase	0.127	-0.065	0.150	-0.114	0.037	0.065	0.107	0.057
	Phase B	0.040	-0.202	0.095	-0.116	0.046	0.186	0.085	0.012
	Phase E	-0.191	-0.320*	-0.335*	-0.362***	0.355**	-0.150	0.222	-0.066

P-values ≤ 0.05 indicated with *, ≤ 0.01 with **, and ≤ 0.005 with ***

crops, including E ≥ 10% and E. This implies that a scarcity of pollinators lengthens receptivity, and the staggered pollination leads to the prolongment of these later phases. This is corroborated by observation that despite synchronous initiation of syconia within plants, developmentally consecutive stages often overlap temporally (C.K. Yeo, pers. obs.).

Taken together, it is strongly suggestive that even with apparently aseasonal initiation of reproduction, temporal variation in pollinator availability influences not just the duration of receptivity, but also reproductive output through the percentage of fruit set, and the duration of availability of ripe syconia for frugivores. The same is likely to apply to *Ficus* species with more seasonal reproduction. These possibly significant deviations from expectation are not apparent from phenological studies focused on crop initiation alone.

Dependence of pollination rate on meteorological factors

Correlations between the occurrence of Phase B and meteorological variables are the strongest with mean relative humidity and mean temperature, at a 4-week lead (Table 2). As timing of initiation of reproduction is not related to weather variables, and the duration of receptivity has been linked to pollination rate, it seems likely that this could be due to the direct effect of weather on the population dynamics or dispersal of the pollinator, which in turn affects pollination rate.

This could happen during the short lifespan at the dispersal of the immediate predecessors of the pollinators of the affected crops, measurable in days (Kjellberg et al. 1988); or more likely, during the predecessors' development within syconia, as pollinator development (Phase C) takes about 3 weeks (C.K. Yeo, pers. obs.). Seasonal weather has been reported to affect the rate of syconium development (e.g. Zhang et al. 2006; Pereira et al. 2007), and cause seasonality in the initiation and synchrony of reproduction within and between plants (e.g. Milton et al. 1982; Bronstein 1989; Bronstein and Patel 1992; Smith and Bronstein 1996; Harrison et al. 2000; Tweheyo and Lye 2003).

However, this study has shown for *F. superba* that the initiation of reproduction is aseasonal, and significant positive correlations exist between the duration

of Phase B and all subsequent phases, inclusive of Phase C. This suggests that the staggering of pollination leads to the staggering and lengthening of later developmental phases. Furthermore, the narrow spread of Phase C duration (2.75 ± 0.86 weeks, coefficient of variation = 0.313) (C.K. Yeo, pers. obs.) suggests that the variation in the rate of syconium development is minor compared to what Zhang et al. (2006) and Pereira et al. (2007) observed for *Ficus* species in more seasonal climate. Thus, the less seasonal climate may not affect syconium development directly except through pollination.

Furthermore, as pollinator dispersal is wind-dependent (Ware and Compton 1994a, b), the stochasticity in the arrival of the pollinator may be sensitive to prevailing wind conditions. This is worth further investigation, as the occurrence of Phase B was found to peak in February, which coincides roughly with the Northeast Monsoon coming in from the South China Sea. This has the strongest and most directional winds in the year (Chia and Foong 1991). Thus, the possibility that it may be a poorer source of the pollinator compared to winds coming in over regions rich in coastal habitats inhibited by *F. superba*, merits further investigation.

Despite the prolongment of receptivity attributable to lower pollination rates, as shown by the significant positive correlation between the duration of Phase B and percentage of failed female syconia, there is no corresponding pattern found in the temporal distribution of reproductive failures and near-failures. This could be indicative of the success of Phase B extension in damping out out-right reproductive failures caused by the stochasticity of pollinator arrival. However, such a conclusion should be substantiated by more direct evidence.

Further study should furnish data on the temporal variation in pollinator arrival, quantify crop size, abscission, as well as pollination rate. Pollinator arrival may be gauged as Compton et al. (2000) did using non-attracting sticky traps. Owing to the potentially great distances the pollinator wasps regularly traverse (Nason et al. 1998), a large representative area may need to be sampled. However, local factors such as habitat fragmentation and density of individuals are known to affect pollination and parasitization rates (Wang et al. 2005), thus they should also be addressed as well in a well-considered study.

Persistence of ripe syconia

Although the non-random persistence of ripe syconia could have simply resulted from fluctuation in Phase B duration, as suggested by the strong correlation between durations of Phase B, Phase E and Phase E $\geq$ 10%, the departure from complete congruence between the mean duration of Phases B and E $\geq$ 10% (Fig. 1), suggests that factors other than delayed pollination may be important. Seasonal variation in frugivory comes to mind, though not addressed in the present study, as frugivore numbers and species have been observed to vary over both space and time (Bronstein and Hoffmann 1996), and has been linked with seasonal availability of alternative food sources (Ragusa-Netto 2002).

The syconia of *F. superba* are consumed by birds of various families, such as house crow (*Corvus splendens* (Corvidae)), pink-neck pigeon (*Treron vernans* (Columbidae)), white-vented myna (*Acridotheres javanicus* (Sturnidae)), glossy starling (*Aplonis panayensis* (Sturnidae)), and straw-headed bulbul (*Pycnotus zeylanicus* (Pyconotidae) (C.K. Yeo, pers. obs.). Richard T. Corlett (pers. comm.) also observed fruit bat, *Cynopterus brachyotis* (Pteropodidae), feeding on the ripe syconia.

A predominantly bird-dispersed species, *F. superba* would be expected to have syconia that ripen gradually rather than synchronously, in the light of the study of Korine et al. (2000), which demonstrated the relationship between synchrony of crop ripening, and bird or bat frugivory in *Ficus* species. Thus, the prolonged availability of ripe syconia may not just be caused by the staggered pollination, but may also be an adaptation to its avian dispersers. However, as combined data on frugivore activity and alternative food source availability were not systematically collected for the present study, such conclusion cannot be drawn until a proper study is done. This would contribute significantly to our understanding of the keystone genus and its interactions with frugivores.

Possible adaptive significance of crop size

Small events in *F. superba* have higher mean number of foundresses per syconium, and shorter Phase B, implying that crop size can modulate pollination rate. This is unexpected, if the amount of pollinator attractant produced is proportional to crop size and

synchrony (Janzen 1979a; Bronstein 1987; Windsor et al. 1989; Smith and Bronstein 1996), and olfactory in nature (Ware et al. 1993; Hossaert-McKey et al. 1994). If so, a larger receptive crop should attract more pollinator wasps over a greater distance and secure greater pollination success. Instead, pollinator scarcity seems to be widespread, as shown by the prevalence of unvisited syconia, found in 60 percent of examined crops, and making up on average 23% of the affected crops (C.K. Yeo, pers. obs.).

The present study shows that small crops tend to produce a slightly greater proportion of pollinated syconia. Thus more small crops are expected be initiated if crop set is to be maximized. That crops of both classes are initiated apparently aseasonally raises the question of whether varying crop sizes could be adaptive. If reproductive success is conceived to consist of two components, seed set and pollinator production, the production of seeds or pollinator progenies could be seen as a tradeoff between the male or female functions in monoecious species (Janzen 1979b; Ansett et al. 1998, 1996b). Thus, it is hypothesized that crop size could be a viable way of modulating such a tradeoff.

How could this work out for monoecious *Ficus* species? Ansett et al. (1996b) have reported that the number of seeds produced by a syconium of *F. aurea* Nutt. is inversely related to the number of foundresses. Herre (1989, 1996) has reviewed it to be generally true for several other species, and that there is a negative relationship between seed and wasp production. If applicable to *F. superba*, crop size could tip the investment toward seeds or wasps by modifying pollination intensity.

Large crops of *F. superba*, having fewer pollinators per syconium, are expected to produce more seeds and fewer pollinator wasps. Should large crops attract more frugivores as Korine et al. (2000) observed, and promote the establishment of new plants, that would further augment the female function. Large crops also have somewhat greater proportions of syconia with single-sexed broods, and pollinators failing to eclose or disperse. The former could be attributed to the arrhenotokous haplodiploid reproduction of the pollinator (West et al. 1997), with single-foundress broods more prevalent in large crops. Thus, it appears the gain in female function comes with some loss of male function.

On the other hand, small crops have slightly higher rates of parasitisation by *Camarothorax* and *Apocryptophagus*, suggesting that emphasizing male function of pollinator wasp production comes with higher parasitisation. This seems to be in line with the expectations of Harrison and Yamamura (2003), who broadened the reproductive tradeoff to include exploitation by non-pollinating fig wasps in accounting for the evolution of dioecy. Harrison and Yamamura (2003) suggested that dioecy evolved to result in female plants bearing a lower parasite load compared to male and monoecious plants. Thus, similar trends may be occur when monoecious *F. superba* produces crops biased toward fulfilling the male or female functions.

These tentative trends and speculations merit larger scale, multi-population, longer duration studies to corroborate their consistency. Although the categorizing of crops into two size classes is sufficient to reveal some significant trends, more could be accomplished if finer standardized quantitative measures of reproductive success could be adopted for future studies. Unfortunately, few phenological studies quantify the size of crops, the numbers of seeds, wasps and galls per syconium in each syconium, and frugivory at the crop level. More detailed studies on these aspects, e.g., along the line of work conducted by Corlett et al. (1990), Yang et al. (2000, 2005), Wang et al. (2005), and Korine et al. (2000) would be beneficial. Certainly, such data would be necessary to corroborate the hypothesized adaptive function of crop size in *Ficus* species.

Conclusions

This study has shown the effect of pollination rate on the duration of receptive Phase B in *F. superba*, despite the underlying aseasonal reproduction and equable climate. This could in turn affect crop set and quality, and in combination with frugivore availability, the persistence of ripe syconia. Thus, even though reproductive initiation may be random, reproductive output may not be. Surprisingly, the plant also shows some influence over pollination rate and persistence of ripe syconia through variation in crop size. The possible adaptive value of this has been discussed in terms of its modulation of the tradeoffs between seed production, pollinator production, and guarding

Springer

against parasitisation. This highlights that pollinator phenology, and possibly frugivore phenology, should be fully considered for a more complete explanation of *Ficus* reproductive output and phenology.

The plant-pollinator-frugivore interactions, and the pollinator and frugivore tracking of the low-density, asynchronous resources, are unquantified. This makes it difficult to determine the impact of climate change on the long-term survival of the pollinator-plant mutualism. Climate change could affect the plant reproductive timing, output and quality both directly, through the phenology of plants, and indirectly, through the recursive interactions between the mutualists. These points have yet to be addressed to date in a comprehensive study.

Finally, *F. superba* could be a valuable model species to study for the impact of climate change on *Ficus* species. It is found in coastal and monsoon forest habitats (Berg and Corner 2005), thus it may be more at risk from climate change, as sea-level rises, and droughts and floods intensify in the tropics (IPCC 2007). The thinning of the host plant populations and resulting synchronization of pollinator population dynamics through synchronization of plant phenology in the remaining populations will affect it sooner than species inhabiting less marginal habitats. Therefore, what befalls this species may be a harbinger of what will happen to other *Ficus* species as the climate and environmental changes progress.

References

Ansett MC, Bronstein JL, Hossaert-McKey M (1996) Resource allocation: a conflict in fig/fig wasp mutualism? J Evol Biol 9:417–428. doi:10.1046/j.1420-9101.1996.9040417.x

Anstett MC, Gibernau M, Hossaert-McKey M (1998) Partial avoidance of female inflorescences of a dioecious fig by their mutualistic pollinating wasps. Proc R Soc Lond Biol Sci 265:45–50. doi:10.1098/rspb.1998.0262

Anstett MC, Hossaert-McKey M, McKey D (1997) Modeling the persistence of small populations of strongly interdependent species: figs and fig wasps. Conserv Biol 11:204–213. doi:10.1046/j.1523-1739.1997.95436.x

Anstett MC, Kjellberg F, Bronstein JL (1996) Waiting for wasps: consequences for pollination dynamics of *Ficus pertusa* L. J Biogeogr 23:459–466. doi:10.1111/j.1365-2699.1996.tb00007.x

Anstett MC, Michaloud G, Kjellberg F (1995) Critical population size for fig/wasp mutualism in a seasonal environment: effect and evolution of the duration of female receptivity. Oecologia 103:453–461. doi:10.1007/BF00328683

Batschelet E (1981) Circular statistics in biology. In: Sibson R, Cohen JE (eds) Mathematics in biology. Academic Press, London

Berg CC, Corner EJH (2005) Moraceae: Ficeae. In: Nooteboom HP (ed) Flora Malesiana, series I, part 2, vol 17. The National Herbarium Nederland, Leiden, pp 610–614

Borchert R (1983) Phenology and control of flowering in tropical trees. Biotropica 15:81–89. doi:10.2307/2387949

Borchert R (1998) Responses of tropical trees to rainfall seasonality and its long-term changes. Clim Change 39:381–393. doi:10.1023/A:1005383020063

Boucek Z (1988) Australasian Chalcidoidea (Hymenoptera): a biosystematic revision of genera of fourteen families, with a reclassification of species. C.A.B. International, Wallingford, Oxon

Bronstein JL (1987) Maintenance of species-specificity in a neotropical fig-pollinator wasp mutualism. Oikos 48:39–46. doi:10.2307/3565686

Bronstein JL (1988) Limits to fruit production in a monoecious fig: consequences of an obligate mutualism. Ecology 69:207–214. doi:10.2307/1943176

Bronstein JL (1989) A mutualism at the edge of its range. Experientia 45:622–639. doi:10.1007/BF01975679

Bronstein JL, Hoffmann K (1996) Spatial and temporal variation in frugivory at a neotropical fig, *Ficus pertusa*. Oikos 49:261–268. doi:10.2307/3565760

Bronstein JL, Hossaert-McKey M (1995) Hurricane Andrew and a Florida fig pollination mutualism: resilience of an obligate interaction. Biotropica 27:373–381. doi:10.2307/2388922

Bronstein JL, Patel A (1992) Causes and consequences of within-tree phenological patterns in the Florida strangling fig, *Ficus aurea* (Moraceae). Am J Bot 79:41–48. doi:10.2307/2445195

Chapman CA, Chapman LJ, Zanne AE, Poulsen JR, Clark CJ (2005) A 12-year phenological record of fruiting: Implications for frugivore populations and indicators of climate change. In: Dew JL, Boubli JP (eds) Tropical fruits and frugivores: the search for strong interactors. Springer, The Netherlands, pp 75–92

Chia LS, Foong SF (1991) Climate and weather. In: Chia LS, Rahman A, Tay DBH (eds) The biophysical environment of Singapore. Singapore University Press, Singapore, pp 13–49

Compton SG, Ellwood MDF, Davis AJ, Welch K (2000) The flight heights of chalcid wasps (Hymenoptera, Chalcidoidea) in lowland Bornean rain forest: fig wasps are high fliers. Biotropica 32:522–525

Corlett RT, Boudville V, Seet K (1990) Seed and wasp production in five fig species (*Ficus*, Moraceae). Malay Nat J 44:97–102

Corlett RT, Lafrankie JV Jr (1998) Potential impacts of climate change on tropical asian forests through an influence on

phenology. Clim Change 39:439–453. doi:10.1023/A:1005328124567

Fenner M (1998) The phenology of growth and reproduction in plants. Perspect Plant Ecol Evol Syst 1:78–91. doi:10.1078/1433-8319-00053

Foo SL (2002) Singapore facts and pictures 2002. Ministry of Information, Communications and the Arts, Singapore

Galil J, Eisikowitch D (1968) Flowering cycles and fruit types of *Ficus sycomorus* in Israel. New Phytol 67:745–758. doi:10.1111/j.1469-8137.1968.tb05497.x

Harrison RD (2000) Repercussions of El Niño: Drought causes extinction and breakdown of mutualism in Borneo. Proc Proc R Soc Lond Biol Sci 267:911–915. doi:10.1098/rspb.2000.1089

Harrison RD, Yamamura N (2003) A few more hypotheses for the evolution of dioecy in figs (*Ficus*, Moraceae). Oikos 100:628–635. doi:10.1034/j.1600-0706.2003.11829.x

Harrison RD, Yamamura N, Inoue T (2000) Phenology of a common roadside fig in Sarawak. Ecol Res 15:47–61. doi:10.1046/j.1440-1703.2000.00319.x

Herre EA (1989) Coevolution of reproductive characteristics in 12 species of new world figs and their pollinator wasps. Experientia 14:637–647. doi:10.1007/BF01975680

Herre EA (1996) An overview of studies on a community of Panamanian figs. J Biogeogr 23:593–607. doi:10.1111/j.1365-2699.1996.tb00020.x

Hossaert-McKey M, Gibernau M, Frey JE (1994) Chemosensory attraction of fig wasps to substances produced by receptive figs. Entomol Exp Appl 70:185–191. doi:10.1007/BF02380526

IPCC (2007) Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Janzen DH (1979a) How to be a fig? Annu Rev Ecol Syst 10:13–51. doi:10.1146/annurev.es.10.110179.000305

Janzen DH (1979b) How many babies do figs pay for babies? Biotropica 11:48–50. doi:10.2307/2388172

Khadari B, Gibernau M, Ansett MC, Kjellberg F, Hossaert-McKey M (1995) When figs wait for pollinators: the length of fig receptivity. Am J Bot 82:992–999. doi:10.2307/2446228

Kjellberg F, Doumesche B, Bronstein JL (1988) Longevity of a fig wasp. In: Proceedings of the Koninklijke Nederlandse Akademie Wetenschappen series C, vol 91(2), pp 117–122

Kjellberg F, Maurice S (1989) Seasonality in the reproductive phenology of *Ficus*: its evolution and consequences. Experientia 45:653–660. doi:10.1007/BF01975682

Korine C, Kalko EKV EA, Herre EA (2000) Fruit characteristics and factors affecting fruit removal in a Panamanian community of stranglers. Oecologia 123:560–568. doi:10.1007/PL00008861

Lambert FR, Marshall AG (1991) Keystone characteristics of bird dispersed *Ficus* in a Malaysian lowland rain forest. J Ecol 79:793–809. doi:10.2307/2260668

Leighton M, Leighton DR (1983) Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton SL, Whitmore TC, Chadwick AC (eds) Tropical rain

forest: ecology and management. Blackwell, Oxford, pp 181–196

Milton K (1991) Leaf change and fruit production in six neotropical Moraceae species. J Ecol 79:1–26. doi:10.2307/2260781

Milton K, Windsor DM, Morrison DW, Estribi MA (1982) Fruiting phenologies of two Neotropical *Ficus* species. Ecology 63:752–762. doi:10.2307/1936796

Nason JD, Herre EA, Hamrick JL (1998) The breeding structure of a tropical keystone plant resource. Nature 391:685–687. doi:10.1038/35607

Pereira RAS, Rodrigues E, de Oliveira Menezes A Jr (2007) Phenological patterns of *Ficus citrifolia* (Moraceae) in a seasonal humid-subtropical region in southern Brazil. Plant Ecol 188:265–275. doi:10.1007/s11258-006-9161-0

Ragusa-Netto J (2002) Fruiting phenology and consumption by birds in *Ficus calyptroceras* (Miq.) Miq. (Moraceae). Braz J Biol 62:339–346

Shanahan M, So S, Compton SG, Corlett R (2001) Fig-eating by vertebrate frugivores: a global review. Biol Rev Camb Philos Soc 76:529–572

Smith CM, Bronstein JL (1996) Site variation in reproductive synchrony in three neotropical figs. J Biogeogr 23:477–486. doi:10.1111/j.1365-2699.1996.tb00009.x

Terborgh J (1986) Keystone plant resources in the tropical forest. In: Soulé ME (ed) Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts, U.S.A., pp 330–344

Tweheyo M, Lye KA (2003) Phenology of figs in Budongo forest Uganda and its importance for chimpanzee diet. Afr J Ecol 41:306–316. doi:10.1111/j.1365-2028.2003.00475.x

Wang RW, Yang CY, Zhao GF, Yang JX (2005) Fragmentation effects on diversity of wasp community and its impact on fig/fig wasp interaction in *Ficus racemosa* L. J Integr Plant Biol 47:20–26

Ware AB, Compton SG (1994a) Dispersal of adult female fig wasps 1. Arrivals and departures. Entomol Exp Appl 73:221–229. doi:10.1007/BF02382473

Ware AB, Compton SG (1994b) Dispersal of adult female fig wasps 2. Movement between trees. Entomol Exp Appl 73:231–238. doi:10.1007/BF02382474

Ware AB, Kaye PT, Compton SG, van Noort S (1993) Fig volatiles: their roles in attracting pollinators and maintaining pollinator specificity. Plant Syst Evol 186:147–156. doi:10.1007/BF00940794

West SA, Herre EA, Compton SG, Godfray HCJ, Cook JM (1997) A comparative study of virginity in fig wasps. Anim Behav 54:437–450. doi:10.1006/anbe.1996.0494

Wiebes JT (1994) The Indo-Australian Agaoninae (pollinators of figs). Verhandelingen der Koninklijke Nederlandse akademie van wetenschappen. Afdeling natuurkunde. Tweede Reeks, Deel 92. North-Holland, Amsterdam

Windsor DM, Morrison DW, Estribi MA, de Leon B (1989) Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Island, Panama. Experientia 45:647–653. doi:10.1007/BF01975681

Yang D, Peng Y, Zhao T, Wang Q, Xu L (2005) Relationship between activity of *Ceratosolen fusciceps* and seasonal changes of the seed number of *Ficus raceomsa*. Scientia Silvae Sinicae 41:25–29

Yang D, Wang R, Song Q, Zhang G, Zhao T (2000) Rule of seasonal changes of the *Ceratosolen* sp. in the tropical rainforest of Xishuangbanna, China. For Res 13:477–484

Zhang G, Song Q, Yang D (2006) Phenology of *Ficus racemosa* in Xishuangbanna, southwest China. Biotropica 38:334–341. doi:10.1111/j.1744-7429.2006.00150.x