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The reproductive success of *Ficus altissima* and its pollinator in a strongly seasonal environment: Xishuangbanna, Southwestern China

Yan-Qiong Peng · Stephen G. Compton · Da-Rong Yang

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Abstract Fig trees (*Ficus* spp.) are of great ecological significance, producing fruits that are fed on by more birds and mammals than any other plants in the tropics. They are pollinated by host-specific pollinator fig wasps (Hymenoptera, Agaonidae), and their fruit phenology and reproductive success are, therefore, modulated by symbiotic fig wasps. However, there are few studies focusing on the variation of *Ficus* reproductive success in strongly seasonal environments. We examined the phenology and reproductive success of *Ficus altissima* growing in a highly seasonal climate towards the northern limit of the range of fig trees in Xishuangbanna, China. Leaf production occurred at irregular intervals throughout the year, with new leaves and syconia initiated together, producing between three and seven crops over a 3-year period. Syconia were produced in synchronous crops with asynchrony between trees. The syconia produced more seeds than pollinators, and those syconia with more seeds also produced more pollinators. Reproductive success (measured as the number of seeds and pollen-carrying agaonid females produced by each syconium) varied greatly between seasons. It was highest for crops that matured during the cooler, relatively dry periods from February to March and October to November, and was lowest during the summer months from April to August. This variation corresponded to small differences in the number of flowers in the syconia, but was mainly driven by large seasonal differences in the relative abundance of non-pollinating fig wasps.

Keywords *Ficus* · Fig wasps · Mutualism · Phenology · Seasonality

Y.-Q. Peng · D.-R. Yang (✉)
Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, 88 Xuefu Road, 650223 Kunming, Yunnan, People's Republic of China
e-mail: yangdr@xtbg.ac.cn

S. G. Compton
Faculty of Biological Sciences, University of Leeds, Leeds, UK

Introduction

Plants often exhibit reduced reproductive success towards the edge of their ranges (Jump and Woodward 2003; Jump et al. 2006) and in more seasonal environments (Totland 2001; Munoz and Arroyo 2006), where the timing of reproduction becomes more critical (Kozlowski 1992). Phenological studies address the timing of recurring biological events. For plants, these include seasonal patterns of leaf flushing, leaf shedding, flowering and fruiting. Plant phenology impacts on animal populations by generating temporal changes in resource availability, but may, in turn, be affected by biotic factors through responses to competition, herbivory, pollination and seed dispersal, in addition to underlying climatic variables (van Schaik et al. 1993; Brody 1997). The link between flowering phenology and reproductive success is, therefore, modulated by interactions with both mutualists and antagonists (Elzinga et al. 2007), and is likely to be particularly significant for plants with highly specialised pollination requirements.

More than 750 species of fig trees (*Ficus* spp., Moraceae) (Berg 1989) depend on host-specific fig wasps (Hymenoptera: Agaonidae) for pollination and the fig wasps, in turn, depend on the syconia (colloquially known as figs) for oviposition sites (Weiblen 2002; Machado et al. 2005). Most of the fig trees are limited to tropical and subtropical areas, where they are the most important group of plants for fruit-eating vertebrates (Shanahan et al. 2001), and few are found at higher latitudes. Nonetheless, some temperate fig tree species are resistant to frost (*F. carica* in Europe and *F. tikoua* in China are examples), and the factors that limit the distribution of fig trees are unclear. In particular, it not known whether their climatic tolerances are dictated by the trees themselves, by the insects that pollinate them or by factors that limit the effectiveness of their interactions (Bronstein 1989). In particular, the needs of the pollinators (adult fig wasps survive for at most a few days) provide a constraint that dictates aspects of the phenology of fig trees, leading to a unique all-year-round flowering pattern that is characteristic of the genus, but may not be well-suited to more seasonal environments.

Although *Ficus* populations necessarily include some plants with syconia throughout the year, their phenology is often influenced by climatic conditions, leading to periods when relatively few trees are fruiting. Periods of decreased flowering frequency are typically associated with dry or cold seasons (Hill 1967; Janzen 1979; Compton 1993), and the initiation of syconium was shown to be negatively correlated with rainfall in *F. fulva* at Lambir Hills National Park, Sarawak (Harrison et al. 2000). Leaf production by *F. variegata* in northern Australia is similarly related to seasonal rainfall patterns (Spencer et al. 1996), but the initiation of syconium can also be negatively correlated with leaf flushing on individual trees (Compton 1993).

Syconia are shaped like a hollow ball, lined on the inside by large number of tiny uniovulate flowers. Foundress female fig wasps gain entry to the ovules of their particular *Ficus* species through the ostiole, a bract-lined tunnel that opens temporarily when the syconium is ready to be pollinated (receptive). Once inside, the foundress attempts to gall and lay eggs in some of the ovules and pollinates others. Consequently, each syconium (in monoecious *Ficus* species) produces both seeds and fig wasp offspring. Agaonid generation times are typically 1–2 months, depending on temperature, and mated females of the next generation (loaded with pollen) emerge from the syconia and fly off to seek new receptive syconia. These are generally to be found on other trees, because many monoecious fig trees exhibit flowering synchrony at the individual level and asynchrony at the population level (Bronstein et al. 1990; Compton 1993; Cook and Power 1996; but see Lin et al. 2008).

Here, we describe seasonal variation in the reproductive success of the monoecious fig tree *Ficus altissima* close to the northern limit of its range in China, and close to the northern limit of fig trees in general. We address three questions: (1) What are the leaf and syconium phenological patterns of *F. altissima* in a highly seasonal environment? (2) Does the plants reproductive success (measured as the number of seeds and pollen-carrying fig wasps produced by individual syconia) vary between seasons? (3) What factors are responsible for the variation?

Methods

Study site

The study was carried out around Menglun town, Xishuangbanna in tropical Southwest China (21°55′N, 101°15′E, at about 555 m asl). Temperature and rainfall data collected for 40 years at Xishuangbanna Forest Ecology Station (XTBG), less than 3 km from the research area, show that annual temperature averages 21.8°C, with means of 25.7°C in the hottest month (June) and 16.0°C in the coldest month (January). Average annual relative humidity is 85.0% and rainfall is variable, with distinct rainy (May–October) and dry (November–April) seasons (Xishuangbanna Forest Ecology Station 2001). Figure 1 summarises local temperature and rainfall patterns during the period of the study.

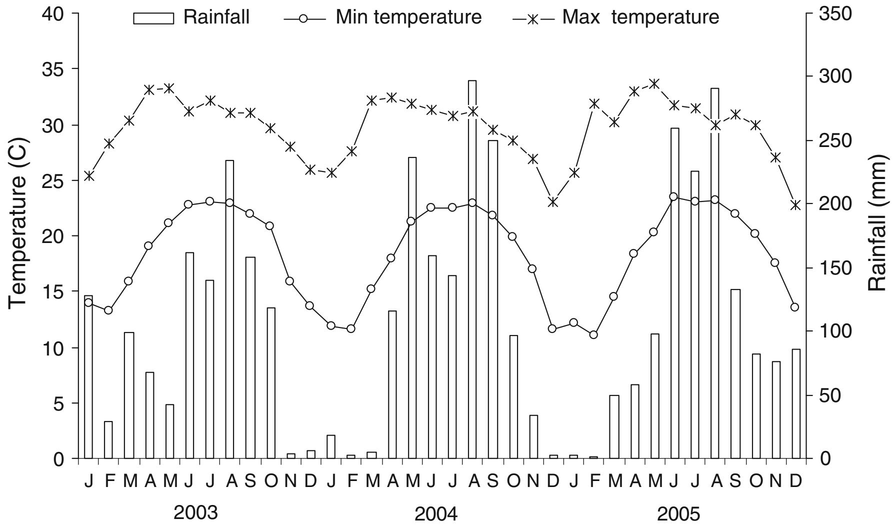

Fig. 1 Temperatures and rainfall at XTBG during the period of the study

Study species

Ficus altissima (subgenus *Urostigma*, section *Conosycea*: Berg and Corner 2005) is distributed across Asia (Corner 1965). At Xishuangbanna, the species occurs naturally in tropical forest, but it is also frequently planted in cities, villages or near temples as an ornamental or sacred plant. The syconia are axillary and paired (rarely solitary). At the time, they release their fig wasps they are yellow in colour and average 14.0 mm in diameter (SE = 0.99, $n = 679$), after which they soften and turn red/orange to attract fruit-feeders (mainly birds). Large crops can number many thousands of syconia. *Ficus altissima* is actively pollinated by the agaonid *Euptistina altissima*, but also supports an undescribed congener (*Eupristina* sp.) which has reduced pollen pockets and fails to pollinate (Peng et al. 2008). *Eupristina* sp. can develop independently of *E. altissima*, and can be the only agaonid in a syconium, or even a whole crop of syconia. The syconia entered by the two *Eupristina* species nonetheless mature and ripen in the same way, even though syconia entered only by *Eupristina* sp. contain no seeds. In addition to the two agaonids, *F. altissima* also locally supports at least 25 further species of non-pollinating fig wasps (NPFW) belonging to families other than the Agaonidae (Gu et al. 2003). Their detailed biology is largely unknown, but they include ovule gallers and parasitoids. Some of these species can also develop in syconia that have not been pollinated.

Data collection

Phenological censuses of seven *F. altissima* trees were conducted weekly from 13 January 2003 to 6 December 2005. The presence or absence of the following leaf character states was recorded: young yellow or red leaves, matured green leaves and senescing leaves. Five syconium developmental phases were also distinguished: A (pre-female), B (female phase, when syconia are entered and pollinated), C (inter-floral phase, when seeds and wasp offspring are developing), D (male phase, when the next generation of wasps emerges from the syconia) and E (post-floral phase, after the syconia have been vacated and become attractive to seed dispersers). When present, 30 D phase syconia per tree were collected. Each syconium was placed individually in a fine-mesh bag (20 × 20 cm), and the fig wasps were allowed to emerge. All the fig wasps, including those remaining inside the syconia, were collected and preserved in 70% ethanol. The number of fig wasps, seeds and female flowers were counted. During the 3 years, a total of 679 syconia were collected from 23 crops. Daily temperatures and rainfall for the survey period were provided by the Xishuangbanna Forest Ecology Station.

Analysis

The proportions of the trees with new leaves and new syconia were calculated after every census, and related to average temperature and total rainfall during the preceding week. Kendall correlations were used to determine the correlation between the two variables. Paired-samples T tests were used to compare differences in the number of seeds and female pollinators per syconium. In order to determine relationships amongst seed and pollinator numbers and biological variables at the syconium level, we first calculated the proportion of total female flowers used by seeds and pollinators. A Generalised Linear Mixed (GLM) Model with binomial errors was applied (poisson and quasi-poisson distributions did not adequately describe the data), with trees as a block treatment in the analysis. At the crop level, a GLM Model with quasi-poisson errors was used to examine relationships between seed and pollinator numbers and climatic variables. All the analyses were conducted in R 2.6.2 Professional Edition.

Results

Syconium and leaf phenology

Syconia were present on the seven *F. altissima* trees at all times of the year, with between zero and five trees with syconia at any one time (Fig. 2). Individual trees produced from three to seven crops over the 3-year period, with no synchrony between trees in crop initiation dates. Syconia were present on some trees for much of the year, but others were less successful and rarely had syconia present. Reflecting their longer durations, A-phase (pre-female) syconia and C-phase (inter-floral) syconia were recorded more frequently than the other developmental stages (Fig. 2). The trees generally produced highly synchronous crops, with most syconia at the same stage of development, but there were exceptions. A total of 12 of the weekly surveys recorded crops with phase-B receptive syconia (the short period when pollinators enter the syconia), whereas 32 surveys recorded crops with phase-D syconia, where fig wasps were emerging. There was overlap of phases B and D on only two occasions, when self-pollination would have been possible. The duration of phase C (when seeds and fig wasps develop in the syconia) varied between 20 and 70 days. This partially reflected temperature-related variation in development times, but three of 23 crops also aborted early, producing no seeds or fig wasps.

Ficus altissima at XTBG is deciduous, but because flushing occured immediately after leaf drop there were always some leaves present on the trees (Fig. 2). The trees produced 1–4 flushes of new leaves each year, but small quantities of new leaves could also appear more or less continuously. Leaf phenology was usually synchronised with syconium production (Fig. 2). Before the initiation of a crop, the trees typically shed all or some of their leaves and the branches would then initiate new leaves and syconia simultaneously; syconium and leaf initiation were highly correlated (Kendall correlation: $T = 0.23$, $n = 145$, $P < 0.01$). Temperature, but not rainfall, was significantly negatively correlated with new leaf initiation (Kendall correlation: $T = -0.13$, $n = 145$, $P < 0.05$), whereas fig crop initiation was negatively correlated with both rainfall and temperature (Kendall correlation: $T = -0.23$, $n = 145$, $P < 0.01$ for rainfall; $T = -0.24$, $n = 145$, $P < 0.01$ for temperature).

The reproductive success of *Ficus altissima* and its fig wasps

The contents of the 679 syconia sampled from 23 crops were highly variable, with mean number of seeds in different crops ranging from just above zero to over 250, and mean number of female pollinators ranging from zero to over 200 (Fig. 3). Overall, significantly more seeds than female pollinators were present in the syconia (paired-samples *t*-test: $t = 6.53$, df $= 678$, $P < 0.001$) and those syconia with more seeds also produced more pollinators (GLM: $\beta = 0.006 \pm 0.0005$, $P < 0.001$).

The non-pollinating agaonid *Eupristina* sp. was present in almost all of the crops (22 from 23, Table 1), but varied considerably in abundance from crop to crop. Comparison of the contents of syconia containing one or both agaonids (Table 1) shows that mean seed production averaged about 50% higher and pollinator numbers were twice as high in syconia where *Eupristina* sp. was absent. Consequently, *Eupristina* sp., significantly reduced pollinator female numbers within shared syconia (GLM: $\beta = -0.03 \pm 0.0003$, $P < 0.001$), and had a significant negative impact on seed numbers (GLM: $\beta = -0.002 \pm 0.0006$, $P < 0.001$). The relationship between *Eupristina* sp. and *E. altissima* is apparently asymmetric, because the former produced almost as many offspring in shared

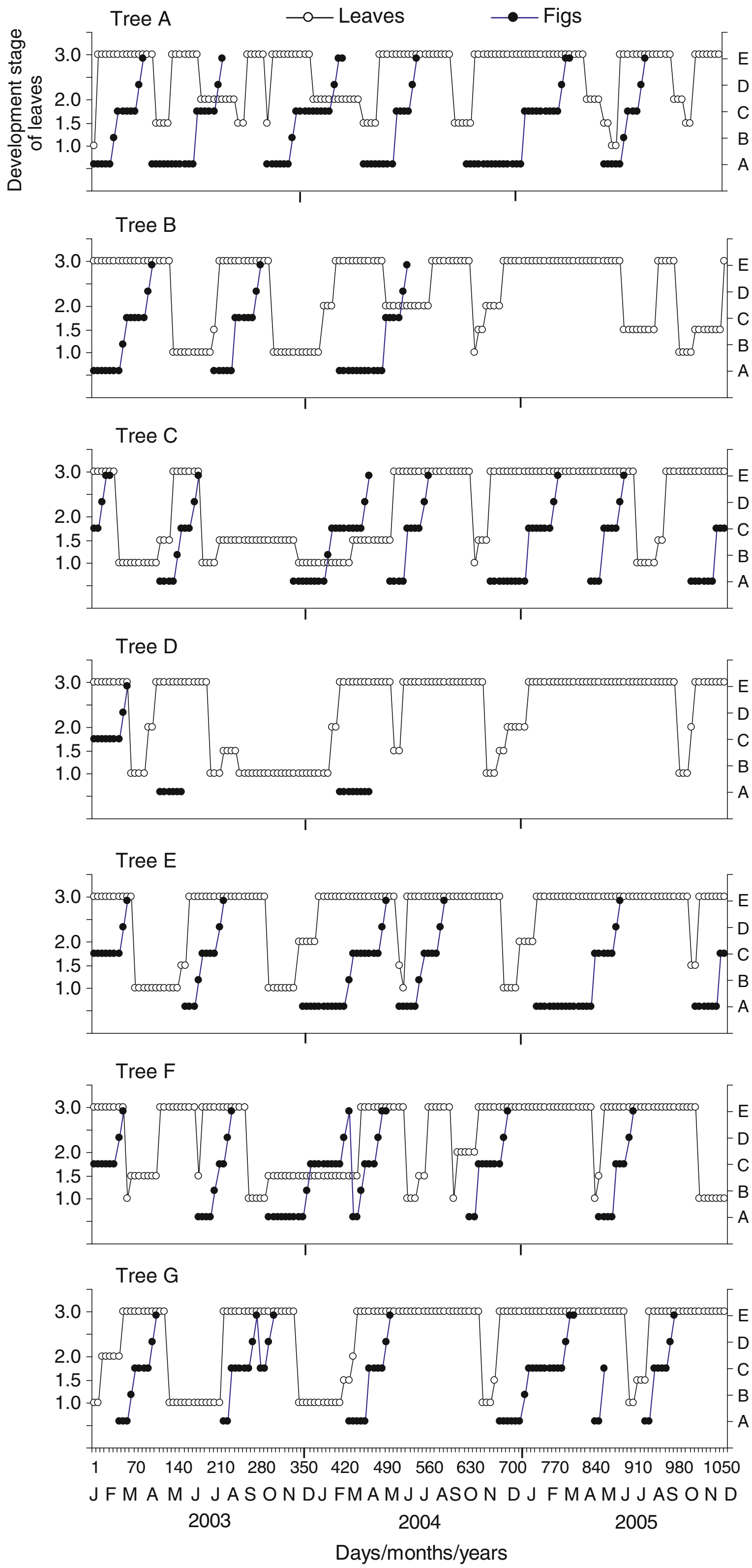

Fig. 2 The phenology of leaf and syconium production by *Ficus altissima* at XTBG. The developmental phases of the leaves are summarised as: 1.0 (senescing leaves), 1.5 (senescing + new yellow and red leaves), 2.0 (new yellow and red leaves) and 3.0 (mature green leaves). The developmental phases of the syconia are summarised as phases A (pre-female), B (female), C (inter-floral), D (male) and E (post-floral)

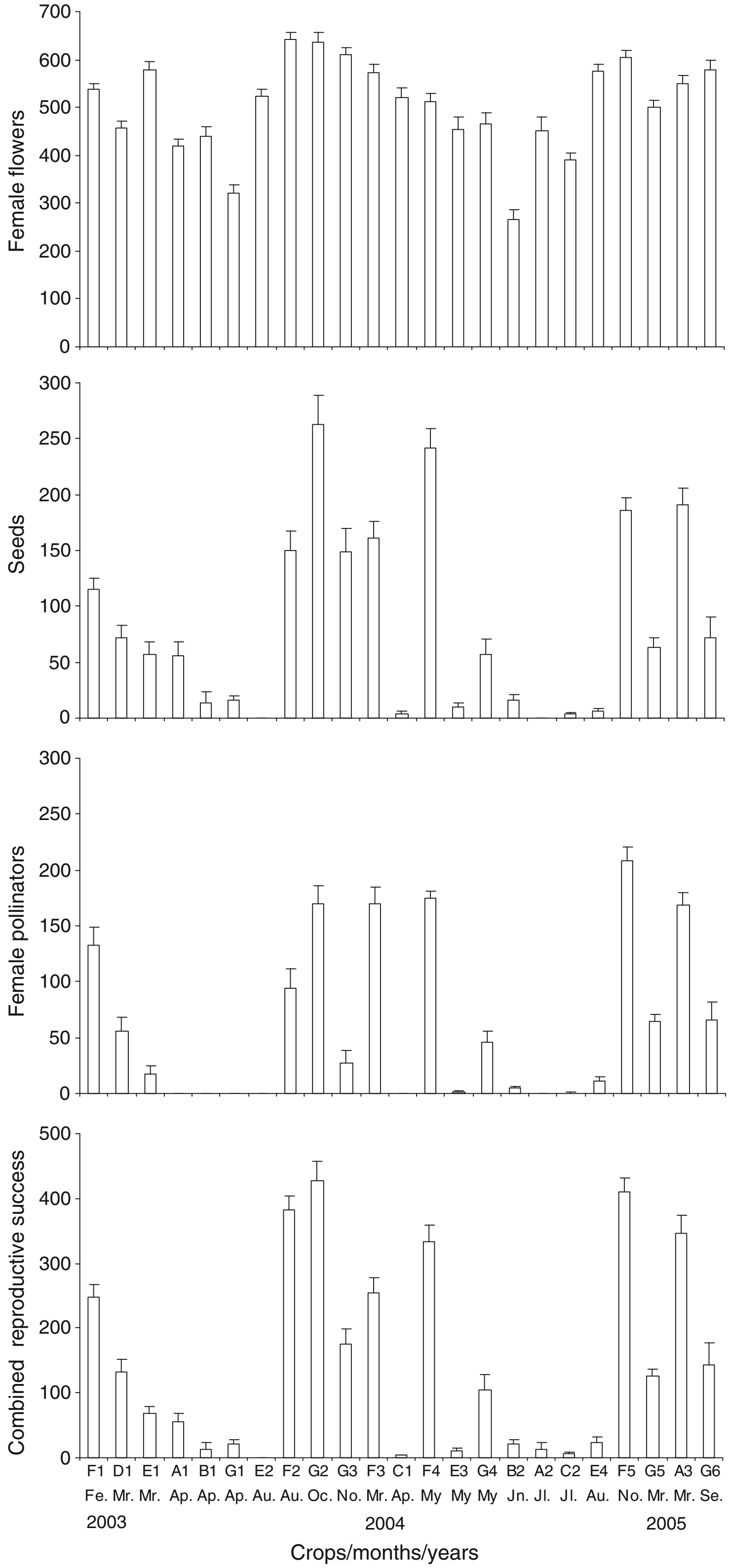

Fig. 3 Seasonal variation in the number of flowers that produced seeds and fig wasps in *Ficus altissima* syconia at XTBG (Mean/syconium and SE). The *dates* indicate when the mature syconium crops were sampled. Each female flower can potentially produce one seed, one pollinator, or neither. Combined reproductive success includes the number of both pollen-carrying female fig wasps and seeds and summarises the number of flowers that successfully contributed to either male or female reproductive function

Table 1 The contents of *Ficus altissima* syconia that produced different combinations of agaonids (means/syconium and SE)

Occupants	Syconia	Seeds	Female *E. altissima*	Female *Eupristina* sp.
E. altissima alone	261	151.03 ± 6.63	147.06 ± 5.09	–
Eupristina sp. alone	303	35.13 ± 4.29	–	78.08 ± 4.63
Both *Eupristina* species	52	103.83 ± 14.53	71.42 ± 8.99	56.10 ± 8.98
No agaonid wasps	63	18.83 ± 7.21	–	–

Syconia are combined from all crops. The presence of seeds in some syconia that did not produce *Eupristina altissima* indicates that foundresses of this species entered the syconia, but failed to reproduce

syconia as in syconia where it was the only agaonid (Table 1).

In addition to the two agaonids, there were 2–19 species of NPFW recorded from different crops, with dramatic variation in the number of individuals present (Fig. 4). This diverse group of species includes parasitoids and seed gallers. In crops, where NPFW fig wasps were abundant, there were many syconia that produced no agaonids of either species, suggesting that some NPFW were independently capable of stimulating syconium development. Syconia with more NPFW species contained more NPFW individuals (GLM: $\beta = 0.09 \pm 0.03$, $P < 0.05$), and NPFW numbers had a significant negative impact on seed and pollinator production within individual syconia (GLM: $\beta = -0.005 \pm 0.0002$, $P < 0.001$ for seeds, $\beta = -0.004 \pm 0.0002$, $P < 0.001$ for pollinator females).

Seasonal variation in seed and pollinator production

The climate at Xishuangbanna (Fig. 1) has distinct rainy (May–October) and dry seasons (November–April), with average monthly temperatures and rainfall (over a 40-year period) that are positively correlated (Kendall correlation: $T = 0.69$, $P < 0.001$). Seed and pollinator female production per syconium (measures of the trees' female and male reproductive fitness, respectively) showed similar annual variation (Fig. 3), with peaks in the cool dry season. In contrast, few seeds and female pollinators were produced from April to August, when five crops did not produce any female pollinators at all. Despite this, neither temperature nor rainfall significantly predicted the number of seeds in the syconia (GLM: $P = 0.23$ for temperature; $P = 0.77$ for rainfall) and pollinators (GLM: $P = 0.15$ for temperature; $P = 0.79$ for rainfall). However, there was a significant negative correlation between temperature and the number of female flowers in the syconia (GLM: $\beta = -0.07 \pm 0.03$, $P < 0.05$), which also showed that seasonal variation (Fig. 3). Climatic factors could, therefore, have been acting indirectly, via syconium size, to influence the plant's reproductive success, as syconia with fewer female flowers produced both fewer seeds (GLM: $\beta = 0.002 \pm 0.0005$, $P < 0.001$) and fewer female pollinators (GLM: $\beta = 0.001 \pm 0.0005$, $P < 0.001$).

In addition to seasonal variation in the number of female flowers in the syconia, there was also variation in the fate of those flowers, with crops in the cool dry season having syconia with a higher proportion of their female flowers that contained seeds (Fig. 4). Periods of higher seed production corresponded with production of a higher proportion of pollinator females, compared to the fig wasp community as a whole, with a lower proportion of the 'cheater' *Eupristina* sp., and NPFW (Fig. 4).

Discussion

Despite its northerly location, the fruiting phenology of *F. altissima* at XTBG is similar to that described for most other monoecious *Ficus* species, in that individual trees generally produced syconia in synchronous crops (preventing self-pollination), and that there was asynchrony between trees in the timing of syconium production (Bronstein et al. 1990; Compton 1993; Lin et al. 2008). A flush of new leaves usually took place immediately after leaf drop, though some individuals produced small quantities of new leaves more or less continuously. This is a pattern similar to that described by Milton (1991) from six neotropical *Ficus* species, but contrasts with that seen in the highly seasonal south of South Africa,

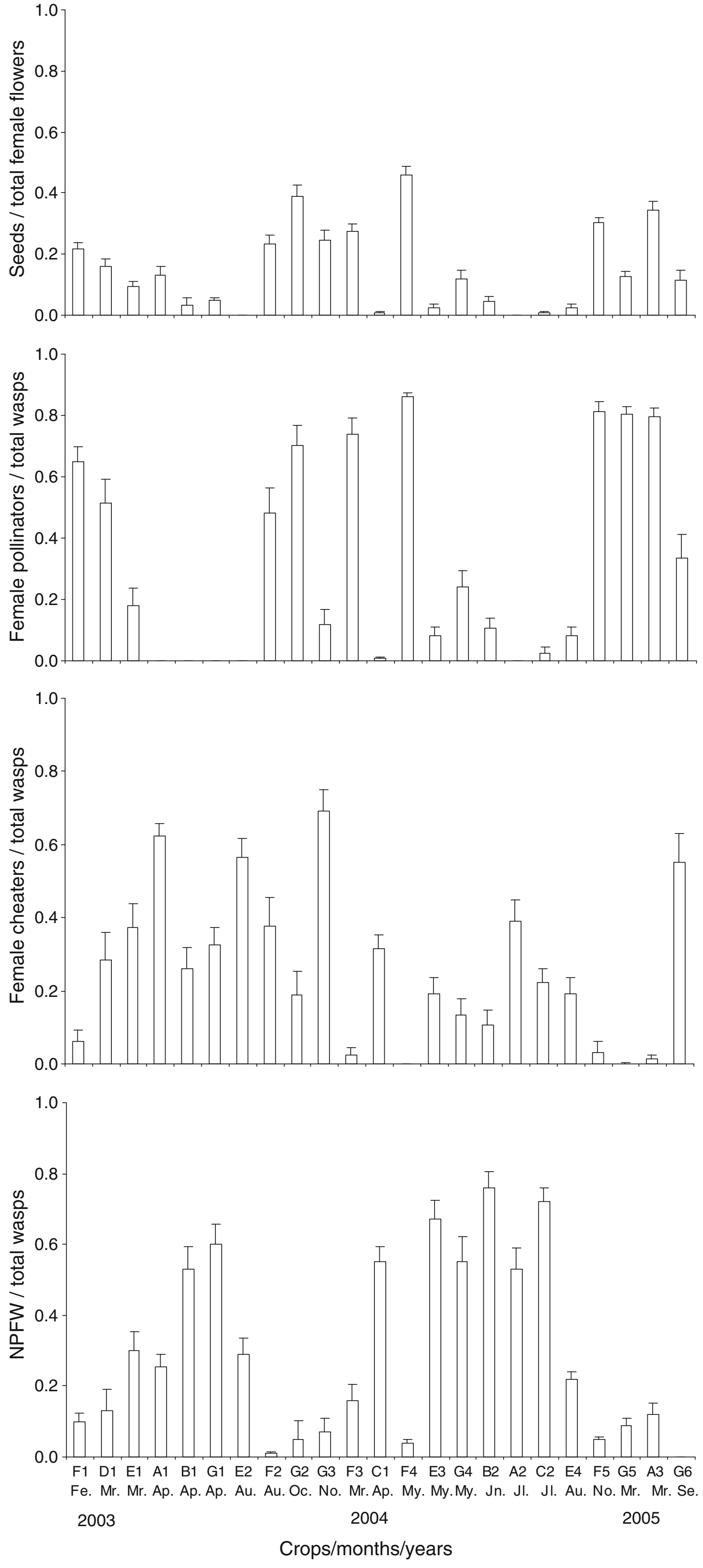

Fig. 4 Seasonal variation in the contents of *Ficus altissima* syconia at XTBG, expressed as a proportion of the total female flowers that produced seeds or as a proportion of the total number of fig wasps (all species) that were present in the syconia (Mean/syconium and SE). *Eupristina altissima* is the pollinator and *Eupristina* sp. is a 'cheater' agaonid that no longer pollinates the syconia

where *F. burtt-davyi* was found to often be leafless for extended periods during winter (Compton 1993). Leaf flushing and syconium initiation in *F. altissima* generally occurred at the same time, again as recorded by Milton (1991) for six neotropical *Ficus* species, but in contrast to *F. burtt-davyi*, where new syconium crops were initiated at any time except when a tree was flushing.

Syconia that contained more seeds also contained more pollinator females. This suggests that wasps were not overexploiting their hosts, and there was no detectable trade-off between pollinators and seeds (Anstett et al. 1996). The plant's reproductive success (as measured by seed and pollinator female numbers per syconium) varied greatly between crops, with a strong seasonal pattern. Number of both seeds and pollinator females were highest in crops that ripened during the cooler, relatively dry periods from February to March and October to November, whereas some crops produced almost no seeds and no pollinators from April to August (the end of the dry season and into the rainy season). This latter period included the months when the most crops ripened (March and June).

Seasonal highs and lows in *F. altissima* reproductive success coincided with variation in the number of female flowers in the syconia (and therefore the maximum number of flowers that could be utilised for seed or pollinator production), as shown for some New World *Ficus* species (Bronstein 1988; Bronstein and Hossaert-McKey 1996). In addition, there was marked seasonal variation in the proportion of the female flowers that produced either seeds or pollinator fig wasps. This resulted from changes in the composition of the fig wasp community, particularly in the relative abundance of fig wasps that were parasites or mutualists. As with many monoecious fig trees, *F. altissima* is host to numerous species of NPFW, but it is unusual in that it also supports a 'cheater' agaonid that enters the syconia, but no longer pollinates them. Like some NPFW, it does not need to share a syconium with the tree's pollinator, and can independently stimulate occupied syconia to grow and mature. The syconia ripen in the same way as if pollinator offspring were present, but contain no seeds. *Eupristina* sp. enters the syconia to oviposit, unlike the NPFW associated with *F. altissima,* but like many NPFW it feeds on galled ovules, and competes for oviposition sites with the pollinator. Other NPFW have a parasitoid life style, but their host ranges are unknown.

The two *Eupristina* species displayed clear seasonal differences in abundance, with crops where the cheater was abundant producing few, or even no pollinator females. This appears to reflect an asymmetry in competitive ability between these species, with the cheater *Eupristina* sp., the more effective competitor. Periods when *Eupristina* sp. were abundant also coincided with greater number of NPFW, which are also competitors or parasitoids, and in combination, they reduced the number of the pollinator and the seeds it generates. The factors driving the peaks and troughs in agaonid and NPFW abundance are unknown, but given their seasonal nature, may reflect climatic conditions experienced by the adults outside the syconia. Adult females of the two *Eupristina* species are unusually long-lived for agaonids (Y.-Q. Peng, unpublished), exposing them to environmental factors for longer than is the case for most pollinator fig wasps.

In conclusion, *F. altissima* growing in the highly seasonal environment of XTBG, close to the northern limit of the distribution of the species, is most successful at producing seeds and pollinators during the colder periods of the year, because antagonistic fig wasps are less frequent at those times. An understanding of how seasonality differentially influences the population dynamics of the fig wasp species will be required to explain the underlying causes.

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