Original article

Living on the edge: Fig tree phenology at the northern range limit of monoecious *Ficus* in China

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A B S T R A C T

Fig trees (*Ficus*) are a species-rich group of mainly tropical and subtropical plants that are of ecological importance because of the large numbers of vertebrates that utilise their figs for food. Factors limiting their distributions to warmer regions are still poorly understood, but are likely to include factors linked to their specialised pollination biology, because each *Ficus* species is dependent on one or a small number of host-specific fig wasps (Agaonidae) for pollination. Adult fig wasps are short-lived, but some species are capable of dispersing extremely long distances to pollinate their hosts. Close to its northern range limit we investigated the phenology of *Ficus virens*, the monoecious fig tree that reaches furthest north in China. Relatively few trees produced any figs, and very few retained figs throughout the winter. Despite this, new crops produced in spring were pollinated, with seasonally migrant pollinators from plants growing further south the most likely pollen vectors. An inability to initiate new crops at low temperatures may limit the distribution of monoecious fig trees to warmer areas.

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1. Introduction

Geographic ranges are one of the fundamental characteristics of species. Current and predicted changes in the distribution of many species in response to climate change have stimulated much recent interest in the determinants of range boundaries (Parmesan et al., 1999; Parmesan and Yohe, 2003; Sexton et al., 2009; Hill et al., 2011). Extensions in ranges are normally in response to factors that influence the demographics of peripheral populations (Geber, 2008), via changes in death and birth rates, immigration or emigration (Sagarin et al., 2006; Gaston, 2009). Mortalities are likely to increase towards range edges because physiological tolerances may be tested in less suitable, marginal environmental conditions. Birth rates also respond to physiological stresses and are considered to be among the more common demographic constraints on range expansion (Gaston, 2009).

Physiological tolerances limit both the northern and southern ranges of plant species in Europe (Normand et al., 2009). Co-distribution with suitable pollen vectors is also clearly a requirement for plants that depend on animals for pollination (Moeller et al., 2012), as is illustrated by declines in plants that result from reductions in pollinator numbers (Potts et al., 2010). The range limits of plants that depend on the services of a small range of specific pollinators are especially likely to be determined by the abundance and distribution of their pollinators, given that these may display a narrower range of physiological tolerances than the plants themselves.

Ficus (Moraceae) is among the largest genera of angiosperms, with more than 750 included species, each of which relies on one or a small number of host species-specific fig wasps (Agaonidae) for pollination (Herre et al., 2008). Most species of fig trees are restricted to tropical or subtropical regions, where they are perhaps the single most significant source of food for frugivorous vertebrates (Shanahan et al., 2001). A small number of species have ranges that extend into temperate areas and a few species are largely or entirely extra-tropical in distribution (Weiblen, 2002). Temperatures and water availability (Coelho et al., 2014), as well as survivorship of their species-specific pollinators (Kjellberg and Valdeyron, 1990) have all been suggested as factors limiting the distributions of fig trees in different regions, but the reasons why fig trees are largely tropical in distribution remain poorly understood.

It has been suggested that species with a dioecious breeding system may be better suited to more seasonal, temperate climates than monoecious species (Berg, 1989). This suggestion was based on one of the major constraints on fig tree life cycles that results from the biology of their unusual pollinators. Adult agaonids are small insects that are sensitive to extremes of temperature and humidity (Peng et al., 2010; Warren et al., 2010) and typically

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survive for just one or two days (Kjellberg et al., 1987). Foundress females enter figs to lay their eggs in the numerous female flowers present inside. Pollination is active or passive, depending on the species, and in fig trees with monoecious breeding systems it results in some female flowers in each fig producing seeds, while others contain the offspring of the fig wasps. All year round fruiting is required in order to maintain pollinator populations, with individual trees typically fruiting at different times, to allow pollinator populations to cycle between trees. This results in monoecious fig trees producing seeds throughout the year, rather than during seasons when their survival is most likely. This constraint does not apply to dioecious *Ficus* species, where individual trees are specialized for either a male or female reproductive function, and have figs that contain only pollinator offspring or seeds, respectively. This allows flowering among female trees to be seasonal, because only male trees need to support pollinator populations. The *Ficus* species with northerly-centred distributions in Europe and Asia are all dioecious and both sexes exhibit strongly seasonal fruiting phenologies that allow the fig wasps to remain as larvae throughout the long winter periods. Northerly specialists are absent among monoecious *Ficus* species. In the southern hemisphere, monoecious species nonetheless penetrate further south in Africa than dioecious species (and are the only fig trees in southern Australia and South America).

Patterns of seed dispersal, the availability of suitable germination sites, competitive interactions and physiological tolerances to local conditions will all influence whether a fig tree can establish, grow and reach maturity, but whether the plants can then successfully reproduce will depend upon the ability of the plants to produce figs and the ability of their host-specific pollinators to reach the figs. Fig trees are capable of growing in areas where their pollinators are absent. For example, naturally-occurring *Ficus carica* are found along the Atlantic coast of France, whereas the tree's pollinator is restricted to areas with a more Mediterranean climate (Bronstein, 1989) apparently because it cannot complete its unusual bivoltine life cycle (Kjellberg and Valdeyron, 1990). Fig trees growing in areas where they cannot maintain local pollinator populations throughout the year may remain sterile, or seasonal migrations by pollinators that developed on trees elsewhere may allow seeds to be produced. Fig wasps, especially those associated with monoecious host plants, can disperse many kilometers and pollinate even very isolated fig trees (Nason et al., 1998; Ahmed et al., 2009), but pollinator limitation leading to reduced seed set or fruit abortions has nonetheless been reported among isolated populations (Bronstein, 1988; Compton et al., 1994; Harrison, 2000; Ma et al., 2009). Fig trees also support numerous additional species of non-pollinating fig wasps (NPFW). Some NPFW can develop in figs that lack pollinators. Where NPFW distributions extend beyond those of their pollinators (utilizing planted trees), seasonal colonization patterns have been reported, with species extending their distributions during the summer months (Galil et al., 1970).

Fruiting patterns in fig trees often respond to seasonal changes in climatic conditions, and many species have been found to produce more crops of figs, or produce larger crops, during the warmer months of the year, even in tropical latitudes (Hill, 1967; Valdeyron and Lloyd, 1979; Corlett, 1987; Pereira et al., 2007). By extension, fig trees growing towards their northern range limits might be expected to entirely cease fig production during the winter, and depend entirely on pollinators that migrate northwards each summer, at least for their first crops each year. Trees growing even further north would then be predicted to fail entirely to reproduce, either because they fail to produce any figs, even in summer, or if they do so, then they are growing too far away from fig wasp source populations for the figs to be pollinated.

We tested this prediction with populations of *Ficus virens* growing towards their northern range limit in China, where this is the Chinese monoecious fig tree with a distribution that extends furthest north (Fang et al., 2009). We recorded the leaf and fruiting phenologies of the plants, with the aim of determining whether 1) pollinator populations associated with *F. virens* at the northern edge of its range die out in the north each winter, but dispersal by pollinators moving north each summer results in a "rescue effect" or 2) Figs are present throughout the year and their development simply slows in winter, allowing the fig wasps to overwinter in the figs even at the northern limit of the trees.

2. Materials and methods

F. virens Ait. is a monoecious fig tree species belonging to subgenus *Urostigma*, section and subsection *Urostigma* (Berg and Corner, 2005). Its wide native range covers tropical and subtropical regions of south and south-east Asia, Melanesia and North Australia (Berg and Corner, 2005), and also extends northwards into China, where, in Sichuan Province, it grows further north than any other monoecious fig tree species in China and is one of only two monoecious species with distributions that extend beyond 25° north in China (Fang et al., 2009). Considerable morphological variation is present within its large range, with two varieties described (Berg and Corner, 2005). *F. virens* is also widely planted as a street tree in Thailand, China and elsewhere. In Sichuan Province it is mainly planted within the recorded northern limit of natural populations (Fang et al., 2009). *F. virens* is described as being deciduous or semi-deciduous (Chang et al., 1998; Fang et al., 2009). Its figs are located in the leaf axils, and reach 7–12 mm when mature. The pollinator recorded for *F. virens* is *Platyscapa coronata* (Grandi), but molecular screening has revealed that several distinct but closely related agaonid species are associated with this tree in different parts of its range (J-Y Rasplus, Pers. Comm.). *Platyscapa* adults may be the most widely-dispersing fig wasps in Asia (Compton and McCormack, 1999; Harrison and Rasplus, 2006). In addition to the pollinator there are numerous species of NPFW associated with *F. virens* but there have been no detailed studies of the fauna (Universal Chalcidoidea Database, online resource http://www.nhm.ac.uk/research-curation/research/projects/chalcidoids). In Sichuan these include parasitoids and gallers, some of which can develop independently in figs that have not been entered by the pollinators (Y. Chen et al., unpublished).

Mianyang is located in South-Central Sichuan Province and has a monsoon-influenced humid subtropical continental climate with four distinct seasons. Frosts occur regularly in winter, but snow is rare. Summers are hot and humid. Rainfall is highly seasonal and occurs mostly in summer. The natural range of *F. virens* extends only as far north as Mianyang, and it is also commonly planted in this city.

To assess the effect of temperature on the leaf and fruiting phenology of *F. virens*, minimum and maximum daily temperatures in Mianyang during the observation period were obtained from http://www.tianqihoubao.com/. The meteorological station is about five km. from the study site.

To monitor the seasonal dynamics of *F. virens* and its pollinator at its northern range margin, we followed seasonal changes in thirty five roadside trees greater than 5 m in height weekly from 1 April 2010 to 30 April 2011. The trees were planted in the Mianyang Normal University old campus (31°29′N, 104°44′E). The presence of different leaf stages (active buds, green leaves, yellow senescing leaves), was recorded, together with the developmental phases of any figs that were present. At least 10 figs on each of five well-separated branches
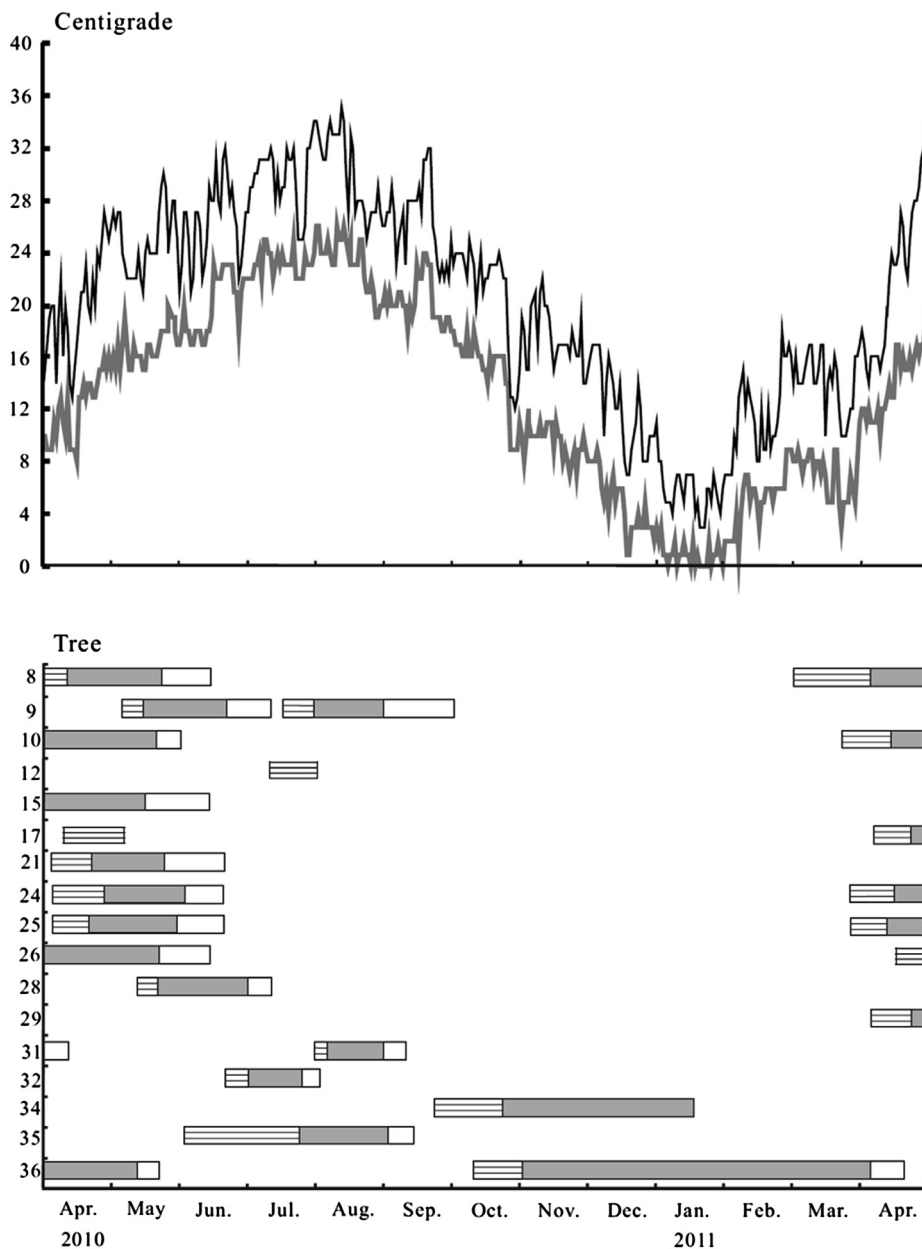
Fig. 1. The daily maximum (black) and minimum (grey) temperatures in Mianyang during the study period in relation to the fruiting phenology of 17 individuals of *Ficus virens*. Bars with horizontal lines, grey bars and open bars indicate AB, C and DE phase figs respectively.

were checked closely, together with general scans of the trees. The developmental phases of the figs were recorded as being either pre-female (A-phase), female (B-phase, when foundress female pollinators enter to oviposit), interfloral (C-phase, when fig wasp larvae and seeds develop), male (D-phase, when the next generation of fig wasps emerge from galled ovules) or postfloral (E-phase, after the fig wasps have emerged and the figs become attractive to frugivores) (Galil and Eisikowitch, 1968a). The B- and D-phases of each fig are brief and they were combined with A- and E-phases respectively in the analyses. Obvious signs of ripening were often slow to appear after the first fig wasps emerged, and emergence could continue for several days. The presence of C-phase figs did not necessarily indicate that pollination had taken place, because figs also entered this phase if they had been colonized by NPFW, irrespective of whether pollinators had also entered the figs.

3. Results

Temperatures in Mianyang varied greatly between seasons. They peaked in late August, when minimum temperatures were over 20 °C and maximum temperatures over 30 °C (Fig. 1). The coldest temperatures were recorded in January, when maximum temperatures were generally below 10 °C and several nights were at or below freezing.

Most of the 35 *F. virens* trees had healthy green leaves present throughout almost all the year (Figs. 2 and 3). They lost their old leaves over a short period in spring immediately before or at the same time as new leaves were appearing on the trees. The remaining 14 trees lost all their leaves during autumn or winter (mostly by January, some in December). There were some differences between years, with seven trees that still had the previous year's green leaves in spring 2010 losing all their leaves by January
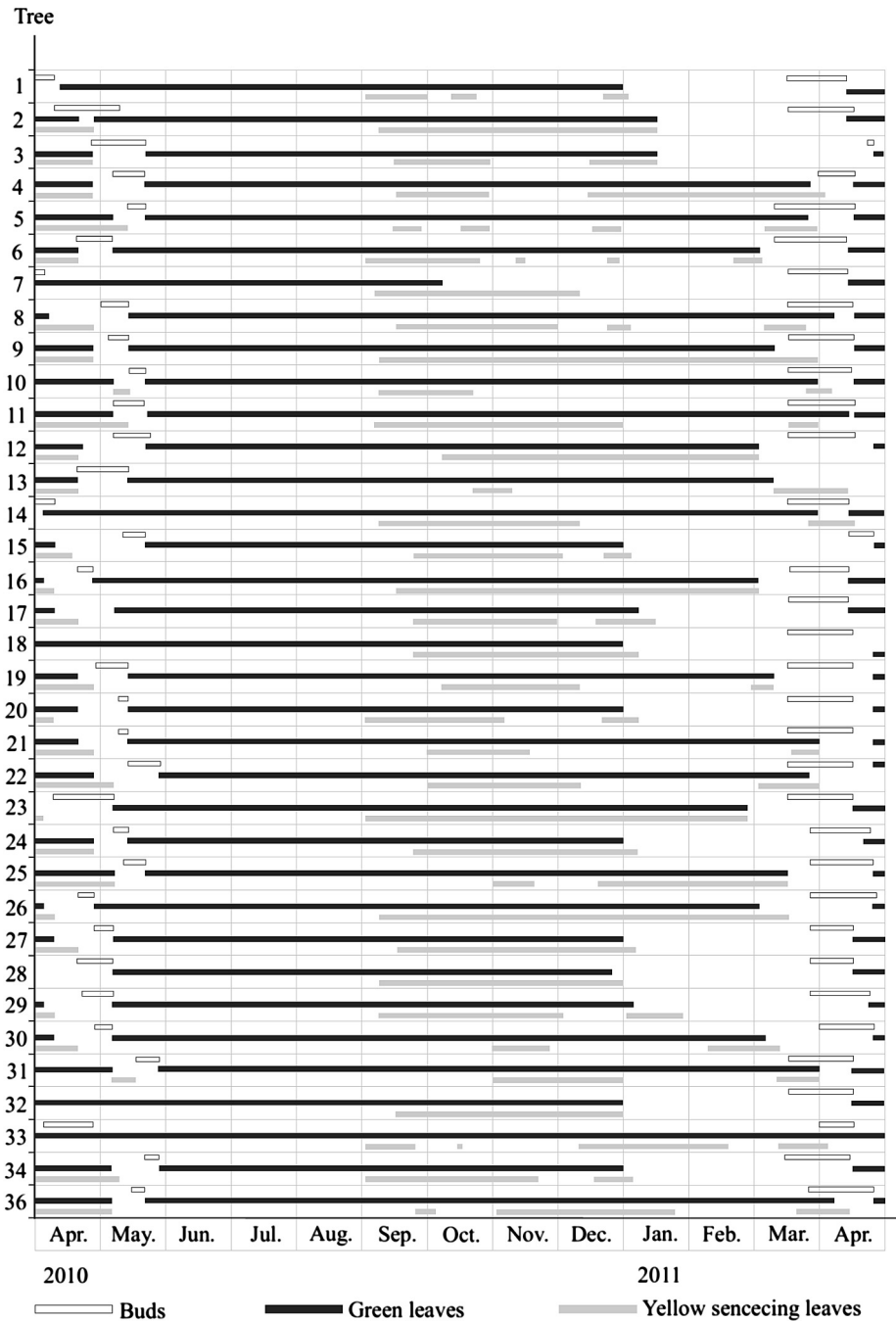
Fig. 2. The leaf phenology of *Ficus virens* individuals in Mianyang. The open, black and grey bars show the times when active buds, green leaves and yellow senescing leaves were present respectively.

2011. All the trees produced new leaf buds in spring. Senescing yellow leaves were present from September or October 2010 on all trees, but abscissions meant that they were not necessarily present continuously. Progressive senescence sometimes continued through to the spring, resulting in some overlap with the first appearance of active leaf buds.

Figs were recorded on 17 trees of the trees during the 12 months of observation (Fig. 1). Fig production was synchronized within trees, with well-defined crops, but was asynchronous across the population as a whole. Most trees produced a single annual crop, but some managed two crops. New crops were mainly produced in the spring, but new crops continued to appear through to October. This resulted in the total number of crops being highest in spring, when they were present on up to 10 of the trees. In contrast, only two trees bore figs through the winter period. One of these crops had many figs that aborted and the remainder became shriveled on the branches at a late stage without allowing any wasps to complete their development. No new crops were initiated throughout the winter period, and no wasps were released. The single healthy crop that survived the winter took six months to complete its development, whereas crops initiated in summer took less than two months. Figs from two crops aborted without being pollinated, one in spring and one in summer.
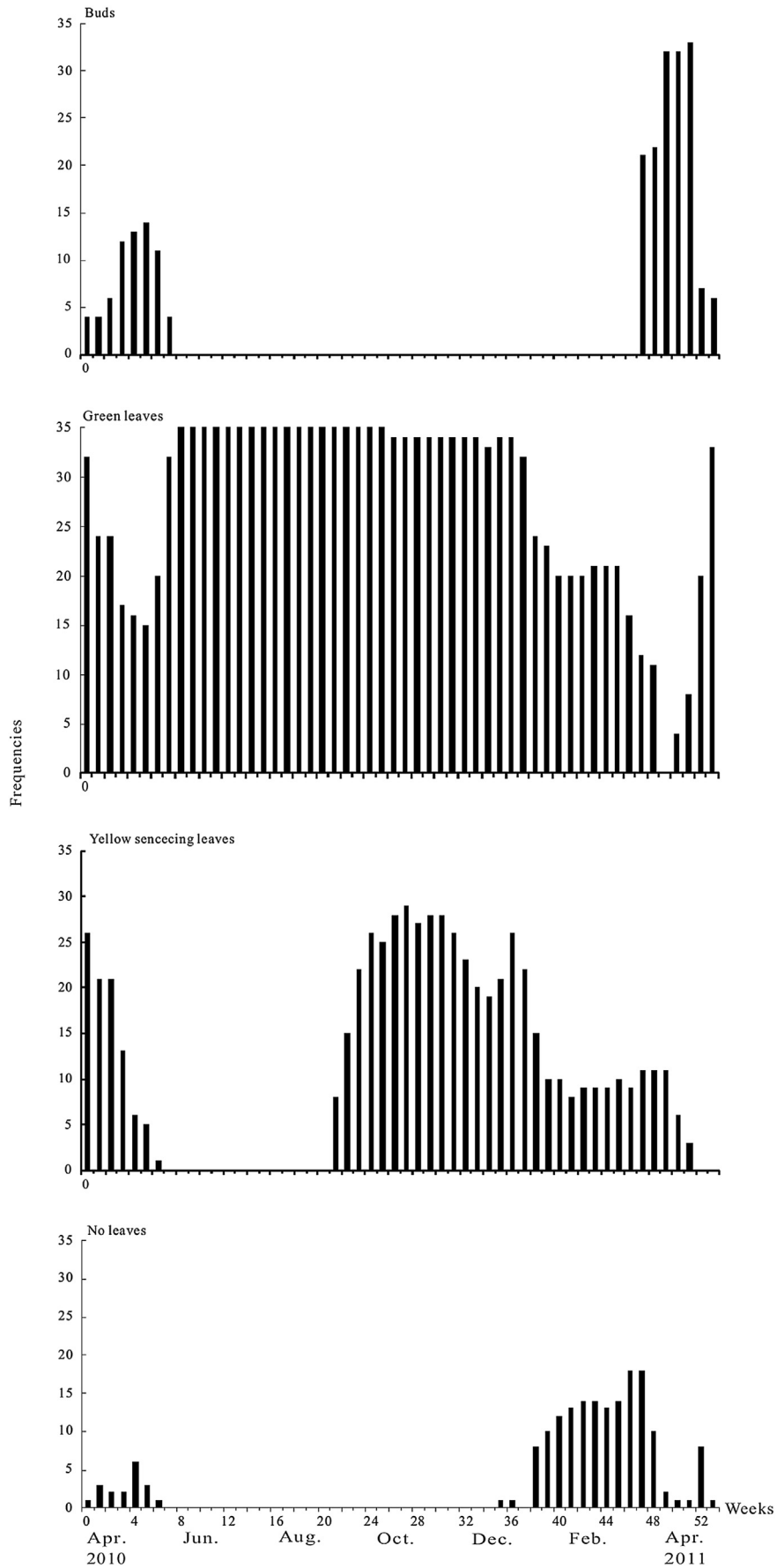
Fig. 3. A summary of leaf phenology among *Ficus virens* trees in Mianyang.

Despite the winter hiatus in fig production, *F. virens* supported a rich fig wasp fauna in Mianyang with at least ten genera represented (Supplementary Table 1). Fewer taxa were present in Spring than Summer crops, but the pollinator was present in mature figs collected in the Spring (Y. Chen et al. unpublished).

4. Discussion

The production of leaves on *F. virens* trees growing in Mianyang varied among individuals, but there was a clear response to the marked seasonal temperature changes. Although some trees did bear green mature leaves almost year-round, senescing leaves were produced by all the trees when temperatures decreased in the Autumn. A burst of new leaves were observed in spring on all the trees. Seasonal influences on leaf production have been described in many *Ficus* species, though rarely at the edge of a species' range (Spencer et al., 1996; Zhang et al., 2006; Pereira et al., 2007; Ballestrini et al., 2011). *F. virens* may be unusual in that leaf loss is often gradual and can occur over an extended period. This contrasts with the rapid leaf turnover of species such as *Ficus obtusifolia* (Ballestrini et al., 2011) and even *Ficus burtt-davyi* when it is growing at the latitudinal limit of the species in South Africa (Compton, 1993). Bursts of new leaf production accompany the induction of large fig crops in some *Ficus* species (Harrison et al., 2000; Pereira et al., 2007; Peng et al., 2010). The same pattern was present in *F. virens* in Mianyang insofar as all the trees renewed their leaves in spring, and new fig crops were also routinely produced at this time.

Both abiotic and biotic factors play important roles in determining the range limits of plants, with availability of suitable pollinators a fundamental constraint for many species (Pauw and Bond, 2011; Chalcoff et al., 2012; Moeller et al., 2012). Pollinator limitation at the northern edge of its range was expected to be particularly important for a species such as *F. virens*, because it is dependent on a single species of insect for pollination and pollinator fig wasps are not capable of surviving for more than one or two days outside its host figs. However, shortage of pollinators did not appear to be the main constraint on *F. virens* reproduction in Mianyang, where the plant's fruiting phenology, especially during the winter period, had a significant influence. In Mianyang, about half the mature-sized and apparently healthy *F. virens* trees failed to produce any figs during the year-long study period. Among the 17 trees that did flower, fig production was strongly seasonal and largely restricted to the spring and summer months. No female (B-phase) figs were present during the winter months, in marked contrast to the pattern recorded for *F. virens* growing under less harsh conditions in Australia, where female phase figs were present at similar frequencies throughout the year (McPerson, 2005). Crops on two of the trees in Mianyang also failed to mature any of the figs they produced, apparently as a result of a lack of pollinators, and the figs of one of two other crops that were pollinated in the Autumn entirely failed, even though they contained developing fig wasps. This meant that only one of the 35 trees we surveyed had succeeded in supporting the local fig wasp population through the winter period. Despite this, the figs produced on other trees during the spring were usually pollinated. This apparent 'rescue effect' from more southerly populations is not unexpected given the dispersal abilities of pollinator fig wasps (Yu and Nason, 2013), but requires quantification.

The responses of monoecious fig trees to low winter temperatures vary between species. *Ficus sycomorus* in the Near East rarely produces figs during the winter and populations of its pollinator have failed to become established there, despite a history of cultivation that has lasted for many hundreds of years (Galil and Eisikowitch, 1968b). Conversely, *F. burtt-davyi* growing towards the edge of its range in temperate South Africa continues to produce figs throughout the winter, with crops that fail to mature before the winter taking up to six months to complete their development (Compton, 1993). We postulated two possible ways in which *F. virens* might continue to set seed at the northern edge of its range, despite experiencing low winter temperatures: that populations of its pollinator die out locally each winter, but pollinators migrate each summer from natal figs further south, or that figs continue to develop throughout the year, allowing local fig wasp populations to be maintained. It appears that a combination of these scenarios is operating in Mianyang, with very limited local over-wintering survival of pollinators supplemented by the arrival of wasps from elsewhere. *F. virens* growing under even more extreme winter conditions might be expected to cease winter fig production entirely, and depend solely on the seasonal migration of suitable pollinators from elsewhere. The proportion of trees that produce even summer crops may also decline further, and this, in combination with limitations generated by the dispersal abilities of the tree's pollinator, may determine the northern limit at which this plant can reproduce. More generally, an inability to initiate new crops at low temperatures may limit the distribution of monoecious fig trees to warmer areas.

The seasonal variation in temperatures experienced by *F. virens* growing in Mianyang are rather similar to those experienced by *F. burtt-davyi* in Grahamstown, South Africa, though the winters are a little colder (Compton, 1993). *F. burtt-davyi* displays a less extreme response to the winter conditions it experiences and routinely supports its associated fig wasp populations through this period. *F. burtt-davyi* is restricted to Southern Africa, whereas *F. virens* has a far larger distribution, where it experiences a wider range of climates. The *Platyscapa* that pollinates *F. virens* is expected to disperse its pollen widely, an attribute that may inhibit local adaptation by this tree at its northern range margin (Savolainen et al., 2007).

Acknowledgements

Appendix A. Supplementary material

Supplementary material related to this article can be found at http://dx.doi.org/10.1016/j.actao.2013.09.002.

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