



Adaptation in a changing climate: The phenology of two closely related sympatric *Ficus* species in Taiwan

Yun-Peng CHIANG¹, Hsy-Yu TZENG², Lien-Siang CHOU¹, Anthony BAIN^{3,*}

1. Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan.

2. Department of Forestry, National Chung Hsing University, Taichung, Taiwan.

3. Department of Biological Sciences, National Sun Yat-sen University, Taiwan.

*Corresponding author's email: anthonybain22@mail.nsysu.edu.tw

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ABSTRACT: Climate change affects precipitation patterns and seasonal temperatures and disrupts the development and distribution of organisms. In the obligate mutualism between *Ficus* trees (Moraceae) and fig wasps (Hymenoptera: Agaonidae), the trees live mostly in the tropics and rely on short-lived pollinators, and climate change challenges this relationship. In this study, a 25-month phenological survey of *Ficus subpisocarpa* and *Ficus caulocarpa*, closely related sympatric *Ficus* species with different suitable development areas, was conducted in tropical southern Taiwan. The effects of temperature-related meteorological factors were analyzed and compared with data obtained previously for trees in northern Taiwan to identify possible phenological trends caused by climate change. The results revealed that the phenological characteristics of the two *Ficus* in southern Taiwan are similar to those in northern Taiwan; however, the trees exhibited stronger correlations with meteorological factors in northern Taiwan. In southern Taiwan, the onset of fig crops for the two species was not related to any meteorological variable, and the trees produced figs throughout the year. The leaf changing in southern Taiwan followed no seasonal pattern, and only the renewal of leaves in *F. subpisocarpa* trees was linked to seasonal increases in temperature. The lowest temperature in northern Taiwan might effect *F. subpisocarpa* and *F. caulocarpa* trees to drop their leaves at the same period. Fig trees are likely resilient to climate change and can maintain their mutualism in a warming climate in the near future.

KEY WORDS: *Ficus subpisocarpa*, *Ficus caulocarpa*, phenology, sympatric, climate change.

INTRODUCTION

The next decades will be challenging for many organisms as the modeled climate changes become a reality (IPCC, 2014). These climate changes can be substantial at high latitudes (Box *et al.*, 2019) but more subtle near the equator, causing changes in precipitation patterns and seasonal temperature (IPCC, 2014). For many landmasses, the northernmost distribution limit tends to extend northward in a warming climate, causing species living in certain temperature areas to move to boreal areas (Gallant *et al.*, 2020) and tropical species to live outside the tropics (Osland *et al.*, 2021).

Environmental changes can disrupt the mutualistic relationship between organisms (Gilman *et al.*, 2012), especially the pollination mutualism (Bascompte *et al.*, 2019). The disruption can be functional (Miller-Struttman *et al.*, 2015) or phenological (Parmesan and Yohe, 2003). A functional change can cause a shift toward more generalist pollinators and traits (Miller-Struttman *et al.*, 2015). Many pollination mutualisms are obligate, with two partners depending on each other to fulfill their lifecycles, thus indicating that the phenological disruption of one of the two partners may affect both species. *Ficus* trees and agaonid pollinating wasps (Hymenoptera: Chalcidoidea) are part of a nursery pollination mutualism (Kjellberg *et al.*, 2005). Each *Ficus* species is pollinated by one or more pollinating agaonid

species (Rodriguez *et al.*, 2017) and lives mostly in the tropics, with some species living in temperate areas (Berg *et al.*, 2005).

Taiwan is located in tropical and subtropical zones. A total of 27 *Ficus* species, 6 monoecious and 21 dioecious species, have been recorded in Taiwan (Bain *et al.*, 2015). Among the six monoecious species, *Ficus subpisocarpa* and *Ficus caulocarpa* are closely related, both belonging to the subgenus *Urostigma* and the section *Urostigma*, sympatric distributed in northern and southern Taiwan, and have similar in morphology, life form, habitat and appearance (Tzeng, 2004). *Ficus caulocarpa* is considered a tropical species at the northernmost limit of its distribution, whereas *F. subpisocarpa* has a more northern distribution limit but is mostly distributed from subtropical Taiwan to temperate Japan (it is not found in the Philippines, Berg, 2007). This similarity in their biogeography allows for an investigation of the behavior of two similar species with different climatic affinities under nontypical climates, that is, *F. subpisocarpa* in a tropical zone and *F. caulocarpa* outside the tropics. *Ficus* trees have a highly asynchronous phenology that allows them to maintain a population of pollinators (Bain *et al.*, 2014a; Chiu *et al.*, 2017) in seasonal area. Their unique phenology can be affected by genetic diversity (Yang *et al.*, 2014) and the climate throughout their distribution range (Bain *et al.*, 2014a). Thus, an investigation of the phenology of species that obligate depend on their rightly

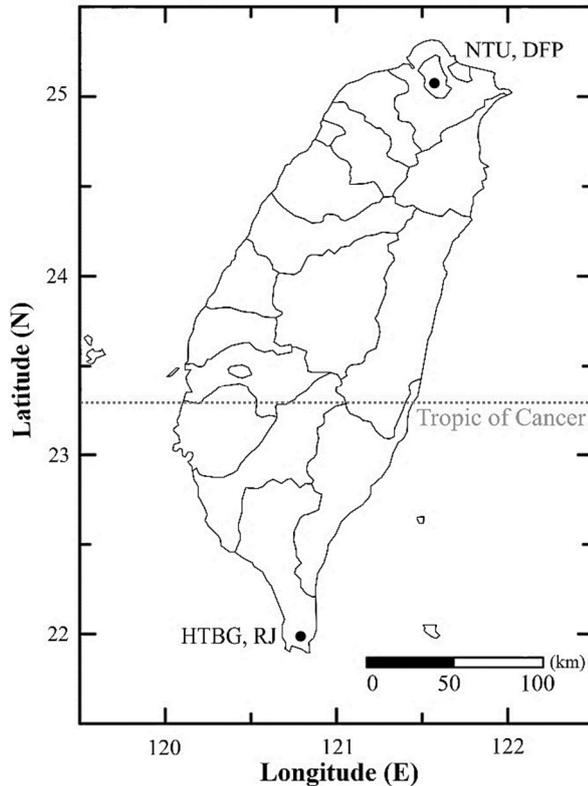


Fig. 1. Locations of the study sites. The study sites in this study were in Pingtung County in southern Taiwan, including Hengchun Tropical Botanical Garden (HTBG) and the road to Jialeshuei (RJ). The study sites in Chiang *et al.* (2018) were also showed in this map, including National Taiwan University campus (NTU) and Taipei Da'an Forest Park (DFP).

timed phenology for the completion of their lifecycle can reveal shifts in their distribution and the behavior of tree species under climate change. Therefore, this study collected the phenological data of *F. subpisocarpa* and *F. caulocarpa* in southern Taiwan, examined associated meteorological factors, and compared the data with those obtained from these species in northern Taiwan to determine whether the species can maintain their unique phenology and sustain their mutualistic pollinator partner populations. Moreover, this study investigated whether the *Ficus* phenology in northern and southern Taiwan is independent from climatic variables and estimated the behavior of these species under climate change.

MATERIALS AND METHODS

Study species and site

Ficus subpisocarpa Gagnep. (Ex. *Ficus superba* (Miq.) Miq. var. *japonica* Miq.) and *F. caulocarpa* (Miq.) Miq. are closely related species, and differentiating between them is often difficult (Tzeng, 2004; Berg *et al.*, 2005). Both species are monoecious hemiepiphytic trees, and they differ mainly in their geographical distribution.

Ficus caulocarpa is distributed in insular Malesia from New Guinea to Taiwan, which is its northern limit (Berg *et al.*, 2005), whereas *F. subpisocarpa* has a more continental distribution from Peninsular Malaysia to southern Japan (Berg, 2007). The insular geographical distribution of *F. subpisocarpa* is limited to Taiwan and Japan.

Monoecious figs have five developmental phases: phase A (prefloral), phase B (female wasp receptivity), phase C (development of the seeds and wasp larvae), phase D (adult wasp emergence from the fig), and phase E (ripening) (Galil and Eisikowitch, 1968; Chiang *et al.*, 2018). These two fig species provide a sustainable source of food for birds and mammals (Shanahan *et al.*, 2001; Chiang *et al.*, 2018; Walther *et al.*, 2018). In Taiwan, the common names of these two fig species mean “bird (or sparrow) fig tree,” alluding to the birds that frequently perch on their crown.

The study site was in Pingtung County in southern Taiwan. Sample trees were mostly located in the Hengchun Tropical Botanical Garden (HTBG, 21°57'36.4"N, 120°48'49.28"E) of the Hengchun Research Center, Taiwan Forestry Research Institute. One *F. caulocarpa* tree and four *F. subpisocarpa* trees were located near the HTBG, and 10 *F. caulocarpa* trees were located along the roadside from the HTBG to Jialeshuei (22°0'13.01"N, 120°52' 24.41"E), which is 8 km from the HTBG (Figure 1).

Data collection and analysis

Phenological surveys were conducted twice a month from April 2011 to April 2013. One of the *F. subpisocarpa* trees was cut down in September 2012, and the surveys of the other two *F. subpisocarpa* trees began in May 2012 and August 2011, respectively (gray areas in Figure 2). The observations and analyses were conducted using the same methods described by Chiang *et al.* (2018); the leaf and fig development phases were recorded, and the proportions on every single tree were estimated during each survey. The leaf phase was divided into five categories: no leaves, leaf buds, tender leaves, mature leaves, and yellow leaves. The fig development phase was also divided into several stages: no figs, fig buds, phase A, phase B, phase C, phase D, and phase E. Only the crops with figs in at least phase C and one other phase were used to calculate the crop duration, the crop duration would be counted from the first survey date of the fig crop to the last survey date. We compared phenology in different climatic zones (Table 1) by using phenological data from northern Taiwan (Chiang *et al.*, 2018).

Because the phenological records of fig and leaf growth were time series data, the Durbin-Watson statistic and the first-order autoregressive model (AR1 model) were applied to identify the temporal autocorrelation and control autocorrelation errors. The Durbin-Watson statistic is used for understanding if the residuals from a

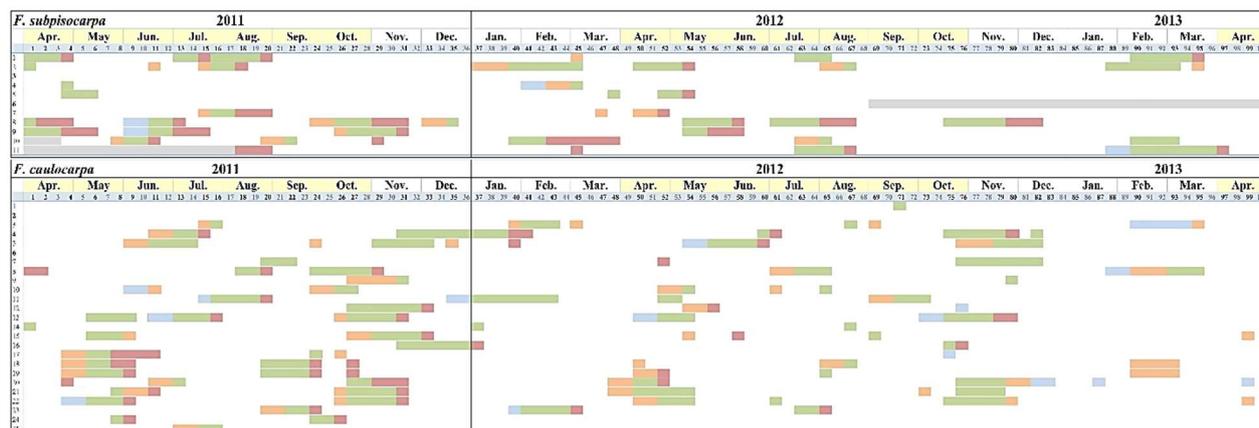


Fig. 2. Fig phenology of *Ficus subpisocarpa* and *Ficus caulocarpa* in Southern Taiwan from April 2011 to April 2013. Each row represents a different sampling tree. A total of 11 *F. subpisocarpa* trees and 25 *F. caulocarpa* trees were sampled. The numbers with blue backgrounds represent different survey weeks, the black numbers represent the surveys conducted in southern Taiwan, and the gray numbers represent the weeks in which surveys were not conducted. The color bars represent fig development stages: phase A (blue), phase B (orange), phase C (green), and phases D and E (pink). The gray bars represent nonsurveyed periods.

Table 1. Differences between survey sites. Only survey data from before April 2013 were considered to compare the two geographical locations. National Taiwan University campus (NTU); Taipei Da'an Forest Park (DFP); Hengchun Tropical Botanical Garden (HTBG); Road to Jialeshuei (RJ).

	Taipei City	Pingtung County
Sampling sites	NTU, DFP	HTBG, RJ
Climatic zones	Subtropical	Tropical
Survey duration	Apr. 2011–Dec. 2014 ^a	Apr. 2011–Apr. 2013
Survey frequency	once a week	twice a month
Survey amount to Apr. 2013	100	54
Sample size to Apr. 2013		
<i>F. subpisocarpa</i>	46 (2, no figs)	11 (2, no figs)
<i>F. caulocarpa</i>	21 (3, no figs)	25 (2, no figs)

^aPhenological study has been published in Chiang *et al.*, 2018.

regression analysis had autocorrelation. The value of the Durbin–Watson statistic (d) will range from 0 to 4, and be compared to lower and upper critical values (dL and dU). There is statistical evidence for positive autocorrelation when $d < dL$, and there is no statistical evidence for positive autocorrelation when $d > dU$. If $dL < d < dU$, the test is inconclusive. In addition, the AR1 model was used to investigate the presence of any meteorological effect on plant phenology. For better comparing the results between the northern and southern survey areas, we reanalyzed the data from Chiang *et al.* (2018) in northern Taiwan with the same survey period. Test factors were total rainfall, average temperature, and total solar radiation (data collected from the Central Weather Bureau of Taiwan). Factors related to temperature were subdivided into average diurnal temperature variation, weekly temperature variation, average lowest temperature, and average highest temperature. An independent t-test was performed to identify differences in the meteorological factors between the northern and

southern survey areas. All statistical analyses were performed using SPSS Statistics 20.0 (IBM SPSS Statistics, Chicago, IL, USA).

RESULTS

Plant phenology in southern Taiwan

The fig development of *F. subpisocarpa* and *F. caulocarpa* in southern Taiwan remained highly synchronous within a single individual until the figs reached phase D. After wasp emergence (phase D), the figs lost synchrony and gradually shifted to phase E, so the fig trees would have phase D and phase E figs at the same time (Chiang *et al.*, 2018). Therefore, we combined phases D and E in the figures due to the difficulty to separate these two phenophases. Two trees of each *Ficus* species did not produce any figs during the survey period. In each survey, 20.7% (2.2 ± 1.5 trees) of *F. subpisocarpa* and 17.9% (4.4 ± 2.8 trees) of *F. caulocarpa* were bearing figs. A complete absence of figs was observed during eight surveys for *F. subpisocarpa* and three surveys for *F. caulocarpa* (Figure 4). The highest peaks (>50% of trees) in fig production were mostly noted in summer and late winter for *F. subpisocarpa* (Figure 3A) and in late spring and autumn 2011 for *F. caulocarpa* (Figure 3B).

The changes in the leaves of the two *Ficus* species followed no clear seasonal patterns (Figure 4). However, leaf flushing was at its lowest for *F. subpisocarpa* at the beginning of winter (Figure 4A). In addition, leaf abscission in *F. caulocarpa* was less common during winter (Figure 4D). The two species regularly abscised a few leaves in addition to the abscission of the entire tree. Most of the leaf changing events of *F. subpisocarpa* were small, with <20% of branches having tender or yellow leaves, and *F. caulocarpa* displayed events with >20% of branches having tender or yellow leaves.



Table 2. Significant correlations between fig phases and meteorological factors. The factors total rainfall, total solar radiation, average temperature, average diurnal temperature variation (DTV), weekly temperature variation (WTV), average lowest temperature (LT), and average highest temperature (HT) were tested using the Durbin–Watson test and the first-order autoregressive (AR1) model. The tests using previous phenological data (Chiang *et al.* 2018) were reperformed for this study period. (Insignificant correlations were omitted)

Area	Species	Analyze	β	t	p-value
Northern Taiwan	<i>F. subpisocarpa</i>	Phase C with Rainfall	-0.252	-2.551	0.012
		Phase D with Rainfall	0.295	3.028	0.003
		Phase E with Rainfall	0.265	2.696	0.008
		Yellow leaf with DTV	0.291	2.984	0.004
		Yellow leaf with LT	-0.393	-4.187	0.000
	<i>F. caulocarpa</i>	Phase A with Solar radiation	0.299	3.107	0.002
		Phase A with Temperature	0.262	2.693	0.008
		Phase A with LT	0.237	2.416	0.018
		Phase A with HT	0.263	2.703	0.008
		Phase D with Temperature	0.213	2.133	0.035
		Phase D with LT	0.215	2.156	0.034
		Phase E with LT	0.219	2.200	0.030
		Yellow leaf with LT	-0.284	-2.902	0.005
Southern Taiwan	<i>F. subpisocarpa</i>	Phase D with HT	0.282	2.075	0.043
		Phase E with Temperature	0.271	2.029	0.048
		Phase E with HT	0.282	2.120	0.039
		Leaf flushing with Solar radiation	0.276	2.070	0.043
		Leaf flushing with Temperature	0.442	3.549	0.001
		Leaf flushing with DTV	0.293	2.170	0.035
		Leaf flushing with LT	0.412	3.263	0.002
		Leaf flushing with HT	0.469	3.832	0.000

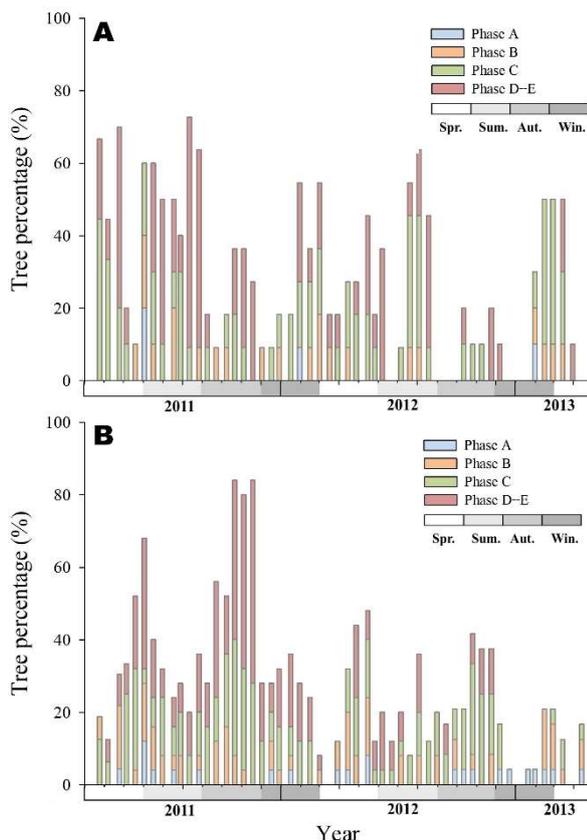


Fig. 3. Fig production in different phases of *F. subpisocarpa* and *F. caulocarpa* in Southern Taiwan from April 2011 to April 2013. **A:** fig production of *F. subpisocarpa*. **B:** fig production of *F. caulocarpa*. Different colors show different fig phases.

The crop duration was divided into two categories according to the season: a shorter crop duration between April and October (30.05 ± 12.35 [range: 11–58] days, $n = 41$) and a longer crop duration between November and March (45.38 ± 14.55 [range: 16–73] days, $n = 21$). More crops were observed for only one survey for *F. caulocarpa* than for *F. subpisocarpa* in southern Taiwan. The crops either matured rapidly (<4 weeks) or dropped before reaching maturation.

Meteorological factors and time series analysis

Figure 5 presents the climatic patterns of the area investigated in this study and those of northern Taiwan (for more specific information see Table S1 in supplementary data). The values of most of the climatic variables differed between the two regions (Table S1). Seasonal precipitation was mostly similar between the northern and southern Taiwan, with differences observed in the summer and winter of 2011 and in the autumn and winter of 2012.

Most of the values generated using the Durbin–Watson test were <1.654 (dL for data on northern Taiwan; $\alpha = 0.05$) and 1.528 (dL for data on southern Taiwan; $\alpha = 0.05$), indicating positive autocorrelations. The only exceptions were phase A of fig development in both areas, phase E and the leaf flushing for *F. subpisocarpa* in southern Taiwan, and phase B for *F. caulocarpa* in southern Taiwan (Table S2 and S3 in supplementary data).

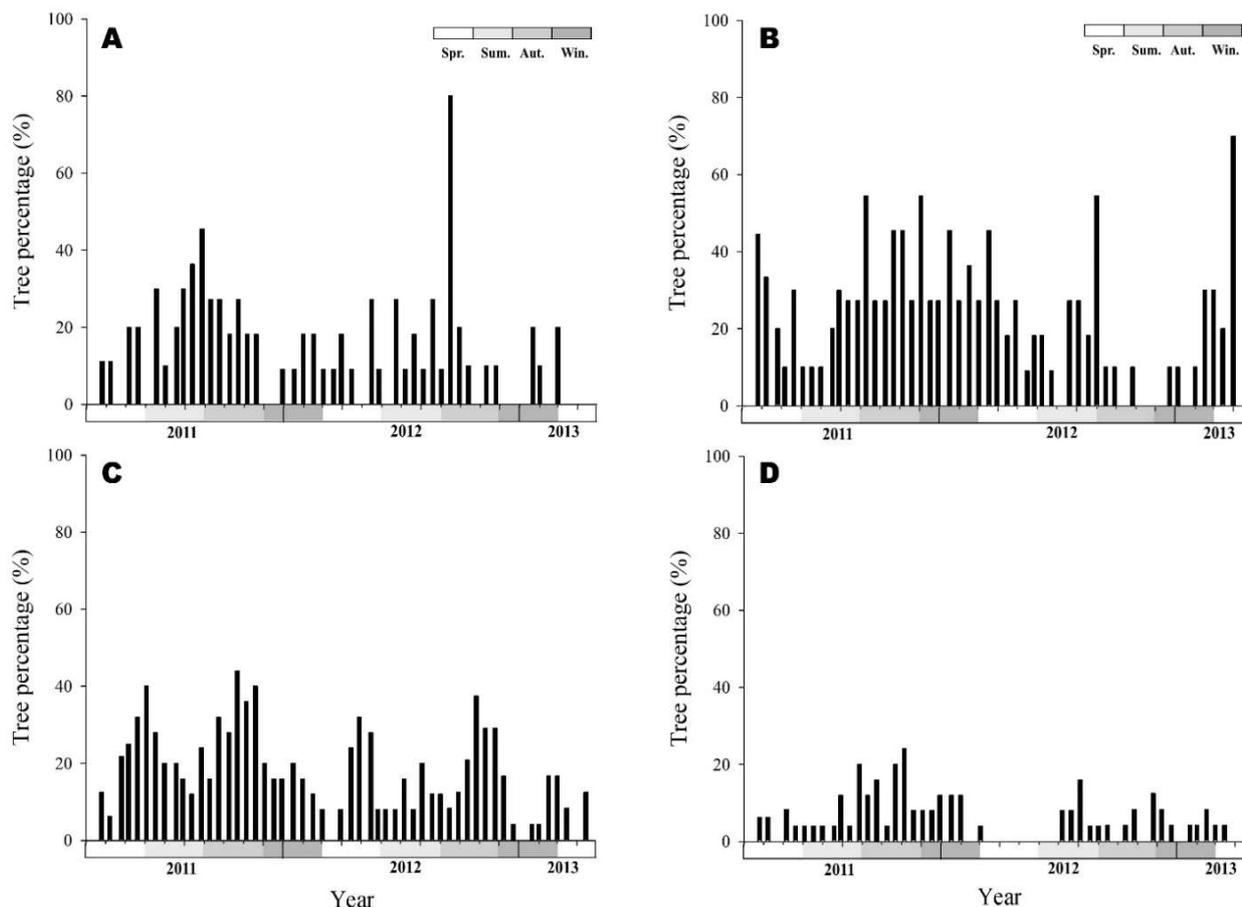


Fig. 4. Leaf phenology of *F. subpisocarpa* and *F. caulocarpa* in Southern Taiwan from April 2011 to April 2013. **A:** Leaf flushing of *F. subpisocarpa*. **B:** yellow leaf of *F. subpisocarpa*. **C:** leaf flushing of *F. caulocarpa*. **D:** yellow leaf of *F. caulocarpa*.

The trees in northern Taiwan with the same survey period exhibited stronger correlations with meteorological factors than did those in southern Taiwan (Table 2). No correlation was detected for the *F. caulocarpa* phenology in southern Taiwan (Table S2 and S3), whereas phases A and D of *F. caulocarpa* in northern Taiwan exhibited stronger correlations with temperature-related factors, particularly with average temperature and the lowest temperature (Table 2). The fig phenology of *F. subpisocarpa* and *F. caulocarpa* in northern Taiwan was correlated with many meteorological factors, and both species exhibited a correlation between leaf abscission and the lowest temperature (Table 2).

The results revealed a difference in the correlations of *F. subpisocarpa* between northern and southern Taiwan: phases C, D, and E were related to rainfall in northern Taiwan, whereas phases D and E were related to the highest temperature in southern Taiwan (Table 2). The leaf flushing of *F. subpisocarpa* exhibited a correlation with all four temperature-related factors in southern but not northern Taiwan (Table 2).

DISCUSSION

The following phenological characteristics of *F. caulocarpa* and *F. subpisocarpa* in southern Taiwan were similar to those of the trees in northern Taiwan (Chiang *et al.*, 2018): (1) a strong within-tree synchrony of fig development and a complete asynchrony between trees; (2) the loss of within-tree synchrony after wasp emergence to extend the fruiting and seed disperser visitation periods; and (3) a complete aseasonality in the reproductive phenology.

In southern Taiwan, the onset of fig crops for the two species was not related to any meteorological variable, and the trees produced figs throughout the year. Even in the tropical zone, plants displayed a seasonal pattern of flowering and fruiting (Morellato *et al.*, 2013); this finding highlights the peculiarity of *Ficus* reproductive phenology. Continuous fig production has been observed in fig trees worldwide (Gautier-Hion *et al.*, 1985; Harrison *et al.*, 2000; Kuaraksa *et al.*, 2012; Kattan and Valenzuela, 2013) and in different species in Taiwan (Bain *et al.*, 2014a; Lin *et al.*, 2015a; Huang *et al.*, 2019). Thus, the mutualism with the associated pollinating wasp

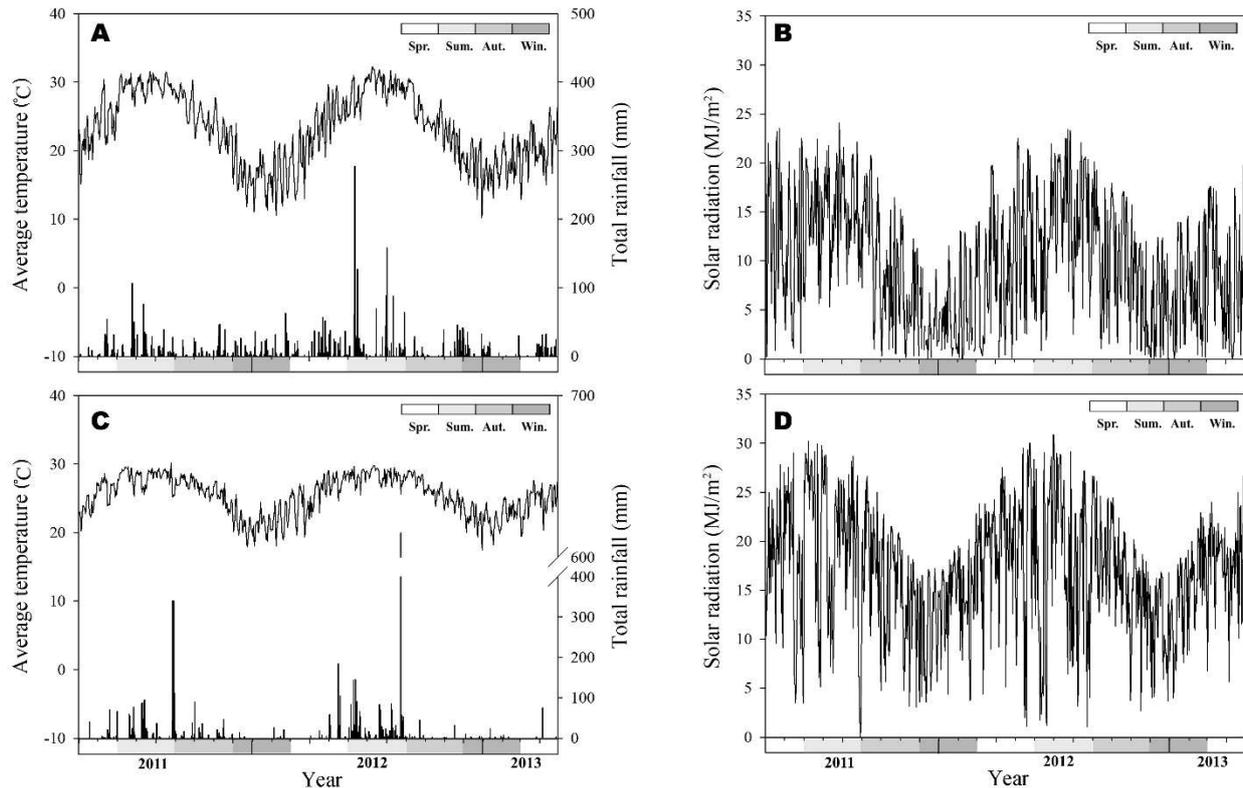


Fig. 5. Meteorological factors in Northern (upper figures **A** and **B**) and Southern Taiwan (lower figures **C** and **D**) from April 2011 to April 2013. Figures on the left display the average temperature and total rainfall, and those on the right display the solar radiation during the survey period.

requires frequent crop production to allow short-lived pollinating wasps to find a receptive fig and complete their life cycle in time. This is especially true for trees in southern Taiwan that exhibited no correlation between crop onset and climatic variables.

However, *F. caulocarpa* in northern Taiwan exhibited positive correlations between the onset of fig production (phase A) and some meteorological variables (temperature and solar radiation). The north of Taiwan is the northernmost limit of *F. caulocarpa* distribution and can reach temperatures below 10°C in winter. Similar to *Ficus septica* in the same area (Bain *et al.*, 2014a), *F. caulocarpa* trees may synchronize some of their crops with meteorological variables to produce crops. Outside the tropics, *F. caulocarpa* trees that synchronize their crops with an increase in temperature during the spring may be selected because their crops are more successful than those of other *F. caulocarpa* trees. Indeed, as the most part of the *F. caulocarpa* distribution area is overlapping with the tropics we assume that their pollinators may have difficulty to handle a colder winter outside the tropics. Pollinating wasps are known to be sensitive to temperature and rather fragile organisms (Dunn *et al.* 2008; Conchou *et al.* 2014). Thus, the correlation between the production of the figs in spring and meteorological factors may be come from the higher

pollination rate of spring figs that are accessible by pollinating wasps when the temperatures are more welcoming for them. This phenomenon can be linked to the multiple observations of the early crops dropping from the trees at phase B or early phase C. Moreover, the crops of *F. caulocarpa* drop less often than the crops of *F. subpisocarpa* but in both species, these crop drops may probably be attributed to a very low pollination rate. Even if, the causes of these problematic crops are unclear, trees can receive pollinators from other parts of Taiwan as pollinating fig wasps can disperse over large distances (Ahmed *et al.*, 2009; Kobmoo *et al.*, 2010). Some crops of trees in northern Taiwan may rely on pollinators from southern Taiwan, even if fig production is somehow continuous in northern Taiwan (Chiang *et al.*, 2018).

The vegetative phenology of these two fig species exhibited few correlations with climate, especially leaf flushing (although more meteorological variables were tested than those in the study conducted by Chiang *et al.* (2018)). Only renewal of the leaves in *F. subpisocarpa* trees in southern Taiwan was linked with the seasonal increase in temperature. The lowest temperature in northern Taiwan seemed to effect *F. subpisocarpa* and *F. caulocarpa* to drop their leaves at the same time. These findings indicate that fig tree phenology will be little affected by future changes in climate (in addition to



extreme weather events). Climate changes in Taiwan will be similar to those in other countries, with a projected increase in temperature of approximately 3°C by 2100 (Lin *et al.*, 2015b), a decrease in nontyphoon rainfall, and an increase in typhoon rainfall (Tu and Chou, 2013). Nontyphoon rainfall will decrease with an increase in drought periods (Huang *et al.*, 2012). These changes are particularly true for urban areas (Bai *et al.*, 2011) where *F. subpisocarpa* and *F. caulocarpa* are commonly found (Walther *et al.*, 2014; Chiang *et al.*, 2018). Thus, the phenological independence from meteorological variables would be beneficial for these fig species and their associated fig wasps in a changing climate; however, the effects of climate change may differ from those expected (Guan *et al.*, 2012).

One expected consequence of increasing temperatures is that the development of wasps and figs may accelerate. Summer crops develop faster than winter crops (Zhang *et al.*, 2006; Chiang *et al.*, 2018). Whether wasp and seed development will differ under a warmer climate remain unclear, but it may affect *Ficus* species. Nevertheless, the phases D and E of *F. subpisocarpa* and *F. caulocarpa* are independent from wasp development because the final phases of fig development considerably varied within a crop.

In a period of changing environmental politics in Taiwanese cities (Hu *et al.*, 2016; Mabon and Shih, 2018), *F. caulocarpa* and *F. subpisocarpa* are a major asset in the stability and efficiency of green spaces in urban areas in Taiwan. With their continuous fruit production, these fig species can sustain birds, mammals (Shanahan *et al.*, 2001; Walther *et al.*, 2014; Chiang *et al.*, 2018), and various insects (Bain *et al.*, 2014b). Fig trees in general are highly resilient to climate change (Yang *et al.*, 2013; Chiu *et al.*, 2017; Chen *et al.*, 2018; Kuo, 2018), and the species in the geographical range investigated in this study would be particularly resistant to future changes. Nevertheless, long-term phenological studies with circular statistics and additional studies on the physiological aspects of their growth, ecology, and phenology and their obligate mutualistic partner, the pollinating fig wasp, should be conducted.

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