Flowering and fruiting phenology of woody trees in the tropical-seasonal rainforest, Southwestern China

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The reproductive phenology of tropical plants is potentially driven by a number of abiotic and biotic factors. However, it is still unclear as to which climatic factors and biotic interactions drive the reproductive phenology of woody trees in the tropical seasonal rainforest of Xishuangbanna region in Southwest China. We conducted observations on woody plants (including trees and shrubs) phenology between November 2004 and October 2007 at biweekly intervals in the one hectare permanent plot of tropical seasonal rainforest in Southwest China. A total of 357 individuals of 76 species (70 genera, 37 families), comprising of 59 (78%) woody trees and 17 (22%) shrub species were observed. Our results demonstrate that flowering and fruiting frequencies show slight temporal variation between years. Flowering was significantly correlated with day-length, temperature and rainfall and fruiting was significantly correlated with rainfall and temperature. This finding indicates that woody tree reproductive phenology was primarily associated with temperature and rainfall and to a lesser extent with day-length. Reproductive phenology is also linked to seasonal patterns with flowering peaking in the late dry season and fruiting peaking in the late wet season. Moreover, reproductive phenology is also significantly associated with reproductive ecological guilds such as pollination types and dispersal modes. Community reproductive phenology is associated with climatic seasonality and biotic interactions. It also suggests that seasonal phenology patterns may play a fundamental role in community reproductive success in the tropical seasonal rainforest of Xishuangbanna region of Southwest China.

Keywords: Biotic factors, climatic variables, plant phenology, seasonal patterns, south China.

PATTERNS of reproductive phenology in tropical forest plant species are correlated with a number of abiotic and biotic factors^{1–9}. Many studies show that reproductive phenology (flowering and fruiting) is associated with rainfall, temperature, day-length, radiation levels and photoperiod in both seasonal and aseasonal tropical rainforests throughout the world^{10–21}. For instance, temperature is an important factor that acts directly on the phenology of flowering and fruiting production in both seasonal and aseasonal and aseasonal climates^{12,14,20,22}. Analogously, rainfall influences fruiting seasonality^{23,24} and germination success^{4,14}.

Over evolutionary time, seasonal changes in environmental conditions and biotic resources may provide selective pressures that shape community reproductive patterns. Thus, the study of timing of community reproductive events in response to environmental and biotic resource availability may provide insights into community plant reproductive success and the subsequent ability to compare these across different forest types. For example, in the aseasonal tropics, flowering and fruiting events are often irregular and peaks of these events can occur within their plant communities during most seasons^{25–27}.

Conversely, in neotropical seasonal environments, flowering peaks are often distinct and correspond to climatic variation. For instance, flowering was observed to peak between May and July, with a subsequent but smaller peak from August to October at the La Selva Biological station of Costa Rica²⁸. Analogously, several other neotropical studies of seasonal environments show that the majority of flowering took place during mid-dry season (April– May)^{3,10,28–30}. Supporting this idea, flowering generally occurs towards the end of dry season or beginning of wet season in the aseasonal rainforests of Southeast Asia^{25,31}.

In addition, flowering and fruiting of plants may synchronize with climatic events to optimize offspring survival^{3,10,14,21}. This demonstrates that reproductive phenology is highly correlated with climatic conditions in seasonal and dry environments^{8,30–33}. For instance, seasonal activities of pollinators, seed predators or seed

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dispersers may also be associated with plant reproductive mechanisms^{34,35}. Moreover, peak flowering events may coincide with the peak in temporal abundance of pollinators whilst peak fruiting of fleshy-fruited species may coincide with the period when dispersers are most abundant^{34,36,37}. Thus, the analysis of phenological events can provide important insights into plant community reproductive success in the seasonal tropics.

Numerous studies have exhibited the reproductive phenology pattern of tropical seasonal and aseasonal rainforests of Southeast Asia and have been well studied. But there is no information on community reproductive phenology of the tropical seasonal rainforest of Southwest China, and it is still unclear. Thus, in this study, we concentrated on the reproductive phenology of woody plant species, fortnightly, in a one-hectare, permanent plot of tropical seasonal rainforest, over three consecutive years from November 2004 to October 2007. This is the first comprehensive study of reproductive phenology of woody species in the latitude 21°N in Southwestern China. Our study focused on how community level phenology relates to climatic factors and biotic interactions. As such, we address the following questions: (1) how does reproductive phenology correlate with climatic variables such as day length, temperature and rainfall?; (2) how does flowering and fruiting frequency vary between years?; (3) do flowering and fruiting times correlate with seasonal climate patterns?; (4) are flowering and fruiting seasons associated with individual species pollination mode, fruit type and dispersal mode?

Materials and methods

Study site

The study was conducted in a one-hectare permanent plot of the tropical seasonal rainforest, in Menglun, Xishuangbanna prefecture, Southwest China. The plot is located at 21°57′47.14″N and 101°12′09.10″E, at an elevation of 730 m asl (Figure 1)^{38,39}. In this plot, topography, plant community composition, population and forest structure have been previously studied^{38,39}. As such, the known dominant tree species are *Pometia tomentosa*, *Barringtonia macrostachya*, *Gironniera subaequalis* and *Chisocheton siamensis* and the dominant plant families are Euphorbiaceae, Lauraceae, Myrsticaceae and Meliaceae^{38,39}. Additionally, bamboos are known to exist at a high density on the fringes of secondary forests in the region^{38,39}, though the one-hectare plot was not disturbed by any human interference.

Phenological studies

Phenological observations were conducted fortnightly throughout the study period from November 2004 to October 2007. Within the one-hectare plot, we used five transects of 10×100 m to observe the reproductive phonological events such as flowering and fruiting. Specifically, within these transects, we observed the reproductive phenology of 357 individual plants (capable of producing buds, flowers and fruits) and additionally marked all plant species for ease of comparison. During each fortnightly observation, we recorded the percent of open/ripe flowers and fruits on each individual. During observation, flowering and fruiting percentages were categorized into 10%, 25%, 50% and 75% categories for each individual plant and these data were recorded through direct visual estimation until flowers and fruits completely fell off each individual. Additionally we counted the number of individuals within each species of plant that were flowering and/or fruiting each month over the three-year study period. Plant species were collected and identified using a floral key (www.efloras.org), and identifications confirmed at the Xishuangbanna Tropical Botanical Garden (XTBG) herbarium. All voucher specimens were deposited in the XTBG Herbarium Centre.

Climatic patterns

Xishuangbanna has a markedly seasonal climate, with a distinct dry season (November-April) and rainy season (May-October). In the one-hectare plot, there was no meteorological station. Hence all climatic variables were calculated from the records of XTBG meteorological station, Menglun covering the years 1990-2014. The XTBG meteorological station is located 4 km east of the onehectare study plot. There was no major difference in topography or climatic conditions between the examined one-hectare plot and XTBG. Rainfall was automatically recorded daily at the meteorological station (using a rain gauge) on an hourly basis. Between 1990 and 2014, the average annual rainfall was 1500.2 mm, and the annual rainfall ranged from 866.8 to 1948.3 mm. Temperature sensors and a pyranometer were setup inside XTBG garden in an open area (the name of the equipment brand is VAISALA, Made in Finland, Milos 520). We automatically recorded the temperature and solar irradiance at every hour and then averaged these across various time intervals. The average annual temperature for XTBG was 22°C (Figure 2 a), ranging from 16.7°C in January to 25.7°C in June. Day-length from January 2004 to December 2007 was recorded at 20°N and the day of the year was determined from the available website http://www.dateandtime.info. Day length was then averaged monthly for further analysis. The average day length in the studied period was 11.95 h, and ranged from 10.48 h in December to 13.24 h in July (Figure 2 *b*).

Flowering frequency

We observed 357 flowering individuals comprising 76 species. Eight of the observed species had less than three

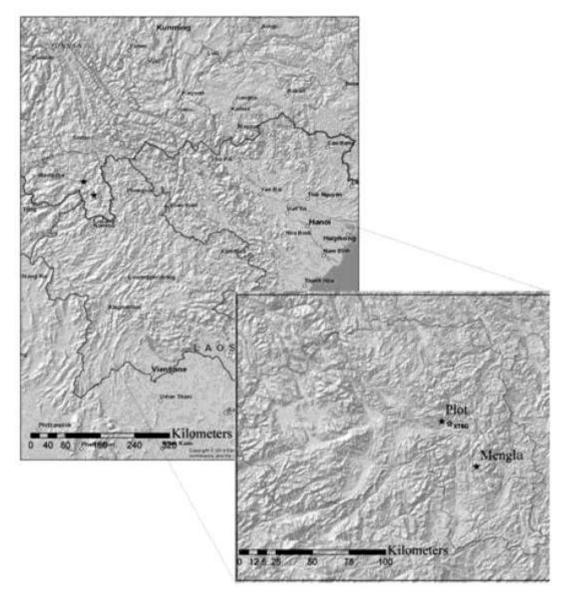


Figure 1. Phenology observation conducted in one hectare permanent plot of tropical seasonal rainforest of Southwest China. This one hectare permanent plot is located near Xishuangbanna Tropical Botanical Garden, Mengla County, Xishuangbanna Prefecture, Yunnan Province, Southwest China.

flowering individuals, whilst the remaining 68 species had observations from ≥ 4 individuals (see <u>Supple-mentary Table 1</u>). We classified the flowering frequency of species based on the flowering occurrence of the individual plant in each species. We classified flowering patterns as annual, supra-annual, sub-annual and non-flowering^{25,26,30,33,40}. Annual species flowered once annually; supra-annual species flowered once every two years or less; sub-annual species flowered twice a year and species of individuals which did not flower during the observation period were considered as non-flowering. In the study, we did not focus on intraspecific variation of flowering frequency among individuals due to low sample size and those aspects were excluded. We found that the 76 studied species did not show any significant intraspecific variation in flowering frequency among the observed individuals within the examined one-hectare plot.

Seasonal patterns

Flowering and fruiting seasons of each species were categorized into two classes of seasons, either dry or wet season. We defined dry season as months which have an average monthly rainfall of ≤ 99 mm and the wet season as months with an average monthly rainfall ≥ 100 mm. This classification was done for all months over the 23year period of 1990–2014. Over this 23-year period, the dry season usually fell between November and April and the wet season fell between May and October. As such,

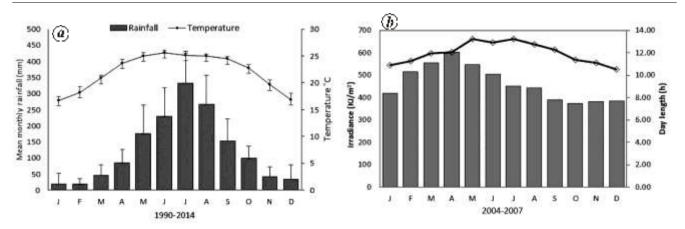


Figure 2. a, Rainfall and temperature pattern over 25 years from 1990 to 2014. b, Total monthly irradiance and mean monthly day length of the study areas during the study period from 2004 to 2007. The weather data was obtained from XTBG. The distance between study plot (one-ha) and XTBG was about 4 km and the study plot was located towards the western side of XTBG.

for this study, we classified November–April as dry season flowering/fruiting of any species which flowers and fruits during this period. Predictably, we classified May– October as wet season flowering/fruiting of any species which flowers and fruits during this period.

Pollination and dispersal mode

For this study, the pollination mode was categorized into two classes, abiotic and biotic pollination, which was assessed based on pollination syndrome and direct observation. Abiotic pollination was regarded as pollination which occurs without involving other organisms, that is, usually pollination occurred by either wind or water. Biotic pollination was regarded as pollination mediated by organisms such as insects, birds, butterflies. We did not expect or find any animal pollination syndrome in this study. Dispersal mode was assessed based on fruit types. Fruits were classified into fleshy or dry fruits. Fleshy fruits included berries, syncarps, drupes and pomes. Dry fruits included dehiscent fruits such as legumes, follicles and capsules. Indehiscent dry fruits such as achenes, samaras, nuts, caryopsis and schizocarps were assessed by direct observation and later confirmed through literature survey^{41,42}. All the fleshy fruits were categorized as zoochorous dispersers, commonly referred to as plant species which use mammals and birds for seed dispersal⁴³. Dry fruits were classified as either autochorous or anemochorous dispersers. Autochorous species are dispersed by an explosive mechanism, whilst Anemochorous species are dispersed by the wind. These species were assessed based on direct observation and later confirmed through literature survey^{41,42}.

Data analyses

For data analysis, all fortnightly observations of each species, flowering and fruiting recorded over the three

consecutive years of study were pooled into monthly phenology frequency records. The flowering frequency pattern was then estimated based on the temporal frequency distribution found to occur over three consecutive years. Additionally, we calculated the percentage of flowering frequency and observed the pattern for all the 76 studied species. The average number of concurrently flowering and fruiting species per month and season was also estimated across the three years. The month and season where the highest number of flowering species occurred were considered as the peak flowering month and season respectively. Similarly, the month and season where the greatest number of species were found to be fruiting were considered as the peak fruiting month and season.

Correlation coefficients for each observed species were calculated between each phenophase (such as flowering and fruiting) in relation to the following climatic factors: monthly average rainfall, mean monthly temperature, and average day length. Spearman's rank correlation coefficients were then computed for the number of species in each phenophase (flowering and fruiting) per month by the monthly climatic factors. The percentage of flowering and fruiting was also related with average day length that occurred over the three study years.

The frequencies of monthly flowering and fruiting per study year were analysed by ANOVA (pairwise comparison was tested by Tukey's HSD) to find out whether the flowering and fruiting frequencies differed significantly between the three study years. Similarly, the frequencies of flowering and fruiting per studied climatic season (e.g. dry and wet) were tested by G-test, to find out whether reproductive phenology and seasonal patterns were significantly associated. To compare the proportion of flowering and fruiting species in each season these data were also tested using a G-test analysis, in order to understand which season produced proportionately higher flowering and fruiting. Additionally, the frequencies of flowering

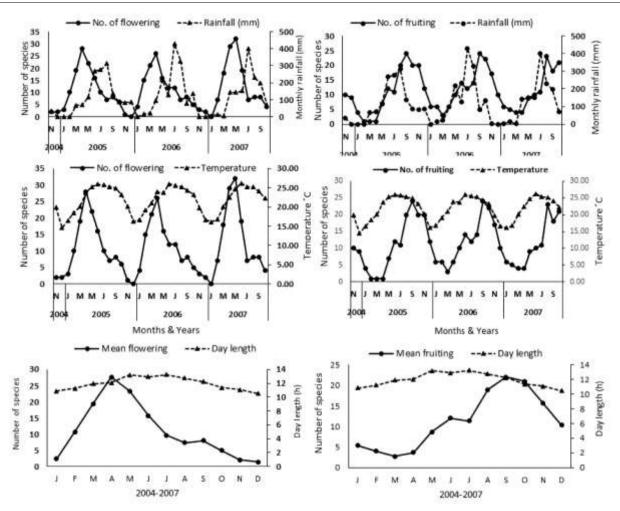


Figure 3. Frequency of flowering and fruiting in relation with rainfall, temperature and day length among species (N = 76 species) in the tropical seasonal rainforest of Southwest China. The temporal annual variation of flowering and fruiting species is shown from November 2004–October 2007 over a three-year period.

species in each of the pollination modes were tested using a G-test, as were the frequencies of fruiting species in each fruit type and dispersal mode category. For all, percentage calculation was added up to 100% in each frequency of species in order to normalize the data. SPSS statistical software version 17.0 and PAST version 3.01⁴⁴, were used for all statistical analyses.

Results

Phenology patterns

A total of 357 plants of 76 species (70 genera, 37 families) were observed, comprising 59 (78%) woody tree species and 17 (22%) shrub species. The majority of these species showed annual flower production (54 species or 71%), followed by supra-annual (14 species or 18%), sub-annual (4 species or 5%) and non-flowering (4 species or 5%) with no continuously flowering species recorded (see <u>Supplementary Table 1</u>). Most species

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flowered for 1–2 months at the end of the dry-season or early wet-season (April–May). Fruiting periods ranged from 1 to 4 months with most fruiting occurring during the late wet-season and early dry-season from August to November (Figure 3). Very few species had fruiting events which bridged yearly boundaries.

The average number of concurrently flowering species throughout the study period was 11.03 (SD \pm 8.81). The maximum number of concurrently flowering species found over the three studied years occurred during March, April and May, with a mean of 26.3 (35%) species flowering. The average number of concurrently fruiting species was 11.31 (SD \pm 7.02), whilst, maximum peak fruiting was found to occur in August, September and October with a mean of 20.7 (27%) fruiting species recorded. There was annual variation in the peak number of concurrent flowering species. In 2005 and 2006, peak flowering of 28 and 26 species respectively, occurred in April, whereas peak flowering of 32 species in 2007 occurred during May (Figure 3). Peak fruiting varied only slightly between years with 24 species concurrently fruiting in 2005 and 2006 during September whilst in 2007, 23 species concurrently fruited in August (Figure 3).

Reproductive phenology and climatic variability

A positive correlation was found to exist between the number of species flowering and individually: the average day length (rs = 0.689, P < 0.0001), mean temperature (rs = 0.523, P < 0.001) and rainfall (rs = 0.324, P < 0.053). Additionally, in the years 2005, 2006 and 2007, peak flowering events of 65%, 57% and 74% respectively of the plant community occurred during March–June; when the average day length was >12 h.

Similar to flowering events, the number of species fruiting showed a positive correlation individually with mean temperature (rs = 0.406, P < 0.013) and rainfall (rs = 0.34, P < 0.042). However, there was no significant correlation between the number of species fruiting and average day length (rs = 0.107, P = 0.532; Figure 3). Peak community fruiting events of 63%, 53%, 56% were found to occur during the period August–November in three successive study years (2005–2007), when the day length was <12 h. Longer day lengths of >12 h appear to be correlated with peak flowering events whilst, shorter day lengths of <12 h, appear to be correlated with peak fruiting events (Figure 3).

Flowering and fruiting temporal distributions

There was no significant difference in annual variation of peak flowering ($F_{69,72} = 0.585$, P = 0.561) over the three studied years (Tukey pairwise test HSD = 1.521, P = 0.534 between 2005 and 2006; HSD = 0.608, P = 0.903 between 2006 and 2007 and HSD = 0.912, P = 0.796 between 2005 and 2007 respectively). Similarly, there was no significant difference in the annual variation of fruiting events ($F_{69,72} = 0.992$, P = 0.3786). Tukey's pairwise HSD = 0.067, P = 0.998 between 2005 and 2007 and HSD = 1.758, P = 0.462, between 2006 and 2007 and HSD = 1.69, P = 0.3786 between 2005 and 2007 respectively (Figure 3).

Reproductive phenology and seasonal patterns

The phenology of flowering and fruiting was found to be significantly associated with seasons (dry and wet) over the three year study period (*G*-test = 25.57, *P* = 0.0001). For example, in 2005 and 2006, flowering was significantly higher during the dry season (2005: $\chi^2 = 9.09$, *P* = 0.0026; 2006: $\chi^2 = 5.49$, *P* = 0.019) (Figure 4). However, in 2007, there was no significant difference ($\chi^2 = 0.68$, *P* = 0.41) in flowering frequency between the dry and wet season. Analogously, fruiting frequency was

found to be significantly associated with season with increased fruiting occurring in the wet season for all three study years (in 2005: $\chi^2 = 8.11$, P = 0.004; in 2006: $\chi^2 = 5.13$, P = 0.023; in 2007: $\chi^2 = 9.45$, P = 0.002).

Flowering and fruiting seasons in relation to individual species' pollination mode, fruit types and dispersal mode

In addition, the peak flowering season, per examination year, was found to be significantly associated with the pollination mode employed by the species (2004–2005: G-test = 89.75; P = 0.00001; 2005–2006: G-test = 69.48; P = 0.00001; 2006–2007: G-test = 84.24; P = 0.00001). For instance, during 2004–2005, a majority of the biotically pollinated species flowered during dry season (41%) and early wet season (27%) whilst, 12% flowered during the peak of wet season, and 11% in the late wet season. However, in 2005-06, half of the biotically pollinated species flowered in the wet season and half in the dry season. In contrast, in 2006–07, biotically pollinated species flowered at a higher frequency during wet season (59%) than dry season (41%), perhaps due to the fact that flowering frequency was higher during the wet season in 2007 (Figure 5).

The recorded peak fruiting seasons were found to be significantly associated with the fruit type of species (*G*-test = 52.14, df = 20, P = 0.0001), across the three study years. For instance, peak fruiting of fleshy fruited species occurred during the late wet season (September–October) in 2004–2005, 2005 and 2006. However, in 2006–07, peak (35% of species) fruiting of fleshy fruited species occurred during wet-season (July–August) and late (32% of species) wet-season (September–October). Fleshy fruited species were also found to consistently display their lowest fruiting occurrence during the dryseason in each of the examined study years (Figure 6).

The timing of peak fruiting varied significantly between species which utilize differing dispersal mechanisms (G-test = 559.8, df = 32, P = 0.0001). For instance, the peak fruiting events of zoochorous dispersed species in both 2004-05 (28%) and 2005-06 (36%) occurred during the late wet-season whilst, in 2006-07, it occurred during the peak wet-season (35%) and late wet-season (34%). Similarly, peak fruiting of autochorous dispersed species occurred during the peak wet-season in two years (2005 and 2007), and during the late-wet season in 2006. In contrast, the timing of peak fruiting events of anemochorous dispersed species was inconsistent across study years. Specifically, peak fruiting of anemochorous dispersed species in 2004-05 occurred during the late wet-season and early dry-season; in 2005-06, it occurred during the peak dry season (67%), and in 2006-07 the frequency of flowering events was equally shared (33%) over the seasons (Figure 7).

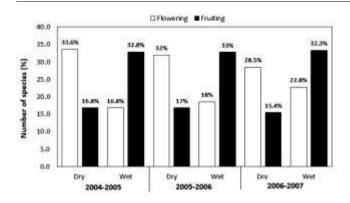


Figure 4. Seasonal pattern of flowering and fruiting species showed variation on frequency between year intervals over three-year period. Number of species was normalized as percentage in each year on flowering and fruiting through the observation.

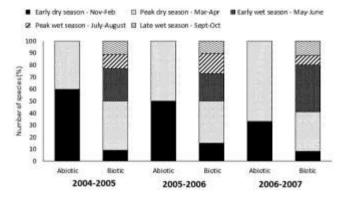


Figure 5. Frequency of seasonal flowering pattern in relation to abiotic and biotic pollination mode over three-year period in the tropical seasonal rainforest of Southwest China. Percentage values of species frequency are presented.

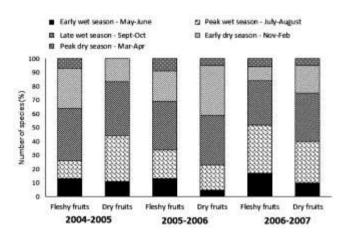


Figure 6. Frequency of seasonal fruiting pattern in relation with fruit types over three-year period in the tropical seasonal rainforest of Southwest China. Percentage values of species frequency are presented.

Discussion

The majority of woody-plant species in the seasonaltropical rainforest of south-west China display seasonal

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peaks in their reproductive cycles. Over three consecutive years of study, slight annual variations in the flowering and fruiting frequency of the examined woody-tree species were noted. For instance, in 2007, flowering frequency was higher (12%) than in 2005 and 2006 (Figure 3). Similarly, over the three-year study period, the of peak-flowering month varied but generally occurred in the same period that is during the late dry-season to early wet-season (Figure 5). Analogously, although fruiting of individual species started in the early wet season and extended into the early dry season, the number of species fruiting usually peaked sometime during the end of the late wet-season (September-October) (Figure 5). We also found that flowering was positively related to day-length, temperature and rainfall and fruiting was positively associated with rainfall and temperature, but not day-length. Therefore reproductive phenology at the community level is highly seasonal and correlated with climatic factors.

In addition to overall flowering frequency, woody-tree species whose flowers were biotically pollinated also displayed a distinct seasonality in their flowering with peakflowering occurring in the period between late-dry and early-wet season. Moreover, there was a clear seasonality in fruiting events displayed by species within individual fruit types and dispersal modes. For instance, fleshy fruited tree species displayed a peak in fruiting during the period between early-wet season and late-wet season. These seasonalities found in flowering and fruiting events of woody-tree species have been reported in previous studies of various tropical seasonal forests at other geographic localities^{3,8,10,14,30,45}. However, this is the first report of these reproductive phenology patterns occurring at the latitude of 21°N in the seasonal-forests of Southwest China.

Reproductive phenology: climate and seasonal patterns

Seasonal variation in flower and fruit production in tropical seasonal-forests has previously been correlated with annual variations in rainfall and temperature, and with the presence of a dry season in which the precipitation is usually >60 mm (refs 1, 3, 14, 20, 29, 46). In this study, seasonal flowering of woody species peaked in the late dry season indicating that temperature and rainfall may play a major role in shaping flowering. Interestingly, we also found that rainfall showed a positive association with flowering in that, it contributed to the physiological processes which promote bud-breaking and subsequent flowering⁴⁷. Conversely, although day length showed a significant positive association with flowering, we believe day length is not an important cue for community phenology in this study. We suggest this as although there were variations in the timing of peak flowering and fruiting events and day length was consistent across the examined study years, there was no significant variation between

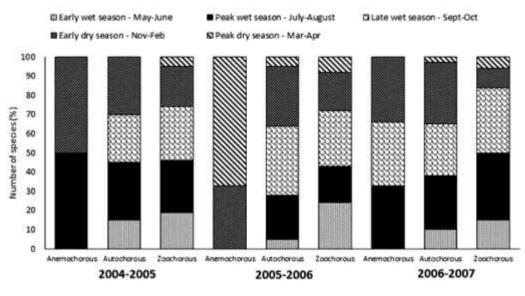


Figure 7. Frequency of seasonal fruiting pattern in relation with dispersal mode (such as Anemochorous, Autochorous and Zoochorous) over three-year period in the tropical seasonal rainforest of Southwest China. Percentage values of species frequency are presented.

year intervals. However, there was considerable variation in rainfall and temperature and as such we suggest that these variables may be an important abiotic factor driving seasonal variations in flowering and fruiting in the tropical seasonal rainforests of the Xishuangbanna region of Southwest China. In support of these suggestions, previous studies of flowering events have also noted that water availability^{20,48} and temperature^{12,13,15,20,29,49–51} act directly on flowering events in the tropics. Consequently, our findings reveal that flowering and fruiting were significantly associated with rainfall and temperature in the seasonal forests examined and that this pattern is similar to that described in many previous studies^{3,10,14,20,29,51}.

Phenology patterns with biotic interactions

The flowering seasonality observed in the seasonal-rainforests of south China is a flowering pattern similar to that found in other tropical seasonal environments^{14,20,29,30,51}. For instance, this seasonal flowering pattern is known to occur in the tropical seasonal-rainforests of South America, Malaysia and Australia^{3,25,52}. We suggest that the observed seasonal and synchronized flowering events might be employed as a mechanism to maximize pollination success through peak-flowering occurring when pollinators are most abundant^{2,53-55}. For instance in the examined forests of Southern China, during the dry season, pollinators are abundant^{56,57} which may contribute to plant community reproductive success. The potential for pollinators to influence woody-tree phenology is additionally plausible as it has been previously found that pollinator behaviour is an important selective force for flowering phenology^{58,59}. It must be noted, however, that given the lack of temporal segregation in flowering at the community level, pollinator competition between tree species may be possible in particular seasons (i.e. the dry season) though this could only be determined through further study.

We found that peak fruiting in the seasonal-rainforest of southern China falls during the wet season (September to October). Consequently, peak-fruiting coincides with the period of greatest soil moisture availability⁶⁰ which may subsequently influence seed germination and seedling regeneration success^{3,7,61}. Additionally, previous studies of Southeast Asian forests have reported that peak fruiting of fleshy fruited species often coincides with the period when dispersers are most abundant^{8,36,37}, as this may facilitate increased spatial seed dispersal³⁴. In support of these previous findings, we also found that during the peak fruiting season, 59% of all animal dispersed (zoochory) woody-tree species fruited. However, in addition to this fruiting peak, we also found that the remaining animal-dispersed fruits were produced sporadically throughout the year which may provide a constant supply of fruits for resident dispersers⁶²⁻⁶⁴. Therefore, in the examined seasonal rainforests, the timing of fruiting synchronization and the remaining sporadic fruiting may benefit common local and migratory seed dispersal agents.

Conclusions

In the tropical seasonal rainforest of south China (at latitudes of 21°N) flowering and fruiting patterns of woodytree species display seasonal peaks in their reproductive cycles and these are associated with climatic seasonality. The dry season is associated with peak-flowering periodicity and subsequent fruiting peak occurs during the early wet to late wet seasons. The day length recorded in the study site did not show significant variation across the three years of study, and as such we suggest that rainfall and temperature appear to be the main climate factors that drive local woody-tree community phenological events. However, further long-term observations of phenological patterns in response to rainfall and temperature patterns, in particular, may provide a clearer understanding of localized phenological patterns. In addition, subsequent analyses of biotic interactions between woody-tree species and pollinators and seed dispersers will aid in a clear understanding of the likely impact of future climate change.

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