

# Phenological response of tropical plants to regional climate change in Xishuangbanna, south-western China

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**Abstract:** The phenology of temperate plants is vulnerable to climate change. Yet, the phenological responses of tropical plants to climate change are still unclear. In this study, temporal trends (1973–1999) of four phenological events (budburst, growing season, flowering and flowering duration) were studied among 21 plant species in Xishuangbanna Tropical Botanical Garden (south-western China). Fourteen species (67%) showed significant phenological trends during the study period. Seven species (33%) presented delaying trends in budburst (average  $1.4 \text{ d y}^{-1}$ ) and such trend was more likely to be presented in those that started budburst earlier in the dry season. Four species (19%) showed trends of extension in growing season (average of  $3.5 \text{ d y}^{-1}$ ). These vegetative events appeared to be mainly influenced by increasing temperature. Rainfall showed little effects directly, however, the effects of temperature seemed to largely depend on the moisture condition. Flowering duration of five species (24%) was shortened by average  $2.1 \text{ d y}^{-1}$  which was most likely to be the result of the decline in sunshine duration during the rainy season. Our results suggest that the phenology of tropical plants has changed significantly in response to the regional climate change but these reactions are somewhat different from those of temperate plants.

**Key Words:** budburst, flowering, flowering duration, growing season, phenological trend, tropical plant

## INTRODUCTION

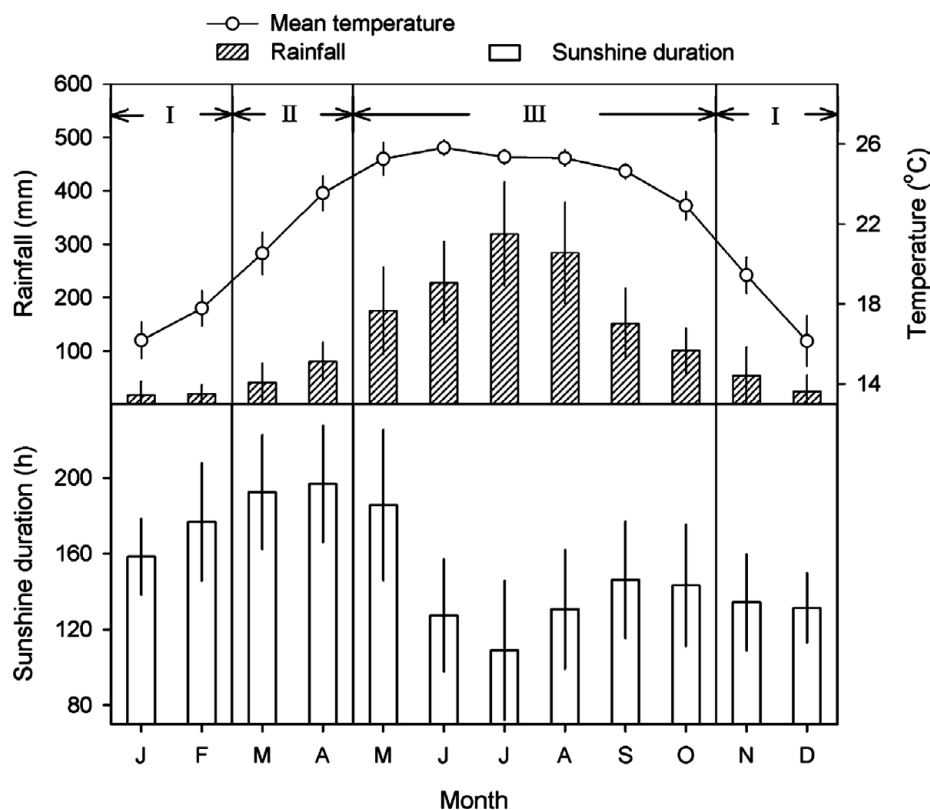
Plant phenology is strongly controlled by climate and has consequently been considered as a reliable indicator of ongoing climate change (Gordo & Sanz 2010, Keatley *et al.* 2002, Parmesan & Yohe 2003, Root *et al.* 2003). In response to the warming climate, many species in temperate regions have advanced the dates of spring leaf development (e.g. leaf budburst and leaf flushing) and flowering over the past half century (Abu-Asab *et al.* 2001, Ahas *et al.* 2002, Doi & Katano 2008, Dose & Menzel 2004, Fitter & Fitter 2002, Gordo & Sanz 2009). Such temperature increase also has led to a prolonged growing season in most cases (Chen *et al.* 2005, Matsumoto *et al.* 2003, Menzel & Fabian 1999).

In the tropics, instead of temperature, light condition is usually more important (Nemani *et al.* 2003, Wright & van Schaik 1994, Zimmerman *et al.* 2007). Some

authors have addressed the importance of day-length variation in manipulating bud break or flowering in tropical trees (Bollen & Donati 2005, Rivera & Borchert 2001, Rivera *et al.* 2002). In regions near the equator where day-length variation is small across the year, Borchert *et al.* (2005) proposed an assumption based on times of sunrise or sunset to explain synchronous flowering. Recently, studies in tropical America suggested the daily insolation, which is a function of day-length and intensity of irradiation, to be the main factor controlling bud break and flowering of many perennials in the tropics, instead of day-length only (Calle *et al.* 2009, 2010).

Water availability is another important factor for the phenology of tropical plants. In tropical monsoon forests, synchronous leaf flushing and flowering are triggered by the first heavy rain after the dry season (Borchert 1994a, Eamus 1999, Opler *et al.* 1976). For evergreen species, leaves are kept hydrated during the dry season by using the water taken from subsoil (Jackson *et al.* 1995). Deciduous species in dry forests also use subsoil water for shoot growth or flowering at the end of dry

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**Figure 1.** Monthly mean temperature, rainfall and sunshine duration in Xishuangbanna during 1971–2008. Three seasons are noted as: I, cool-dry season; II, hot-dry season; III, rainy season. The error bar represents 1 SD.

season (Borchert 1994b, 1994c). Due to the multiple drivers, phenology of tropical plants is more complicated compared with temperate plants.

Under the scenario of climate change, whether plant phenology in the tropics is affected by global warming is still inconclusive. Calle *et al.* (2010) suspected that in the tropics, especially some lowland forests, where temperature is over 25 °C, global warming is not likely to affect the plant phenology there. By contrast, a study from the forest in Costa Rica found reductions in tree growth accompanied by the increasing temperature (Clark *et al.* 2003), implying a change in vegetative phenology could have also occurred. Although the phenology of tropical plants has attracted much attention, its response to climate change is generally unclear because of the lack of long-term phenological records.

In this study, we analysed the phenological data (1973–1999) of the tropical plants in Xishuangbanna Tropical Botanical Garden, where the mean temperature has increased by 1.33 °C  $y^{-1}$  since the 1960s (Zhao *et al.* 2012), to test the hypothesis that the warming climate has led to consistent changes in the phenology of tropical plants (i.e. advanced the date of leaf budburst and flowering and prolonged growing season and flowering duration) as it has performed in temperate species. The

result will improve current knowledge of how tropical plants are affected by climate change.

## METHODS

### Site description

The study site is in Xishuangbanna Tropical Botanical Garden (XTBG, 21°41'N, 101°25'E), located at the northern edge of the Asian tropical zone (Zheng *et al.* 2010) at an altitude of 570 m asl. The annual mean temperature is 22 °C and the rainfall is 1496 mm. The climate is typically seasonal, which is dominated by the tropical southern monsoon from the Indian Ocean during May–October and by subtropical jet streams during November–April. Consequently, three seasons are exhibited (Figure 1) which were defined by former studies in this region (Cao *et al.* 1996, 2006; Zhang 1966). They are a cool-dry season (November–February), hot-dry season (March–April) and rainy season (May–October). The cool-dry season is the coolest period with a mean temperature of 17 °C. There is dense fog in the morning but hardly any rainfall (average 29 mm  $mo^{-1}$ ). The following hot-dry season is a transitional period with more

rainfall (average  $61 \text{ mm mo}^{-1}$ ) and higher temperature (average  $22 \text{ }^\circ\text{C}$ ). In the rainy season, rainfall comprises about 84% of the annual amount and mean temperature is the highest ( $25 \text{ }^\circ\text{C}$ ).

### Phenology and climate

With the phenological records of more than 15 y, 21 deciduous tree species from five families (Bignoniaceae, Combretaceae, Dipterocarpaceae, Mimosaceae and Papilionaceae) were selected to study. The studied phenological events include onset of leaf budburst (the day that first leaf bud begins to open), growing season (the days from onset of leaf budburst to all leaves shed in a year), onset of flowering (the day that first flower bud totally opens) and flowering duration (days from the onset of flowering to all flowers shed in a year). Seeds or seedlings of the trees were introduced from other seasonal tropical regions (Appendix 1) and planted around 1960. They were not artificially pruned, irrigated or fertilized, which makes the study of climate impact possible. The study periods vary slightly among species and generally cover 1973–1999 (Appendix 1). Data after 1999 are, unfortunately, not available because phenology observation has been suspended since then.

For each species, phenology of five randomly chosen healthy mature individuals were monitored in accordance with the Method of Phenology Observation in China (Wan & Liu 1979), where the dates that three (out of the five) individuals began to open leaf buds, shed leaves, flower and drop all flowers were recorded. Thus, the observation is an estimation of the phenology on species-level rather than on specific individuals. The observation was conducted by fixed staff members once a week. During the period of phenological occurrence, it was scheduled on a daily basis.

Climatic data, including air temperature, rainfall and sunshine duration, from a meteorological station in the botanical garden during 1971–2008 were used to reveal the climatic impacts on phenology. The monitoring procedure has followed relevant requirements stipulated by the China Meteorological Administration (CMA).

### Statistical methods

Phenological dates were transcribed to day of year (DOY) for analysis. To improve the reliability of this phenological dataset, outliers beyond twice standard deviation (i.e. 95% confidence interval) from each phenological series were discarded.

Mann–Kendall (MK) test was applied to determine if any consistent phenological trends were presented during the study period. MK test is a non-parametric test based

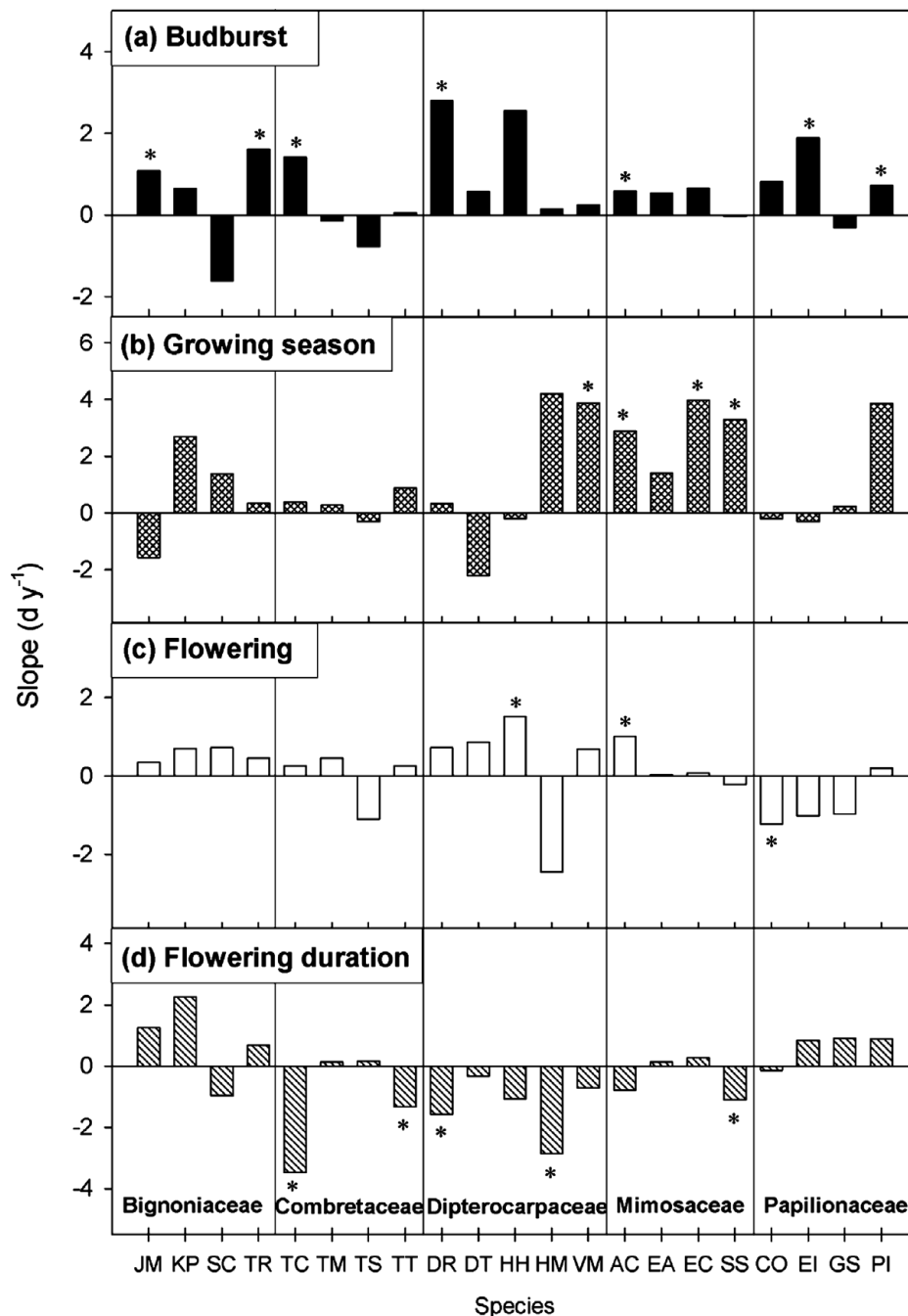
on the Kendall rank correlation to identify monotonic trends in time series, and it is not sensitive to data interruption (Jaagus 2006). From MK test, a final statistic  $Z$  was computed, which indicates the direction of the possible trend (see Kendall 1975 for detailed calculation). Trend significance is determined by comparing  $Z$  to  $Z_{1-\alpha/2}$ , which is obtained from the standard normal cumulative distribution tables (Partal & Kahya 2006, Tabari & Marofi 2011). In this study, significance level of  $\alpha = 0.05$  was applied, and a significant positive  $Z$  represents a delaying trend in budburst and flowering or a prolonging trend in growing season and flowering duration, while a significant negative  $Z$  indicates an advancing trend in budburst and flowering or a shortening trend in growing season and flowering duration. This  $Z$  was then correlated with average onset date (day of year) of each event across the 21 species to investigate whether the trend of each event was related to its occurrence time. Slopes of linear regressions between dates/days of the events and time (year) over the study period were computed to indicate the average inter-annual change rates of the events. These slopes share the same directions (i.e. signs of the values) with the statistic  $Z$  in each data series.

Correlation analysis is a direct and effective approach to reveal the impact of climate on phenology (Bendix *et al.* 2006, Bollen & Donati 2005). To find the climatic factors that affected the inter-annual variation of each phenological event, Spearman correlation coefficient between dates (or days) of the phenological events and climatic factors was computed over the study period. Factors used are mean temperature, mean maximum temperature, mean minimum temperature, rainfall and sunshine duration in the three seasons. Annual factors were also involved in the cases of growing season and flowering duration because they may better explain the events that lasted for more than one season.

## RESULTS

### Trends in phenological events

Of the 21 studied species, 14 species (67%) showed significant trends in the studied phenological events (Figure 2). In budburst, seven species (33%) delivered significant trends which delayed budburst by  $1.4 \pm 0.8 \text{ d y}^{-1}$  (Figure 2a). In the growing season, four species (19%), including three species of Mimosaceae, presented significant trends and prolonged the length by  $3.5 \pm 0.5 \text{ d y}^{-1}$  (Figure 2b). Besides the species with significant trends, eight and nine species also showed positive slopes in budburst and growing season, respectively, indicating the phenological shifts (i.e. delay of budburst and extension of growing season) were prevalent among the species.



**Figure 2.** Temporal shift rates (slopes of linear regression) of the phenological events for the species in Xishuangbanna. Species with significant trend, determined by MK test ( $P < 0.05$ ), are noted with asterisks (\*). A positive slope indicates a delay in date of budburst/flowering or an extension in growing season/flowering duration. A negative slope indicates an advance in date of budburst/flowering or a shortening in growing season/flowering duration. Species codes as given in Appendix 1.

In flowering, significant trends were shown in three species (Figure 2c), where two (10%) delayed (positive) the date of flowering and one (5%) advanced it (negative). Over all the species, positive slopes (delaying) were dominant, being presented in 15 species (67%). In flowering duration (Figure 2d), negative (shortening) trends ( $2.1 \pm 1.0 \text{ d y}^{-1}$ ) were presented in five species

(24%). Besides, 10 species (48%) showed positive slopes (prolonging) but failed to present any significant trends.

**Relationship between phenology and climatic factors**

Overall, 68 of the 84 studied phenological cases (81%) are correlated with climatic factors (Appendix 2). For the

19 cases with significant trends, 18 of them are climate-correlated, indicating that these changes in phenology were most likely to be induced by climate change.

Onsets of budburst occurred during the hot-dry season in most species (Appendix 2). Budburst is the only event with all the species well correlated with climatic factors. Of the seven species that presented significant trends, sunshine duration in the cool-dry season (Sun-C) positively correlated with three species, while mean maximum temperature in the cool-dry season (Tmax-C) negatively correlated with another four species, indicating the increase of Sun-F advances budburst while increase of Tmax-C delays it. For other species with no significant trends, temperature factors are also important and, interestingly, temperatures in the cool-dry season were usually negatively correlated with budburst while temperatures in the hot-dry season positively correlated with budburst. By contrast, factors of rainfall and sunshine were less important for budburst, as they only correlated with five and three species, respectively.

Length of growing season varied from 5 to 8 mo (Appendix 2). Temperature factors were in correlation with 13 species (62%, including the four species with a significant trend), and the coefficients were mostly positive (but see exceptions *Dipterocarpus turbinatus*, *Hopea hainanensis* and *Erythrina indica*), indicating thermal conditions are crucial for growth of the trees. Significant coefficients of rainfall and sunshine duration only presents in four and two species, respectively. Still, there are four species (19%) not correlating with any climatic factors.

Compared with vegetative events, flowering was less affected by climatic factors as six species were not climate-correlated, which includes all the four Bignoniaceae species (Appendix 2). Dates of flowering varied among species and the factors that influenced them were also different. For example, the species of Combretaceae, Mimosaceae and Papilionaceae were mostly correlated with temperature factors in the dry season, while Dipterocarpaceae species were mainly correlated with sunshine duration or rainfall. Moreover, the same factors presented different effects on different species, e.g. increase of sunshine duration in cool-dry season can advance flowering date in *D. retusus* but delay the date in *D. turbinatus*. It seems that flowering is relatively conservative and the conditions required for flowering are particularly different among species.

Flowering duration was generally 1–2 mo (Appendix 2) and mainly correlated with temperature and sunshine duration. Yet, rainfall presented little effects on flowering duration (apart from in *Kigelia pinnata*). For the species with significant trends, sunshine duration in rainy season (Sun-R) was a common factor that positively correlated with all of them. Besides, there were still five species not correlated with climatic factors.

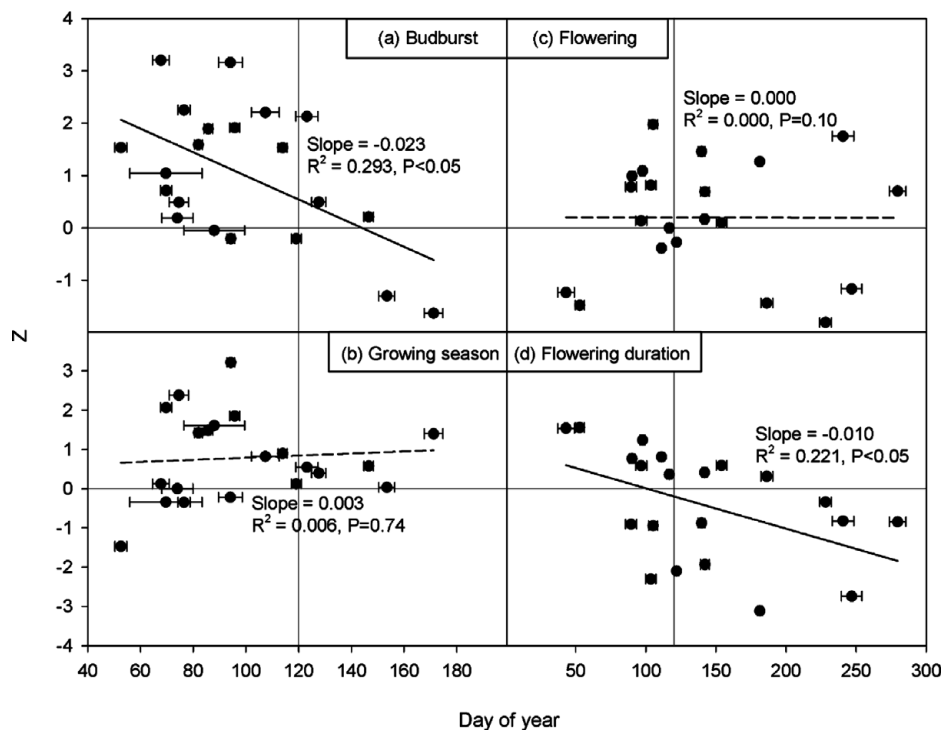
### Effect of occurrence time on trends delivery

The occurrence time showed a significant effect on the trend performance in the events of budburst and flowering duration (Figure 3). This means the early-budburst species were more likely to present a delaying trend and the late-flowering species (especially those that flowered in the rainy season) tended to show a shortening trend in flowering duration.

### DISCUSSION

During the study period, 14 species (67%) showed consistent trends in phenology and the regional temperature increase appears to be one of the major forces that cause these changes, which agrees with our hypothesis. Our knowledge of how climate change has affected the phenology of tropical plants has long been limited due to the lack of long-term data. Borchert (1998) argued that, rather than temperature itself, the significant reduction in rainfall induced by global warming is more likely to exert influences on plant phenology in tropical areas, however, failed to provide direct evidence. This assumption is not consistent with our results, where the rainfall, which showed a slight increase (but not significant, Figure 4) during 1971–2008, only presented minor effects on inter-annual variations of the plant phenology directly. By contrast, the relatively inadequate thermal conditions (i.e. the mean temperature of  $21.9\text{ }^{\circ}\text{C} \pm 3.7\text{ }^{\circ}\text{C}$  is generally lower than typical tropical regions due to the location of Xishuangbanna) was made more crucial to the phenology of tropical plants there.

In vegetative events, the trend of budburst delay, which was unexpected, is mostly like to be driven by the increase of the maximum temperature in the cool-dry season (Tmax-C, Figure 4) in four species. This can be explained by the severe drought in the cool-dry season (Figure 1). During the driest period of a year, temperature (especially the maximum temperature) increase would enhance water loss from soil and further reduce the positive turgor pressures necessary to expand growing cells (Green & Cummins 1974), which could, then, postpone the development of leaves. By contrast, rainfall in the hot-dry season is twofold that in the cool-dry season and most species started to develop their leaves during this period. With relatively more water available, a sufficient thermal condition would shorten the time of temperature accumulation for plants and cause an earlier budburst. This led to the positive correlation between temperature in the hot-dry season and budburst dates in many species. Although rainfall hardly presented a direct impact on budburst, it seems that the effects of temperature depended largely on the moist conditions.



**Figure 3.** Correlations between occurrence time (day of year  $\pm$  SE) of the phenological events and statistic Z (from MK test) across 21 species in Xishuangbanna, where Z represents the significance of temporal trends of the events. A higher absolute value of Z indicates the trend is more significant. A positive Z denotes a delay in budburst/flowering or an extension in growing season/flowering duration, and a negative Z denotes an advance in budburst/flowering or a shortening in growing season/flowering duration. Vertical lines denote the start of rainy season.

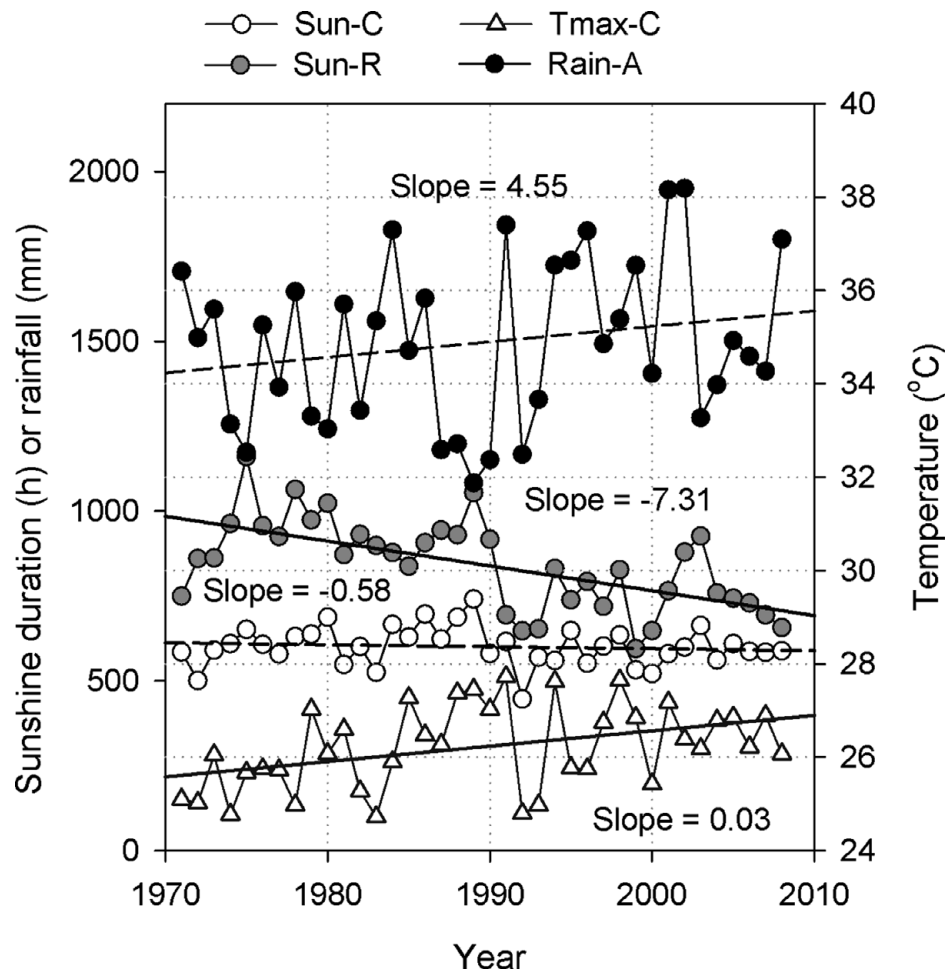
The delay of budburst, accompanied by the increasing maximum temperature in the dry season, is probably unique for those drought-sensitive species in such tropical areas with a typical dry season.

Furthermore, we found that the early-budburst species (i.e. those presented budburst during periods with little rainfall) were more likely to delay the budburst dates, which may result in a more synchronous budburst pattern among species. This result contradicts the finding in temperate plants that the species with earlier spring phenology (e.g. budburst) can advance more days in the corresponding event as temperature increases (Menzel *et al.* 2006, Wolkovich *et al.* 2012). Under different environmental conditions, the delay of budburst in our study seems to be an avoidance of unfavourable conditions (i.e. drought), while the budburst advance in temperate plants is probably a strategy to maximize their length of growing season under more favourable conditions (i.e. warmer climate).

Although delay of budburst was performed in many species, the extension in growing season is still prevalent, which, considering the strong correlation with temperature, could generally be attributed to the warming climate. This agrees with most studies in temperate areas (Chen *et al.* 2005, Matsumoto *et al.* 2003, Menzel & Fabian 1999). Increase in length of growing season is regarded as a cause that can enhance

the carbon fixation by plants and further accelerates the growth (White *et al.* 1999). In this regard, for the tropical plants in Xishuangbanna, the warming climate could be a compensation for the thermal deficit and may benefit their growth.

In reproductive events, five species shortened the flowering duration and, according to the correlation with the occurrence time, such change was more likely to present in plants that flowered during the rainy season. A short flowering duration shortens the period of pollination, and may further reduce the chance of successful pollination, especially in the rainy season when pollinating insects are less active because of the frequent rainfall. In this regard, such change in flowering duration could be a threat for the propagation of these plants. By contrast, length of pollen season (i.e. period of pollination) of many plants in temperate regions was found to have extended due to the warming environment (D'Amato *et al.* 2002, Frenguelli 2002, Ziska *et al.* 2011). This difference may result from the different climatic drivers. For tropical plants, light condition, rather than temperature, is of more importance in controlling the flower phenology (Calle *et al.* 2009, 2010; Zimmerman *et al.* 2007). In this study, the decreasing sunshine duration in the rainy season (Sun-R, Figure 4) was most likely to have influenced the flowering duration, mostly in the species with high light demand (e.g. *Terminalia*



**Figure 4.** Inter-annual variations of four climatic factors (1971–2008) in Xishuangbanna, which are mean maximum temperature in cool-dry season (Tmax-C), sunshine duration in cool-dry season (Sun-C), sunshine duration in rainy season (Sun-R) and annual rainfall (Rain-A). Lines of linear regression were added to show temporal trends, where a solid line indicates a significant trend (MK test,  $P < 0.05$ ) and a dashed line indicates an insignificant trend. Slopes of the fitted lines show the shift rates ( $^{\circ}\text{C y}^{-1}$ ,  $\text{h y}^{-1}$  or  $\text{mm y}^{-1}$ ).

*catappa*, *Dipterocarpus retusus*, *Samanea saman*; Appendix 1). In Xishuangbanna, sunshine duration in the rainy season is relatively lower (Figure 1) due to the cloudy weather and frequent rainfall, and its further reduction could become a restriction for these species that led to the decline of flowering duration. Therefore, plants that flower during the dry season with peak irradiance may have more advantages in reproduction.

To our knowledge, this is the first study regarding the inter-annual phenological trends in tropical plants with data series of more than 10 y. Although the study periods are slightly different among species (Appendix 1), the results demonstrated the fact that the phenology of tropical plants has been affected by climate change significantly but the reaction has been somewhat different from temperate plants. Yet, as phenological responses of tropical plants vary across regions of different climatic features, more studies of phenological trends from other tropical areas are still needed.

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**Appendix 1.** A list of the names of the studied species and their study periods, origins of their seeds or seedlings, codes (which were used in the figures and appendix), native range and habitat, potential ecological trait and the sources of the information. Names of the species are in accordance with Li *et al.* (1996). NA: no authoritative reference available.

Family / Species	Period	Origin	Code	Native range and habitat	Potential trait	Reference
<b>Bignoniaceae</b>						
<i>Jacaranda mimosifolia</i>	1984–1999	Zaire	JM	Highland areas in Argentina and Brazil	High light demand	Bein <i>et al.</i> 1996
<i>Kigelia pinnata</i>	1984–1998	Tropical China	KP	Wet savanna woodland or along rivers throughout Africa	Drought tolerant	Bein <i>et al.</i> 1996
<i>Spathodea campanulata</i>	1978–1999	Ghana	SC	Deciduous, transition and savanna forests throughout Africa	Drought tolerant	Bein <i>et al.</i> 1996
<i>Tabebuia rosea</i>	1982–1999	Mexico	TR	Wet land in Central and South America	High moisture demand	Streets 1962
<b>Combretaceae</b>						
<i>Terminalia catappa</i>	1978–1999	Tropical China	TC	Tropical coastal areas of Indian Ocean	Drought tolerant, high light demand	Morton 1985
<i>T. muelleri</i>	1982–1998	Cuba	TM	Beach or monsoon forest in north-eastern Australia	High light demand	Boland <i>et al.</i> 2006
<i>T. superba</i>	1977–1998	Ghana	TS	Deciduous forest throughout Africa	High light demand, drought sensitive	Bein <i>et al.</i> 1996
<i>T. tomentosa</i>	1973–1998	Cuba	TT	–	–	NA
<b>Dipterocarpaceae</b>						
<i>Dipterocarpus retusus</i>	1974–1996	Tropical China	DR	Evergreen and monsoon forests in South-East and East Asia	High light demand	Luna 1996
<i>D. turbinatus</i>	1973–1998	Tropical China	DT	Tropical evergreen and moist deciduous forests in South-East Asia	Shade tolerant, high moisture demand	Yang <i>et al.</i> 2008
<i>Hopea hainanensis</i>	1973–1996	Tropical China	HH	Tropical forests in China and Vietnam	High light demand, frost tolerant	Yang & Qiu 2007
<i>H. mollissima</i>	1976–1998	Vietnam	HM	–	–	NA
<i>Vatica mangachapoi</i>	1979–1998	Tropical China	VM	Dry ridges in China and South-East Asia	Drought tolerant	Fang <i>et al.</i> 2004
<b>Mimosaceae</b>						
<i>Albizia chevalieri</i>	1978–1998	Mali	AC	–	–	NA
<i>Entada africana</i>	1974–1996	Mali	EA	Wet savanna in central Africa	High moist demand	Bein <i>et al.</i> 1996
<i>Enterolobium cyclocarpum</i>	1978–1998	Cuba	EC	Tropical and dry forests in Central America	Drought tolerant	Allen 1956
<i>Samanea saman</i>	1978–1998	Ghana	SS	Lowland dry forests and grassland/savanna in Central America	Drought tolerant, high light demand, frost sensitive	Clarke & Thaman 1993
<b>Papilionaceae</b>						
<i>Centrolobium ochroxylum</i>	1973–1998	Cuba	CO	–	–	NA
<i>Erythrina indica</i>	1973–1998	India	EI	Lowland deciduous forests in India	Frost sensitive	Luna 1996
<i>Gliricidia sepium</i>	1981–1998	Ghana	GS	Tropical dry forests in Central America	Drought tolerant, frost sensitive	Clarke & Thaman 1993
<i>Pterocarpus indicus</i>	1982–1998	Tropical China	PI	Riverine tropical forests in South-East and East Asia	High light demand, drought tolerant	Clarke & Thaman 1993

**Appendix 2.** Climatic factors in Xishuangbanna that correlated with the phenological events. It shows average day of year (DOY) or duration ( $\pm$  SD) that the events occur or last for, and a list of three (some less than three) significant climatic factors ( $P < 0.05$ ) for each event. Species codes as given in Table 1. Factors (i.e. Tave, Tmax, Tmin, Rain and Sun) represent average temperature, mean maximum temperature, mean minimum temperature, rainfall and sunshine duration, respectively. Periods that the factors cover are showed following them (C, cool-dry season; H, hot-dry season; R, rainy season; A, annual). Correlation coefficients (r) of the factors are presented within parentheses, where a positive r indicates that the increase of the factor advances or prolongs the event, and a negative r delays or shortens it. NS, no significant factors are available ( $P > 0.05$ ).

Family/Species	Budburst		Growing season		Flowering		Flowering duration	
	DOY	Factors (r)	Duration (d)	Factors (r)	DOY	Factors (r)	Duration (d)	Factors (r)
<b>Bignoniaceae</b>								
JM	77 $\pm$ 9	Sun-C (0.692)	236 $\pm$ 22	Sun-H (0.543)	90 $\pm$ 8	NS	65 $\pm$ 22	NS
KP	82 $\pm$ 6	Sun-C (0.701) Rain-C (-0.551)	223 $\pm$ 50	Sun-C (-0.597)	98 $\pm$ 7	NS	68 $\pm$ 37	Tmax-A (-0.624) Tmax-C (-0.610) Rain-C (0.521)
SC	171 $\pm$ 16	Tave-H (0.474)	229 $\pm$ 24	Tave-H (0.671) Tave-A (0.494) Tmin-C (0.496)	280 $\pm$ 27	NS	118 $\pm$ 28	NS
TR	123 $\pm$ 16	Sun-C (0.518)	217 $\pm$ 21	Rain-A (0.559)	97 $\pm$ 16	NS	31 $\pm$ 20	Sun-C (-0.574) Tmax-A (-0.561)
<b>Combretaceae</b>								
TC	68 $\pm$ 15	Rain-C (0.540) Tmax-C (-0.461)	244 $\pm$ 34	Rain-R (0.454)	104 $\pm$ 16	Tmax-C (-0.505)	87 $\pm$ 41	Sun-R (0.491) Sun-H (0.481)
TM	119 $\pm$ 8	Tave-H (0.582)	198 $\pm$ 30	NS	154 $\pm$ 15	NS	18 $\pm$ 6	Tave-A (0.752) Tmin-H (0.599) Sun-C (0.553)
TS	153 $\pm$ 13	Tave-H (0.679) Tmin-C (-0.580)	219 $\pm$ 34	NS	186 $\pm$ 20	Tave-H (0.586) Tmax-C (0.569) Tmax-H (0.555)	34 $\pm$ 11	NS
TT	147 $\pm$ 8	Sun-H (0.551)	184 $\pm$ 29	Tmax-A (0.440)	181 $\pm$ 8	Tmax-R (-0.478)	32 $\pm$ 12	Sun-R (0.476)
<b>Dipterocarpaceae</b>								
DR	107 $\pm$ 22	Tmax-C (-0.544)	240 $\pm$ 18	Tmin-C (0.490) Tmin-R (0.448)	142 $\pm$ 12	Sun-C (0.539)	48 $\pm$ 15	Sun-R (0.624) Sun-A (0.575)
DT	53 $\pm$ 10	Tmin-H (0.556)	183 $\pm$ 41	Tmax-H (-0.592)	89 $\pm$ 16	Sun-C (-0.766) Tmax-C (-0.596)	25 $\pm$ 9	Sun-C (0.656) Sun-A (0.628) Sun-R (0.498)
HH	70 $\pm$ 61	Tmax-C (-0.587) Rain-C (0.527)	245 $\pm$ 73	Tmax-A (-0.518) Tmax-C (-0.426)	241 $\pm$ 27	NS	42 $\pm$ 28	Sun-C (0.587) Sun-A (0.569) Sun-R (0.553)
HM	88 $\pm$ 45	Tave-C (-0.685) Rain-C (0.656) Tmax-C (-0.637)	235 $\pm$ 62	NS	247 $\pm$ 25	Rain-R (0.685)	33 $\pm$ 23	Tave-H (-0.699) Sun-R (0.524)
VM	70 $\pm$ 10	Tmin-H (0.483)	225 $\pm$ 41	Tave-C (0.522) Tave-R (0.484)	140 $\pm$ 11	Sun-R (0.476)	33 $\pm$ 19	Sun-R (0.493)

## Appendix 2. Continued.

Family/Species	Budburst		Growing season		Flowering		Flowering duration	
	DOY	Factors (r)	Duration (d)	Factors (r)	DOY	Factors (r)	Duration (d)	Factors (r)
Mimosaceae								
AC	96 ± 8	Sun-C (0.522)	207 ± 36	Tmin-C (0.519) Tmax-A (0.497) Tave-A (0.457),	105 ± 14	Sun-C (0.520)	28 ± 14	Tave-H (-0.511)
EA	114 ± 7	Tmax-H (-0.496)	152 ± 26	Tave-R (0.498)	142 ± 8	Rain-C (-0.617) Tmax-C (0.595)	24 ± 6	NS
EC	75 ± 16	Tave-H (0.471)	255 ± 43	Tmin-R (0.441)	111 ± 7	Tmin-C (-0.503) Tave-H (0.466)	20 ± 7	Tmax-H (-0.831) Tmin-C (0.541) Tmax-A (-0.527)
SS	94 ± 6	Tave-H (0.697) Tmin-C (-0.462)	245 ± 27	Tave-H (0.480)	122 ± 7	Tmin-C (-0.491)	40 ± 13	Sun-A (0.535) Sun-R (0.499) Sun-H (0.458)
Papilionaceae								
CO	128 ± 11	Rain-H (0.559) Tmin-H (0.497)	206 ± 23	Rain-H (0.664) Tmin-H (0.634) Tave-C (0.535)	228 ± 19	Tmax-C (0.583) Rain-C (-0.505)	92 ± 24	NS
EI	94 ± 20	Tmax-C (-0.476)	258 ± 28	Tave-A (-0.432) Tave-H (-0.410)	43 ± 25	Tave-C (0.464)	52 ± 20	Tmax-H (-0.508)
GS	74 ± 25	Tmax-C (-0.513) Rain-H (-0.499)	247 ± 36	Tmax-C (0.597) Rain-C (0.472)	53 ± 13	Tave-C (0.535)	49 ± 16	Tave-R (-0.510)
PI	86 ± 7	Tmax-C (-0.510)	195 ± 47	NS	117 ± 7	Tmin-C (0.498)	21 ± 14	Tmax-R (0.705) Tave-R (0.669) Tmin-R (0.634)