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Phenological Patterns of Six *Xylopia (Annonaceae)* Species in Central Amazonia

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With 2 Figures

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Summary

WEBBER A. C. & GOTTSBERGER G. 1999. Phenological patterns of six *Xylopia (Annonaceae)* species in Central Amazonia. – Phyton (Horn, Austria) 39 (2): 293–301, 2 figures. – English with German summary.

The phenological patterns of six *Xylopia* species occurring in different vegetation types in the vicinity of Manaus, Central Amazonia, were studied. The observation period extended from August 1992 to July 1994. The data were recorded at biweekly intervals or at shorter intervals during the flowering season. Phenological parameters registered were flower buds, flowers, fruits, and young leaves. *X. aromatica* showed continuous flowering, at least at the population level. Individuals with flower buds, flowers, young and ripe fruits were found all the year round. Young leaves were also produced continually. *X. amazonica* showed only a three-months flowering period in the year, which coincided with the low rainfall season. The fruits ripened synchronously about six or seven months after flowering. Young leaves flushed around the year. *X. benthamii* flowered once a year, also within the low rainfall period. Flowering lasted around five months, beginning at the end of June and finishing at the end of October; fruits could be observed from October to February. *X. crinita* had an annual period of flowering that began when rainfall diminished. Flowering lasted about three months, starting in March and ending in May. The fruits of a season were ripe only in the next flowering season. *X. excellens* flowered once a year in the rainy season. The flowering period lasted for about three months, beginning at the end of September and ending in December. Fruits were found up to April

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and occasionally up to May in some of the individuals. *X. emarginata* was observed flowering only once in a three-year period; flowering lasted about two months showing a supra-annual pattern.

Zusammenfassung

WEBBER A. C. & GOTTSBERGER G. 1999. Phänologische Muster von sechs *Xylopia (Annonaceae)*-Arten in Zentral-Amazonien. – Phyton (Horn, Austria) 39 (2): 293–301, 2 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die phänologischen Muster von sechs *Xylopia*-Arten unterschiedlicher Vegetationstypen wurden in der Umgebung von Manaus in Zentralamazonien untersucht. Die Beobachtungszeit erstreckte sich von August 1992 bis Juli 1994. Die Daten wurden in zweiwöchentlichem Rhythmus erfasst und während der Blühperioden auch in kürzeren Zeitabständen. Die phänologischen Parameter umfassten Blütenknospen, offene Blüten, Früchte und junge Blätter. *X. aromatica* zeigte auf die Population bezogen kontinuierliches Blühen. Das ganze Jahr über gab es Individuen mit Blütenknospen, Blüten, sowie jungen und reifen Früchten. Auch neue Blätter wurden kontinuierlich gebildet. *X. amazonica* hatte pro Jahr eine nur drei Monate dauernde Blühzeit, die in die regenärmere Zeit fiel. Die Früchte reiften gleichzeitig etwa sechs oder sieben Monate nach dem Blühen. Junge Blätter wurden das ganze Jahr über gebildet. *X. benthamii* blühte einmal pro Jahr ebenfalls in der regenärmeren Zeit. Das Blühen dauerte etwa fünf Monate, beginnend mit Ende Juni und war gegen Ende Oktober abgeschlossen. Früchte konnten von Oktober bis Februar beobachtet werden. Auch *X. crinita* hatte annuelle Blühperioden, die bei Abnahme der Regenfälle anfingen. Das Blühen dauerte etwa drei Monate, begann im März und war im Mai beendet. Die Früchte waren erst nach beinahe einem Jahr in der nächsten Blühperiode reif. *X. excellens* blühte ebenfalls einmal im Jahr und zwar in der Regenzeit. Das Blühen erstreckte sich auf etwa drei Monate, von Ende September bis Ende Dezember. Früchte waren bis zum darauffolgenden April vorhanden und auf einigen Individuen bis Mai. *X. emarginata* blühte nur einmal innerhalb von drei Jahren. Diese supra-annuelle Blühperiode dauerte etwa 2 Monate.

Introduction

Phenological studies of tropical plants aim for a better understanding of the intricate relationship of species maintenance through the processes of pollination and seed dispersal (FRANKIE & al. 1974, GENTRY 1974, BAWA 1983, NEWSTROM & al. 1994).

It has been often suggested that the variability of phenological patterns lowers the effects of competition of plants for their pollinators and dispersers, which, in turn will have a better food presentation (BAWA 1983, SARMIENTO & MONASTERIO 1983, BORCHERT 1983, NEWSTROM & al. 1994).

The absence of a marked seasonality in tropical wet forests difficults our comprehension of the processes that govern the different phenological patterns. The causal factors of flowering and fruiting are still not totally clear (BAWA & NG 1990, STEEGE & PERSAUD 1991).

Phenological data are of great importance for the correct use and protection of the ecosystems (MACHADO & al. 1997). These data may also con-

tribute to the recuperation of disturbed areas, allowing a planning of collection of seeds of species that will be used for restoration projects (KNOWLES & PARROTA 1997).

The present paper shows the phenological patterns of six *Xylopia* species which occur in different vegetation types in the vicinity of Manaus.

Material and Methods

The species were studied in the region of Manaus, Central Amazonia, mainly in the Reserva Ducke (2°55′–3°08′S, 59°59′W, alt. 80–100 m) and in the Campus of the University of Amazonas (03°04′S, 59°57′W, alt. 70 m). Some observations were also made in the Ponta Negra area at the border of the Rio Negro.

The region of Manaus, has an Afi climate type, which is a tropical climate practically without winter, and with rains along the year and isothermy (RIBEIRO 1976). At Reserva Ducke the mean annual temperature is 26° C and mean annual rainfall is 2362 ± 400 mm (MARQUES FILHO & al. 1981).

Five individuals of each species were observed (except for *X. emarginata*, where only one individual was observed). Each tree was tagged with an aluminum label and characteristics such as habit, height, diameter at breast height (DBH) were recorded. The distances of each individual of a *Xylopia* species in relation to the three more close individuals were measured, in a total of five conspecifics in a given area, and then the mean distance between individuals of a species was calculated.

The observation period extended from August 1992 to July 1994. The data were recorded at bi-weekly intervals or lower intervals during the flowering season. Phenological parameters recorded were flower buds, flowers, fruits, and young leaves. The patterns were described according to the ones proposed by NEWSTROM & al. 1994 and compared with those proposed by GENTRY 1974.

Results

The localities, vegetation types, soil characteristics, ground water level and further features of the studied species are shown in Table 1.

Table 1

Characteristics of studied species

Species	Locality	Vegetation	Vegetation state	Soil	Ground water level
X. aromatica	3	secondar	disturbed	sandy	deep
X. amazonica	1	secondary	little disturbed	sandy	deep
X. benthamii	2	campinarana	little disturbed	sandy	deep
X. crinita	1	forest	undisturbed	clay	deep
				sandy	superficial
X. excellens	2	secondary	little disturbed	sandy	superficial
X. emarginata	1	forest	undisturbed	sandy	superficial

Locality: (1) Reserva Ducke (2) Campus da Universidade do Amazonas
(3) Ponta Negra

Table 1. continued

Species	Mean distance between individuals (m)	Population densit	Mean individual height	DBH of individuals (cm)	Maximal species height (m)	Flower size (cm)
X. aromatica	10.3	high	3.0	3.3–5.7	4.5	3.8–5.2
X. amazonica	7.6	high	13.5	11–16.5	16.0	1.3–1.8
X. benthamii	7.3	medium	10.0	5.9–10.6	12.0	3.4–5.3
X. crinita	>100	very low	11.5	5.7–11.2	15	3.7–4.3
X. excellens	11.0	medium	5.3	3–5	7.5	3.6–4.3
X. emarginata	>50	low	10.0*	10.5*	25.0	1.9–2.1

(*) only 1 individual

Xylopia crinita and *X. emarginata* are found only in the primary forest and show low individual density. *X. benthamii* occurs in campinarana (a forest-like white-sand vegetation) and the other species occur in disturbed areas. *X. excellens* and *X. emarginata* occur only at stream borders, and *X. crinita* occurs on both sandy and clayey soil.

X. aromatica showed continual flowering, at least at the population level. Individuals with flower buds, flowers, young and ripe fruits were found all the year round (Fig. 1). Young leaves were also produced continually. Occasionally, some individuals could be found in the vegetative state. The number of open flowers per day in a given individual varied from one to eight. There is flowering synchronism both at the individual and population level. Fruiting was also synchronized.

X. amazonica showed only a three-months flowering period in the year (Fig. 1), which coincided with the low rainfall season. The number of open flowers per day reached around 200, but generally it was around 50. This species therefore showed the greatest amplitude of open flowers per day.

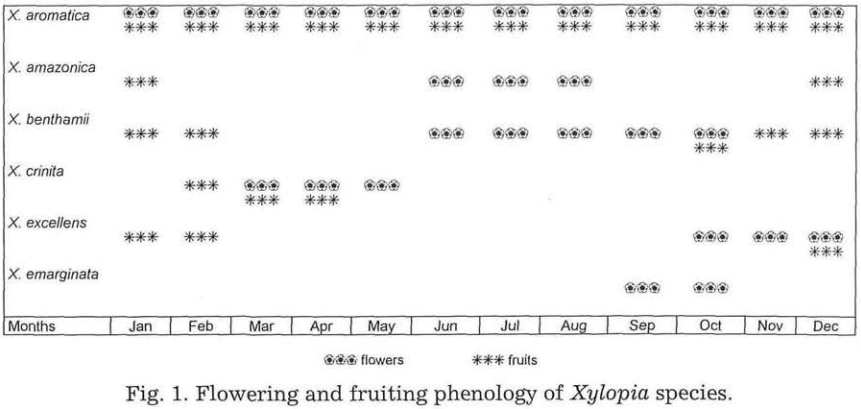

Fig. 1. Flowering and fruiting phenology of *Xylopia* species.

Flowering synchrony occurred in and between individuals. The fruits ripened synchronously about six or seven months after flowering. Young leaves flushed around the year.

X. benthamii flowered once a year, also at the low rainfall period. Flowering lasted around five months beginning at the end of June and lasting until the end of October; fruits could be observed from October to February. Flowering was to some extent synchronized in and between individuals, but there were individuals which started flowering earlier and others which started later. The number of open flowers at the same time in one individual was observed to reach 17, but generally, the number was lower. The individuals may not open their flowers for some days.

X. crinita had an annual period of flowering (Fig. 1) that began when rainfall diminished. Flowering lasted about three months, started in March and ended in May. The fruits of a season were ripe only in the next flowering season. Flowering appears also synchronic, at both the individual and population level. Some individuals may be without flowers for one or more days. The number of open flowers per day in one individual never was more than four; this species therefore has the lowest flower amplitude (Table 2).

X. excellens flowered once a year at the rainy season. The flowering period lasted for about three months, beginning at the end of September and ending in December. Fruits were found up to April and occasionally

Table 2

Comparison of phenological patterns

Species	regularity	duration	amplitude
X. aromatica	regular	extended	low
X. amazonica	regular	intermediate	high
X. benthamii	regular	intermediate	low
X. crinita	regular	intermediate	reduced
X. excellens	regular	intermediate	low
X. emarginata	irregular	intermediate	medium

Table 2. continued

Species	date	synchrony	pattern (NEWSTROM & al. 1994)	pattern (GENTRY 1974)
X. aromatica	Jan–Dec	yes	continual	cornucopia
X. amazonica	Jun–Aug	yes	annual	steady state
X. benthamii	Jun–Oct	yes	annual	cornucopia
X. crinita	Mar–May	yes	annual	cornucopia
X. excellens	Oct–Dec	yes	annual	cornucopia
X. emarginata	Sep–Oct	?	supra–annual	–

up to May in some of the individuals. Flowering was synchronic in individuals and between them; the maximal flower number of an individual was nine.

X. emarginata was observed flowering only once in the two-year-period; its flowering lasted about two months. The number of flowers open in one individual can be up to 70; this species, therefore, has the second largest flowering amplitude. In this species it was not possible to observe any synchrony. In spite of the short period of observation this species seems to have a supra-annual pattern. Table 2 shows a comparison of flowering phenology of the studied species.

Discussion

The species studied showed three distinct phenological patterns, the continual, annual, and supra-annual. The most common pattern was the annual one.

When comparing the flowering periods with the rainfall distribution over the year, it could be seen that some species flowered in the period of more rain and others in the period with less rain. Only *X. aromatica* flowered around the year. This seems to indicate that more rains may stimulate flowering of some species while less rain seems to favor flowering of others. In *X. aromatica*, at least at the population level, rainfall quantity appears not to interfere in the process of flowering and fruiting. This species shows seasonality in the cerrado vegetation in Central Brazil (Silberbauer–Gottsberger, pers. comm.). For *X. emarginata* more studies are necessary to know if flowering occurs always at the same season also in subsequent years. Variation in periods of flowering and fruiting related to rainfall are frequent in tropical wet forests (Heideman 1989, Newstrom & al. 1993, 1994, Knowles & Parrota 1997).

X. emarginata was the only species with irregular flowering. Regarding duration, *X. aromatica* has an extended flowering period and all other species an intermediate period. Rathcke & Lacey 1985 consider that more extended flowering periods may have advantage in lowering the risk of an uncertain pollination.

Considering flowering amplitude, a great variation between species is observable. The size of flowers seems to be correlated with the number of flowers produced. *X. aromatica*, *X. benthamii*, *X. crinita*, and *X. excellens* have larger flowering and a smaller flowering amplitude, while *X. amazonica* and *X. emarginata* have smaller flowering and a greater flowering amplitude.

In relation to synchrony of flowering (*X. emarginata* could not be compared), all the species showed synchrony within one individual and between several individuals. In these context, synchrony at the individual level in *X. crinita* seems to be important, because of the very low popula-

tion density and also because this species has very small pollinators, viz., Staphylinidae (WEBBER 1996). Flowering synchrony influences not only the genetic quality of the descendants but also the quantity of descendants produced in a season and over an individual plant lifetime (AUGSPURGER 1985). On the other hand a certain degree of asynchrony between flowers of the same individual promotes a larger cross-pollination rate, because the pollinators need to move between individuals (RATHCKE & LACEY 1985).

Continuous leafing processes around the year were observed for all species. This continuous leafing pattern is common in wet forests (ARAUJO 1970, FRANKIE & al. 1974, ALENCAR 1990, NEWSTROM & al. 1993). In seasonal forests, rainfall has direct influence in phenology (FRANKIE & al. 1974, SARMIENTO & MONASTERIO, 1983, MACHADO & al. 1997).

The distribution of flowering in different periods seems not to have direct influence on pollination of the studied species, as they do not compete for pollinators (WEBBER 1996). Other *Annonaceae* compete for the same pollinators and therefore distribution of flowering at different periods is of great importance (GOTTSBERGER 1989, WEBBER 1996, WEBBER & GOTTSBERGER 1996). To GENTRY 1974 the differences in flowering phenology represent one of the mechanisms for maintenance of the high species diversity in tropical plant communities. These different phenological patterns permit a better partition of the pollinators (that many times are the same) by different species and, on other hand enhances better food presentation to the visitors that may obtain it practically all the year. Differences in flowering periods may be also a selection against hybridization (RATHCKE & LACEY 1985).

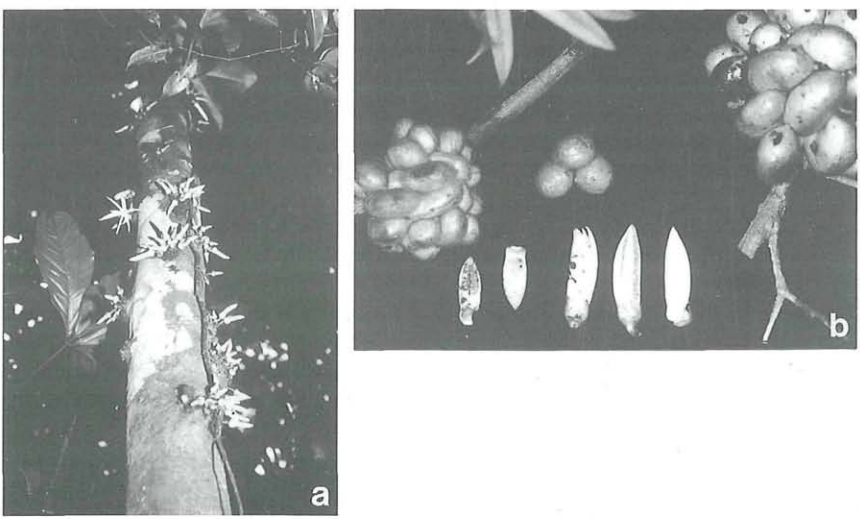

Fig. 2. – a. *Xylopia benthamii* with flowers. – b. *Xylopia crinita*, flowers and fruits.

The distribution of fruiting is relevant because all species have ornithochorous fruits. In this context, certainly there is a better partition of the fruits to the dispersers. Within individuals of each species and in between them a synchronism of fruit ripening occurred. This synchronism within an individual could be a disadvantage if dispersers are on a tree for a long time and drop many seeds under the parent plant (RATHCKE & LACEY 1985).

In the studied *Xylopia* species, there is a great variation of the phenological patterns and different parameters analyzed. Interpretation of the factors that determine these variations, however, is very complex. STEEGE & PERSAUD 1991 enumerate a series of factors that could trigger the flowering process, but consider that this process is still not clear enough. PIRES-O'BRIEN 1994 suggests that there are two types of phenological control, an environmental one and an endogenous one. FRANKIE & al. 1974 suggest that interactions between plants and animals may have influence on the diversification of flowering and fruiting patterns.

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