A REVIEW OF TREE PHENOLOGY IN CENTRAL AMAZONIAN FLOODPLAINS

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Abstract

Trees in central Amazonian floodplains are subjected to periodical inundations of up to seven months every year. The present paper summarizes the available data of tree phenology in Amazonian floodplains in the vicinity of Manaus, Brazil. The phenological observations included presence of leaves, leaf flush, flowering and fruiting of 76 species from 30 families. Leaves are shed mainly in the flooded period, new leaves are flushed when water recedes. The species from nutrient-rich várzea flush new leaves towards the end of the flooded period, in nutrient-poor igapó the peak of leaf flush is in the terrestrial, non-flooded period. Flowering occurs mainly at the beginning of the flooded period in igapó, while in várzea the peak is at highest water levels. The peak of fruiting is in the flooded period, in várzea later than in igapó. In both várzea and igapó, the amount of deciduous species is around 50%. In igapó a leafless period is not as evident because it is less synchronized. Although in most species analysed phenological changes occurred during the flooded period, it is not clear whether it is flooding that triggers the phenological events.

Key words: *evergreen trees, deciduous trees, leaf flush, flowering, fruiting, floodplain forest, várzea, igapó.*

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Resumo

As árvores das áreas inundáveis da Amazônia central estão sujeitas a inundações periódicas de até sete meses de duração por ano. O presente estudo faz um sumário dos dados de fenologia disponíveis para as florestas inundáveis nas proximidades de Manaus, Brasil. As observações fenológicas incluem presença de folhas, broto de novas folhas, floração e frutificação de 76 espécies de 30 famílias. A perda de folhas ocorre no período inundado, e novas folhas são produzidas antes do fim da enchente. As espécies de várzea, floresta rica em nutrientes, brotam folhas novas no final da enchente, enquanto no igapó, pobre em nutrientes, o pico de brotação de novas folhas é na fase terrestre, não inundada. A floração ocorre no começo do período inundado no igapó, enquanto na várzea durante o pico da cheia. O pico da frutificação ocorre na fase inundada, na várzea mais tarde do que no igapó. A porcentagem de espécies decíduas em várzea e igapó é de 50 %. No igapó há pouca sincronia quanto ao período de desfolha das árvores. A maioria das mudanças fenológicas ocorreram na fase inundada. Mesmo assim, não é claro quais são os fatores responsáveis pela ocorrência dos eventos fenológicos.

Palavras chave: *árvores sempreverdes, árvores deciduas, brotamento de folhas, floração, frutificação, florestas inundáveis, várzea, igapó.*

Introduction

The floodplains along the Amazon river and its main tributaries are subjected to a hydrological regime described by the 'flood pulse concept' (Junk *et al.*, 1989): a regular and predictable oscillation of the river levels causes periodical inundations of large forested areas which can last up to seven months every year. According to the quality of the flooding rivers, two types of floodplains can be distinguished in Central Amazonia, the nutrient-rich várzea flooded by whitewater rivers, and the nutrient-poor igapó flooded by blackwater rivers (Prance, 1979). Both ecosystems, especially the productive várzea, have high economic importance concerning fishing, timber extraction and small-scale agriculture (Parker, 1989; Klenke & Ohly, 1993; Junk, 1997; Parolin, 2000 a). Nevertheless, little is known about the ecology of the forests, and only a few tree species have been studied with respect to reproduction, physiology, morphology or anatomy (e.g. Worbes, 1986, 1988; Schlüter, 1989; Meyer, 1991; Waldhoff *et al.*, 1998; Parolin, 2000 b). Phenological traits are mentioned for some species (Table 1), but for most species it is not even known if they are deciduous or evergreen, or which precise dispersal modes they have. With the exception of a recent six-year study on the flowering phenology of *Ceiba pentandra* (Gribel *et al.*, 1999), continuous recordings over many years are almost completely lacking, as are publications summarizing and describing the phenological traits of trees in Central Amazonian floodplains. Most information about phenology is available only in the chapters of unpublished theses. The first continuous recordings were made in a two-year study by Revilla (1981). He dealt with six tree communities at Praia Grande, a blackwater floodplain of the Rio Negro near Manaus. This study showed that flooding can act as a regulating factor for phenology in some species, but there was a high diversity in the timing of phenological events in the six communities, with evergreen, semi-deciduous, and deciduous species which flush their leaves before, during or after flowering, when the water receded, or at high water. The same diversity was documented by Ferreira (1991) who analysed 30 tree species in an igapó community of the Rio Tarumã-Mirim near Manaus. The phenological cycles were not necessarily triggered by the flood periodicity, as indicated by monitoring trees growing at different elevations in the flooding gradient (Ferreira, 1991, 1998). There was a high inter- and intraspecific diversity of phenological traits in the analysed igapó community, which was found also when comparing pioneer and non-pioneer species of the várzea (Worbes, 1983; Parolin, 1997; Wittmann, 1997; Oliveira, 1998; Armbrüster, 1999; Wittmann & Parolin, 1999; Parolin, 2000 b). The only homogeneous trait among the floodplain trees was the period of fruit maturation, which was during high water or at the end of the flooded period, linked to dispersal by water (hydrochorous) or fish (ichthyochorous). This was documented by Ziburski (1990) for 33 tree species from várzea and igapó. Based on these studies and further, mostly single observations, some general statements and hypotheses concerning the timing and triggers of phenological events in Central Amazonian floodplains can be found in the literature:

1. Leaves are shed mainly in the flooded period (Worbes, 1983; Revilla, 1990; Ayres, 1993).
2. New leaves are flushed in the periods when the water is receding (August – September) or onset of rains (November – December), and in várzea also when the trees are still flooded (Worbes, 1997).
3. Flowering occurs mainly at the beginning of the flooded period (Worbes, 1997).
4. Fruits are produced mainly in the flooded period (Adis *et al.,* 1979; Worbes, 1986; Ziburski, 1990; Ayres, 1993), as an adaptation to water and fish dispersal (Ziburski, 1991; Goulding, 1983).
5. Differences between várzea and igapó: várzea forests are mainly deciduous, while in igapó evergreen species prevail (Klinge *et al.*, 1983; Worbes, 1983, Revilla, 1990).
6. The flood pulse is the main driving force which is predictable and responsible for the existence, the productivity and the interactions of the biota in the floodplains (Junk *et al.*, 1989). This implies that flooding also operates as a regulator for the timing of phenological events.

These statements have been formulated in spite of the high number of co-occurring species and the inter- and intraspecific variation. The influence of the different nutrient availability in várzea and igapó on phenology has not been considered, although it has been shown to affect plant distribution and floristic composition (Worbes, 1986; Ferreira, 1997; Pires & Prance, 1985), tree growth and productivity (Klinge *et al.*, 1983, 1995), wood density (Parolin *et al.*, 1998; Parolin & Ferreira, 1998; Parolin & Worbes, 2000), and seed mass (Parolin, 2000 c).

The present paper summarizes the existing data on tree phenology in Central Amazonian floodplain forests. It has the aim to review the available phenological data in a descriptive manner, and to compare the cited statements and hypotheses with detailed data recordings for consistency and underlying patterns.

Study sites

All studies reviewed here (Table 1) were carried out in the vicinity of Manaus, Brazil, near the confluence of the Amazon (Solimões) River with the Negro River (approximately 3ºS, 58º-60ºW). The tree species of várzea were studied mainly along the Amazon River (Ilha de Marchantaria, Costa do Catalão, Solimões). Species of the igapó were studied in the floodplains of Rio Tarumã-Mirim and the Negro River up to the Anavilhanas Archipelago.

Climate and water regime

The climate and water regime of the study areas are shown in Figure 1. All study sites were situated between 21 and 27 m above sea-level (asl) and were subjected to a mean annual water level fluctuation of 10 m, which corresponds to a period of inundation of up to seven months per year (Junk, 1989). Variation in river water level is markedly seasonal. The rising period occurs between December and June, and the draining period from July to November. Mean monthly temperature ranges from 26.3º to 27.2ºC. Mean annual precipitation varies between 1700 and 2550 mm (Ribeiro & Adis, 1984), with a marked dry season from June to November (42-162 mm precipitation per month, Adis, 1992) and a rainy season from December to May (211-300 mm precipitation per month).

Methods

The phenological events recorded in the reviewed studies included presence of leaves, leaf flush, flowering and fruiting. The definition of these phenological events is subjective in the various studies, which means the comparison of species and sites has to be interpreted with caution.

In summarizing the vegetative phenology (Table 2), a tree was considered to be deciduous when it was bare of leaves for at least three weeks (e.g. *Tabebuia barbata*) or when it had exclusively senescent and dead leaves (e.g. *Crateva benthami*). A tree was called evergreen if it changed leaves continuously (e.g. *Ce-*

cropia latiloba, *Senna reticulata*), or 'semi-deciduous', if it had periods of strong leaf loss and a subsequent flush of new leaves without a leafless period (e.g. *Swartzia polyphylla*, *S. argentea*, *S. laevicarpa*, Revilla, 1981; *Nectandra amazonum* and *Psidium acutangulum*, Wittmann, 1997; *Laetia corymbulosa*, Armbrüster, pers. comm.).

Results

In this review, detailed phenological data for 76 species from 30 families are presented (Table 3). Of these, 24 species were studied in the várzea, 49 species in the igapó, and three species (*Astrocaryum jauari*, *Macrolobium acaciifolium*, *Tabebuia barbata*) in both várzea and igapó. All additional published data on leaf phenology in the form of single references are presented in Worbes (1983); Kahn & Henderson (1998).

Duration of phenological events

In the deciduous species, the mean deciduous period was 2.3 ± 1.1 months (n = 11) in várzea, and 2.6 ± 0.8 months (n = 23) in igapó. Maximum duration of the leafless stage was four months in both várzea (*Crescentia amazonica*, *Pseudobombax munguba*) and igapó (*Buchenavia ochnopnuma*, *B. suaveolens*, *Myrciaria dubia*).

The duration of flowering and fruiting ranged from continuous flower and fruit production during the whole year to one month only (*Tabebuia barbata*). The longest period of flowering in várzea was 12 months (*Salix humboldtiana*), but in igapó only 7 months (*Astrocaryum jauari*). Mean flowering duration was 3.4 ± 2.5 months (n = 22) in várzea, and 2.9 ± 1.2 months (n = 51) in igapó.

Mature fruits were present for 4.9 ± 2.8 months (n = 41) in várzea, with a maximum of 12 months (*Crescentia amazonica*, *Pouteria glomerata*, *Salix humboldtiana*). In igapó, the mean fruiting period was 3.7 ± 1.4 months (n = 54), with a maximum duration of 8 months (*Hevea spruceana*).

Timing of leaf flush

The flush of new leaves in várzea occurred in August in most species. In igapó, most species flushed their leaves in July and August, but many did so also in the rest of the year, such as in October, December, or February, which was not the case in the várzea.

Intraspecific comparisons of phenological events

Eight species from várzea and 12 species from igapó were monitored by different authors in different years. Three species which occur in both várzea and igapó were monitored by different authors. *Eschweilera parviflora* was monitored by the same author (Ferreira, 1998) on different elevations in the flooding gradient of igapó. Intraspecific comparisons in the várzea, or in the igapó, show similarities but not congruence. Whether this is linked to the different years of recording, and thus to climatic and hydrological differences, or to different methodologies of the authors, cannot be differentiated. The same is due for intraspecific comparisons between the two ecosystems. Therefore a further analysis and the interpretation of intraspecific differences is omitted here.

Differences at 'high' and 'low' elevations in the flooding gradient

The duration of the leafless period was longer at high elevations than at low elevations in the várzea, whereas in the igapó it was shorter at high elevations (Figure 2). In várzea, flowering was longer at high elevations, and fruiting was shorter than at low elevations. In igapó it was the opposite: flowering was shorter at high elevations, and fruiting was longer than at low elevations (Figure 2).

Discussion

Deciduousness vs. evergreenness in várzea and igapó

The high number of deciduous tree species in both várzea and igapó (Figure 3) can be explained if deciduousness is advantageous at times of low tree water status: water loss of the trees is reduced by the reduction of the transpiring area through the shedding of leaves (Borchert, 1991). If leaf shedding cannot be afforded, for instance because of low nutrient availability, other protections against water loss can be found, such as sclerophyllous leaves which are typical for evergreen species (Medina, 1983) and are found especially in igapó trees (Prance, 1979). Due to the differences of nutrient status of the two ecosystems, it is surprising that among the documented species in igapó the strategy of deciduousness (26 species) is as common as that of leaf sclerophylly (24 species). Also, some species which were excluded from show deciduous behaviour in some years and evergreen in others, for example *Couepia paraensis*, *Maprounea guinanensis* (Revilla, 1981; Ferreira, 1991), and *Laetia corymbulosa* (Armbrüster, pers. comm.). This makes a classification difficult, as does the fact that many species which here are treated as typical for igapó, according to other authors might occur in várzea as well and vice versa (Prance, 1979; Worbes, 1983; Revilla, 1981, 1991; Ferreira, 1991; Rohwer & Kubitzki, 1992; Amaral *et al.*, 1997; Parolin *et al.*, 1998), and therefore might not show typical strategies expected for the nutrient-rich várzea or the nutrient-poor igapó.

Periodicity of flowering and fruiting

Since long-term studies of several years are lacking completely, and the results presented by various authors are not congruent, little can be said about the periodicity of flowering and fruiting with the present data. Most species have annual rhythms, but some species have supra-annual cycles. *Ceiba pentandra* has flowers and fruits every three years (Gribel *et al.,* 1999). *Aldina latifolia* has two-year cycles (Ferreira, pers. comm.) and no definite ring structures can be found in the wood of this species (Worbes, 1997 p. 241). Also other floodplain species, for example *Sloanea guianensis* in Lago Teiú várzea forest near Tefé, have supra-annual cycles of flowering and fruiting (Ayres, 1993 p. 49). Long-term studies are needed to detect and understand these periodicities.

Differences at 'high' and 'low' elevations along the flooding gradient

Flood duration is linked to the elevation at which a tree grows along the flooding gradient (Junk, 1989) and can determine the timing and duration of flowering and fruiting, as was documented for individuals of *Eschweilera parviflora* growing at different elevations in the flooding gradient (Ferreira, 1998). Trees from upper elevations began to produce flowers several months later and when unflooded (September) compared with trees from lower elevations (May-July). At the community level, in Lago Teiú várzea forest near Tefé, the fruiting peak in a high-lying community ('restinga alta') was a little later than in a low-lying community ('restinga baixa') (Ayres, 1993). Other species, such as *Macrolobium acaciifolium*, did not show intraspecific differences of phenology at different elevations (Schlüter & Furch, 1992).

The species of the present review were grouped according to their occurrence at 'high' (25-28 m asl) or 'low' (21-25 m asl) elevations along the flooding gradient (Ferreira, 1991; Ayres, 1993; Parolin & Ferreira, 1998; Parolin, 2000 c). The duration of flowering and fruiting did not show clear trends and was different in várzea and igapó (Figure 2). There were slightly more deciduous species at low elevations, compared with evergreen species, in both várzea and igapó, whereas at high elevations there were slightly more evergreen species (Figure 4). This might indicate that deciduousness is an adaptation to long periods of flooding, but further data are needed to confirm this statement.

Timing of phenological events

In the analysed species, the timing of leaf shedding and leaf flush, and the duration of the leafless period, were closely related to flooding (Figure 5). In seasonally dry regions like savannas, where many species from the floodplains originate (Kubitzki, 1989), trees shed their leaves and reduce the production of new leaves in a period of dry conditions (Reich & Borchert, 1982; Bullock &

Solis-Magalhaes, 1990; Wright & Cornejo, 1990; Gribel *et al.,* 1999). This pattern is described as a strategy of 'drought-avoidance' (Medina, 1983). In floodplains, the flooding disturbs the root function, i.e. water uptake, and reduces the water status of a tree (Gill, 1970; Kozlowski, 1984; Meyer, 1991; Blom & Voesenek, 1996). In fact, in the Amazonian tree species the leafless period began at highest water levels, and lasted until the end of flooding, or until the terrestrial period in igapó (e.g. until November in *Parkia discolor*, *Sclerolobium hypoleucum* and *Simaba guianensis*). Worbes (1992) found that most tree species had a cambial rest during this period which leads to the formation of annual increment rings. The period of regular growth reductions corresponded to the period of maximum leaf fall. The same observation led Gessner (1968) to the concept of the 'physiological winter' hypothesis, where flooding represents a stress factor for trees like winter in temperate regions, and leaves are shed to cope with the unfavourable environmental conditions. However, the high phenological and physiological activity during the flooded period (Schlüter, 1989; Schlüter *et al.,* 1993; Parolin, 1997; Maia, 1997; Armbrüster, 1999) does not support this statement.

A second peak of leaf shedding can occur in the non-flooded period in October, when precipitation is very low (about 50 mm per month) and leaf fall occurs as a reaction to the rapidly drying soil (Worbes, 1983). Measurements of litter production show the same trends as the phenological observations. In várzea, litter fall has a peak between May and July (high water) which was measured in the years 1981/2 by Adis (see Worbes, 1997), and in 1996 by Wittmann (1997). A second peak was measured in the dry period in November (Worbes, 1997 p. 251). In igapó leaf litter production had a peak between July and August (Adis *et al.,* 1979).

The timing of fruiting is important to guarantee optimization of dispersal, most species of the floodplains having hydrochoric and ichthyochoric dispersal syndromes (Ziburski, 1991). The close relationship between the period of fruiting and water level is emphasized by the adaptations for floating which most fruits and seeds display in this environment (Kubitzki & Ziburski, 1994; Williamson *et al.,* 1999). Some seeds are dormant as long as they are covered by water (Ziburski, 1991), but many seeds lack dormancy, and a precise timing of diaspore release during inundation is important for the dispersal and germination immediately after the water retreats. The period between the floods sometimes lasts only a few weeks, and some seedlings which do not tolerate complete flooding (e.g. *Senna reticulata* in várzea, Parolin, 1998, and *Aldina latifolia, Mora paraensis, Swartzia polyphylla* in igapó, Ziburski, 1991), apparently depend on an efficiently timed release for establishment and survival. Fruiting in várzea occurs later than in igapó (Figure 5), perhaps as an adaptation to the strong sediment deposition in várzea (Ziburski, 1991): this permits the colonization of freshly deposited sediments without the danger of burial, as shown for *Vitex cymosa* and *Cecropia latiloba* (Kubitzki & Ziburski, 1994).

Triggers for phenological events

The variety of abiotic factors such as temperature, precipitation and air humidity trigger phenological events in tropical forests (Alvim & Alvim, 1978; Bullock & Solis-Magalhaes, 1990; Wright & Cornejo, 1990; Seghierei *et al.*, 1995). In floodplains, a main additional trigger is the periodical flooding, such as in East African riverine forests, flowering is triggered by the dry conditions at low river levels (Kinnaird, 1992). In the igapó forest of Tarumã-Mirim near Manaus, the flowering and fruiting of more than half of 29 tree species was significantly correlated with changes in the river level (Ferreira, 1991). However, precipitation was also significantly correlated with the phenological events of these species, indicating that several factors act together. As mentioned earlier, flooding acted as a trigger for phenological events in *Eschweilera parviflora* growing at different elevations along the flooding gradient (Ferreira, 1998), whereas Schlüter & Furch (1992) did not find intraspecific differences of phenology in *Macrolobium acaciifolium* at different elevations. The timing of flowering and fruiting in this species was independent of the beginning of the flood and its duration. Other triggers may act here, such as inherent genetic factors linked to the ecogeographical distribution and origin of the species. Some species are widespread also in non-flooded upland forests (e.g. *Ormosia excelsa, Hevea brasiliensis*, and *Triplaris weigeltiana*): their phenology is independent of flooding periodicity and is more linked to precipitation (Kubitzki & Ziburski, 1994).

To what extent genetically differentiated populations have differing phenologies and are specifically adapted to particular flooding conditions is not known. The plasticity of the genotypes might be tested with transplantation experiments, where seedlings from trees in upper elevations are transplanted to lower levels and vice-versa. In five *Senna reticulata* trees which were transplanted to the non-flooded terra firme in Manaus, the production of flowers and fruits occurred at the same time as in individuals growing in the várzea (Parolin, 1997), suggesting that precipitation and other climatical parameters are the main trigger for flowering and fruiting of this species. Leaf production, on the other hand, remained constantly high in the *Senna reticulata* trees grown in terra firme which did not suffer water shortage or flooding, while at the same time in várzea, with flooding, leaf number and leaf area were strongly reduced (Parolin, 1997). This indicates that in *Senna reticulata* the change of water status caused by flooding is the trigger responsible for leaf shedding and production. Two identical flooding experiments with seedlings of six species from várzea, performed at different times of the year, showed that leaf phenology was linked to the flood condition, and not to precipitation or inherent cycles (Parolin 2001). On the other hand, *Macrolobium acaciifolium* which was transplanted to terra firme was deciduous at the same time as in the várzea (Schlüter & Furch, 1992) showing that for this species the trigger is not flooding. These experiments point out that different species of the floodplains react to different triggers. What the triggers are, and how they interact, is not yet understood.

Comparison with the statements

The data summarized in this review supports some of the statements and hypotheses found in the literature, but not all:

- 'Leaves are shed mainly in the flooded period' (Worbes, 1983; Revilla, 1990; Ayres, 1993). This statement is supported by the data (Figure 5), especially concerning species in the várzea, where most species shed their leaves in June and July, when the river levels are at their peak. In the species from igapó, the period of leaf shedding is more towards the end of the flooded period and the beginning of the terrestrial period (September and October), which is congruent with the statements of Revilla (1981) and Worbes (1997) that in the igapó a maximum of shedding occurs in the end of the flooded period.
- 'New leaves are flushed in the periods when the water is receding (August – September) or onset of rains (November – December), in várzea also when the trees are still flooded' (Worbes, 1997). This statement is supported by the data (Figure 5): one can infer from the decrease in leaf shedding that the species from várzea flushed new leaves in August and September, towards the end of the flooded period, whereas in igapó many leaves were flushed at high water (July, August), but the peak of leaf flush was in November and December, in the non-flooded period.
- 'Flowering occurs mainly at the beginning of the flooded period' (Worbes, 1997). This statement is not supported by the data (Figure 5): in várzea, there is a peak of flowering in May and June, i.e. at highest water levels. In igapó many trees had flowers in February when the flood begins, but there was a rapid decrease of flowering in March and April.
- 'Fruits are produced mainly in the flooded period' (Adis *et al.,* 1979; Worbes, 1986; Ziburski, 1990; Ayres, 1993). This is obviously supported in both várzea and igapó, although the peak of fruiting in várzea (June-July) occurred later than in igapó (February-April; Figure 5).
- 'Várzea forests are mainly deciduous, while in igapó evergreen species prevail' (Klinge *et al.*, 1983; Worbes, 1983; Revilla, 1990). This is clearly not the case: in várzea there were even slightly more evergreen than deciduous species, and in igapó more deciduous than evergreen species. An explanation for the origin of the statement might be found in the timing of the deciduous period. The clear peak of deciduousness in várzea in June/July (Figure 5) might give the observer the impression that the forest is deciduous. In igapó the period of deciduousness is less synchronized among the species and more distributed over the year, therefore a leafless period is not as evident.
- 'Flooding operates as a regulator for the timing of phenological events' ('flood pulse concept', Junk *et al.,* 1989). This statement is difficult to test, since there are no long-term studies which compare annual cycles and allow the determination of triggers. Only few studies (Ferreira, 1991;

Schlüter & Furch, 1992; Ferreira, 1998; Ayres, 1993) compared species at different elevations in the flooding gradient, but they also do not give clear insights into the role of flooding as trigger.

Conclusions

This study tries to give an overview of the phenology of trees in Central Amazonian floodplains. The main trends that were found in the analysed species show that most phenological changes occurred during the flooded period, when the tree roots and stems were flooded. However, with the present knowledge, it is not possible to answer the question which triggers are responsible for the phenological events in Amazonian floodplains. Long-term studies are needed, including intraspecific comparisons of trees in different ecosystems, i.e. in várzea, igapó, and even terra firme. Comparisons of trees on different elevations in the flooding gradient, and transplantation experiments might give the key to the role that different triggers play for the tree species in the floodplains.

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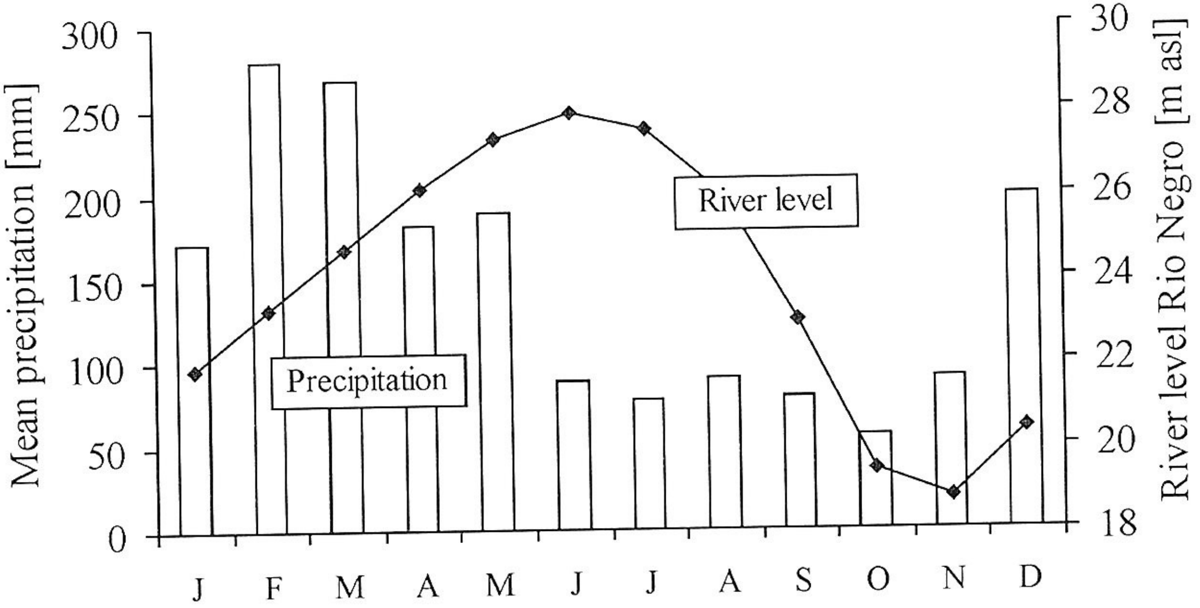


Figure 1 – Mean monthly precipitation [mm], measured at the Ilha de Marchantaria, Manaus, 1991 – 1995; mean monthly water level of the Negro River [m above sea-level], measured at the Capitania dos Portos, Manaus, 1987 – 1997.

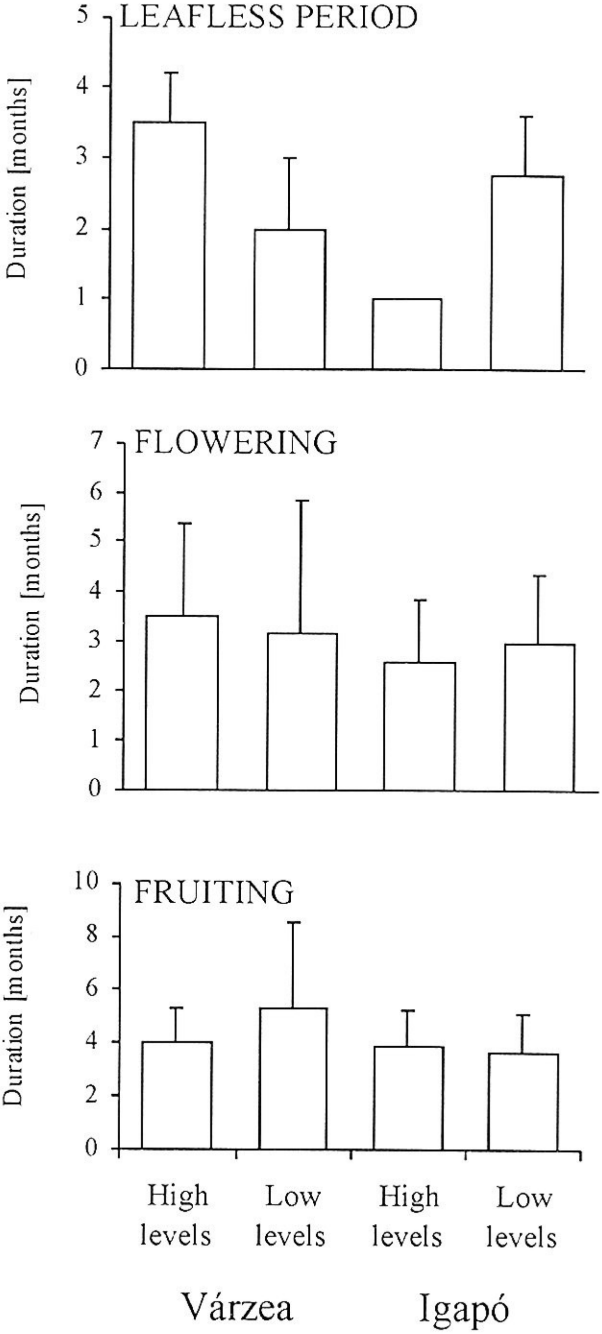


Figure 2 – Duration of the leafless period, flowering and fruiting in várzea and igapó at high (25-28 m asl) and low (21-25 m asl) elevations in the flooding gradient.

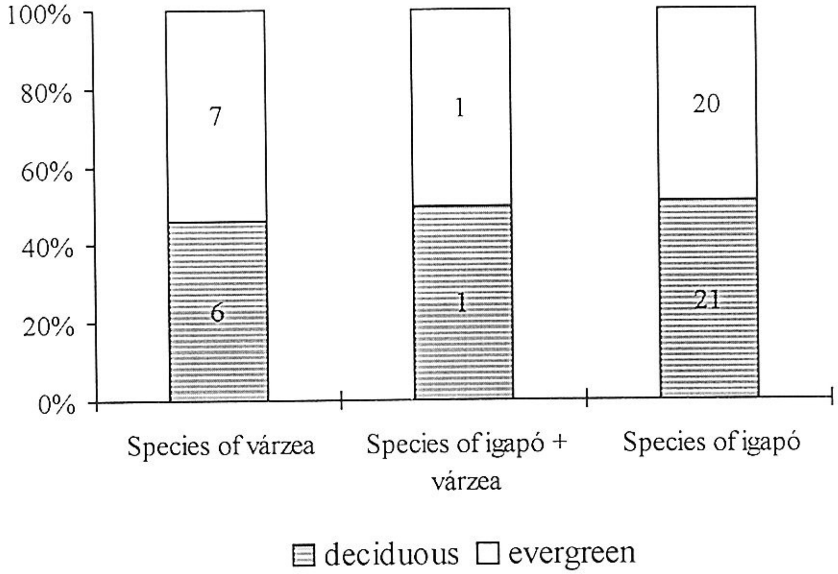


Figure 3 – Percentage of evergreen and deciduous species among the chosen species (with number of species), based on Table 2.

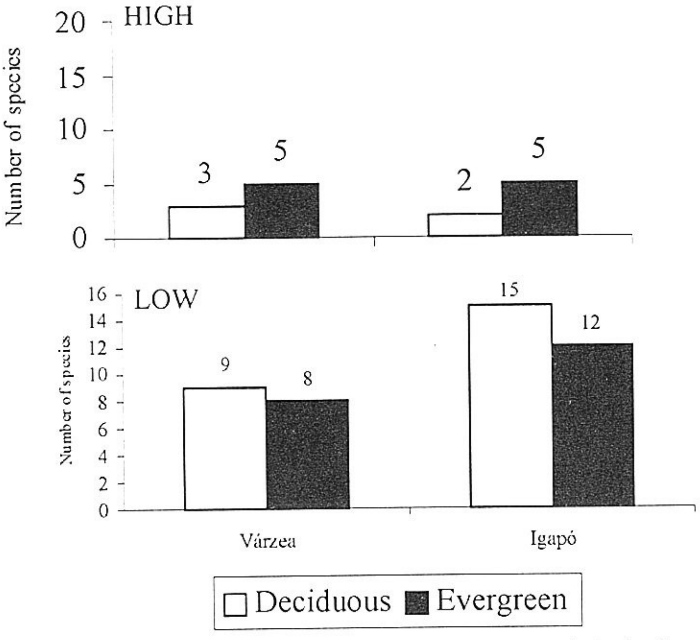


Figure 4 – Number of deciduous and evergreen species at high and low elevations in the flooding gradient (high = 25-28 m asl, low = 21-25 m asl) in várzea and igapó.

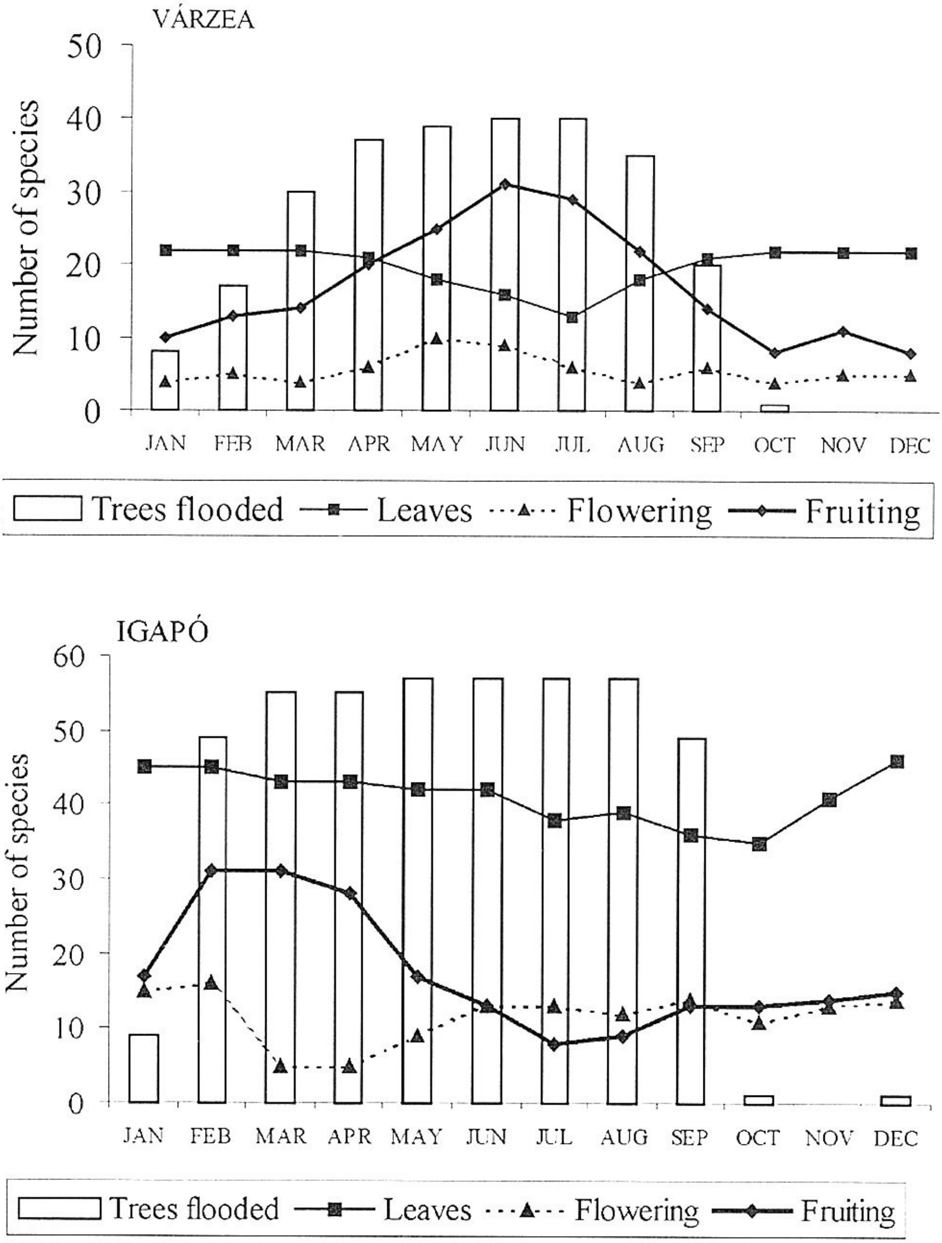


Figure 5 – Summary of species with leaf loss / flush, flowers, and fruits (calculated from data in Table 3) in várzea (A) and igapó (B).

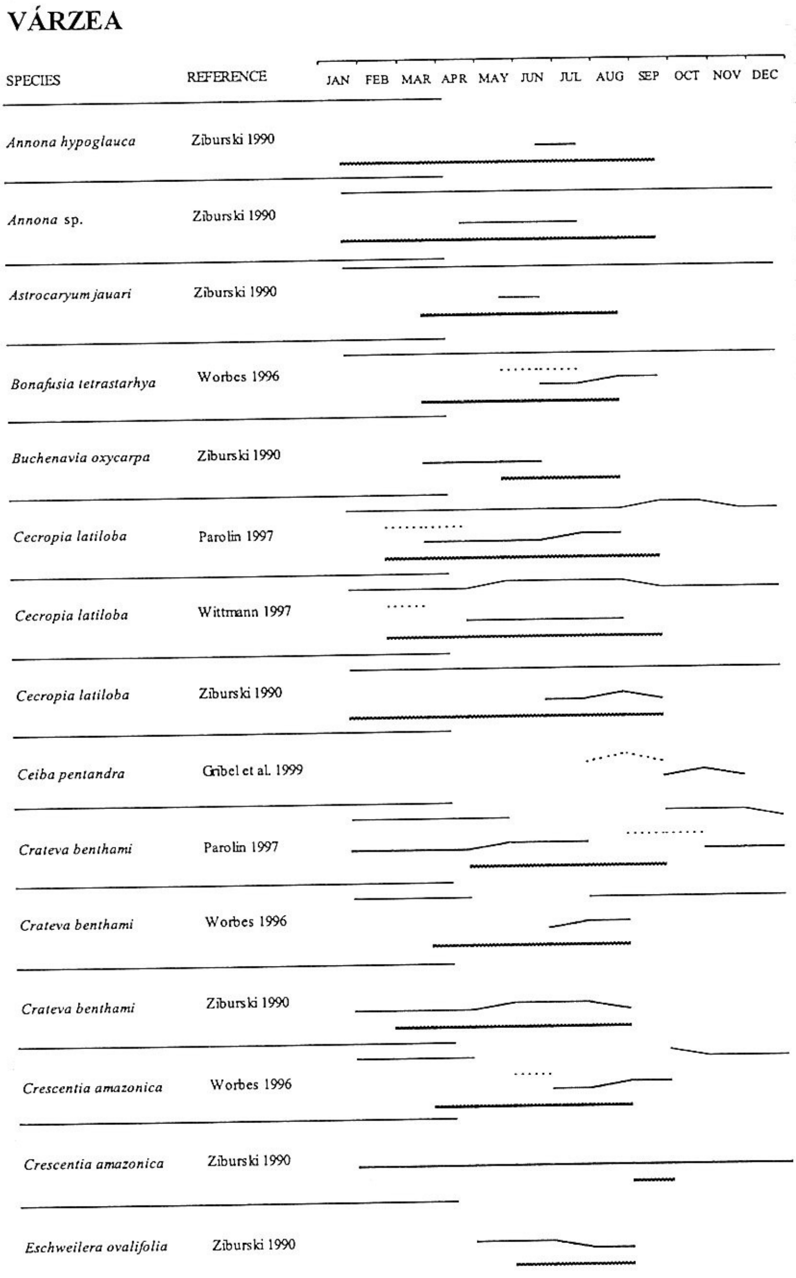
Table 1: Studies with phenological observations considered in the present review, in chronological order, with study sites, species and number of individuals per species (n).

Author, year of publication	**Study sites**	**Species** **n per species**	**Duration of phenol. recordings**
Revilla, 1981	Igapó: Praia Grande / Rio Negro	37 species n = 3	20 months (4/1978-11/1979)
Piedade, 1985	Igapó: Rio Negro	Astrocaryum jauari	12 months (1981)
Ziburski, 1990	Várzea: Marchantaria Igapó: Tarumã Mirim, Praia Grande, Rio Negro	18 species in várzea 15 species in igapó	16 months (1/1988-4/1989)
Ferreira, 1991	Igapó: Tarumã Mirim	30 species n = 15-19	12 months (5/1989-5/1990)
Worbes, 1996	Várzea: Marchantaria	7 species	12 months? (1981/82)
Parolin, 1997	Várzea: Costa do Catalão, Marchantaria.	6 species; n = 5	15 months (4/1994-6/1995)
Maia, 1997	Igapó: Tarumã Mirim	Eschweilera tenuifolia, Hevea spruceana n = 15	18 months (7/1993-12/1994)
Wittmann, 1997	Várzea: Marchantaria	6 species n = 2	4 months (6/1996-9/1996)
Ferreira, 1998	Igapó: Tarumã Mirim	Eschweilera parviflora n = 24	12 months (5/89-5/90)
Oliveira, 1998	Várzea: Marchantaria, Rio Solimões	*Salix humboldtiana* (= *S. martiana*) n = 75	14 months (4/1993-5/1994)
Armbrüster, 1999	Várzea: Marchantaria	Laetia corymbulosa, Pouteria glomerata n = 1	11 months (4/1997-6/1998)
Gribel *et al.*, 1999	Várzea: Costa do Catalão	Ceiba pentandra n = 12	5 years (1992-1997)

Table 2 – Species considered for the present review, with vegetative phenology (deciduous / evergreen), elevation at which they mainly grow in the flooding gradient (high = 25-28 m asl, low = 18-25 m asl), and floodplain type where the species' phenology was studied (data from references in Table 1, and additional data from Worbes 1983, Kahn & Henderson 1998, and pers. obs.); in alphabetical order. D deciduous, E evergreen, L low, H high, – no data, I igapó, V várzea.

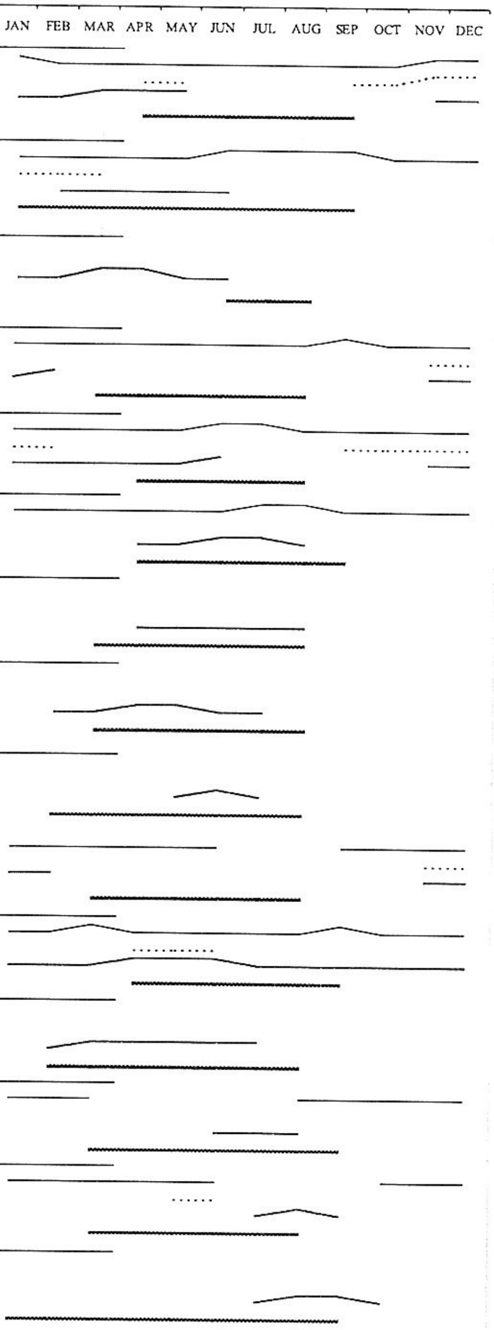
Species	Family	Leaf periodicity	Elevation in flood gradient	Floodplain type	Reference
Acosmium nitens	Papilionaceae	D	L?	I	Revilla 1981
Alchornea castaneifolia	Euphorbiaceae	D	L	V	Parolin pers. obs.
Alchornea schomburgkiana	Euphorbiaceae	D	L?	I	Revilla 1981
Aldina latifolia	Papilionaceae	D	H	I	Revilla 1981, Ziburski 1990, Ferreira 1991
Aniba affinis	Lauraceae	E?	-	I	Ziburski 1990
Annona hypoglauca	Annonaceae	-	L	V	Ziburski 1990
Annona sp.	Annonaceae	-	-	V	Ziburski 1990
Astrocaryum jauari	Arecaeceae	E	L	V - I	Piedade 1985, Ziburski 1990
Banara guianensis	Flacourtiaceae	E	L	I	Ferreira 1991
Bonafusia tetrastarhya	Apocynaceae	E	L	V	Worbes 1996
Buchenavia ochnopnuma	Combretaceae	D	L	I	Revilla 1981
Buchenavia oxycarpa	Combretaceae	D?	L?	V	Ziburski 1990
Buchenavia suaveolens	Combretaceae	D	L?	I	Revilla 1981
Burdachia prismatocarpa	Malpighiaceae	D	-	I	Revilla 1981
Byrsonima chrysophylla	Malpighiaceae	E	-	I	Revilla 1981
Campsiandra comosa	Caesalpiniaceae	D	L	I	Revilla 1981, Ziburski 1990
Caryocar microcarpum	Caryocaraceae	E	L	I	Ferreira 1991
Cecropia latiloba	Cecropiaceae	E	L	V	Ziburski 1990, Parolin 1997, Wittmann 1997
Cecropia membranacea	Cecropiaceae	E	H	V	Parolin pers. obs.
Ceiba pentandra	Bombacaceae	D	H	V	Gribel et al. 1999
Clitoria amazonum	Papilionaceae	D	L	V - I	Parolin pers. obs.
Couepia paraensis	Chrysobalanaceae	D-E	L	I	Revilla 1981, Ferreira 1991
Crateva benthami	Capparidaceae	D	L	V	Ziburski 1990, Worbes 1996, Parolin 1997
Crescentia amazonica	Bignoniaceae	D	L	V	Ziburski 1990, Worbes 1996
Crudia amazonica	Caesalpiniaceae	D	L	I	Ziburski 1990
Elaeoluma glabrescens	Sapotaceae	E	-	V	Worbes 1983
Elvasia calophyllum	Ochnaceae	D	L	I	Revilla 1981
Eschweilera coriacea	Lecythidaceae	D	-	I	Revilla 1981
Eschweilera ovalifolia	Lecythidaceae	E?	L	V	Ziburski 1990
Eschweilera parviflora	Lecythidaceae	E?	H + L	I	Ferreira 1998
Eschweilera tenuifolia	Lecythidaceae	E	L	I	Ziburski 1990, Maia 1997
Eugenia cachoerensis	Myrtaceae	E	-	I	Revilla 1981
Eugenia inundata	Myrtaceae	D	L	V – I	Parolin pers. obs.
Eugenia longiracemosa	Myrtaceae	D	-	I	Revilla 1981
Eugenia tefensis	Myrtaceae	D	-	I	Revilla 1981
Euterpe precatoria	Arecaceae	E	L?	V	Kahn & Henderson 1998
Genipa spruceana	Rubiaceae	D	L	V	Parolin pers. obs.
Hevea spruceana	Euphorbiaceae	E	L	I	Maia 1997
Himatanthus attenuata	Apocynaceae	D	L?	I	Revilla 1981
Humiria balsamifera	Humiriaceae	E	H?	I	Revilla 1981
Ilex inundata	Aquifoliaceae	E	L	I	Parolin pers. obs.
Ilex sp.	Aquifoliaceae	D	L?	V	Worbes 1983
Laetia corymbulosa	Flacourtiaceae	E	H	V	Ziburski 1990, Wittmann 1997, Armbrüster 1999
Laetia suaveolens	Flacourtiaceae	D	L	I	Revilla 1981, Ziburski 1990
Leopoldinia pulchra	Arecaeceae	E	L	I	Revilla 1981
Licania apetala	Chrysobalanaceae	D	L	I	Revilla 1981
Macrolobium acaciifolium	Caesalpiniaceae	E	H	V - I	Ziburski 1990, Worbes 1996
Macrolobium multijugum	Caesalpiniaceae	D	L	I	Revilla 1981, Ziburski 1990
Maprounea guianensis	Euphorbiaceae	D-E	L	I	Revilla 1981, Ferreira 1991
Mollia speciosa	Tiliaceae	E	H	I	Revilla 1981
Mora paraensis	Caesalpiniaceae	D	H	I	Ziburski 1990
Myrciaria dubia	Myrtaceae	D	L	I	Revilla 1981, Ziburski 1990
Nectandra amazonum	Lauraceae	E	L	V	Ziburski 1990, Parolin 1997, Wittmann 1997

Table 3 – Phenology of tree species from Central Amazonian floodplains. – leaves present (line higher = flush of new leaves), – flowers, – fruits (line higher = mature fruits), – flooded period. Study site and period see Table 1.



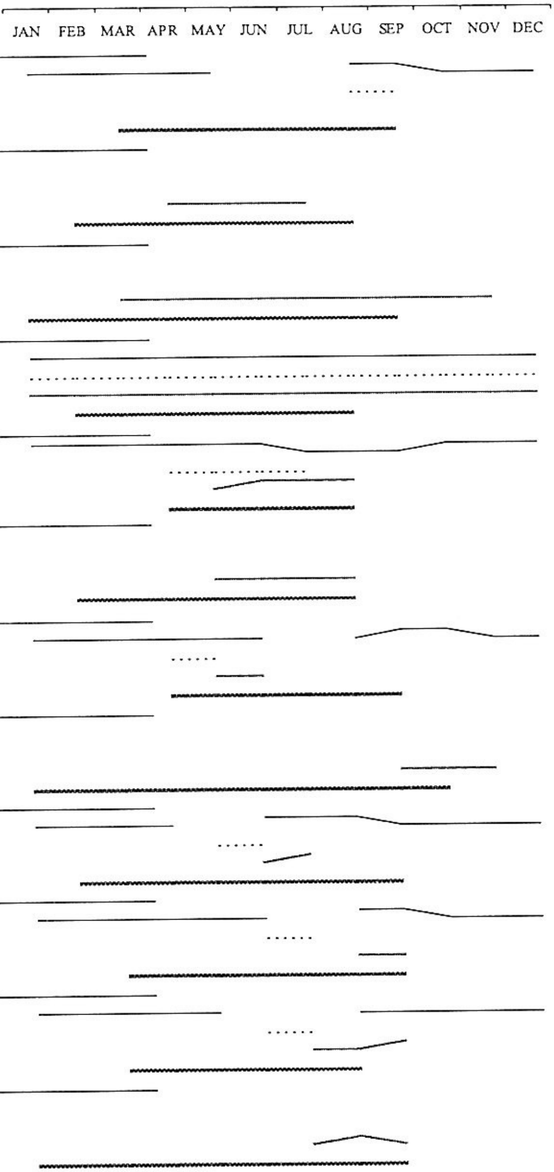
VÁRZEA

SPECIES	REFERENCE
Laetia corymbulosa	Armbrüster 1999
Laetia corymbulosa	Wittmann 1997
Laetia corymbulosa	Ziburski 1990
Macrolobium acaciifolium	Worbes 1996
Nectandra amazonum	Parolin 1997
Nectandra amazonum	Wittmann 1997
Nectandra amazonum	Ziburski 1990
Neolabatia cuprea	Ziburski 1990
Pithecellobium inaequale	Ziburski 1990
Piranhea trifoliata	Worbes 1996
Pouteria glomerata	Armbrüster 1999
Pouteria stylosa	Ziburski 1990
Pseudobombax munguba	Wittmann 1997
Pseudobombax munguba	Worbes 1996
Pseudobombax munguba	Ziburski 1990



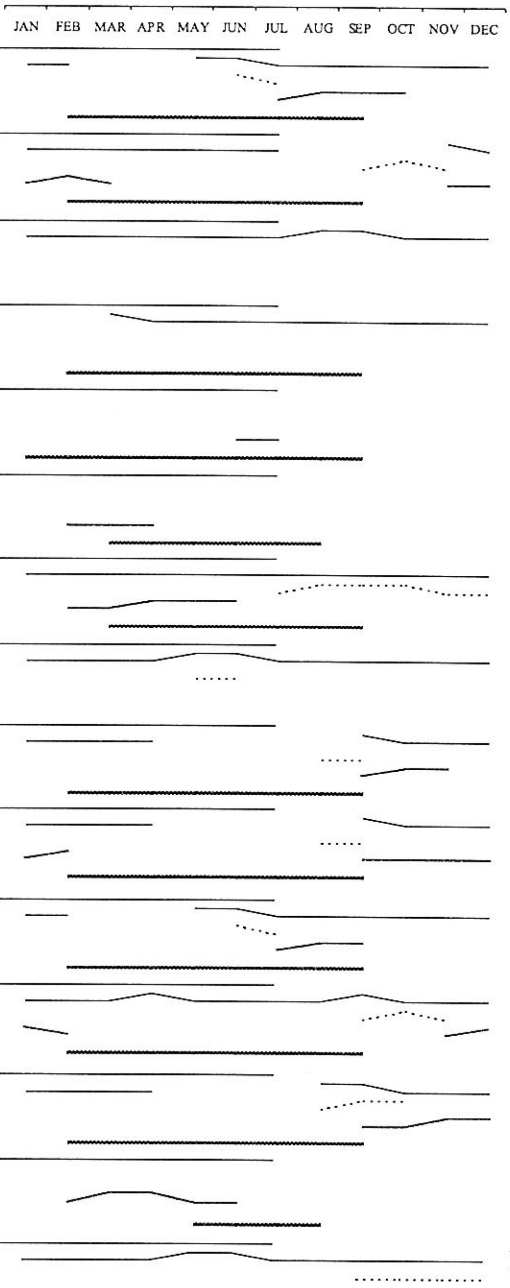
VÁRZEA

SPECIES	REFERENCE
Psidium acutangulum	Wittmann 1997
Psidium acutangulum	Ziburski 1990
Rheedia brasiliensis	Ziburski 1990
Salix humboldtiana	Oliveira 1998
Senna reticulata	Parolin 1997
Sorocea duckei	Ziburski 1990
Tabebuia barbata	Parolin 1997
Triplaris weigeltiana	Ziburski 1990
Vitex cymosa	Parolin 1997
Vitex cymosa	Wittmann 1997
Vitex cymosa	Worbes 1996
Vitex cymosa	Ziburski 1990



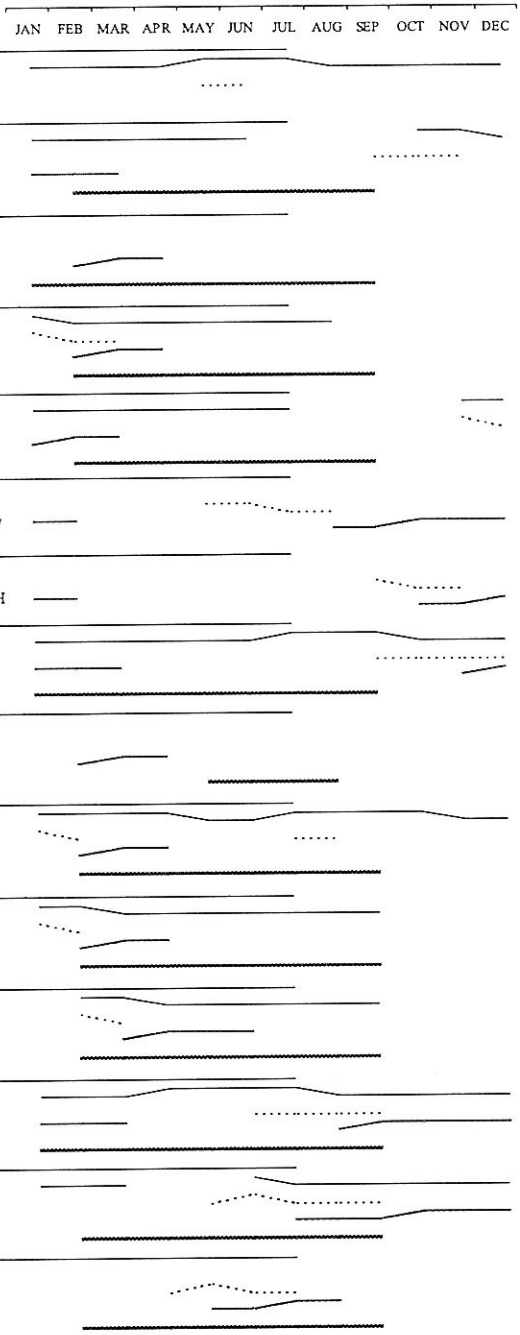
IGAPÓ

SPECIES	REFERENCE
Acosmium nitens	Revilla 1981
Alchornea schomburgkiana	Revilla 1981
Aldina latifolia	Ferreira 1991
Aldina latifolia	Revilla 1981
Aldina latifolia	Ziburski 1990
Aniba affinis	Ziburski 1990
Astrocaryum jauari	Piedade 1985
Banara guianensis	Ferreira 1991
Buchenavia ochnopnuma	Revilla 1981
Buchenavia suaveolens	Revilla 1981
Burdachia prismatocarpa	Revilla 1981
Byrsonima chrysophylla	Revilla 1981
Campsiandra comosa	Revilla 1981
Campsiandra comosa	Ziburski 1990
Caryocar microcarpum	Ferreira 1991



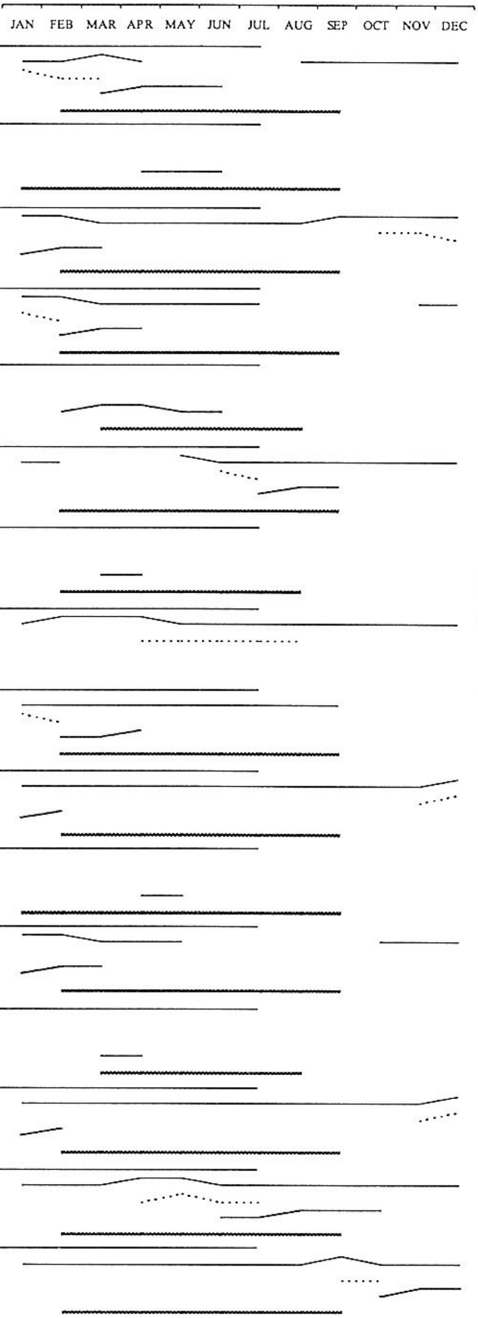
IGAPÓ

SPECIES	REFERENCE
Couepia paraensis	Ferreira 1991
Couepia paraensis	Revilla 1981
Crudia amazonica	Ziburski 1990
Elvasia calophyllum	Revilla 1981
Eschweilera coriacea	Revilla 1981
Eschweilera parviflora	Ferreira 1998: LOW
Eschweilera parviflora	Ferreira 1998: HIGH
Eschweilera tenuifolia	Maia 1997
Eschweilera tenuifolia	Ziburski 1990
Eugenia cachoerensis	Revilla 1981
Eugenia longiracemosa	Revilla 1981
Eugenia tefensis	Revilla 1981
Hevea spruceana	Maia 1997
Himatanthus attenuata	Revilla 1981
Humiria balsamifera	Revilla 1981



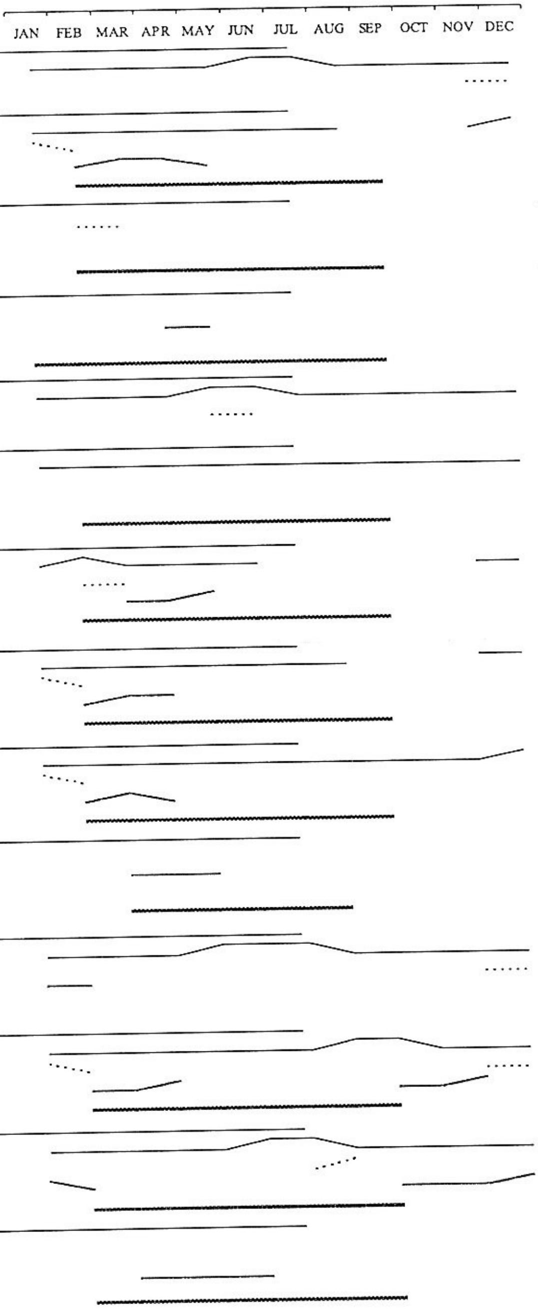
IGAPÓ

SPECIES	REFERENCE
Laetia suaveolens	Revilla 1981
Laetia suaveolens	Ziburski 1990
Leopoldinia pulchra	Revilla 1981
Licania apetala	Revilla 1981
Macrolobium acaciifolium	Ziburski 1990
Macrolobium multijugum	Revilla 1981
Macrolobium multijugum	Ziburski 1990
Maprounea guianensis	Ferreira 1991
Maprounea guianensis	Revilla 1981
Mollia speciosa	Revilla 1981
Mora paraensis	Ziburski 1990
Myrciaria dubia	Revilla 1981
Myrciaria dubia	Ziburski 1990
Ormosia excelsa	Ziburski 1990
Ouratea spruceana	Revilla 1981
Palicourea nitidella	Revilla 1981



IGAPÓ

SPECIES	REFERENCE
Parkia auriculata	Ferreira 1991
Parkia discolor	Revilla 1981
Pithecellobium adiantifolium	Revilla 1981
Pithecellobium adiantifolium	Ziburski 1990
Pithecellobium amplissimum	Ferreira 1991
Rheedia floribunda	Revilla 1981
Sclerolobium hypoleucum	Revilla 1981
Simaba guianensis	Revilla 1981
Simaba obovata	Revilla 1981
Simaba orinocensis	Ziburski 1990
Swartzia argentea	Ferreira 1991
Swartzia laevicarpa	Revilla 1981
Swartzia polyphylla	Revilla 1981
Swartzia polyphylla	Ziburski 1990



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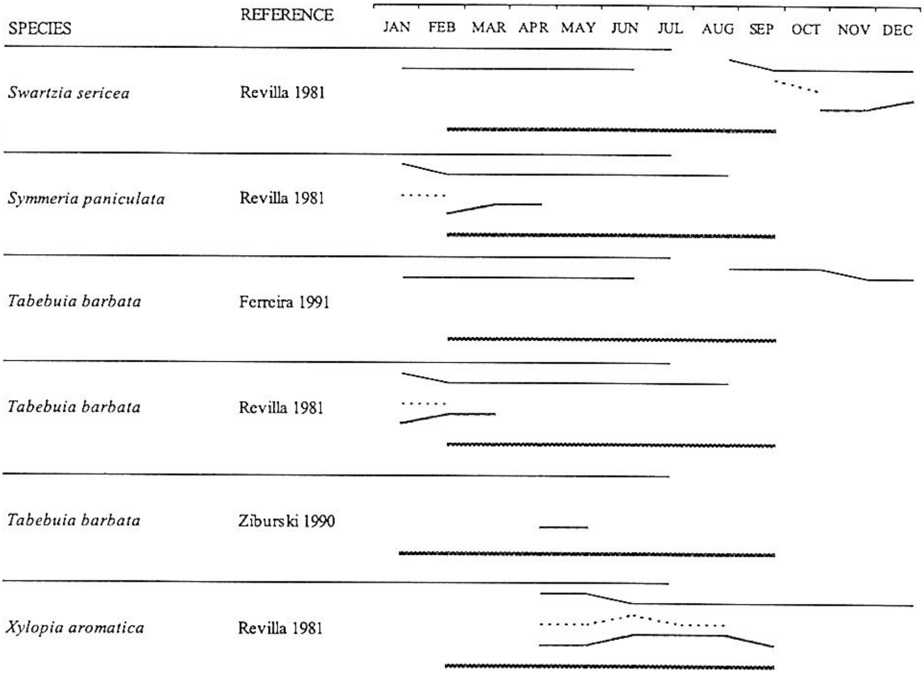
SPECIES
REFERENCE
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
Swartzia sericea
Revilla 1981
Symmeria paniculata
Revilla 1981
Tabebuia barbata
Ferreira 1991
Tabebuia barbata
Revilla 1981
Tabebuia barbata
Ziburski 1990
Xylopia aromatica
Revilla 1981