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TREE PHENOLOGY IN CENTRAL AMAZONIAN FLOODPLAIN FORESTS: EFFECTS OF WATER LEVEL FLUCTUATION AND PRECIPITATION AT COMMUNITY AND POPULATION LEVEL

Leandro Valle Ferreira¹
Pia Parolin²

Abstract

The large rivers in central Amazonia show annual water level fluctuations of about 14 m. The life cycles of the trees growing in this environment are closely linked to the periodicity of the hydrological regime, but there are differences depending on tree position in the flooding gradient. To study the effect of flooding and precipitation on tree reproductive phenology at community and population level, we surveyed the phenological events of 29 species in a black water floodplain forest in Central Amazonia, Brazil. At community level, peak of number of trees with flowers occurred in the falling river phase and dry season, while the peak of fruiting occurred in the period of rising river level and rainy season. At population level, 72% of the species had their flowering periods significantly related with the variation of water level or precipitation, and 85% had their fruiting periods significantly related with the variation of water level or precipitation. In both cases, the trigger of reproduction was more correlated with precipitation level than with the variation of the water level. For some species there were individual variations of the onset of flowering and fruiting, and of mean flowering or fruiting periods in relation to tree position in the flooding gradient. This can indicate that the beginning of flooding – as related to the position in the flooding gradient – is one very strong trigger to explain variation.

Key words: Amazonia, floodplain forest, flooding, flowering, fruiting, tree phenology

Introduction

Amazonian floodplains are subjected to annual water level fluctuations of up to 14 m, which result in annual flood periods of up to 210 days in the forested wetlands (Junk, 1989). In these forests, duration and predictability of the river level fluctuation and flooding have strong effects on the reproductive phenology of trees: regeneration strategies seem to be responses to variations in habitat seasonality and

1 Museu Paraense Emílio Goeldi –MPEG/CCTE, Av. Perimetral 1901 – Bairro Terra Firme - Belém-Brasil - CEP: 66077-530, email: lvalle@museu-goeldi.br

2 Max-Planck-Institute for Limnology, Tropical Ecology, P.O.Box 165, 24302 Plön, Germany, e-mail: piaparolin@gmx.de

predictability (Scarano, 1998). Similar to the hypothesis formulated by Janzen (1967) in relation to the dry season in lowland Central America, trees in Amazonian floodplains appear to have evolved the timing of their flowering and fruiting period to maximize vegetative competitive ability of individuals, and to maximize use of pollinating and dispersal agents in relation to the flooding periodicity. In fact, many tree species have evolved hydrochoric or ichthyochoric dispersal mechanisms (Ayres, 1993; Gottsberger, 1978; Goulding, 1983; Kubitzki & Ziburski, 1994; Moegenburg, 2002). Fruit maturation occurs mainly at high water levels, when water and fish enhance seed dispersal, but the onset of flowering and fruiting may vary between species and along the flooding gradient. Several autecological, ecophysiological and phenological studies have been performed in Amazonian floodplain forests (Ayres, 1993; Ferreira, 1998; Kubitzki & Ziburski, 1994; Parolin *et al.*, 2002; Piedade, 1985; Schöngart *et al.*, 2002; Williamson *et al.*, 1999; Williamson & Costa, 2000; Wittmann *et al.*, 2006; Ziburski, 1991, 2002). These studies report that – at community level – tree flowering and fruiting periods are related to the fluctuation of river level, with peak flowering in the phase of falling to lowest river levels, and peak fruiting in the phase of rising river levels.

In Central Amazonian floodplains, in only one case (Ayres, 1993) the effect of river level fluctuation and precipitation was analysed over tree population, and showed the same results of the community levels of the formerly mentioned studies.

The synchronization of flowering and fruiting with river levels at the community level are expected patterns for this environment, but none of these studies considered the variation of phenology at population level.

The present study aims at analysing the different influence of river level fluctuation and precipitation on the reproductive phenology of Amazonian floodplain trees differentiating between community and population levels to show that the first approach can be biased and decrease the natural variation which can be shown by the population level.

Methods

Study area. We conducted this study in a black water floodplain forest (seasonal igapó, Prance, 1979) on the lower course of the Rio Tarumã-Mirim, on the left bank of Rio Negro (3° 02'S; 60° 17'W), 20 km Northeast of Manaus, Brazil. The climate of the area is hot and humid (Radambrasil, 1978). Mean monthly temperature ranges from 26.3° to 27.2°C, and total annual precipitation ranges from 1800 to 2300 mm. Rain is irregularly distributed throughout the year, with a dry season between June and September, and a rainy season from December to May (Figure 1 + 2).

Variation in river level at the study area is markedly seasonal, with a mean annual amplitude of 14m. The rising period occurs between late December and early July, while the receding period occurs from the end of July to early December (Ferreira, 1991) (Figure 1 + 2).

The study area is situated between 21 and 28 m above sea level (asl)

resulting in annual inundations of 6 meters at the peak of the rising period in June, and a mean flooding period varying between 0.5 and 8.7 months per year (Adis, 1984). River level data for Rio Tarumã-Mirim were calculated based on the maximum river level measured in 1989 in the Rio Negro at the Manaus harbor. Hydrological data collected by Schmidt (1976) in the Rio Solimões, 60 km from Manaus, showed only a few centimeters difference compared to those recorded in Manaus harbor. We assume that river level differences between Rio Tarumã-Mirim and Rio Negro in Manaus were negligible. To calculate the mean flooding period for each tree, we used the data from Junk (1989) who determined the relation between river level and the duration of flooding period of the Rio Negro over the last 80 years. For each tree of the study plot, a measurement of the previous year's watermark on the stem was taken to calculate individual flooding height and duration.

Data collection. Reproductive phenology was monitored monthly on 468 tagged trees with DHB = 5 cm belonging to 29 species (Table 1). The species were selected according to their abundance on the different river levels along the flooding gradient of the study area (Ferreira, 1991). The monitored reproductive characteristics were onset and duration of flowering (buds and flowers) and fruiting (unripe and ripe fruits). Flowering and fruiting periods were defined in this study as the interval between the appearance of the first and the last bud, flower or fruit on a tree. The 29 species were divided in two groups, according to their distribution along the flooding gradient of the study area: group L consisted of 14 species situated in lower region between 21 and 24.9 m asl and group H consisted of 15 species in higher region situated between 25 and 28 m asl (Table 1).

Results

The peak of the flowering period occurred from July to September 1989, which corresponded with the beginning of the receding river phase (Fig. 1) and middle of the season with low precipitation (Fig. 2).

The fruiting period rose from a low number of individuals in August to a peak of individuals in March and April, and declined from April to August (Fig. 1, 2).

The number of trees in flower was positively correlated with the variation of the river level, ($r^2=0.35$, $F_{[1,11]}=5.91$; $P<0.05$, $n=11$, Fig. 3), and negatively correlated with precipitation ($r^2 = -0.67$, $F_{[1,11]}=22.01$; $P<0.001$, $n=11$, Fig. 4).

The number of trees in fruit was not correlated with the variation of the river level ($r^2=0.16$, $F_{[1,11]}=2.15$; $P\geq 0.05$, $n=11$, Fig. 5), and was positively correlated with mean precipitation ($r^2 = 0.91$, $F_{[1,11]}=112.64$; $P<0.0001$, $n=11$, Fig. 6).

Of the 29 species, 8 species (27%) had their flowering periods significantly correlated to the variation of water level, and 17 species (59%) to the variation of precipitation. The fruiting period was significantly correlated with variation of water level in 17 species (55%) and to precipitation in 16 species (55%) (Table 2).

Some species (*Acmanthera latifolia*, *Aldina latifolia*, *Caryocar microcarpum*, *Parkia discolor*, *Tabebuia barbata* and *Talisia elephantiae*) had their flowering period from November 89 to May 90, differing from the community pattern with flowering

peaks in August 89 (see Appendix). Other species (*Erisma calcaratum*, *Eschweilera parvifolia*, *Hevea spruceana*, *Swartzia polyphylla*, and *Virola elongata*) had their fruiting period concentrated between September and January thus differing from the community pattern which was concentrated between March and April (see Appendix).

Of the 29 species of this study, five species (*Acmanthera latifolia*, *Aspidosperma nitidum*, *Mabea nitida*, *Pentaclethra macroloba* and *Virola elongata*) showed individual variation in mean flowering periods in relation to the position of the trees along the flooding gradient. Three species (*Albizia marginata*, *Erisma calcaratum* and *Laetia sauveolens*) showed individual variations in mean fruiting period. Two other species (*Eschweilera parvifolia* and *Parkia discolor*) had individual variation in both mean flowering and fruiting period (Table 3).

Three species had individual variation in the beginning of the flowering period in relation to tree position along the flood gradient, *Aspidosperma nitidum* ($X^2=9.55$, $P<0.001$), *Mabea nitida* ($X^2=3.82$ $P<0.05$) and *Pentaclethra macroloba* ($X^2=5.92$, $P<0.01$) while two species had individual variation in the beginning of the fruiting period, *Laetia sauveolens* ($X^2=4.29$ $P<0.05$) and *Albizia marginata* ($X^2=4.95$, $P<0.05$).

Two species showed individual variation in both the beginning of the flowering and fruiting periods, *Eschweilera parvifolia* ($X^2=18.0$ and $X^2=18.0$, $P<0.001$, respectively) and *Virola elongata* ($X^2=4.26$ and $X^2=4.26$, $P<0.05$, respectively).

Discussion

Duration and predictability of the flood cycle in tropical floodplain forests have a strong impact on reproductive phenology (Ayres, 1993; Kubitzki & Ziburski, 1994; Piedade, 1985; Revilla, 1981). However, this impact is variable, showing different patterns when examined at community and population levels.

At the community level, the flowering period predominantly occurred during the phase of receding water level, and the fruiting period occurred during the phase of rising water, showing that periodic changes in flowering and fruiting are not attributed to endogenous control but to changes in external conditions in the analysed species (Alvim & Alvim, 1978). These results reinforce those of other studies performed in Brazilian floodplain forests (Ayres, 1993; Gottsberger, 1978; Goulding, 1983; Kubitzki & Ziburski, 1994; Moegenburg, 2002; Williamson *et al.*, 1999; Williamson & Costa, 2000), in other neotropical floodplains (Colonnello, 1991) and tropical floodplain forests for example in Ghana, Africa (Kinnaird, 1992).

The season of flowering is related to the season of fruit dispersal, as was described also for upland forests on Barro Colorado Island, Panama (Foster, 1982). The concentration of flowering during the receding river level phase may be a natural strategy to permit species to complete fruit maturation and drop their fruits or seeds during the periods of maximum river level. Water, directly or indirectly

combined with fish, is the main dispersal agent in Amazonian floodplain forests (Gottsberger, 1978; Goulding, 1980). Of the 29 species analyzed in this study, 28 species have their seed or fruits dispersed by water (Ferreira, 1991). Only *Pentaclethra macroloba* (Mimosaceae) has its seeds dispersed by autochory (explosion of fruits). This species occurs in the transition between upland and floodplain forest and the seeds do not tolerate submersion in water.

Kubitzki & Ziburski (1994) extended this pattern demonstrating that seed biology, particularly germination, is closely integrated into the framework determined by inundation. Establishment strategies differ on different positions in the flooding gradient. Seeds of igapó species from the high community were significantly larger and heavier than in species from the low-lying tree community (Parolin, 2000). This was interpreted as a need, at sites with short periods of flooding in igapó forests, for rapid height growth which may have selected for species with larger seeds which enable seedlings to grow fast, independently from the availability of soil nutrients which in igapó forests is extremely low (Furch, 1997; Sioli, 1954; Sombroek, 1984). In igapó high seed mass compensated the lack of nutrients of the environment (Parolin, 2000). In 31 tree species, those from high levels in the flooding gradient germinated earlier and had longer leaves and taller seedlings than those from low levels (Parolin & Junk, 2002). Two hypothesized strategies enable efficient seedling establishment on different levels in the flooding gradient: tolerance of prolonged submergence vs. escape from submergence (Parolin, 2002). Where submergence is unavoidable, on the lower sites in the flooding gradient, seedlings had significantly lower shoot extension than on the higher sites. Large and small seeds produced seedlings with high shoot elongation, enhancing the chances of non-submergence for the seedlings at high elevations. Thus, tree zonation observed at community level (Ferreira & Stohlgren, 1999) may be at least partly related to different establishment strategies of the species occurring in the floodplains, which are linked also to phenological patterns.

Almost all species of this study, 92%, flower once per year (corresponding to the "annual class", Newstrom *et al.*, 1994). This flowering event in the majority of species is closely associated with the regular flood cycle. However, only 8 species (27%) had their monthly flowering, and 16 species (55%) their monthly fruiting periods significantly correlated with variation in mean river level. On the other hand, 17 species (59%) had their flowering, and 16 species (55%) their fruiting periods significantly correlated with the variation in mean precipitation, with the peak of flowers concentrated in the dry and the peak of fruiting in the rainy season. Similar patterns are described for adjacent Amazonian non-flooded forests (Araujo, 1970; Alencar, 1979, 1994; Ducke & Black, 1953), and other tropical forests (Dulmen, 2001, Figueroa & Fournier, 1995, Frankie *et al.*, 1974, Kinnard, 1992, Rathcke & Lacey, 1985). The higher number of species flowering and fruiting in association with precipitation rather than with river level is surprising when one would expect a strong influence of the flood cycle on the reproductive phenologies. However, the evolution of adaptations in trees in floodplain forests may require a longer period of

association with flooding (Kubitzki, 1989). More important, flowering, like vegetative phenology (leaf shedding), is strongly correlated with seasonal changes in tree water status (Borchert, 1994, Eamus & Prior, 2001), which appears to be the principal determinant of phenology, and may be less linked to selection for optimum tree-pollinator interaction than to drought and / or waterlogging of the trees (Borchert, 1983). This stands in contrast to studies, which found that flowering phenology of a plant is not linked to moisture availability (Wright & Cornejo, 1990), and may be the outcome of competition for pollinators (Proctor *et al.*, 1996). Only two autecological studies deal with pollination of Amazonian floodplain trees (*Pseudobombax munguba* and *Ceiba pentandra*, Bombacaceae, Gribel *et al.*, 1999; Gribel & Gibbs, 2002), which state that flowering was related to the dry season. Further studies are urgently needed to get further insights into the selection for timing of flowering in Amazonian floodplains.

Naturalists have recognized variation within species, but its ecological and evolutionary role is still poorly understood (Keeley, 1979). In some species of this study, both the beginning and length of the flowering and fruiting periods varied among individuals in relation to the tree position along the flooding gradient. Keeley (1979) reported that natural selection can produce within the same species genetically differentiated populations specifically adapted to particular conditions, such as flooding duration. She also suggested that the evolution in temperate floodplain forests in the USA has selected intermediate strategies thus preserving genotypes capable of acclimating to either drained or flooded conditions.

The lower number of species which had their individual phenologies affected by tree position along the river level, may indicate that flooding is not the only abiotic factor to explain changes in individual reproductive phenologies. The seven species in this study which showed variation in the initiation of the flowering or/and fruiting periods in relation to tree position along the flooding gradient belong to seven different families, indicating that this pattern may occur independently of phylogeny. Ferreira (1998) also showed an interesting phenological pattern in *Eschweilera parvifolia* (Lecythidaceae) in a floodplain forest in central Amazonia with great differences in the initiation and mean length of flowering and fruiting periods in relation to tree position on the flooding gradient. The trees situated in the lower positions had a significantly longer flowering period than the trees situated in the higher positions. The same was true for the fruiting period.

As shown by Ferreira (2002) for *Himatanthus sukuuba*, a species occurring both in Terra Firme and in Várzea, different populations show different tolerance to flooding. 64 % of submerged seeds of a Terra Firme population germinated, compared to 98 % of submerged seeds of a Várzea population. The differences were even bigger when comparing seedling survival to flooding: waterlogged seedlings survived to 100 % when the seeds originated from a Várzea population, and to 70 % when they were collected in the Terra Firme population. When completely submerged, 70 % of the Várzea seedlings survived, but 0 % of the Terra

Firme. This gives a good idea of population differentiation along the inundation gradient.

In conclusion, the influence of river level and precipitation on the trees in the floodplain forests in the study area occurred at community and population levels. However, the number of species involved and the length of this study are still very limited. Given that the actual understanding of the evolutionary role of abiotic factors on the phenological events in this heterogeneous environment is still poorly studied, a clear prediction about the responses of trees at these levels is difficult. We suggest that further studies involving phenological events at the population level at different points along the flooding gradient are needed, ideally combined with physiological and genetical studies giving insight into the nature of the different phenological patterns observed.

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Literature cited

- ADIS, J. 1984. Seasonal igapo-forest of Central Amazonian black-water rivers and the terrestrial arthropod fauna. Pp:246-268 In: Sioli, H. (ed.). *The Amazon, Limnology and landscape ecology of a mighty tropical river and its basin*. Dodrecht.
- ALENCAR, J.D.C. 1994. Phenology of five Sapotaceae tropical tree species correlated to climatic variables in Ducke Forest reserve, Manaus, AM. *Acta Amazonica* 24:161-181.
- ALVIM, P.d.T. & ALVIM, R. 1978. Relation of climate to growth periodicity in tropical trees. In: Tomlinson, P.B. & Zimmermann, M.H. (eds.). *Tropical trees as living systems*. Cambridge University Press. pp. 445-464.
- ARAÚJO, V.C. 1970. *Fenologia de essências florestais amazônicas*. Bol. Pesq. Florestais 4, Instituto Nacional de Pesquisas da Amazônia, Manaus. 26p.
- AYRES, J.M.C. 1993. *As matas de várzea do Mamirauá*. MCT-CNPq-Programa do trópico úmido, Sociedade civil de Mamirauá, Brasil, 123 p.
- BORCHERT, R. 1983. Phenology and control of flowering in tropical trees. *Biotropica* 15:8-89.
- BORCHERT R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75:1437-1449.
- BORCHERT R. 1983. Phenology and control of flowering in tropical trees. *Biotropica* 15:81-89.

- COLONNELLO, G. 1991. Phenological observations and forest litter production in a floodplain forest (várzea) of the Orinoco river, Venezuela. *Interciencia* 16:202-208.
- DUCKE, A. & BLACK, G.A. 1953. Notas sobre a fitogeografia da Amazônia brasileira. *Bol. Tec. Inst. Agron. Norte* 29:1-69.
- DULMEN, A.v. 2001. Pollination and phenology of flowers in the canopy of two contrasting rain forest types in Amazonia, Colombia. *Plant Ecology* 153:73-85.
- EAMUS, D. & PRIOR, L. 2001. Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies. *Adv. Ecol. Res.* 32:113-197.
- FERREIRA, C.S. 2002. *Germinação e adaptações metabólicas e morfo-anatômicas em plântulas de Himatanthus succuuba (Spruce) Wood., de ambientes de várzea e terra firme na Amazônia Central*. Unpubl. (Master-Thesis) Manaus: Universidade do Amazonas/Instituto Nacional de Pesquisas da Amazônia. pp. 95.
- FERREIRA, L.V. & Stohlgren, T.J. 1999. Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia* 120:582-587.
- FERREIRA, L.V. 1998. Intraspecific variation in phenology in relation to flooding duration in *Eschweilera parviflora* (Lecythidaceae) in central Amazonian floodplain forest. *An. Acad. Bras. Ci.* 70:1-4.
- FERREIRA, L.V. 1991. *O efeito do período de inundação na distribuição, fenologia e regeneração de plantas em uma floresta de black water na Amazonia Central*. (Master's Thesis) Manaus: INPA. 234.
- FIGUEROA, P.G. & FOURNIER, O.L.A. 1995. Phenology and physiology in two populations of *Tabebuia rosea* in Costa Rica. *Revista de Biologia Tropical* 44:61-70.
- FRANKIE, G.W., BAKER, G. & OPLER, P.A. 1974. Comparative phenological studies of trees in tropical wet and dry forest in the lowland of Costa Rica. *J. Ecol.* 62:881-919.
- FURCH, K. 1997. Chemistry of várzea and igapó soils and nutrient inventory in their floodplain forests. In: JUNK W.J. (ed.). *The Central Amazon floodplain: Ecology of a pulsing system*. Ecological Studies 126, Springer Verlag, Heidelberg. pp. 47-68.
- GOTTSBERGER, G. 1978. Seed dispersal by fish in the inundated regions of Humaitá, Amazonia. *Biotropica* 10:170-183.
- GOULDING, M. 1983. The role of fishes in seed dispersal and plant distribution in Amazonian floodplain ecosystems. *Sonderbd. Naturwiss. Ver. Hamburg* 7:271-283.
- GRIBEL, R. & GIBBS, P.E. 2002. High outbreeding as a consequence of selfed ovule mortality and single vector bat pollination in the Amazonian tree *Pseudobombax munguba* (Bombacaceae). *International Journal of Plant Sciences* 163:1035-1043.
- GRIBEL, R., GIBBS, P.E. & QUEIRÓZ, A.L. 1999. Flowering phenology and pollination biology of *Ceiba pentandra* (Bombacaceae) in Central Amazonia. *J. Trop. Ecol.* 15:247-263.
- JANZEN, D.H. 1967. Synchronization of sexual reproduction of trees with the dry season in

Central America. *Evolution* 21:620-637.

JUNK, W.J. 1989. Flood tolerance and tree distribution in central Amazonia. In: HOLM-NIELSEN L.B., NIELSEN I.C., BALSLEV. H. (eds.) *Tropical Forest Botanical Dynamics. Speciation and Diversity*. pp. 47-64. London: Academic Press.

JUNK, W.J., BAYLEY, P.B. & SPARKS, R.E. 1989. The "flood pulse" concept in river-floodplain system. In Proceedings of the International Large River Symposium (D.G. Dodge. ed.) pp. 110-127.

KEEL, S.H. & PRANCE, G.T. 1979. Studies of the vegetation of a black water igapo (rio Negro - Brazil). *Acta Amazonica* 9:645-655.

KINNAIRD, M.F. 1992. Phenology of flowering and fruiting of an east African riverine forest ecosystem. *Biotropica* 24:187-194.

KUBITZKI, K. & ZIBURSKI, A. 1994. Seed dispersal in flood plain forests of Amazonia. *Biotropica* 26:30-43.

KUBITZKI, K. 1989. The ecogeographical differentiation of Amazonian inundation forests. *Pl. Syst. Evol.* 162:285-304

MOEGENBURG, S.M. 2002. Spatial and temporal variation in hydrochory in Amazonian floodplain forest. *Biotropica* 34:606-612.

NEWSTROM, L.E., FRANKIE, G.W. & BAKER, H.G. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* 26:141-159.

PAROLIN, P. 2000. Seed mass in Amazonian floodplain forests with contrasting nutrient supplies. *J. Trop. Ecol.* 16:417-428.

PAROLIN, P. 2002. Submergence tolerance vs. escape from submergence: two strategies of seedling establishment in Amazonian floodplains. *Environm. Experim. Botany* 48:177-186.

PAROLIN, P. & JUNK, W.J. 2002. The effect of submergence on seed germination in trees from Amazonian floodplains. *Boletim Museu Goeldi* 18:321-329.

PAROLIN, P., ARMBRÜSTER, N., WITTMANN, F., FERREIRA, L.V., PIEDADE, M.T.F & JUNK, W.J. 2002. A review of tree phenology in central Amazonian floodplains. *Pesquisas, Botanica* 52:195-222.

PIEPADE, M.T.F. 1985. *Ecologia e biologia reprodutiva de Astrocaryum jauari Mart. (Palmae) como exemplo de população adaptada as áreas inundáveis do rio Negro (black waters)*. (Master's Thesis) Manaus: INPA. 187.

PRANCE, G.T. 1979. Notes on vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. *Brittonia* 31:26-38

PROCTOR, M., YEO, P. & LACK, A. 1996. *The natural history of pollination*. London: Harper Collins Publ.

RADAMBRASIL, 1978. *Projeto Radambrasil. Levantamento e recursos naturais*. Volume 18. Manaus. Ministério das Minas e Energia. 623 pp.

- REVILLA, J.D.C. 1981. *Aspectos florísticos e fitossociológicos de floresta inundável (igapó). Praia Grande, rio Negro, Amazonas, Brasil.* (Master's Thesis) Manaus: INPA. 129.
- SCARANO, F.R. 1998. A comparison of dispersal, germination and establishment of woody plants subjected to distinct flooding regimes in Brazilian flood-prone forests and estuarine vegetation. In: Scarano F.R. & Franco A.C. (eds.) 1998: Ecophysiological strategies of xerophytic and amphibious plants in the neotropics. *Serie Oecologia Brasiliensis* 4:176-193.
- SCHMIDT, G.W. 1976. Primary production of phytoplankton in three types of Amazonian waters. *Amazoniana* 5:517-528.
- SCHÖNGART, J., PIEDADE, M.F.T., LUDWIGSHAUSEN, S., HORNA, V. & WORBES, M. 2002. Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. *Journal of Tropical Ecology* 18:581-597.
- SIOLI, H. 1954. Betrachtungen über den Begriff "Fruchtbarkeit" eines Gebiets anhand der Verhältnisse in Böden und Gewässern Amazoniens. *Forschung Fortschritt* 28:65-72.
- SOMBROEK, W.G. 1984. Soils of the Amazon region. In: SIOLI, H. (ed.). *The Amazon*. Dordrecht, Boston, Lancaster: Dr. Junk Publ. pp. 521-534.
- WILLIAMSON, G.B. & COSTA, F. 2000. Dispersal of Amazonian trees: Hydrochory in *Pentaclethra macroloba*. *Biotropica* 32:548-552.
- WILLIAMSON, G.B., COSTA, F. & MINTE VERA, C.V. 1999. Dispersal of Amazonian trees: Hydrochory in *Swartzia polyphylla*. *Biotropica* 31:460-465.
- WITTMANN, F., SCHÖNGART, J., MONTERO, J.C., MOTZER, T., JUNK, W.J., PIEDADE, M.T.F., QUEIROZ, H.L. & WORBES, M. 2006. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. *Journal of Biogeography* 33:1334-1347.
- WRIGHT, S.J. & CORNEJO, F.H. 1990. Seasonal drought and the timing of flowering and leaf fall in a neotropical forest. In: Bawa K.S. & Hadley M. (eds.). *Reproductive Ecology of tropical forest plants*. Man and the Biosphere Series Paris (Unesco) 7:49-61.
- ZIBURSKI, A. 1991. Dissemination, Keimung und Etablierung einiger Baumarten der Überschwemmungswälder Amazoniens. In: Rauh W. (ed.). *Tropische und subtropische Pflanzenwelt*. Akademie der Wissenschaften und der Literatur. 77:1-96.

Table 1 - Number of individuals per species and occurrence in the flooding gradient of 29 species utilized in this study. Lower = trees situated between 21 and 24.9 m ASL; upper = trees situated between 25 and 28 m ASL.

Species	Family	N	Flooding
<i>Acmanthera latifolia</i>	Malpighiaceae	16	lower
<i>Albizia marginata</i>	Mimosaceae	15	lower
<i>Aldina latifolia</i>	Fabaceae	19	upper
<i>Amphirox surinamensis</i>	Violaceae	15	upper
<i>Aspidosperma nitidum</i>	Apocynaceae	15	upper
<i>Banara guianensis</i>	Flacourtiaceae	15	lower
<i>Caraipa grandiflora</i>	Guttiferae	18	upper
<i>Caryocar microcarpum</i>	Caryocaraceae	16	upper
<i>Couepia paraensis</i>	Chrysobalanaceae	17	lower
<i>Erismacalcaratum</i>	Vochysiaceae	15	upper
<i>Eschweilera parvifolia</i>	Lecythidaceae	18	upper
<i>Eschweilera tenuifolia</i>	Lecythidaceae	16	lower
<i>Ferdinandusa rudgeoides</i>	Rubiaceae	15	lower
<i>Hevea spruceana</i>	Euphorbiaceae	18	lower
<i>Humiriastrum cuspidatum</i>	Humiriaceae	16	upper
<i>Ixora ulei</i>	Rubiaceae	15	lower
<i>Laetia suaveloens</i>	Flacourtiaceae	15	lower
<i>Licania apetala</i>	Chrysobalanaceae	17	lower
<i>Mabea nitida</i>	Euphorbiaceae	15	upper
<i>Macrolobium acaciaefolium</i>	Caesalpinaceae	15	lower
<i>Maprounea guianensis</i>	Euphorbiaceae	16	upper
<i>Parkia discolor</i>	Mimosaceae	18	lower
<i>Pentaclethra macroloba</i>	Mimosaceae	16	upper
<i>Pouteria elegans</i>	Sapotaceae	18	lower
<i>Swartzia argentea</i>	Caesalpinaceae	16	lower
<i>Swartzia polyphylla</i>	Caesalpinaceae	16	upper
<i>Tabebuia barbata</i>	Bignoniaceae	16	lower
<i>Talisia elephantiae</i>	Sapindaceae	16	upper
<i>Tovomitamacrophylla</i>	Guttiferae	16	upper
<i>Virola elongata</i>	Myristicaceae	18	upper

Table 2 - Simple regression analysis of the phenological events of the species in this study in relation to river level and precipitation

Species	RIVER LEVEL				PRECIPITATION			
	flowering period		fruiting period		flowering period		fruiting period	
	R2	F	R2	F	R2	F	R2	F
<i>Acmanthera latifolia</i>	0,12	ns	0,57	14.91 **	0,32	5.23 *	0,04	ns
<i>Albizia marginata</i>	0,37	6.37 *	0,52	11.88 **	0,7	25.88 ****	0,44	8.76 **
<i>Aldina latifolia</i>	0	ns	0,09	1,12	0,48	10.16 **	0,1	ns
<i>Amphirrhox surinamensis</i>	0,29	ns	0,58	15.07 **	0,001	ns	0,27	ns
<i>Aspidosperma nitidum</i>	0,13	ns	0,45	9.01 **	0,77	37.77 ****	0,68	23.34 ***
<i>Banara guianensis</i>	0,29	ns	0,36	6.22 *	0,001	ns	0,67	22.54 ***
<i>Caraipa grandifolia</i>	0,17	ns	0,01	0,15	0,1	ns	0,73	30.00 ****
<i>Caroycar microcarpum</i>	0,76	34.37 ****	0,19	2,53	0,1	ns	0,67	22.57 ***
<i>Couepia paraensis</i>	0,31	4.99 *	0,88	81.09 ****	0,76	34.86 ****	0,1	ns
<i>Erismacalcaratum</i>	0	ns	0,72	27.95 ****	0,37	6.42 *	0,51	11.47 **
<i>Eschweilera parvifolia</i>	0,27	ns	0,68	22.88 ***	0,78	39.34 ****	0,001	ns
<i>Eschweilera tenuifolia</i>	0,24	ns	0,05	0,62	0,03	ns	0,6	16.22 **
<i>Ferdinandua rudgeoides</i>	0,02	ns	0,71	22.76 ****	0,62	18.08 ***	0,01	ns
<i>Hevea spruceana</i>	0,16	ns	0,67	22.48 ***	0,8	ns	0,1	ns
<i>Ixora ulei</i>	0,63	18.36 ***	0,53	12.42 **	0,55	13.58 **	0,57	14.70 **
<i>Laetia suaveolens</i>	0,003	ns	0,28	4,21	0,52	12.05 **	0,17	ns
<i>Mabea nitida</i>	0,18	ns	0,37	6.51 *	0,39	6.94 *	0,42	7.84 *
<i>Macrolobium acaccifolium</i>	0,19	ns	0,57	14.76 **	0,59	15.76 **	0,14	ns
<i>Maprounea guianensis</i>	0,13	ns	0,7	25.76 ****	0,2	ns	0,54	13.07 **
<i>Parkia discolor</i>	0,4	7.34 *	0,11	1,35	0,46	9.48 **	0,38	6.76 *
<i>Pentaclethra macroloba</i>	0,05	ns	0,33	5.31 *	0,18	ns	0,82	48.46 ****
<i>Pouteria elegans</i>	0,004	ns	0,44	8.73 *	0,26	ns	0,71	26.26 ****
<i>Sacoglottis amazonica</i>	0,54	13.17 **	0,53	12.56 **	0,23	ns	0,1	ns
<i>Swartzia polyphylla</i>	0,16	ns	0,03	0,31	0,36	6.27 *	0,001	ns
<i>Swartzia argentea</i>	0,03	ns	0,11	1,29	0,45	8.91 *	0,81	47.05 ****
<i>Tabebuia barbata</i>	0,04	ns	0,08	0,1	0,47	9.83 **	0,21	ns
<i>Talisia elephantiasse</i>	0,61	17.52 **	0,005	0,05	0,1	ns	0,67	22.60 ***
<i>Tovomitamacrophylla</i>	0,29	ns	0,2	2,78	0,84	55.80 ****	0,7	ns
<i>Virola elongata</i>	0,4	7.32 *	0,16	2,03	0,69	24.69 ****	0,36	6.28 *

**** P>0.0001, *** P>0.001, ** P>0.01, * P>0.05, and ns= not significant

Table 3 - Nine species occurring in both lower and upper regions, with variation of mean length of phenological events related to position of the trees in the flooding gradient.

Species	Phenological events	Mean length of phenological event [months]?	
		low position	high position
<i>Acmanthera latifolia</i>	flowering	1.50 (1.00)	3.33 (1.41)
<i>Aspidosperma nitidum</i>	flowering	5.00 (0.00)	4.25 (0.50)
<i>Mabea nitida</i>	flowering	2.00 (1.00)	1.10 (0.38)
<i>Pentaclethra macroloba</i>	flowering	5.00 (1.15)	1.90 (0.88)
<i>Virola elongata</i>	flowering	4.00 (1.07)	3.20 (0.45)
<i>Albizia marginata</i>	fruiting	9.57 (0.54)	8.83 (0.41)
<i>Erismacalcaratum</i>	fruiting	7.50 (0.93)	6.33 (0.58)
<i>Laetia suaveolens</i>	fruiting	4.00 (0.58)	5.00 (0.54)
<i>Eschweilera parvifolia</i>	flowering	3.67 (1.50)	2.17 (0.41)
	fruiting	7.92 (1.31)	4.17 (0.41)
<i>Parkia discolor</i>	flowering	4.00 (0.00)	3.57 (0.54)
	fruiting	5.30 (0.46)	4.43 (0.98)

NUMBER IN PARENTHESIS ARE STANDARD DEVIATION (* P>0.05, ** P>0.01, *** P>0.001)

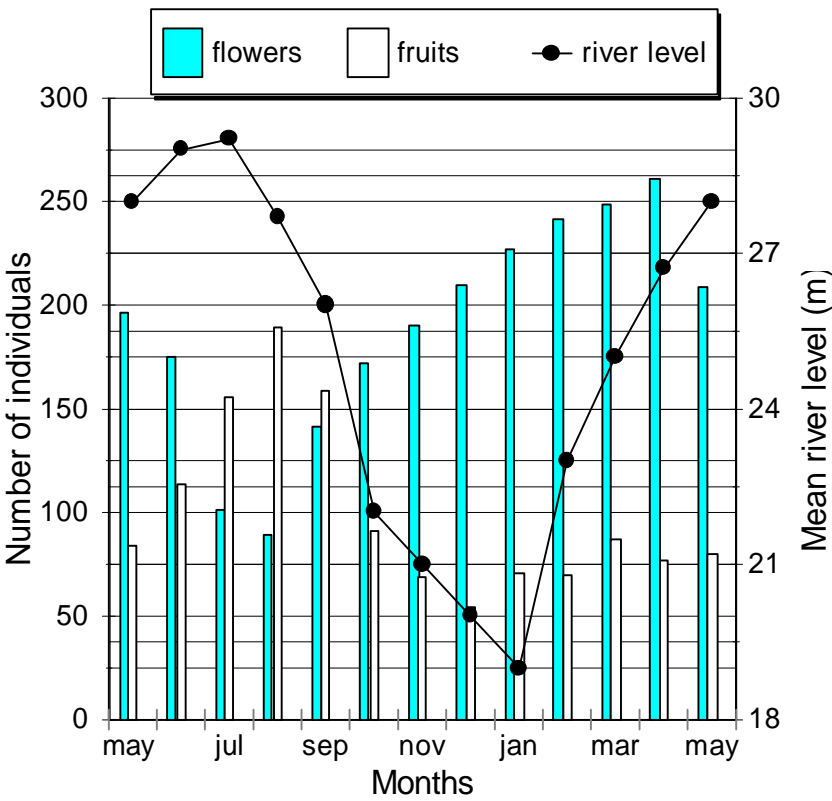


Figure 1: Monthly number of trees in flowers and fruits, and river level.

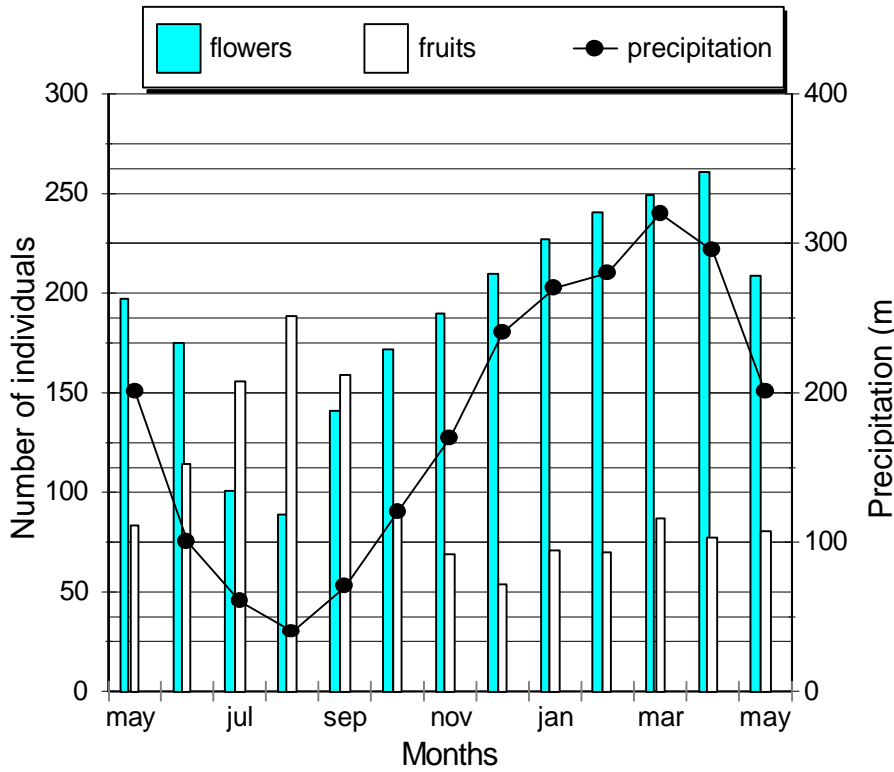


Figure 2: Monthly number of trees in flowers and fruits, and precipitation.

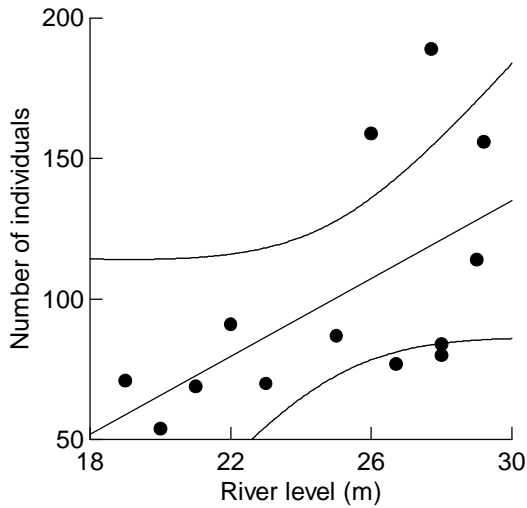


Figure 3: Relation between the number of individuals in flower and river level ($r^2=0.35$, $P<0.05$, $n=11$).

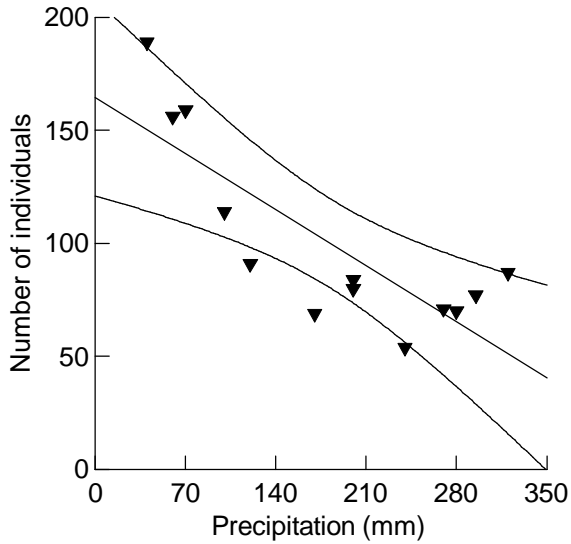


Figure 4: Relation between the number of individuals in flower and precipitation ($r^2 = -0.67$, $P<0.001$, $n=11$).

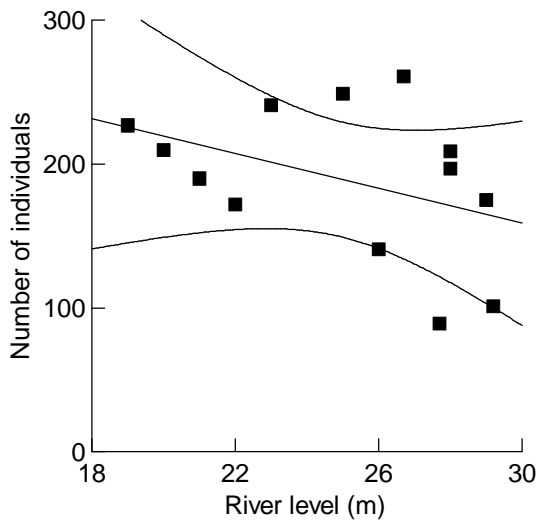


Figure 5: Relation between the number of individuals in fruit and river level ($r^2 = 0.16$, $P > 0.05$, $n = 11$).

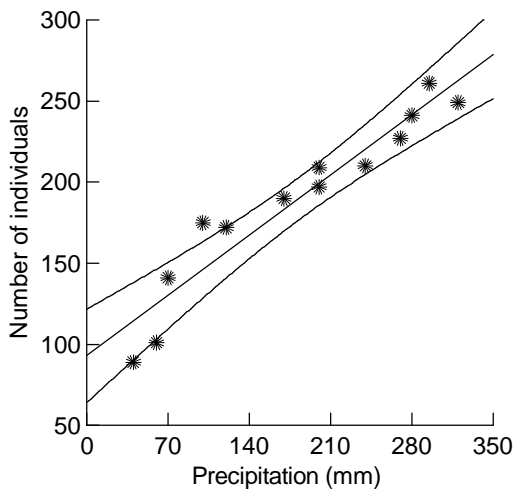


Figure 6: Relation between the number of individuals in fruit and precipitation ($r^2 = 0.91$, $P < 0.0001$, $n = 11$).

