

SHORT COMMUNICATION

Phenology and CO₂-assimilation of trees in Central Amazonian floodplains

PIA PAROLIN¹

Max-Planck-Institute for Limnology, Tropical Ecology, P.O. Box 165, D-24302 Plön, Germany

(Accepted 1st December 1999)

KEY WORDS: Amazon, CO₂-assimilation, flooding stress, floodplain forest, phenology

INTRODUCTION

In Central Amazonian floodplains (called seasonal várzea, Prance 1979), trees are subjected to periodic changes between a terrestrial and a flooding phase, which can last up to 230 d (Junk *et al.* 1989). During this aquatic phase, the soil is covered by a water-table that reaches a height of 10 m. Seedlings and small trees are then completely flooded. High, adult trees, or trees standing on higher levels in the flooding gradient, suffer inundation of the roots and parts of the stems that causes a lack of oxygen in the rhizosphere (Crawford 1989). Gessner (1968) compared the growth conditions in the aquatic phase with temperate winters and introduced the term 'physiological winter'. Leaf-fall and reductions of growth and metabolic activity, which he observed in the aquatic phase, led him to the assumption that trees in floodplains reduce their activity as do trees of temperate forests during the period of unfavourable conditions (Gessner 1968). Annual growth rings are formed in the wood of most tree species in Central Amazonian floodplains as a consequence of regular growth reductions (Worbes 1986, 1989).

Changes of root formation and function, leaf respiration, leaf metabolite and chlorophyll content, water potential and photosynthetic O₂-production were observed in flooded tree seedlings in the várzea (Meyer 1991, Schlüter 1989,

¹ Correspondence address: Universität Hamburg, Institut für Allgemeine Botanik, AB Systematik, Ohnhorststr. 18, 22609 Hamburg, Germany. E-mail: piaparolin@gmx.de.

Schlüter & Furch 1992, Schlüter *et al.* 1993, Scholander & Perez 1968). These studies indicated that flooding induces a series of physiological, anatomical and morphological changes. In particular, submerged leaves showed significant differences of metabolic activity when compared with leaves that emerged above the floodwater (D. Waldhoff, *pers. comm.*). However, all of these studies were performed during a restricted part of the year and no information is available concerning the timing and seasonal variation of the metabolic activity. Quantitative measurements of the changes that occur with flooding of the roots and stems are lacking. The aim of this study was to describe and quantify seasonal variation of growth and its timing. Suitable parameters for this analysis include vegetative phenology and photosynthetic CO₂-assimilation of the trees *in situ*. Leaf-fall and the production of new leaves can be used as indicators of tree growth. Trees shed their leaves and reduce the production of new leaves in a period of unfavourable hydrological conditions (Reich & Borchert 1982, Wright & Cornejo 1990). Leaves are shed to reduce the transpirational surface, an adaptation that regulates tree water status and reduces drought and flood stress (Borchert 1994, Medina 1983). Tree growth is then reduced leading to the formation of growth rings (Worbes 1989, 1997). When tree water status has recovered, new leaves can be flushed and tree growth is regained (Borchert 1994). Photosynthetic CO₂-assimilation is a direct expression of the metabolic activity of a tree. Reductions are caused by leaf senescence, nutrient supply and environmental factors, e.g. flooding (Pezeshki 1993, Pezeshki *et al.* 1996, Sesták 1985).

Timing and seasonal variation of phenology and photosynthetic CO₂-assimilation are used here to answer the question: Does the aquatic phase represent an unfavourable period that is comparable to the temperate winter as postulated by Gessner (1968)? A second question deals with the high diversity of growth strategies found in trees of the Central Amazonian floodplains. Among the several hundred tree species that grow in the várzea, there are evergreen and deciduous ones, as well as fast-growing, light-demanding pioneers and slow-growing, shade-tolerant non-pioneers (*sensu* Swaine & Whitmore 1988). The present study attempted to consider the role of the different growth strategies by comparing species that were typical pioneers and non-pioneers, and that were evergreen and deciduous. Does photosynthetic activity change with flooding in a similar way in species with different growth strategies?

SPECIES AND STUDY AREA

Six tree species, which represent a range of different growth strategies, were chosen for this study. *Cecropia latiloba* Miq., *Senna reticulata* (Willd.) Irwin & Barn and *Nectandra amazonum* Nees are evergreen, while *Crateva benthami* Eichl. in Mart., *Tabebuia barbata* E. Mey. and *Vitex cymosa* Benth. are deciduous. *Cecropia latiloba* and *Senna reticulata* are fast-growing, light-demanding pioneer species with low wood density (Parolin *et al.* 1998). *Nectandra amazonum*, *Crateva benthami*,

Tabebuia barbata and *Vitex cymosa* are non-pioneer species, and are shade-tolerant, with slow growth and high wood density. The terms pioneer/non-pioneer are used according to the definition of Swaine & Whitmore (1988). All of the chosen species are widespread in Central Amazonian white-water floodplains and represent different successional stages (Prance 1979, Worbes *et al.* 1992).

Four study sites (Costa do Catalão, Fazenda Lira, Ilha da Marchantaria, Fazenda Pec Terra Nova/Careiro) were located in white-water floodplains in the vicinity of Manaus. The floodplain forests of these sites are situated between 21 and 27 m above sea level (asl) and are subject to a maximum high water level of 8 m, corresponding to a mean period of inundation of up to 9 mo per year (Junk 1989). The vegetation on the chosen sites is typical várzea forest with a high diversity of species (Worbes *et al.* 1992) and secondary forest dominated by *Cecropia latiloba* and *Senna reticulata*.

METHODS

Climate and flooding regime

The precipitation is markedly seasonal with a rainy season from December to May, followed by a dry season from June to November. Three to four months after the onset of the rains, the water level of the rivers rises and reaches the highest peak in June at 28 ± 2 m asl. The lowest level is reached in November at 18 ± 2 m asl. The water level oscillation of *c.* 10 m is very regular and predictable ('flood pulse concept', Junk *et al.* 1989). The study period from April 1994 to June 1995 included one terrestrial and two aquatic phases.

Vegetative phenology

Timing of leaf-fall and of the production of new leaves was monitored qualitatively every month in five selected individuals per species, all occurring on the same elevation in the flood gradient and of similar diameter at breast height (dbh), located randomly in the four study areas. A tree was labelled deciduous if it lost almost all the leaves and the remaining leaves were senescent. Evergreen trees were those that changed leaves continuously.

Measurements of CO₂-assimilation

Photosynthetic CO₂-assimilation was measured once a month between 09h00 and 12h00 using an infra-red gas analyser (IRGA, ADC LCA-2, Analytical Development Co. Ltd., Hoddesdon, Herts, UK) on marked adult individuals of the six selected tree species in the field. Ten fully expanded, non-flooded leaves from each of the previously selected five individual trees of each species were chosen for measurements at high quantum flux density, with photosynthetically active radiation (PAR) over $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ (A_{max}). Access to the leaves in the high-water period was by boat, and in the low-water period by wooden towers and ladders. Only leaves that emerged above the level of

floodwaters were considered. Whenever possible, only adult, healthy leaves of the outer canopy were chosen for measurements. If this was not possible because the deciduous period had begun, measurements were made on senescent leaves.

The significance of differences between measurements of the terrestrial and aquatic period were tested using ANOVA.

RESULTS

Vegetative phenology

Leaf shedding and replacement occurred continuously in the evergreen species (*Cecropia latiloba*, *Senna reticulata* and *Nectandra amazonum*). In the deciduous species (*Crateva benthami*, *Tabebuia barbata* and *Vitex cymosa*), leaf-fall was very pronounced for 2–3 mo in the period of highest water level, but the trees were leafless only for a 4-wk period.

The production of new leaves in the pioneer species (*Cecropia latiloba* and *Senna reticulata*) occurred during the whole year, but was reduced for 2–4 mo in the period of the highest water level (Figure 1). The four non-pioneers (*Nectandra amazonum*, *Crateva benthami*, *Tabebuia barbata* and *Vitex cymosa*) had a strong flush of new leaves at the highest water peak and towards the end of

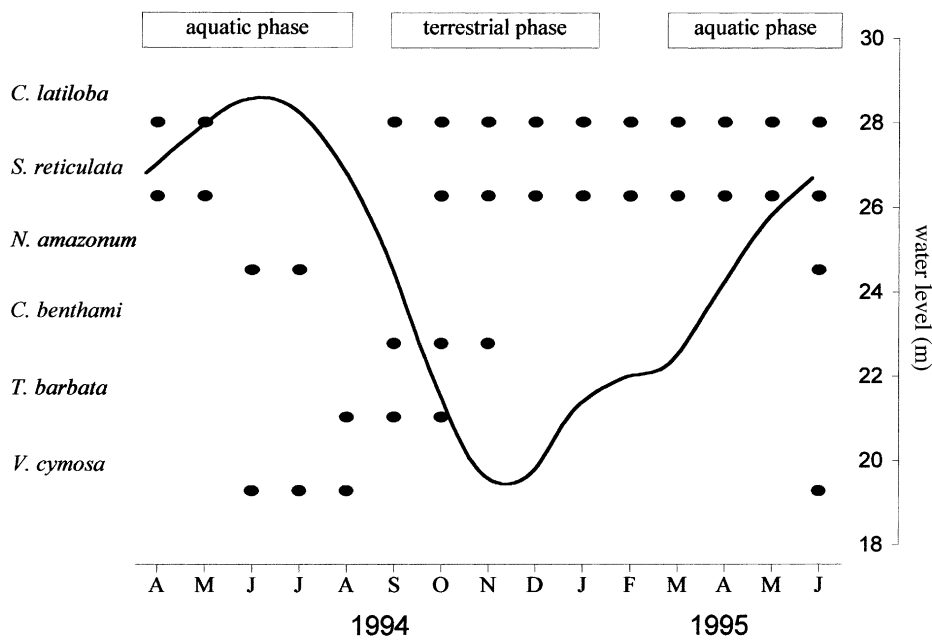


Figure 1. Phenology of six tree species from the Amazonian floodplains showing leaf production during 15 mo, from April 1994 to June 1995. Oval points indicate the production of new leaves, and the line shows the river level measured at the harbour of Manaus (Rio Negro) during the study period. Full species names are given in Table 1.

the aquatic phase. In all species, leaf-flush began or occurred completely before the end of flooding.

Photosynthetic CO₂-assimilation

In all species, CO₂-uptake on average was lower during the aquatic phase than in the non-flooded terrestrial phase (Table 1). In the pioneers, CO₂-uptake in the aquatic phase was *c.* 10% lower than in the terrestrial phase, while in the non-pioneers it was between 20 and 50% lower than in the terrestrial phase. Only in *Cecropia latiloba* were the differences not statistically significant.

A detailed view of the monthly changes of mean CO₂-uptake in the six species is given in Figure 2. During the 15 mo of data recording, in all species mean CO₂-uptake remained high in the first 1–4 mo of flooding, then declined for some weeks to months. In this period, deciduous trees shed their leaves (qualitative observations only). In all species except *Senna reticulata*, mean CO₂-uptake rose again before the end of the aquatic phase and remained high through the terrestrial phase. With the onset of flooding, mean CO₂-uptake was reduced again after several weeks to months.

DISCUSSION

The vegetative phenology and photosynthetic CO₂-uptake of the six chosen species show a high plasticity during the annual cycle. In the aquatic phase, CO₂-uptake is high in the first months of flooding, and is reduced after some months. In the second part of the aquatic phase, CO₂-uptake rises again to levels that are comparable to those of the terrestrial phase, or even more elevated. This takes place before the end of flooding in all species. During the terrestrial phase, the range of photosynthetic assimilation is smaller again, and reductions can occur that are probably related to water shortage in the driest months.

The seasonal changes of photosynthetic assimilation of the chosen species

Table 1. Mean CO₂-uptake at maximum quantum flux density (A_{\max}) in six tree species from the Amazonian floodplain during the terrestrial and the aquatic phase: lowest and highest measured values (min – max), means \pm SD, difference between the terrestrial and the aquatic phase in per cent, F-ratio of the ANOVA; sample size (n) was 80 measurements on separate leaves of five trees per species, each per terrestrial and aquatic phase.

Species	Min–max ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Terrestrial phase ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Aquatic phase ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Difference (%)	F	P
<i>Cecropia latiloba</i>	4.8–21.0	16.8 \pm 1.5	15.0 \pm 4.6	–10.5	2.21	n.s.
<i>Senna reticulata</i>	9.8–24.5	20.0 \pm 4.0	18.4 \pm 4.3	–7.8	18.07	***
<i>Nectandra amazonum</i>	3.2–15.6	9.3 \pm 2.4	7.6 \pm 3.1	–18.7	6.36	*
<i>Crateva benthami</i>	5.4–22.0	10.7 \pm 4.8	8.6 \pm 1.0	–19.7	6.02	*
<i>Tabebuia barbata</i>	3.2–15.1	11.1 \pm 2.3	8.6 \pm 2.6	–21.9	13.38	**
<i>Vitex cymosa</i>	4.1–19.6	16.6 \pm 1.5	8.4 \pm 2.2	–49.2	161.05	***

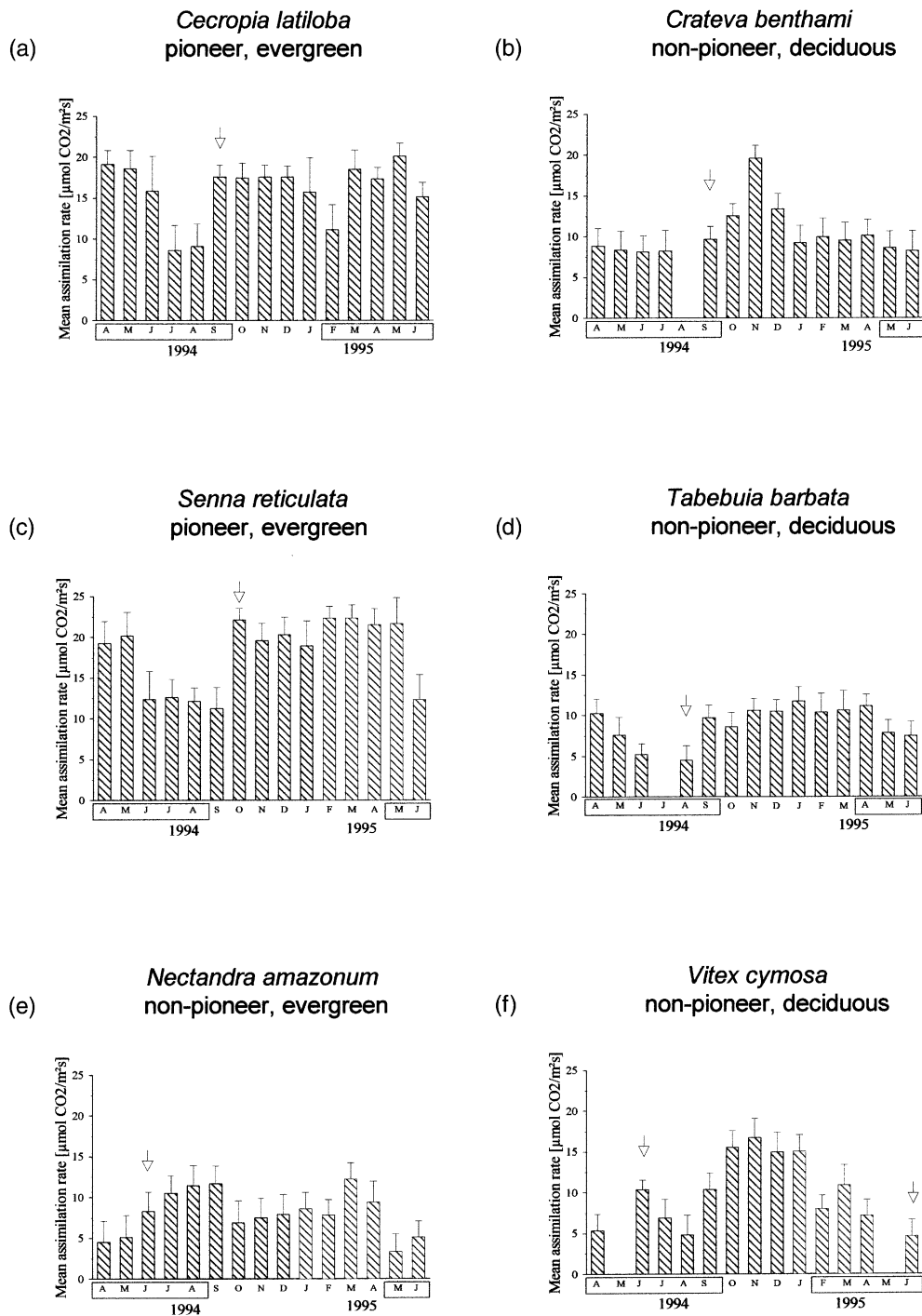


Figure 2. CO_2 -uptake at maximum quantum flux density (A_{max}) of three evergreen species (*Cecropia latiloba*, *Nectandra amazonum*, and *Senna reticulata*) and three deciduous species (*Crateva benthami*, *Tabebuia barbata* and *Vitex cymosa*). Mean monthly values \pm SD in six tree species from Amazonian floodplains between April 1994 and June 1995. Sample size (n) per species and month = 10 leaves from five trees of each species. Months boxed show when the species was flooded. The arrows indicate flushing of new leaves.

were closely related to leaf age and indirectly determined by flooding. With flooding of the roots, tree water status probably decreased, leaves were shed to reduce transpirational surface and water loss, and photosynthetic assimilation decreased as a consequence of the lower photosynthetic capacity of senescent leaves (Reich *et al.* 1999, Sesták 1985). When new leaves were flushed, photosynthetic CO₂-uptake rose again although the roots were still flooded, and reached a maximum when the young leaves were fully expanded.

The aquatic phase represented an unfavourable period for the six tree species, as shown by the shedding of leaves, by the reduced production of new leaves, and by the reduction of photosynthetic assimilation during inundation. The terrestrial phase was the main vegetation period for the six species. Even so, the aquatic phase cannot be considered to be a 'physiological winter' as postulated by Gessner (1968) since this implies a reduction of growth and metabolic activity that lasts for the whole of the unfavourable period. This is clearly not the case in the six species analysed in this study. The trees showed high photosynthetic assimilation for a considerable part of the aquatic phase, where values were reached that were comparable or even higher than those of the terrestrial phase.

Furthermore, in the months when photosynthetic assimilation was reduced, most species produced flowers or fruits (Gottsberger 1978, Kubitzki & Ziburski 1994). The metabolic activity of the trees was high the whole year round, not only during the terrestrial phase. They were probably only shifted from wood increment and photosynthetic assimilation to reproduction. In the six chosen species there was no absolute period of rest or reduced metabolic activity lasting for the whole aquatic period.

The second question dealt with the growth strategies of the six species. There was no association between species and different growth strategies in relation to periodic flooding. Some reactions were similar within strategies, e.g. pioneer species reduced photosynthetic assimilation less than non-pioneers when flooded. But in general, within a group of growth strategies there were few similarities and most reactions did not show a pattern linked to strategy. Several hundred tree species with differing growth strategies manage to adapt to the extreme conditions of Amazonian floodplains. There is no dominance of specific strategies, but a high diversity of species and strategies that coexist and are all efficient under flooding stress. The existence of these different growth strategies shows that flooding cannot be such a strong factor for these species as not to allow a high diversity of life-cycle strategies.

ACKNOWLEDGEMENTS

This study was realized in collaboration between the Max-Planck-Institute for Limnology/Plön, Germany and the National Amazon Research Institute (INPA)/Manaus, Brazil. I thank Martin Bolte, Franz-Josef Risse and Nicole

Armbrüster for their valuable help in the field, and D. Waldhoff and B. Furch for critical comments on the manuscript.

LITERATURE CITED

- BORCHERT, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75:1437–1449.
- CRAWFORD, R. M. M. 1989. The anaerobic retreat. Pp. 105–129 in Crawford, R. M. M. (ed.). *Studies on plant survival: ecological case histories of plant adaptation to adversity*. Blackwell Scientific Publications, Oxford, UK.
- GESSNER, F. 1968. Zur ökologischen Problematik der Überschwemmungswälder des Amazonas. *Internationale Revue der Gesellschaft für Hydrobiologie* 53:525–547.
- GOTTSBERGER, G. 1978. Seed dispersal by fish in the inundated regions of Humaitá, Amazonia. *Biotropica* 10:170–183.
- JUNK, W. J. 1989. Flood tolerance and tree distribution in Central Amazonian floodplains. Pp. 47–64 in Nielsen, L.B., Nielsen I.C. & Balslev H. (eds). *Tropical forests: botanical dynamics, speciation and diversity*. Academic Press, London.
- JUNK W. J., BAYLEY P. B. & SPARKS R. E. 1989. The 'flood pulse' concept in river-systems. Pp. 110–127 in Dodge, D. P. (ed.). Proceedings of the International Large River Symposium. *Canadian Special Publication of Fisheries and Aquatic Sciences* 106.
- KUBITZKI, K. & ZIBURSKI, A. 1994. Seed dispersal in flood plain forests of Amazonia. *Biotropica* 26:30–43.
- MEDINA, E. 1983. Adaptations of tropical trees to moisture stress. Pp. 225–237 in Golley F. B. (ed.). *Ecosystems of the world: tropical rain forest ecosystems*. Elsevier Scientific Publishers,
- MEYER, U. 1991. *Feinwurzelsysteme und Mykorrhizatyphen als Anpassungsmechanismen in Zentralamazonischen Überschwemmungswäldern – Igapó und Várzea*. PhD thesis. Universität Hohenheim, 230 pp.
- PAROLIN, P., FERREIRA, L. V. & JUNK, W. J. 1998. Central Amazonian floodplains: effect of two water types on the wood density of trees. *Verhandlungen des Internationalen Vereins Limnologie* 26:1106–1112.
- PEZESHKI, S. R. 1993. Differences in patterns of photosynthetic responses to hypoxia in flood-tolerant and flood-sensitive tree species. *Photosynthetica* 28:423–430.
- PEZESHKI, S. R., PARDUE, J. H. & DELAUNE, R. D. 1996. Leaf gas exchange and growth of flood-tolerant and flood-sensitive tree species under low soil redox conditions. *Tree Physiology* 16:453–458.
- PRANCE, G. T. 1979. Notes on the vegetation of Amazonia. III. Terminology of Amazonian forest types subjected to inundation. *Brittonia* 31:26–38.
- REICH, P. B. & BORCHERT, R. 1982. Phenology and ecophysiology of the tropical tree, *Tabebuia neochrysantha* (Bignoniaceae). *Ecology* 63:294–299.
- REICH, P. B., ELLSWORTH, D. S., WALTERS, M. B., VOSE, J. M., GRESHAM, C., VOLIN, J. C. & BOWMAN, W. D. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80:1955–1969.
- SCHLÜTER, U.-B. 1989. *Morphologische, anatomische und physiologische Untersuchungen zur Überflutungstoleranz zweier charakteristischer Baumarten des Weiß- und Schwarzwasser Überschwemmungswaldes bei Manaus. Ein Beitrag zur Ökosystemanalyse von Várzea und Igapó Zentralamazoniens*. PhD thesis. Universität Kiel, 147 pp.
- SCHLÜTER, U.-B. & FURCH, B. 1992. Morphologische, anatomische und physiologische Untersuchungen zur Überflutungstoleranz des Baumes *Macrolobium acaciaefolium*, charakteristisch für die Weiß- und Schwarzwasserüberschwemmungswälder bei Manaus, Amazonas. *Amazoniana* 12:51–69.
- SCHLÜTER, U.-B., FURCH, B. & JOLY, C. A. 1993. Physiological and anatomical adaptations by young *Astrocaryum jauari* Mart. (Arecaceae) in periodically inundated biotopes of Central Amazonia. *Biotropica* 25:384–396.
- SCHOLANDER, P. F. & PEREZ, M. O. 1968. Sap tension in flooded trees and bushes of the Amazon. *Plant Physiology* 43:1870–1873.
- SESTÁK, Z. 1985. *Photosynthesis during leaf development*. W. Junk Publishers, The Hague, Netherlands.
- SWAINE, M. D. & WHITMORE, T. C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81–86.
- WORBES, M. 1986. Lebensbedingungen und Holzwachstum in zentralamazonischen Überschwemmungswäldern. *Scripta Geobotanica* 12 pp.
- WORBES, M. 1989. Growth rings, increment and age of trees in inundation forests, savannas and a mountain forest in the neotropics. *IAWA Bulletin* 10:109–122.
- WORBES, M. 1997. The forest ecosystem of the floodplains. Pp. 223–266 in Junk, W. J. (ed.). *The Central Amazon floodplain: ecology of a pulsing system*. Ecological Studies 126, Springer Verlag, Heidelberg.

- WORBES, M., KLINGE, H., REVILLA, J. D. & MARTIUS, C. 1992. On the dynamics, floristic subdivision and geographical distribution of Várzea forests in Central Amazonia. *Journal of Vegetation Science* 3:553–564.
- WRIGHT, S. J. & CORNEJO, F. H. 1990. Seasonal drought and the timing of flowering and leaf-fall in a neotropical forest. Pp. 49–61 in Bawa K. S. & Hadley M. (eds). Reproductive ecology of tropical forest plants. *Man and the Biosphere Series* 7.