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Seasonal Changes of Specific Leaf Mass and Leaf Size in Trees of Amazonian Floodplains

By

Pia PAROLIN*)

With 5 Figures

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Summary

PAROLIN P. 2002. Seasonal changes of specific leaf mass and leaf size in trees of Amazonian floodplains. – *Phyton* (Horn, Austria) 42 (1): 169–185, 5 figures. – English with German summary.

Seasonal changes in specific leaf mass and leaf size were measured at monthly intervals along the annual cycle in six tree species with different growth strategies from Amazonian floodplains (*Cecropia latiloba*, Cecropiaceae; *Crateva benthami*, Cappariaceae; *Nectandra amazonum*, Lauraceae; *Senna reticulata*, Caesalpiniaceae; *Tabebuia barbata*, Bignoniaceae; *Vitex cymosa*, Verbenaceae). In their natural habitat, trees are exposed to extended periods of flooding, and the aim of the present study was to analyse whether there are seasonal changes in leaf specific weight and size, how these changes occur in trees with different growth strategies, and if the changes are related to the periodicity of flooding. Specific leaf mass was higher in waterlogged months in all species except *Crateva benthami*, average leaf age was higher in the aquatic than in the terrestrial period in all species, and mean leaf size was significantly lower in the aquatic period for three species (*Crateva benthami*, *Senna reticulata* and *Tabebuia barbata*). Reductions of leaf size were caused by leaf senescence and a subsequent loss of leaflets. Only for *Senna reticulata* leaf size reduction was a direct response to water stress: in waterlogged months, the newly produced leaves and leaflets were smaller than in the terrestrial period. Data in this study indicate a periodicity in several leaf traits which changes parallel to the flooding periodicity, but which is determined primarily by leaf age and senescence and only indirectly by flooding. The timing of the changes of specific leaf mass and leaf size was similar between species and was con-

*) Dr. Pia PAROLIN, Max-Planck-Institute for Limnology, Dpt. Tropical Ecology, P.O. Box 165, D-24302 Plön, Germany; e-mail: piaparolin@gmx.de

centrated in the aquatic period, but the degree of changes differed among the species. Leaves of pioneer and non-pioneer species, and leaves of deciduous and evergreen species did not show a uniform trend, characteristic for certain growth strategies, as response to flooding. Apparently differences were closely linked to leaf age and can not be considered as adaptive to the changing hydric conditions.

Zusammenfassung

PAROLIN P. 2002. Saisonale Veränderungen der spezifischen Blattmasse und Blattgröße bei Bäumen amazonischer Überschwemmungswälder. – *Phyton* (Horn, Austria) 42 (1): 169–185, 5 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Saisonale Veränderungen der spezifischen Blattmasse und der Blattgröße wurden in amazonischen Überschwemmungswäldern in monatlichen Abständen an sechs Baumarten mit unterschiedlichen Wachstumsstrategien gemessen (*Cecropia latiloba*, Cecropiaceae; *Crateva benthami*, Capparidaceae; *Nectandra amazonum*, Lauraceae; *Senna reticulata*, Caesalpiniaceae; *Tabebuia barbata*, Bignoniaceae; *Vitex cymosa*, Verbenaceae). In ihrer natürlichen Umgebung sind die Bäume lange währenden Überschwemmungsperioden ausgesetzt. Das Ziel der vorliegenden Arbeit war, zu untersuchen, ob saisonale Änderungen der spezifischen Blattmasse und der Blattgröße auftreten, wie diese bei Bäumen mit verschiedenen Wachstumsstrategien ausgeprägt sind und wie sie mit der Periodizität der Überschwemmungen zusammenhängen. Die spezifische Blattmasse war bei allen Arten, mit Ausnahme von *Crateva benthami*, in den vernässten Monaten höher als in der Trockenphase, das Blattalter war in der aquatischen Phase bei allen Arten höher, und die mittlere Blattgröße war bei drei Arten (*Crateva benthami*, *Senna reticulata* und *Tabebuia barbata*) in der aquatischen Phase signifikant geringer als in der terrestrischen. Verminderungen der Blattgröße waren auf das Altern der Blätter zurückzuführen, und auf den daraus resultierenden Verlust von Blättchen. Nur bei *Senna reticulata* war die verminderte Blattgröße eine direkte Antwort auf die Überschwemmung, indem neu produzierte Blätter in der aquatischen Phase kleiner als die neu produzierten in der terrestrischen Phase waren. Die Daten dieser Untersuchung zeigen eine Periodizität auf, die sich parallel zur Überschwemmungsperiodizität ändert, die jedoch vor allem durch das Blattalter determiniert wird, und nur indirekt durch die Überschwemmung. Die Änderungen der spezifischen Blattmasse und der Blattgröße traten besonders in der aquatischen Phase auf, sodaß eine zeitliche Übereinstimmung zwischen den Arten gefunden werden konnte. Die Ausmaße der Änderungen waren jedoch sehr unterschiedlich bei den Arten, und die Blätter der Pionier- und Nichtpionierarten, sowie die Blätter der immergrünen und laubwerfenden Arten zeigten keine einheitlichen Trends bezüglich der Reaktionen auf die wechselnden hydrischen Bedingungen. Die Änderungen waren vielmehr durch das Blattalter bestimmt und die Änderungen der Blattmasse und der Blattgröße können nicht als Anpassung an die wechselnden hydrischen Bedingungen angesehen werden.

Introduction

In Amazonian floodplains trees are exposed to periods of flooding which can last up to 230 days a year (JUNK 1989). The roots, stems, and sometimes crowns of the trees are submerged for several months. Extended periods of waterlogging and drought in the terrestrial period cause un-

favourable conditions for tree growth for several months every year. Flooding and drought affect growth and metabolic activity of trees because root growth is impeded and the absorption of water and nutrients is inhibited (BLOM & VOESENEK 1996, GILL 1970, KOZLOWSKI 1984). Only adapted species can tolerate these conditions, e.g. by a reduction of metabolic activity, as was measured in the temperate flood-tolerant species *Alnus rubra*, *Fraxinus latifolia*, *Nyssa aquatica*, *Taxodium distichum* or *Quercus lyrata* (EWING 1996, PEZESHKI & al. 1996). Some species can maintain or even increase growth and photosynthetic activity under flooding, as was found for the tropical trees *Hymenaea courbaril* and *Chorisia speciosa* (JOLY & CRAWFORD 1982). For some of the hundreds of tree species growing in Amazonian floodplains, physiological, anatomical and morphological adaptations were documented, e.g. the formation of adventitious roots, lenticels, stem hypertrophy, and pressure ventilation (GRAFFMANN 2000, SCHLÜTER & FURCH 1992, SCHLÜTER & al. 1993, WALDHOF & al. 1998). Independent of their growth strategies, whether pioneers or non-pioneers (sensu SWAINE & WHITMORE 1988), evergreen or deciduous species, most trees form annual increment rings indicating periodical growth reductions (WORBES 1989). These may be linked to leaf phenology: leaf fall is increased in the aquatic period (WITTMANN & PAROLIN 1999). Some species shed all the leaves, others shed the submerged leaves, others keep their leaves also if submerged. Respiration, photosynthetic assimilation, leaf chlorophyll content and water potential are lower in waterlogged trees than in non-flooded ones (FURCH 1984, PAROLIN 2000a, SCHLÜTER & FURCH 1992, SCHLÜTER & al. 1993, SCHOLANDER & PEREZ 1968). All of these studies indicate a periodicity imposed by the flooding periodicity. Yet, up to date little is known about ecophysiological changes in the course of the year. Since the assimilating organs are indicators for the vitality of a tree (MEDINA 1984, WALTERS & REICH 1989), and leaf mass and size may change depending on environmental conditions (RODERICK & al. 2000), it may be expected that the trees of Amazonian floodplains reflect the adverse hydric conditions by changes of leaf mass and size in the annual cycle, parallel to the occurrence of waterlogging, submergence or drought. Specific leaf mass expresses the amount of organic substance which is invested in the construction of the leaf and the photosynthetic surface (MEDINA 1984). The size of leaves is closely linked to photosynthetic activity, stomatal conductance and leaf temperature and thus is of fundamental importance for tree ecophysiology (REEKIE & WAYNE 1992). Leaf size variation may well be an adaptation similar to leaf shedding, resulting from the necessity to reduce the transpirational surface in the unfavourable flooded season when tree water status is reduced (BORCHERT 1994).

In the present study, specific leaf mass and leaf size (the size of single leaves, or number and size of leaflets in compound leaves) were measured

along the annual cycle in six tree species with different growth strategies, all common in Amazonian floodplains. The aim was to analyse whether there are seasonal changes in these parameters, how these changes occur in trees with different growth strategies (pioneer / non-pioneer, evergreen / deciduous), and if the changes are related to the periodicity of flooding.

Materials and Methods

Study Trees and Site

Six tree species were chosen, all common to várzea floodplains in Central Amazonia and typical representatives of different growth strategies and flood tolerance (FRANCE 1979, WORRES & al. 1992): *Cecropia latiloba* MIQ. (*Cecropiaceae*, "Embaúba", evergreen pioneer), *Senna reticulata* (WILLD.) IRWIN & BARN. (*Caesalpinaceae*, "Matapasto", evergreen pioneer), *Nectandra amazonum* NEES (*Lauraceae*, "Louro", evergreen non-pioneer), *Crateva benthami* EICHL. in MART. (*Capparidaceae*, "Catoré", deciduous non-pioneer), *Tabebuia barbata* E. MEY. (*Bignoniaceae*, "Capitari", deciduous non-pioneer) and *Vitex cymosa* BENTH. (*Verbenaceae*, "Tarumã", deciduous non-pioneer).

Only adult, healthy trees were chosen which were situated between 21 and 27 m above sea-level (asl) and were subjected to a maximum water level of 7 m on the stem, which corresponds to a period of inundation of eight (*Cecropia latiloba* and *Vitex cymosa*), five (*Crateva benthami* and *Tabebuia barbata*) and four (*Senna reticulata* and *Nectandra amazonum*) months. Five trees per species were marked which were situated at the Costa do Catalão (Barranco and Fazenda Lira) in the vicinity of Manaus, Brazil, near the confluence of the Amazon (Solimões) River with the Negro River (approximately 3°S, 58°–60°W).

Climate and Hydrology

Rainfall is regularly distributed throughout the year, showing a marked dry season between June and September, and a rainy season from December to May. Mean annual rainfall ranges from 1700 to 2300 mm, and mean monthly temperature is between 26.3°C and 27.2°C. Variation of the river water level is markedly seasonal. The rising phase is between late December and early July, while the draining period lasts from the end of July to the end of November (Fig. 1). During the high water period, most deciduous trees lose their leaves.

Measurements

The study was performed between April 1994 and June 1995. 15 intact non-flooded sun-exposed leaves of each of five marked individuals per species were collected at monthly intervals in the field. Only fully expanded leaves from the lower canopy were chosen (MYERS & al. 1987), except for the months where only senescent or young leaves were present on the trees: then these were collected and measured. The collected leaves were transported in plastic bags on ice and in the dark to the Amazon Research Institute in Manaus (INPA) where they were washed with water and dried with a clean cloth before being measured. Leaf fresh weight was determined within maximum five hours after collection. The leaves were dried to constant weight (36 hours) at 60°C and then weighed for the determination of leaf dry weight. The temperature of 60°C was chosen because the same leaves were used for determinations of

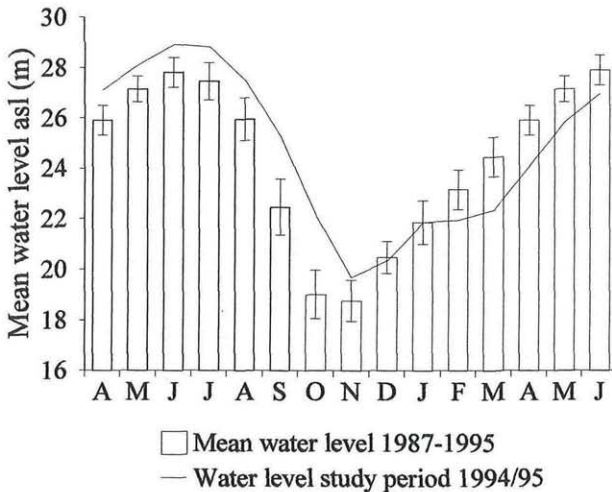


Fig. 1. Monthly water level above sea level (asl) of the Rio Negro measured at the port of Manaus: mean water level in the years 1987 to 1995 (bars) with standard deviation, and in the study period 1994/5 (line).

leaf nitrogen contents (PAROLIN & al. in press). Leaf water content was calculated by the difference between leaf fresh and dry weight. Leaf area was determined with a "leaf area meter" (ΔT Area Meter, Delta-T Devices). Specific leaf mass was calculated by leaf dry weight (g) per leaf area (m^2) (MEDINA 1983, HUANTE & al. 1992). Leaf age was determined by continuous phenological recordings on the marked trees and some leaves were marked individually after expansion to estimate their maximum age. Mean monthly leaf age was calculated as the monthly average age after leaf flush.

Statistics

Statistical analyses of variance (ANOVA) were performed with the computer programme 'SYSTAT', in order to test the significance of differences between terrestrial and aquatic phases for the measured parameters (specific leaf mass, leaf area, leaf water content, number of leaflets and leaflet size). The results were expressed as F-ratio and statistical probability P at an alpha-level of 0.05. The differences between the mean values of the terrestrial and the aquatic phase were expressed in %: the values of the terrestrial phase were set as 100 %, and the values of the aquatic phase were calculated as percentage differing from this.

Results

Specific Leaf Mass

Specific leaf mass in the non-flooded period varied between 48.8 gm^{-2} for the pioneer *Senna reticulata* and 118.9 gm^{-2} for the evergreen non-pioneer *Nectandra amazonum* (Table 1). In waterlogged months, specific leaf mass in an average was 5–33 % higher in all species. Only *Cratogeomys benthami* had significantly lower specific leaf mass with waterlogging.

Table 1

Specific leaf mass and leaf area of the six study species in the non-flooded and waterlogged months: minimum and maximum measured values, average of the measurements in the terrestrial phase, average of the measurements in the aquatic phase, with standard deviations, difference between terrestrial (= 100 %) and aquatic phase, F-ratio and statistical probability P (* $p \geq 0.05$; ** $p \geq 0.01$; *** $p \geq 0.001$; n.s. not significant).

Species	Specific leaf mass					
	Min – max [gm ⁻²]	Terrestrial phase [gm ⁻²]	Aquatic phase [gm ⁻²]	Diffe- rence [%]	F-ratio	P
<i>Cecropia latiloba</i>	43.8 – 112.7	74.6 ± 16	78.0 ± 17	4.6	0.81	n.s.
<i>Senna reticulata</i>	25.3 – 86.7	48.8 ± 11	64.8 ± 12	32.7	54.54	***
<i>Nectandra amazonum</i>	95.0 – 163.9	118.9 ± 14	140.1 ± 17	17.7	54.26	***
<i>Crateva benthami</i>	38.2 – 126.9	94.3 ± 24	80.5 ± 28	-14.6	8.11	**
<i>Tabebuia barbata</i>	33.4 – 133.5	76.3 ± 19	96.5 ± 23	26.4	16.14	***
<i>Vitex cymosa</i>	50.8 – 143.4	83.3 ± 19	106.9 ± 20	28.4	32.51	***
	Leaf area					
	Min – max [cm ²]	Terrestrial phase [cm ²]	Aquatic phase [cm ²]	Diffe- rence [%]	F-ratio	P
<i>Cecropia latiloba</i>	605 – 2380	1051.9 ± 113	1090.3 ± 122	3.7	0.39	n.s.
<i>Senna reticulata</i>	660 – 1588	805.4 ± 218	504.3 ± 262	-37.0	13.69	***
<i>Nectandra amazonum</i>	12 – 101	42.0 ± 12	52.3 ± 18	24.6	17.64	***
<i>Crateva benthami</i>	49 – 531	209.0 ± 81	131.7 ± 47	-37.4	31.49	***
<i>Tabebuia barbata</i>	89 – 670	371.1 ± 105	278.9 ± 122	-24.9	16.16	***
<i>Vitex cymosa</i>	88 – 663	262.1 ± 133	232.9 ± 93	11.1	1.89	n.s.

The new leaves – which were mainly produced in the aquatic period – had higher specific leaf mass than older leaves. In *Cecropia latiloba*, *Crateva benthami*, *Tabebuia barbata* and *Vitex cymosa* there was a constant increase of specific leaf mass in the first months after leaf expansion (Fig. 2).

Leaf Water Content

Leaf water content varied between 49 and 74 %. The evergreen pioneer species had the highest water contents, and the evergreen non-pioneer *Nectandra amazonum* the lowest (Table 2). In the flooded period, leaf water content was lower in all species. While differences were neglectable in *Cecropia latiloba* and *Nectandra amazonum*, where leaf water content was rather constant throughout the year, it changed significantly in the deciduous species and in the pioneer *Senna reticulata*. In all species, the new leaves had higher water contents than the adult and senescent leaves

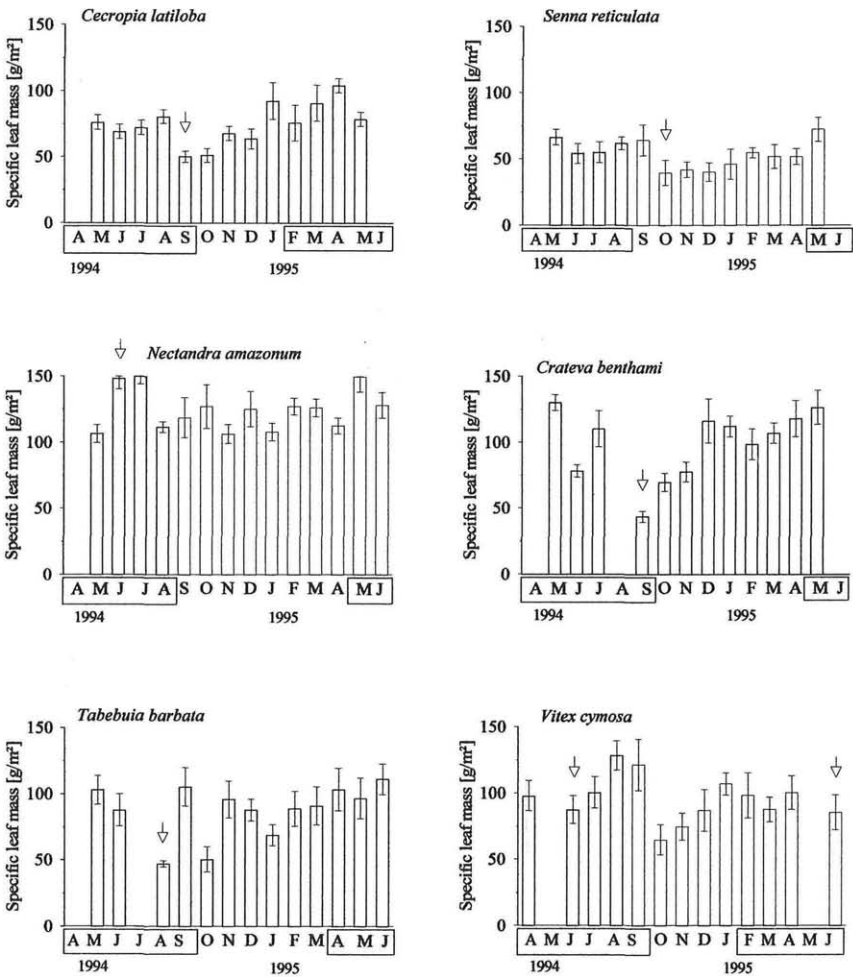


Fig. 2. Specific leaf mass in the annual cycle for the six species chosen. Mean monthly specific leaf mass with standard deviation between April 1994 and June 1995. Sample size per species and month (n) = 75. Months in box = aquatic phase. Arrow = flush of new leaves.

in the subsequent months. Since new leaves were flushed in the high water period, the absolute highest water contents were measured in the aquatic period, but overall means were lower in the flooded period.

Leaf Size

The size of single leaves varied between 12 cm² for *Nectandra amazonum* and more than 2380 cm² for *Cecropia latiloba* (Table 1). Three spe-

Table 2

Leaf water content of the six study species in the non-flooded and waterlogged months: minimum and maximum measured values, average of the measurements in the terrestrial phase, average of the measurements in the aquatic phase, with standard deviations, difference between terrestrial (= 100 %) and aquatic phase, F-ratio and statistical probability P (* $p \geq 0.05$; ** $p \geq 0.01$; *** $p \geq 0.001$; n.s. not significant).

Species	Min – max [g m ⁻²]	Terrestrial phase [g m ⁻²]	Aquatic phase [g m ⁻²]	Difference [%]	F-ratio	P
<i>C. latiloba</i>	55.2 – 83.3	73.6 ± 5	71.8 ± 5	-2.6	3.69	n.s.
<i>S. reticulata</i>	57.0 – 84.4	71.0 ± 5	64.5 ± 4	-9.2	49.89	***
<i>N. amazonum</i>	30.9 – 59.0	48.6 ± 4	48.5 ± 4	-0.2	0.03	n.s.
<i>C. benthami</i>	49.4 – 81.4	67.6 ± 5	61.5 ± 6	-9.1	31.02	***
<i>T. barbata</i>	30.3 – 80.8	62.7 ± 5	54.7 ± 11	-12.8	20.21	***
<i>V. cymosa</i>	44.8 – 90.8	62.7 ± 9	55.0 ± 7	-12.3	28.58	***

cies, the pioneer *Senna reticulata* and two deciduous non-pioneers (*Crateva benthami*, *Tabebuia barbata*), had highly significant reductions of leaf area (25–37 %) in the aquatic period, compared to the terrestrial period (Table 1). The other three species had increased leaf areas in the aquatic period, but only in *Nectandra amazonum* these differences were significant (+25 %).

In the annual cycle, *Cecropia latiloba* and *Nectandra amazonum* produced leaves with a more or less constant size, compared to the other species (Fig. 3). The new leaves of *Senna reticulata*, *Crateva benthami* and *Tabebuia barbata* increased their mean size for 3–4 months, and *Vitex cymosa* had a constant decrease of leaf size after the expansion of new leaves.

Number and Size of Leaflets

In the four species with compound leaves, the mean number of leaflets was lower in the aquatic period compared to the terrestrial period (Table 3). Mean leaflet size was 10–27 % lower in the aquatic period in all species (Table 3).

Senna reticulata had a maximum of 30 leaflets per leaf. This number sank to a minimum of 6 in leaves formed in the aquatic period, mostly because less leaflets were produced, but also because leaflets were lost with senescence and herbivory (Fig. 4). In *Crateva benthami*, *Tabebuia barbata* and *Vitex cymosa*, leaflet number was more constant, and changes were mostly due to the loss of leaflets with leaf senescence, and not because of the production of leaves with fewer leaflets.

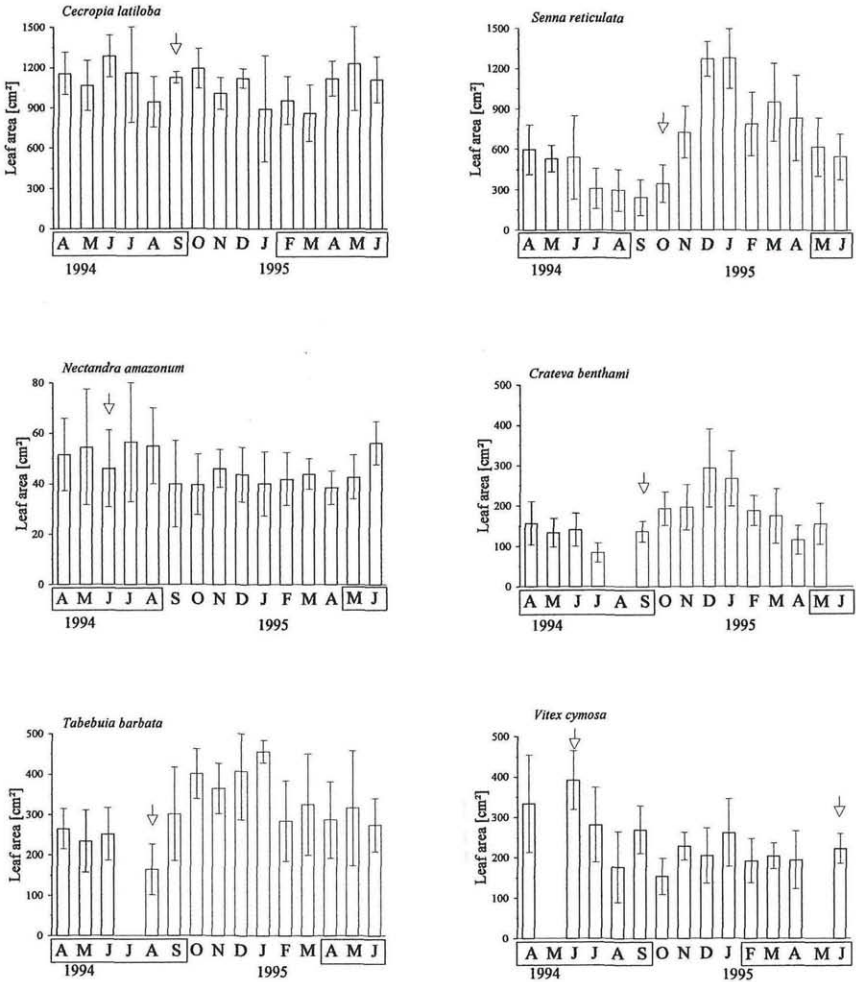


Fig. 3. Leaf area in the annual cycle in the six chosen species. Mean monthly leaf area with standard deviation between April 1994 and June 1995. Sample size per species and month (n) = 75. Months in box = aquatic phase. Arrow = flush of new leaves.

Discussion

Leaf specific mass and size, and their changes in the annual cycle, did not reflect the extreme environmental conditions to which trees in Amazonian floodplains are subjected. The hydric conditions in the floodplains are unfavourable for growth for several months every year, as indicated by regular growth reductions in the wood (WORBES 1989). Changes of leaf mass and size did occur in the annual cycle, average specific leaf mass was

Table 3

Number and size of leaflets of the four study species with compound leaves in the non-flooded and waterlogged months: minimum and maximum measured values, average of the measurements in the terrestrial phase, average of the measurements in the aquatic phase, with standard deviations, difference between terrestrial (= 100 %) and aquatic phase, for leaflet number: F-ratio and statistical probability P (* $p \geq 0.05$; ** $p \geq 0.01$; *** $p \geq 0.001$; n.s. not significant). Sample size (n) = 75.

Species	Min – max	Number of leaflets			F-ratio	P
		Terrestrial phase	Aquatic phase	Difference [%]		
<i>Senna reticulata</i>	6 – 30	21.1 ± 5.1	17.0 ± 6.7	-19.5	16.74	***
<i>Crateva benthami</i>	1 – 3	2.9 ± 0.5	2.5 ± 0.6	-11.7	25.76	***
<i>Tabebuia barbata</i>	3 – 7	5.0 ± 0.5	4.5 ± 0.7	-9.5	13.15	***
<i>Vitex cymosa</i>	3 – 7	5.0 ± 0.5	4.9 ± 0.8	-1.3	0.22	n.s.

	Leaflet size			F-ratio	P
	Terrestrial phase [cm ²]	Aquatic phase [cm ²]	Difference [%]		
<i>Senna reticulata</i>	38.2	29.7	-22.3	20.3	***
<i>Crateva benthami</i>	72.1	52.7	-26.9	35.5	***
<i>Tabebuia barbata</i>	74.1	62.0	-16.5	19.9	***
<i>Vitex cymosa</i>	52.4	47.5	-9.3	2.1	n.s.

higher in the waterlogged months in all except one species (*Crateva benthami*) although intraspecific variability was considerable as shown by the min-max values in Tables 1 and 2.

A relationship between the leaf parameters and the periodicity of flooding was not found in the study species, and the measured variations in leaf mass and size are not understood as adaptations. Leaf size has evolved to regulate leaf temperature, keeping it near an optimum for photosynthesis when the leaf is active and preventing thermal damage or death when the leaf is under stress (GIVNISH & VERMEIJ 1976). The reduction of the transpirational surface, i.e. leaf size, in periods of unfavourable hydric conditions could be an adaptation to the reduced tree water status induced by flooding (BORCHERT 1994). It enables the plant to maintain high photosynthetic activity despite prolonged waterlogging. Only in *Senna reticulata* the reductions of 37 % were a direct response to water stress: in the waterlogged months, the newly produced leaves and leaflets were smaller than those produced in the terrestrial period. Evidence for a reaction to waterlogging with the production of smaller leaves was given in an experiment with seedlings of *Senna reticulata* (Fig. 5, PAROLIN 2001). Since this species constantly produces new leaves, the production of smaller leaves under unfavourable conditions can be seen as adaptation against waterlogging. In the other five species, leaf production was not as fast as in

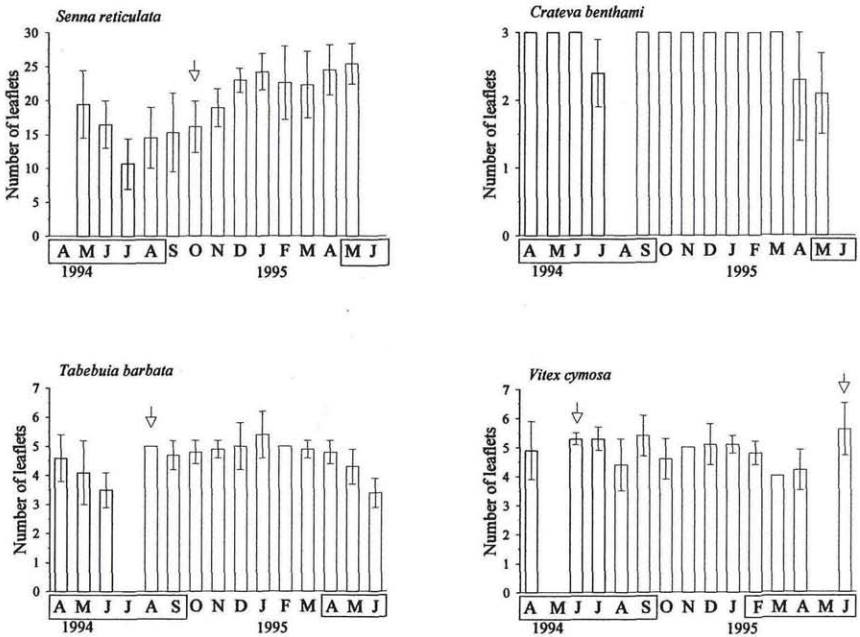


Fig. 4. Number of leaflets in the annual cycle in the chosen species with compound leaves. Mean monthly number of leaflets with standard deviation between April 1994 and June 1995. Sample size per species and month (n) = 75. Months in box = aquatic phase. Arrow = flush of new leaves.

Senna reticulata, and the newly produced leaves were not smaller. On the contrary, in *Nectandra amazonum*, and to a lesser extent in *Cecropia latiloba* and *Vitex cymosa*, in the flooded period a higher average leaf area was measured. This can be typical for highly flood tolerant species which have other physiological, morphological and anatomical adaptations to waterlogging than the regulation of leaf size (ANGELOV & al. 1996). A reduction of mean size of the single leaves in *Crateva benthami* and *Tabebuia barbata* was also related to leaf senescence and a consequent loss of leaflets. Increased herbivory played a role as well: many leaves were partially destroyed by caterpillars.

Leaf Age

Leaf age appears to play a major role for changes of leaf characteristics in the annual cycle. Leaf lifespan varies between the species, ranging from few months in *Senna reticulata* to probably two years in *Nectandra amazonum*. The other four species have leaf lifespans of about one year. Thus, leaves produced in the flooded period are present also in the terrestrial period in all species but *Senna reticulata*. In 23 Amazonian terra-

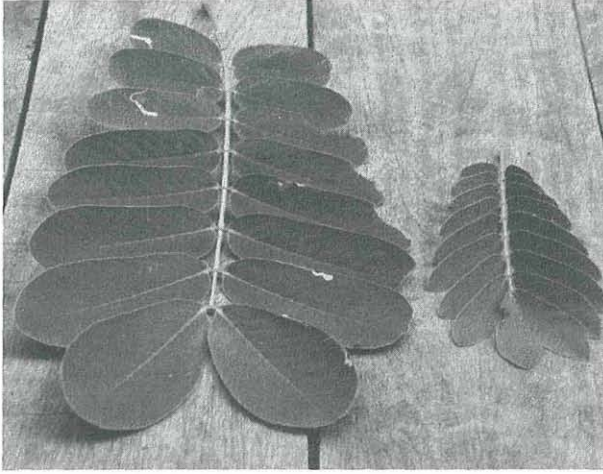


Fig. 5. Leaves of *Senna reticulata* after a flooding experiment (PAROLIN 2001): left leaf from well watered seedlings, right leaf from waterlogged seedlings (treatment lasting 12 weeks). The seedling age was the same in both treatments. Maximum width in the left leaf 26 cm.

firme tree species, leaf structural and functional characteristics like specific leaf area were highly correlated with leaf lifespan (REICH & al. 1991). Specific leaf area (cm^2g^{-1}) – the inverse of specific leaf mass – decreased with increasing leaf age in more than 100 species in distinct tropical and temperate biomes (MEDINA 1984, REICH & al. 1999). In the studied species, new leaves were flushed only towards the end of the flooded period, and leaf senescence occurred almost exclusively in the waterlogged months. Therefore average leaf age was higher in the aquatic than in the terrestrial period, and might be responsible for higher average specific leaf mass. It was especially high in the months prior to leaf shedding, although statistical evidence for the relationship between leaf specific mass and leaf age was found only in *Vitex cymosa* (Table 4). The same was due concerning leaf water content, which in new leaves was higher than in adult and senescent leaves.

Growth Strategies

Although leaves of pioneer and non-pioneer species (BAZZAZ 1991, RAAIMAKERS & al. 1995), and leaves of deciduous and evergreen species (MERINO & al. 1982, SOBRADO 1991, 1998) differ in a number of potentially important properties like drought stress tolerance, a uniform trend of leaf mass and size could not be detected in the study species. Four of the six study species have compound leaves, which are adaptive in warm, seasonally arid situations that favour the deciduous habit – as in *Crateva ben-*

Table 4

Influence of waterlogging and leaf age on specific leaf mass of the six study species:

F-ratio of the analysis of covariance considering leaf age as covariable, with statistical probability P (* $p \geq 0.05$; ** $p \geq 0.01$; *** $p \geq 0.001$; n.s. not significant), and significance of the differences between terrestrial and aquatic phase without considering leaf age.

Species	Waterlogging with covariable leaf age		Waterlogging
	F-ratio	P	P
<i>Cecropia latiloba</i>	2.74	n.s.	n.s.
<i>Senna reticulata</i>	16.75	***	***
<i>Nectandra amazonum</i>	5.05	*	***
<i>Crateva benthami</i>	27.04	***	**
<i>Tabebuia barbata</i>	294.56	***	***
<i>Vitex cymosa</i>	1.14	n.s.	***

thami, *Tabebuia barbata* and *Vitex cymosa* – and in light gap and early successional vegetation – as in *Senna reticulata* – where rapid upward growth and competition for light favor the cheap throwaway branch (GIVNISH 1978).

Leaf Types

The strong hydric changes in the annual cycle, with water deficit linked to submergence and drought, and additional high light intensity, did not cause a uniformity of leaf types, and of changes of their mass and size, as is the case in other extreme environments. A high diversity of leaf forms and sizes can be found among the study species, but also among other trees in the floodplains (pers. obs.). The finding of relatively low diversity of leaf types in tropical lowland rain forests of South America with entire margins, hard consistency, and mesophyll size (MEDINA & al. 1990) cannot be applied to the trees here. The typical mesophyll leaf size of approximately 20–180 cm² which are dominant in the rain forest (MEDINA 1983) are exceeded by far in five study species (all except *Nectandra amazonum*). Since leaf area is controlled by the availability of water and nutrients (RODERICK & al. 2000), perhaps the different leaf sizes found here indicate different tolerance to flooding among the study species. Plants are subjected to periods of water deficit, high light intensity and nitrogen deficiency in the floodplains, but they did not adapt with a rather uniform leaf form. In areas with mediterranean climate, or in the Amazonian 'bana' vegetation with poor soils, the vegetation has typical sclerophyllous leaves which are characterized by high specific leaf mass and high toughness, reduced leaf size, a thick cuticle and outer epidermal walls, and abundant sclerification (LOVELESS 1961, KUMMEROW 1973, SOBRADO & MEDINA 1980,

MEDINA & al. 1990, TURNER 1994). Leaf hardness is of value in relation to water relations chiefly by preventing collapse of the air spaces during desiccation and maintaining cuticular integrity (GRUBB 1986). The lower osmotic potentials at turgor loss point and higher turgor pressure of leaves with high specific leaf mass can be considered as adaptation to water deficits and indicator for drought tolerance (CAVELIER & GOLDSTEIN 1989). Only *Nectandra amazonum* had long-lived leaves with a sclerophyllous character. This species tolerates submergence without leaf shedding, in contrast to the other study species which lose their leaves under water and may have other adaptations to flooding and drought, e.g. leaf shedding, or the production of adventitious roots and lenticels (PAROLIN 2001). Detailed anatomical analyses of the leaves, the abundance of sclerenchyma, thickness of outer epidermal cell walls and cuticles, and leaf thickness are necessary to understand the adaptations to the environment (TURNER 1994, MEDINA & al. 1990). The only available anatomic descriptions of leaves from Amazonian floodplains indicate that the leaves of several species are hygromorphic with a big epidermic layer, thick cuticles and/or epicuticular waxes (WALDHOFF & FURCH 1998).

From an ecological viewpoint, greater leaf mass per area for 52 European woody species is interpreted by CASTRO-DIEZ & al. 2000 as greater allocation to support and defence functions, as shown predominantly by species from resource-poor environments. These findings should be tested for Amazonian floodplain species in a comparison between species from the nutrient-rich whitewater floodplains and the nutrient-poor blackwater floodplains, which have distinct floristics and ecological features, such as wood density and increments, seed mass, or seedling growth patterns (PRANCE 1979, PAROLIN & al. 1998, PAROLIN 2000 b, PAROLIN 2001).

Conclusions

The data of this study indicate a periodicity in several leaf traits which changes with leaf phenology and consequently leaf age. The phenological behaviour is linked to the flooding periodicity (WITTMANN & PAROLIN 1999), and therefore leaf characteristics are indirectly linked to the changing hydric conditions. The timing of the changes of specific leaf mass and leaf size was similar between species and was concentrated in the aquatic period, but the degree of changes differed among the species, and apparently they were closely linked to leaf age and can not be considered as adaptive to the changing hydric conditions.

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