

# 11 The Forest Ecosystem of the Floodplains

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## 11.1 Introduction

The Amazon floodplain forests are of special interest for botanical research due to the special physiognomy, the easy attainability of their margins and their exceptional environmental conditions. They were described in terms of their dominant and conspicuous tree species by Huber (1910), Ducke and Black (1953), Takeuchi (1962), and Hueck (1966). The hydrochemical differentiation of the Amazonian floodplains (Sioli 1954) into white-water (*várzea*) and black-water (*igapó*) inundation areas was confirmed at the botanical level by Prance (1979, 1989) and from a taxonomic point of view by Kubitzki (1989). Detailed forest inventories were carried out by Pires and Koury (1959), Keel and Prance (1979), Revilla (1981, 1990), Worbes (1983), and Campbell et al. (1986). Worbes et al. (1992) defined different forest communities of the *várzea* as successional stages.

Prance (1989) considered edaphic and hydrological aspects in his classification of inundation forests in tropical South America. Ranked by order of increasing length of inundation these classifications are the gallery forest, the floodplains, and the inundation forests (*várzea* and *igapó*). In this chapter *várzea* and *igapó* are combined and classified as floodplains according to the definition of Junk et al. (1989; Sect. 1.2).

## 11.2 Floristics and Forest Structure

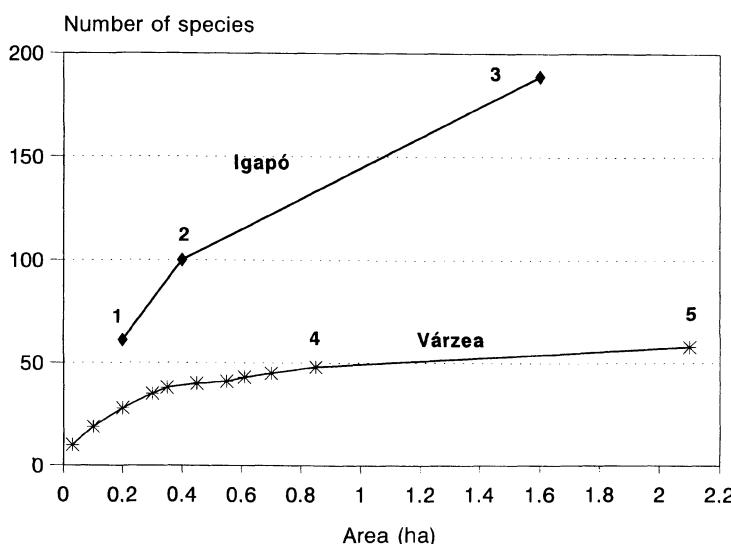
The following description of floristics and forest structure is based on 19 ha of forest inventories in the *igapó* and the *várzea* in Central Amazonia. Detailed information of methods, site conditions, and complete species lists of these inventories were given in Revilla (1981, 1990), Piedade (1985), Worbes (1986), Rankin-De Merona (1988), Ferreira (1991), Worbes et al. (1992). Study sites are described in Section 2.2.

### 11.2.1 Species Diversity

The description of diversity and the discussion of possible reasons for diversity patterns play an important role in the vegetation analysis of tropical forests (Gentry 1982; Prance 1989). There are several underlying problems with the estimation of diversity, i.e., how to choose plot size, dbh size (diameter at breast height) of the selected trees and the selection of stands with a homogenous vegetation structure. A widely accepted method for comparing diversity at different sites is to construct species-area curves.

Within plots with relatively homogenous site conditions and a homogenous vegetation structure the area-species curve flattens out for small plot sizes of 0.22 ha in an igapó stand (Keel and Prance 1979). No flattening point is visible when several igapó stands are considered (Fig. 11.1). The species-area curve of várzea stands at the Ilha de Marchantaria flattens out at about 0.5 ha with 40 species. Within a 12 km area on the same island in an additional 1.21 ha study site only ten new species occur (Fig. 11.1).

In the most diverse record in the várzea, 106 species were found in 1 ha at the Costa de Marrecão. In 10 ha at the same site and 5 ha at the Costa de Barroso the species-area curves flatten at between 2 and 3 ha at different



**Fig. 11.1.** Species area curves from igapó (1–3) and from várzea (4,5). New species were added to the number of species of the previous stand. Stand 1, Tarumá Mirim (Worbes 1983); stand 2, white sand, Negro River (Keel and Prance 1979); stand 3, Praia grande, Negro River (Revilla 1981); stand 4, from Ilha de Marchantaria, Lago Camaleão; stand 5, another stand from Ilha de Marchantaria, Central Lake

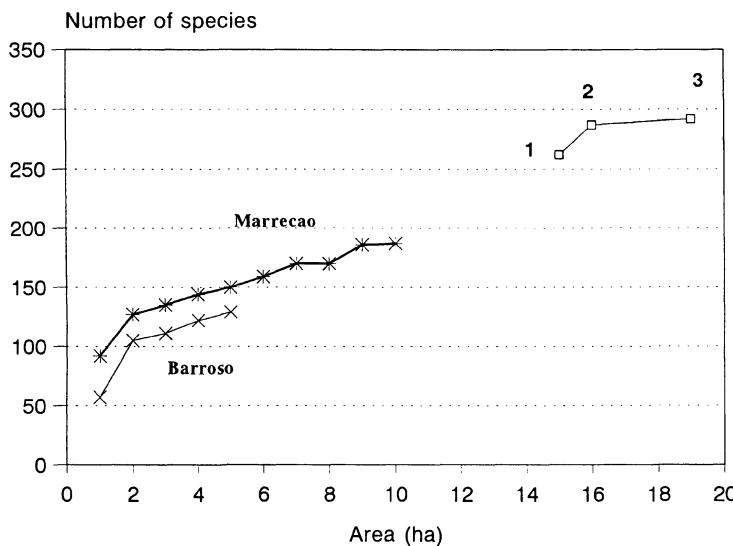


Fig. 11.2. Species area curves for várzea forests from ten 1 ha plots at the Costa de Marrecão, five 1 ha plots at the Costa de Barroso. 1, Combination of Costa de Marrecão and C. de Barroso; 2, additional stand at the Ilha de Carreiro; 3, additional stands at the Ilha de Marchantaria

levels of species numbers, respectively (Fig. 11.2). The species inventory of the two sites differs by approximately 60 species and shows more than 250 species in total. Additional stands at the Ilha de Marchantaria and at the Ilha de Careiro increase the total number of species slightly (Fig. 11.2).

Keel and Prance (1979) and Worbes (1983, 1986) counted in small igapó plots of 0.22 and 0.21 ha 54 and 61 species, respectively. This is almost twice the number of species found on plots of comparable size in the várzea. A total of 292 species are found on 19 ha of várzea forests in the vicinity of Manaus between the Costa de Marrecão (near the city of Manacapuru) and the Ilha de Carreiro (near Manaus). About 200 species were counted on 1.4 ha of investigated igapó forests.

There is not much available information on the neotropical inundation forests outside of Central Amazonia. Most information is on várzea forests. There are 53 species  $\text{ha}^{-1}$  in a tidal várzea forest at the Guamá River, Pará (Pires and Koury 1959), 109 species  $\text{ha}^{-1}$  in a várzea forest at the Tefé River (Ayres 1993) and 149 species  $\text{ha}^{-1}$  at the Napo River, Ecuador (Balslev et al. 1987). Tuomisto (1993) sampled in gallery forests of the white water rivers in the Peruvian foothills of the Andes and found 306 species in an undefined area. On non-flooded sites (terra firme) in the vicinity of Manaus, figures vary between 65 and 176 species  $\text{ha}^{-1}$  (Klinge and Rodrigues 1968; Prance et al. 1976). Gentry (cited in Balslev et al. 1987) counted between 179

and 285 species of trees per hectare in Amazonian Peru. Investigations in floodplain forests and adjacent terra firme stands at the Napo River, Ecuador (Balslev et al. 1987) and at the Xingú River, Brazil (Campbell et al. 1986) show in both cases a higher diversity in the non-flooded areas.

The data suggest that species diversity in igapó forests is higher than in várzea forests. On a local scale, diversity in floodplain forests is lower than in regional neighbouring terra firme forests. Diversity tends to increase in the Amazon basin from east to west in both flood-plains and adjacent terra firme sites.

### 11.2.2 Floristic Relationships Between Amazonian Várzea, Igapó and Terra Firme

Lists of common tree species of igapó and várzea differ considerably depending on the view point of the respective author. Under aspects of taxonomy and species distribution, (Kubitzki 1989), economic interest (Klenke and Ohly 1993) and general descriptions (Prance 1989) the most often cited species are *Ceiba pentandra*, *Hura crepitans*, *Nectandra amazonum*, and *Cecropia* spp. for the várzea, and *Aldina latifolia*, *Swartzia* spp., *Parkia discolor* for the igapó. Abundant species of the igapó are listed in Table 11.1, and abundant species of the várzea are listed in Table 11.2.

The different species compositions in várzea, igapó and the terra firme are traced back to differences in the hydrological regime and, in the case of the floodplain ecosystems, to water chemistry (Kubitzki 1989; Prance 1989). However, the more important factor for plant growth is the soil type. Considerable differences in soil type and soil chemistry occur between várzea and igapó and within the igapó between the sites Tarumã Mirim and Anavilhanas. The content of total phosphorus increases from 13 ppm in the Anavilhanas to 130 ppm at the Tarumã Mirim and to 530 ppm on the Ilha de Marchantaria in the várzea. In other tropical forests the differentiation of vegetation is traced back to differences in P contents of the soil (Tilman 1982).

Nevertheless some tolerant species, i.e., *Alchornea castaneaefolia*, *Tabebuia barbata*, *Piranhea trifoliata*, *Triplaris surinamensis*, *Macrolobium acaciifolium* and others are common in both floodplain forests. Moreover a number of species especially from várzea forests also occur on the terra firme near Manaus, e.g., *Mabea caudata*, *Heisteria spruceana*, *Minquartia guianensis*, *Pithecelobium jupumba*, and *Vatairea guianensis*. Representatives from all leading families of the terra firme (Gentry 1990) are also found in the floodplain forests (Fig. 11.3). Studies on terra

**Table 11.1.** Distribution of abundant and frequent species in the igapó

Stand No:	1	2	3	4	5	6	7	8	9	10	11
Species											
A <i>Borreria capitata</i>	[30]										
<i>Dalbergia inundata</i>	5										
<i>Pithecellobium adiantifolium</i>	15	19	9								
<i>Myrciaria dubia</i>	12	19	6								
<i>Eugenia chachoeriensis</i>		9	9								
<i>E. chrysobalanoides</i>		19	34								
<i>Schistostemon macrophyllum</i>			10								
B <i>Couepia paraensis</i>	9			6	8		+	+	+		
<i>Leopoldinia pulchra</i>	+	+	6			+	+	+	16		
<i>Anacampa rupicola</i>	+		9			+	5			5	
<i>Licania apetala</i>	+				5	+			15		
<i>Himatanthus attenuatus</i>	+	+		+		+	+	+	+	+	
C <i>Malouetia furfuracea</i>				17	+	+	+	+	+		
<i>Mollia speciosa</i>	+			12			+	+			
<i>Duroia velutina</i>	+			6					+		
<i>Neoxythecace elegans</i>				6	+	7	+	+			
<i>Quiina rhytidopus</i>				11			+				
<i>Eschweilera tenuifolia</i>				7			+				
<i>Myrciaria floribunda</i>				8	+			+			
<i>Acmanthera latifolia</i>				10		11	+				
<i>Hevea spruceana</i>				7		7	+		+	+	
<i>Alchornea schomburgkiana</i>				+	53						
<i>Macrolobium acaciifolium</i>					11						
<i>Mabea nitida</i>				+	6	+	+		+	+	
<i>Maprounea guianensis</i>				+	5	+					
D <i>Swartzia argentea</i>							+	+	+	+	
<i>Swartzia polyphylla</i>							+	+	+	+	
<i>Tabebuia barbata</i>							+	+	+	+	
<i>Psychotria lupulina</i>							+	5	5		
<i>Caraipa grandiflora</i>							+	6		+	
<i>Eschweilera parvifolia</i>							+	5		+	
<i>Virola elongata</i>							+	7		5	
<i>Ferdinandusa rudgeoides</i>								+	5	+	
<i>Parkia discolor</i>								+	+	+	
<i>Aldina latifolia</i>								+	+		5
<i>Penthaelethra macroloba</i>											10
<i>Astrocaryum jauari</i>								5	+		66
<i>Calophyllum brasiliense</i>											5

Figures give rel. density (%) in the respective stand; +, density below 5%.

Stands 1–3, white sand; stands 4–11 clay.

Stands 1–4, long-lasting inundation (>260 days/year); stand 5, 200–260 days/year; stands 6 and 7, 150–200 days/year; stands 8 and 9, 75–150 days/year; stands 10 and 11, 25–75 days/year.

Stands 2 and 3 from Rio Negro near Manaus (Keel and Prance 1979).

Stands 1 and 9 from Rio Negro, Praia Grande (Revilla 1981).

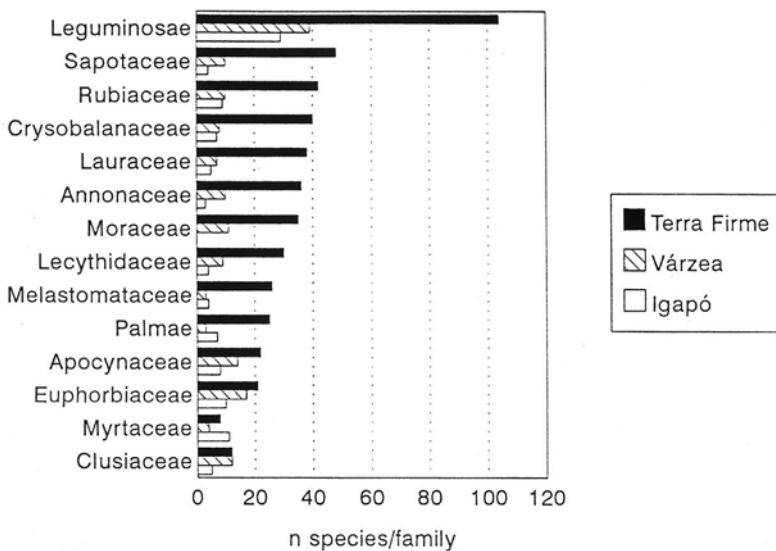
Stands 5, 7, 8, and 10 from Tarumã Mirim (Ferreira 1991).

Stands 4, 6, and 11 from Rio Negro, Anavilhanas (Piedade 1985).

Species group A, low-level community on white sand; species group B, tolerant to different site conditions; species group C, low-level community on clay; species group D, mid-level and high-level community on clay.

**Table 11.2.** Várzea species of low-level shrub communities (Junk 1989), mid-level forest communities (Worbes et al. 1992) and 12 important species from a 10-ha record of a high-level forest community at the Costa de Marreacão. (Revilla 1991)

Low-level shrub community	Mid-level community	High-level forest community
<i>Coccoloba ovata</i>	<i>Casearia aculaeta</i>	<i>Ceiba pentandra</i>
<i>Eugenia inundata</i>	<i>Cecropia latiloba</i>	<i>Hevea spruceana</i>
<i>Ruprechtia ternifolia</i>	<i>Crescentia amazonica</i>	<i>Licania heteromorpha</i>
<i>Symmeria paniculata</i>	<i>Ilex inundata</i>	<i>Malouetia furfuracea</i>
	<i>Labatia glomerata</i>	<i>Manilkara amazonica</i>
	<i>Laetia corymbulosa</i>	<i>Olmedioperebea sclerophylla</i>
	<i>Macrolobium acaciifolium</i>	<i>Piranhea trifoliata</i>
	<i>Nectandra amazonum</i>	<i>Pseudobombax munguba</i>
	<i>Pseudobombax munguba</i>	<i>Pterocarpus amazonum</i>
	<i>Tabebuia barbata</i>	<i>Rollinia exsucca</i>
	<i>Vatairea guianensis</i>	<i>Tapura amazonica</i>
	<i>Vitex cymosa</i>	<i>Virola surinamensis</i>



**Fig. 11.3.** Number of tree species in 12 species-rich families in the Amazonian terra firme (Gentry 1990) in várzea and in igapó

firme and adjacent floodplain forests in the wider Amazon region show concurrences of 18% (Balslev et al. 1987) and 45% (Campbell et al. 1986) at the species level. Taxonomic and chorological investigations (Kubitzki 1989; Prance 1989) show that in general the flora of the igapó is closely related to the flora of the nutrient-poor savannas. On the other hand, close

connections are visible between the flora of the várzea and the flora of more fertile sites on the terra firme.

Many of the tree species from Central Amazonian inundation forests have a wide geographic distribution. Quite a few of them, e.g., *Hura crepitans*, *Casearia aculeata*, *Unonopsis guatteroides* or *Pseudobombax munguba*, are distributed throughout the Neotropis (Prance and Schaller 1982; Prance 1989). There is, however, a recognizable differentiation between those species distributed throughout all of northern South America and those that are found in the eastern or in the western Hylaea (Kubitzki 1989).

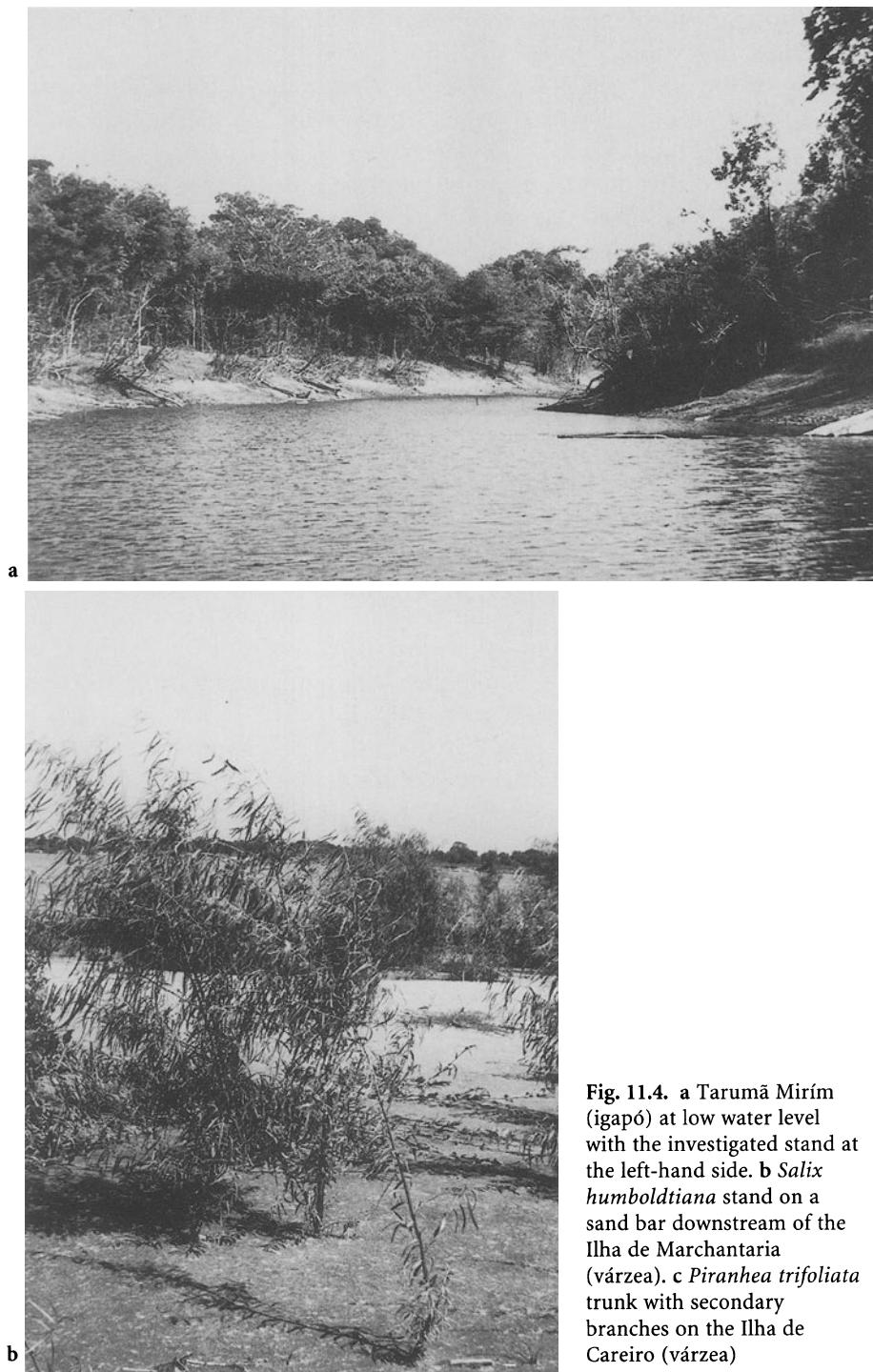
### 11.2.3 Plant Communities and Site Conditions in the Igapó

Most of the vegetational records from the igapó were carried out with regard to the flood gradient. Keel and Prance (1979) and Revilla (1981) give relative positions of recorded subplots or communities with respect to elevation. Piedade (1985), Worbes (1986) and Ferreira (1991) used planimetry to find the actual water level of the Negro River sites. This information together with the daily water level record in the harbour of Manaus makes it possible to calculate the length of inundation in any year or for longer periods of time (Worbes 1985; Junk 1989; Sects. 2.3, 8.2.1).

Besides the flood regime the soil type has been taken into consideration for all records. Two different soil types are distinguishable at the lower Negro River and its small tributaries. The soil is nutrient-poor white sand near the margins of the low level river. At some distance from the low-level shore line the soil is at least 50% clay (Worbes 1986).

We can differentiate between plant communities according to different site conditions (Table 11.1). There is a distinct difference between the species composition on sand and the species composition found in the clay. On clay soils a further differentiation can be made between a low-level community exposed to more than 150 days of annual inundation, a mid-level community with annual inundations between 75 and 150 days and a high-level community which is inundated for less than 3 months. Transitions between these communities are gradual. It is remarkable that a number of species, e.g., *Couepia paraensis*, *Leopoldinia pulchra*, *Anacampa rupicola* and others, are tolerant of long-lasting inundation, very poor soil conditions of the white sand as well as to poor light saturation at the forest floor of the high-level forest community.

According to changes in species composition the structure and the physiognomy of the vegetation change along the flood gradient. On both soil types at sites with a long-lasting mean annual inundation of about 250



**Fig. 11.4.** a Tarumã Mirim (igapó) at low water level with the investigated stand at the left-hand side. b *Salix humboldtiana* stand on a sand bar downstream of the Ilha de Marchantaria (várzea). c *Piranhea trifoliata* trunk with secondary branches on the Ilha de Careiro (várzea)



Fig. 11.4C

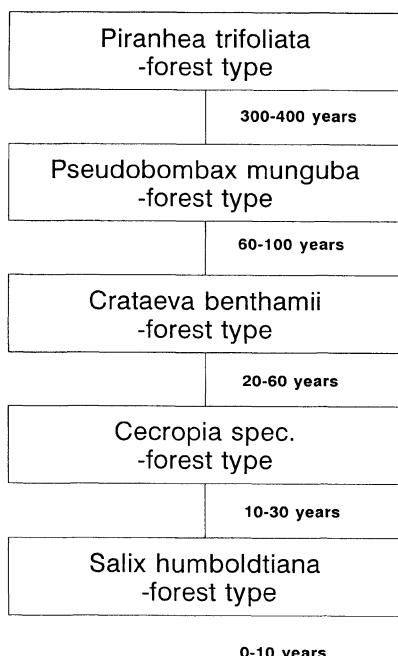
days, the vegetation is composed of relatively few shrubs and small trees of a maximum height of 10 m. This vegetation type turns gradually into a well-structured and diverse forest at inundation levels of less than 200 days year<sup>-1</sup>. At the Tarumã Mirim River site (Fig. 11.4a) the mid-level community is dominated by mighty buttressed trees of *Aldina latifolia* and associated species with a maximum height of 30 m. At the forest floor the herb *Ischnosyphon ovatus* is conspicuous beneath a high number of shrub species. The appearance of *Selaginella stellata* at the forest floor indicates the transition to the never-flooded terra firme (Adis 1984).

#### 11.2.4 Plant Communities and Site Conditions in the Várzea

*Zonation in the Várzea.* The influence of the length of the inundation period on species composition of the várzea forests is often mentioned (Hueck 1966; Junk 1989) (Sect. 8.2). At low-lying sites at the 19.5-m level, which were exposed to inundations 300 days year<sup>-1</sup> on average and fre-

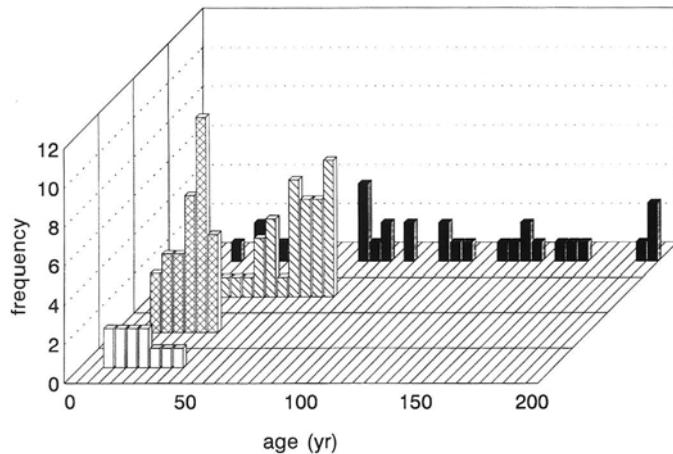
quently experienced in three consecutive years, Junk (1989) found stands of dead shrub communities. At slightly elevated sites (between 20 and 21 m) shrub species may persist. The lower tree line in the várzea is located where average annual inundation is 230 days (22 m). Among others the tree species *Piranhea trifoliata* and *Vitex cymosa* are often found in very low lying locations. In contrast, *Ceiba pentandra* and other species colonize less frequently in shortly flooded areas (Hueck 1966). A species list of low lying shrub communities and a high lying community from a 10-ha record at the Costa de Marrecão is given in Table 11.2.

**Successional Differentiation in Várzea Forests.** Different várzea stands at the same flood level can be dominated by different tree species. Pure stands of *Cecropia* ssp. or *Salix humboldtiana* are frequently distributed at the river margins, the latter also dominate young sand bars (Fig. 11.4b). On sand bars the trees are exposed to high annual sedimentation rates of 50 cm or more. *Salix humboldtiana* tolerates high sedimentation stress by annually forming new root layers at the soil surface to avoid hypoxic conditions in the root zone. The typical tree of the medium sized Marchantaria island is *Pseudobombax munguba*. On the large Careiro island and at the Costa de Marrecão *Pterocarpus amazonum* and *Piranhea trifoliata* are conspicuous and very frequently found (Fig. 11.4c).

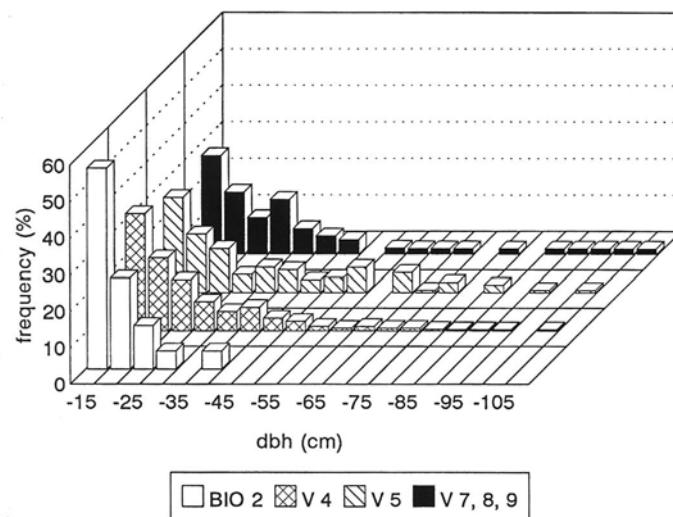


**Fig. 11.5.** Successional pattern of várzea forest types. Approximate time spans of development of the stages are indicated between the boxes. (After Worbes et al. 1992)

Worbes et al. (1992) used an analysis of the species inventories of nine stands located on similar elevations and therefore under equal flood stress to show that different groups of tree species dominate at different sites (Fig. 11.5). Age datings of the dominant trees by means of tree-ring analysis, as described below, showed considerably different age structures for the investigated stands (Fig. 11.6a). The dominating species groups can be differentiated by features such as life span, growth rates and wood density. The



a



b

**Fig. 11.6a,b.** Age structure (a) and distribution of diameter classes (b) of trees in four forest types in the várzea. (*Bio 2, V4, V5* Young forest stands on the Ilha de Marchantaria. *V7–V9* Climax forest stands at the Costa de Marrecão and on the Ilha de Careiro

young stands are dominated by trees with characteristics that are typical of pioneers (Swaine and Whitmore 1988), i.e., low life expectancy, fast growth and low wood density (*Salix humboldtiana*, *Cecropia* ssp., *Pseudobombax munguba*, *Macrolobium acaciifolium*). The oldest stands are dominated by trees with converse features (*Piranhea trifoliata*, *Manilkara* sp., *Tabebuia barbata*).

The presence of tree species with opposing life-history strategies supported by the differences in age structures of the stands allows us to define the investigated stands as a successional time series (Fig. 11.5). The features of the defined successional stages in the várzea also occur in Central American forests (Budowski 1961) as well as in the European floodplain forests (Carbiener et al. 1988).

The initial stage of primary succession in floodplain habitats is dominated by high growing grass communities (Ellenberg 1988) (Sect. 8.2.3). The following pioneer forest community is dominated by representatives of the genus *Salix* (Worbes et al. 1992). Pioneer stages are followed by the "early secondary" stage (Budowski 1961), which is characterized by a species-poor formation dominated by *Cecropia* sp. (examples in Martius 1989). The *Crataeva benthamii* community (stand 4) is analogous to the young "late secondary" stage described by Budowski (1961). This stage soon undergoes a transition to the *Pseudobombax* forest type (stand 5). The *Pseudobombax munguba* community represents the beginning of a dynamic stage between the "late secondary" and the climax community (Hallé et al. 1978). By this time the fast growing dominant species *P. munguba* has reached its maximum age and is eventually replaced by slower growing species from the lower forest canopy. The *Piranhea trifoliata* community (stands 6, 7, 8) represents the typical climax forest. This community is dominated by dense-wood emergents with multisecular rotation and subdominants with a shorter life span.

In general, the successional sequence from pioneer to climax forest is characterized by a decrease in radial growth rates and an increase of wood density of the dominant trees. The division into "light-wood" and "dense-wood" associations of European floodplain forests (*Populion albae* vs. *Ulmenion* with *Quercus*) was originally explained by different degrees of flood tolerance among species. Recently this diversification is interpreted as a consequence of successional development (Carbiener et al. 1988; Ellenberg 1988).

*Structural Changes During Dynamic Development.* The shift in species composition from pioneers to species of climax forests during a successional time sequence is accompanied by basic structural changes (Fig. 11.6b). Along the age gradient the diversity increases continuously from

monospecific stands to stands with about 100 species  $\text{ha}^{-1}$  (Crow 1980). Tree density declines from a maximum of some 1000 stems  $\text{ha}^{-1}$  at the age of about 10 years to 500–700 stems  $\text{ha}^{-1}$ . Biomass increases in the same order. A similar development for the relationship of density to biomass is observed in temperate zones and is known as a self-thinning process (White 1981). The distribution of diameter classes changes rapidly from a high percentage of small diameters in the youngest stand to J-shape distribution observable in any forest community (Fig. 11.7). The differences between the stands that are older than 40 years are very small. Comparison with the age structure of the same stands shows that the age of the stands cannot be determined from diameter development.

According to other tropical forests, the várzea forest appears well structured into different crown layers. The frequency polygon diagrams of tree heights in an 80-year-old stand on the Ilha de Marchantaria shows five crown layers (Fig. 11.8). The layers are composed of trees of different species. Shrubs and trees shorter than 10m in height are *Psidium acutangulum*, *Trichilia singularis*, *Pithecelobium inaequale* and *Pseudoxandra polyphleba*, from 10 to 20m *Crataeva benthamii*, *Ilex inundata*, *Sorocea duckei* and *Vitex cymosa* occur. *Laetia corymbulosa*, *Triplaris surinamensis* and *Eschweilera* sp. can grow to a height of 25 m and

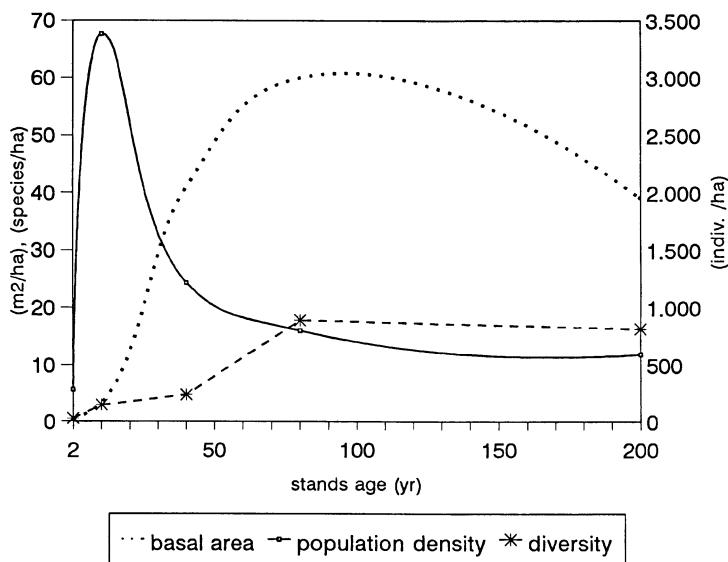


Fig. 11.7. Development of basal area, diversity and tree density along a successional time series in the várzea. Forest stands of different ages are treated as a successional sequence. (Worbes et al. 1992)

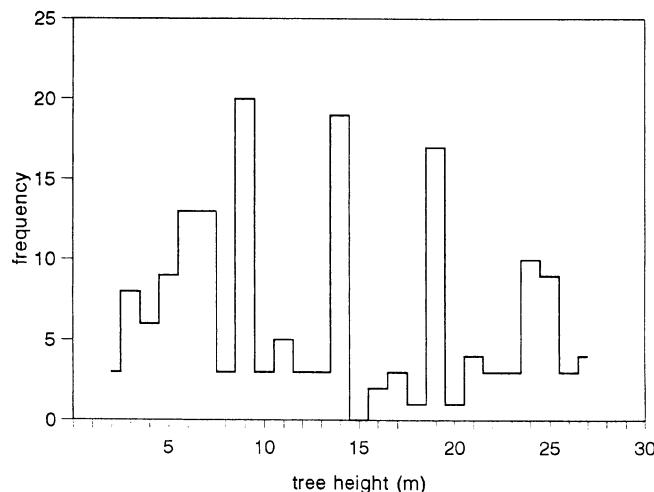


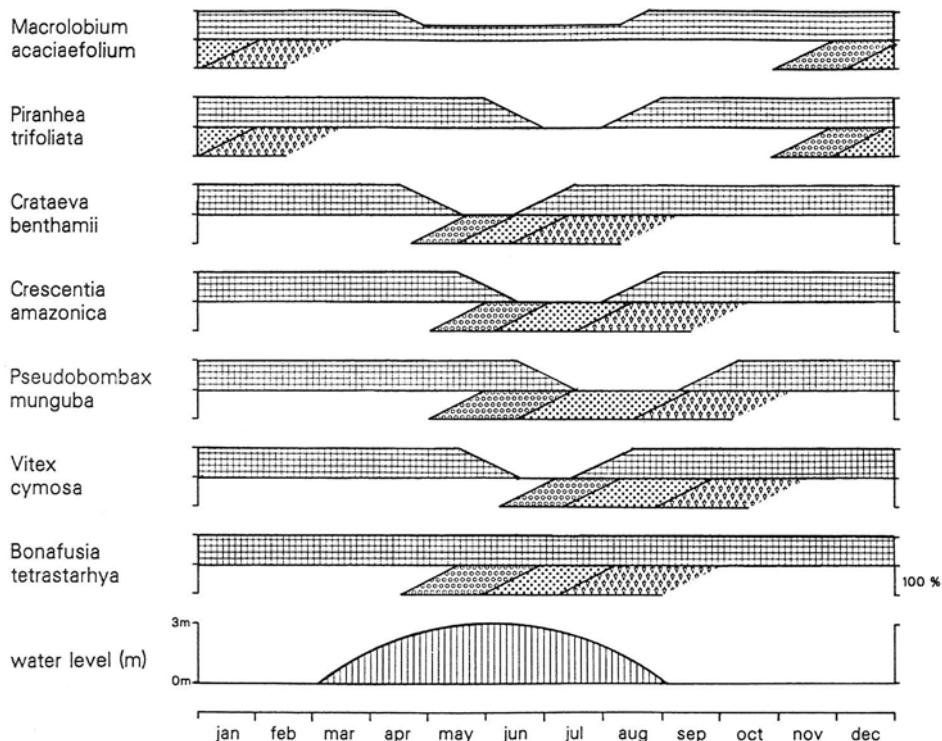
Fig. 11.8. Frequency polygon plot of tree heights measured in an 80-year-old stand on the Ilha de Marchantaria. Five crown layers are indicated by the peaks of the frequency curve

*Pseudobombax munguba* dominates the crown layer with a maximum height of 30 m.

## 11.3 Responses to the Flood Pulse

### 11.3.1 Leaf-Fall Behavior

The casual observer easily recognizes that in the várzea many conspicuous tree species, e.g., *Vitex cymosa*, *Pseudobombax munguba* and others, are defoliated at the end of the submersion phase (Fig. 11.9). The igapó forest seems to be composed more of evergreens (Worbes 1983). A more detailed analysis shows that evergreen and deciduous species exist in both habitats. Species may shed their leaves at the beginning or at the end of the submersion phase. In the igapó a maximum of leafless species is observed during the end of the aquatic phase (Fig. 11.10). In the várzea the maximum leaf fall is observed during the aquatic phase with a smaller peak in November (cf. Fig. 11.21). In the várzea, the outbreak of new leaves may occur when the trees are still flooded (*Crataeva benthamii*, *Vitex cymosa*; Fig. 11.9) or at the beginning of the rainy season in November or December (*Ilex inundata*). Two distinct peaks of leaf flush were observed in igapó stands at Praia Grande (Fig. 11.10). One is in August–September when the water runs

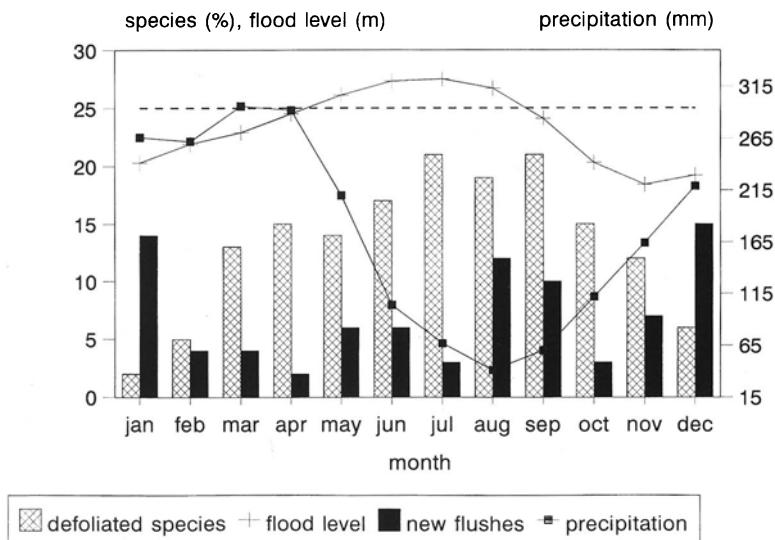


**Fig. 11.9.** Phenology of tree species in the várzea. Cross hatches, Percentage of foliage; open circles, flowering; points, fruiting; triangles, fruit fall. Below, Water level in 1981 in the stand V5 at the Ilha de Marchantaria

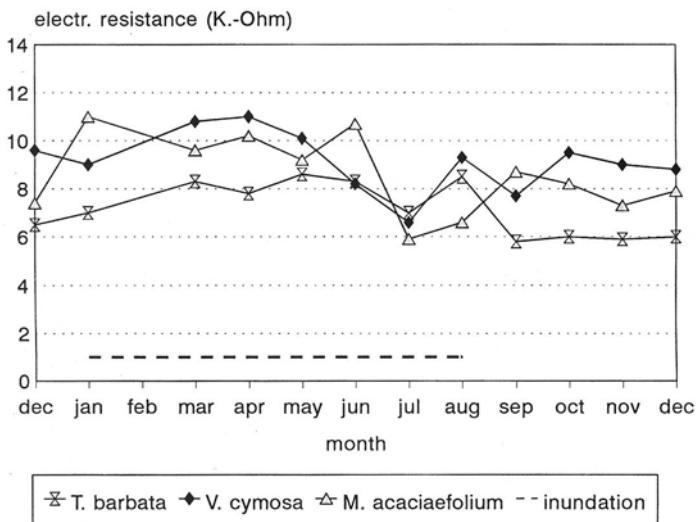
out of the forests. The second is in November and December at the beginning of the rainy season. The peaks of leaf fall and new flushes in November–December may be a reaction to the rapidly drying soil during the months between the end of the aquatic phase and the beginning of the rainy season (Worbes 1986).

### 11.3.2 Periodical Growth of Roots, Wood and Shoots

The electrical resistance of the cambium can be interpreted as the conductivity of the cambium and therefore as cambial activity (Shigo and Shortle 1985). Cambial activity of trees in the várzea measured throughout one year shows lower activity values during the aquatic phase than during the non-flooded period (Fig. 11.11). A small peak of high values was observed during the end of the aquatic phase, probably due to the beginning of flowering or the outbreak of new leaves.



**Fig. 11.10.** Percentage of completely defoliated tree species and percentage of species with new flushes from 95 investigated species in total at the Praia Grande, Rio Negro (igapó) adopted from Revilla (1981). Monthly precipitation (right y-axis) and flood level of the Rio Negro are included. The mean elevation at the stand is 25 m a.s.l. and marked with a dotted line



**Fig. 11.11.** Cambial resistance in *Tabebuia barbata*, Bignoniaceae ( $n = 1$ ), *Vitex cymosa*, Verbenaceae ( $n = 2$ ) and *Macrolobium acaciifolium*, Caesalpiniaceae ( $n = 3$ ) from the Ilha de Marchantaria, várzea from December 1986 until December 1987. High values of resistance indicate low cambial activity and vice versa. The dotted line marks the aquatic phase at the investigation site

The low cambial conductivity in trees lasted throughout several months of the aquatic phase, indicating a cambial dormancy. The dormancy is also reflected by the existence of annual rings in the wood of most species of the inundation forests (Worbes 1985, 1986). Different species were marked by cambial woundings (Mariaux 1967) some weeks before the beginning of the aquatic phase and were felled later (Fig. 11.12). Wood production stopped shortly after water covered the roots of the tree. This proves the existence of annual rings in most trees of várzea and igapó. Annual growth periodicity was proven independently by radiocarbon datings of individual growth zones using the nuclear weapon effect (Worbes and Junk 1989). The increase of  $^{14}\text{C}$  in the atmospheric CO<sub>2</sub> in the 1950s and early 1960s had worldwide effects with an equal increase in the radiocarbon concentration of the wood of trees. The annual variations of  $^{14}\text{C}$  concentration in the growth zones serve as an artificial marker for age dating. Measurements of the ring widths of species with distinct growth zones (Worbes 1985) as well as density estimations of tree-ring series (Worbes et al. 1995) show that the

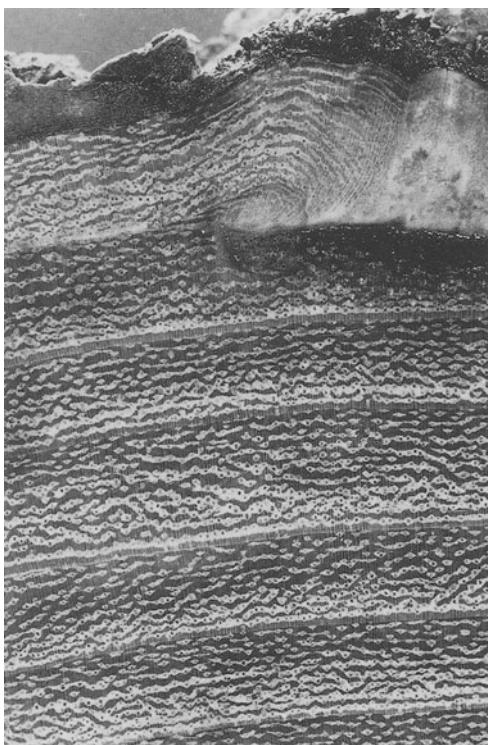


Fig. 11.12. Annual rings and scars from cambial woundings in the wood of *Tabebuia barbata*, Bignoniaceae from the várzea

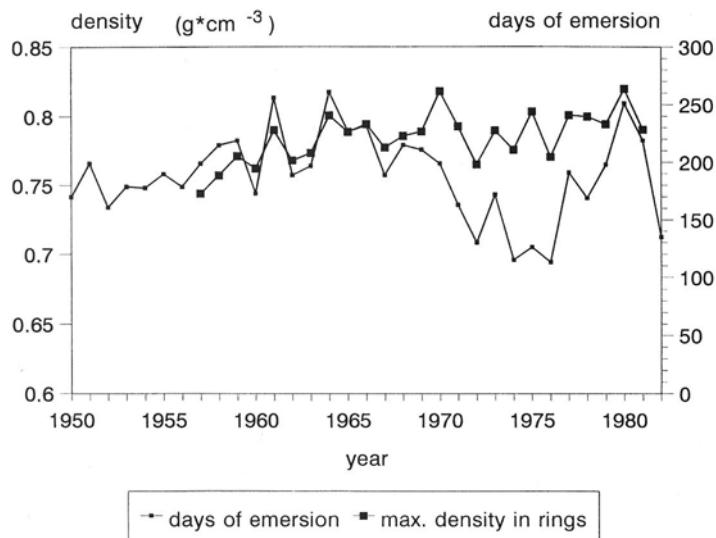


Fig. 11.13. Time series of maximum wood density in annual rings from várzea trees and time series of duration of annual terrestrial phases. The mean density curve is calculated from mean tree curves ( $n = 2$ ) of four species. (Worbes et al. 1995)

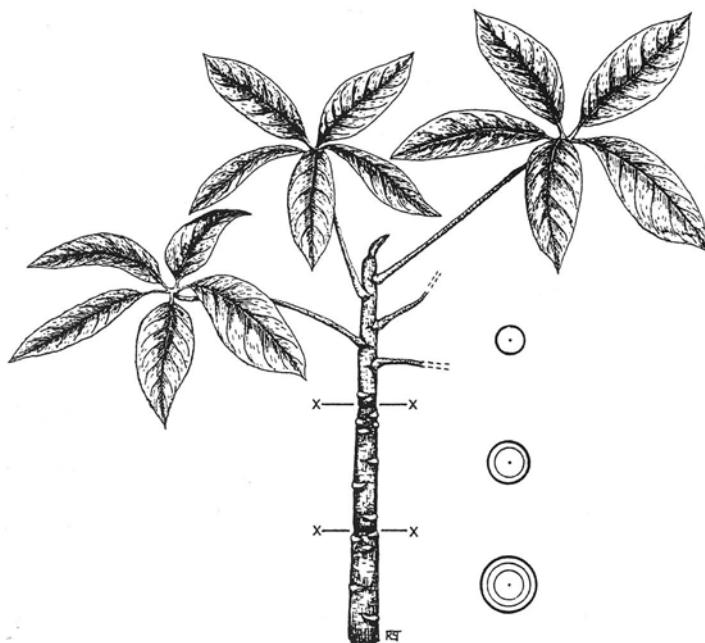


Fig. 11.14. Annual shoot growth in *Pseudobombax munguba*, Bombacaceae, várzea. Distinction between annual shoots is marked with x-x. Cross section with annual rings of the respective shoots is indicated at the right-hand side

widths of the rings and the maximum density are dependent on the length of the terrestrial phase (Fig. 11.13). From the investigation of the occurrence of distinctiveness of growth zones of 82 tree species from the igapó and the várzea we found 67 species have distinct growth zones allowing us to determine the age of individual trees. Fourteen species showed indistinct rings; in *Aldina latifolia* no definite ring structure could be detected.

In congruence with the annual periodicity of radial growth an annual shoot extension can be expected. This congruence is well known for the temperate zones (Rauh 1939). For tropical trees only two positive examples were given by Hallé and Martin (1968) and Gil (1989). Periodical shoot extension can easily be proven by comparison of the number of rings and the number of shoot segments limited by characteristic scars (Fig. 11.14). Six of seven investigated tree species from igapó and várzea show an annual rhythm of shoot extensions (*Pseudobombax munguba*, *Psidium acutangulum*, *Salix humboldtiana*, *Macrolobium acaciifolium*, *Cecropia latiloba* and *Zanthonoxylum compactum*). *Bonafusia tetrastarhyia*, a shrub species in the understory, has very indistinct growth zones. The existence of annual growth periodicity and the presence of annual rings in woody plants allows us to use tree-ring patterns as a tool for ecological analysis ranging from age determinations to the investigation of growth rates and growth behaviour under different ecological conditions, as shown in the preceeding sections.

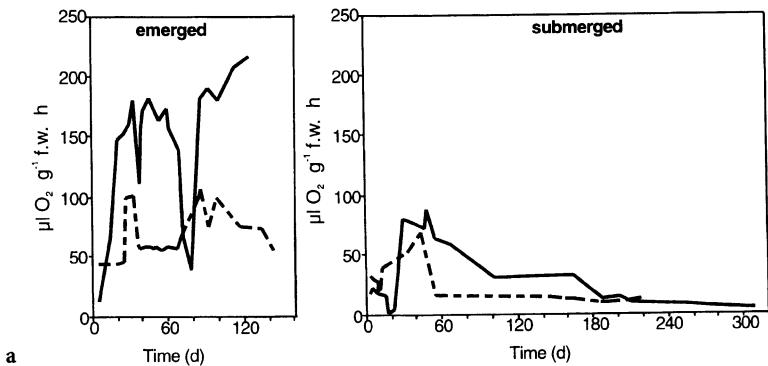
The growth of roots was directly observed with a mini-rhizotron by Meyer (1991). In the várzea, root production increased continuously from October to the following February. During the dry October 1987, the igapó root production was considerably lower than in the other months of the terrestrial phase. A high proportion of living roots at the end of the aquatic phase indicates that roots can survive the anoxic conditions during this period of unfavourable conditions.

### 11.3.3 Morphological and Physiological Adaptations of the Roots

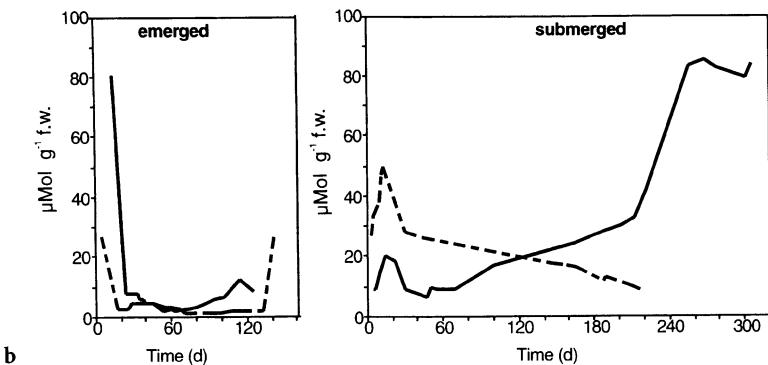
Adaptations and reactions of herbaceous and woody plants to anaerobic soil conditions are summarized by Crawford (1982, 1989). Most investigations were carried out under laboratory conditions and only for short time periods of hours or days with species from temperate zones. Studies on tropical species and on the effects of very long-lasting floodings up to 300 days year<sup>-1</sup> under natural site conditions are rather poor.

When the water floods a site the pore volume in the soil is rapidly filled with water and the gas exchange between soil and atmosphere is hindered. The remaining oxygen in the soil is consumed by the respiration of roots

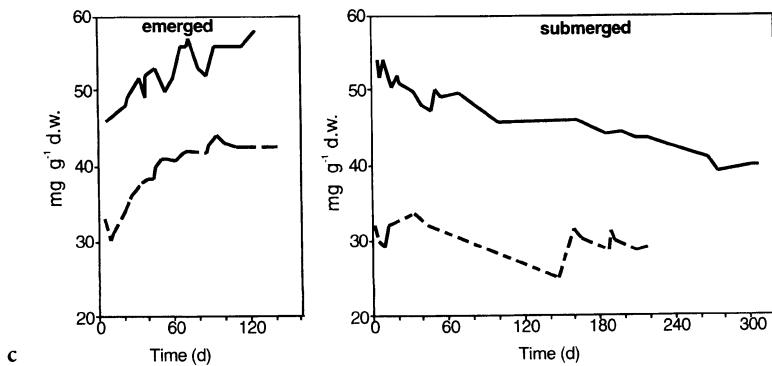
### Respiration



### Ethanol



### Dis. Carbohydrates



— Macrolobium ac. - - Astrocaryum jauari

**Fig. 11.15.** Root respiration (a) and concentrations of ethanol (b), soluble carbohydrates (c), malate (d) and lactate (e) in the roots of *Astrocaryum jauari*, Palmae and *Macrolobium acaciifolium*, Caesalpiniaceae from the várzea during the terrestrial phase (*emerged*) and inundation phase (*submerged*). (After Schlüter 1989)

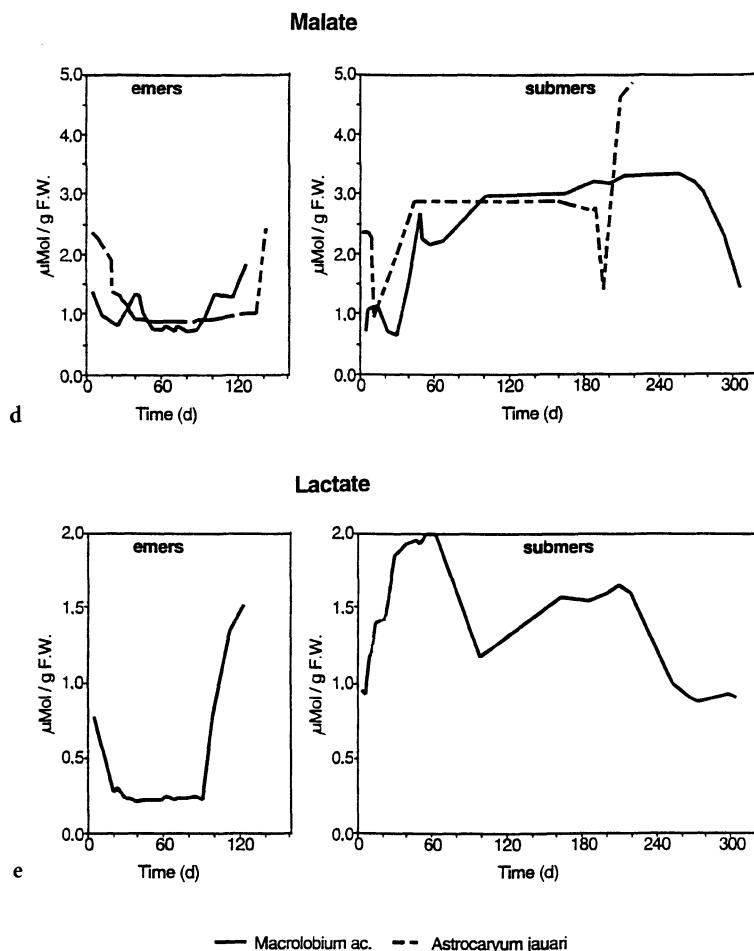


Fig. 11.15d,e

and microorganisms within hours or days (Ponnamperuma 1984). Flooding levels of 5–8 m above the forest floor and root lengths up to 30 m in adult trees preclude the possibility of gas exchange processes between stem and root tips by means of air transport systems of cellular dimensions. Investigations of the xylem from approximately 100 dicotyledonous tree species did not give indications of any aerenchyma (Worbes 1986). Usually trees of the inundation forests cannot support the  $O_2$  demand for the respiration of their roots during the aquatic phase via lenticells in the stems and air conducting systems or via pneumatophores, as can mangroves (Gessner 1959), *Taxodium distichum* and others.

Nevertheless some observations point to morphological and anatomical

stress avoiding systems, e.g., aerenchyma tissues were found in the roots of two-year-old seedlings of the palm species *Astrocaryum jauari* (Schlüter 1989). The connection to an above-ground air transport system remained unclear. In experiments with shallowly flooded seedlings of *Cecropia latiloba* (Junk pers. comm.) and in seedlings of *Macrolobium acaciifolium* on natural sites at the beginning of the aquatic phase (Schlüter 1989), the development of lenticells was observed. Two-and 3-year-old *Salix humboldtiana* trees form a dense layer of adventitious roots on the stem up to a height of 2 m. Under the regular high-rising flooding at the natural sites in várzea and igapó, anoxia-avoiding anatomical and morphological systems (Crawford 1989) are useful only during a short period of rising or falling water level. To tolerate anoxia trees must possess physiological mechanisms to survive the long periods of high flooding. At the beginning of the aquatic phase root respiration decreases to very low values (Fig. 11.15), according to studies of root physiology of the palm species *Astrocaryum jauari* (Schlüter et al. 1993) and the dicotyledonous species *Macrolobium acaciifolium* (Caesalpiniaceae) (Schlüter 1989) in igapó and várzea. After a few more days respiration increases suddenly and reaches its maximum level after 50 days of inundation. During this time, energy metabolism is switched to anaerobic pathways, indicated by the increasing concentrations of ethanol, lactate, alanin and malate in the roots. Whereas production of ethanol, alanin and lactate results in a direct energy gain, the function of malate synthesis is probably as a sink for superfluous CO<sub>2</sub> (Schlüter 1989). The decrease in respiration after 50 days of inundation indicates that the anaerobic pathway of energy gain is only a provisional solution. Moreover in *Macrolobium acaciifolium* after 200 days the concentration of ethanol, which is supposed to be a cell poison (Crawford 1977), increased rapidly. Little information is available on the removal of harmful end products of metabolism. In *Macrolobium acaciifolium* and other species the parenchyma tissue at the ring boundaries produced in the inundation period is filled with undetermined secondary plant substances. These substances may play a role in removal of cell poisons (Worbes 1986).

Carbohydrates as the basic source for the energy gain are transferred into the roots during the terrestrial phase (Fig. 11.15) and will be dissimilated during the aquatic phase. A considerable concentration of soluble carbohydrates in the roots of both investigated species at the end of inundation points to a reduced metabolism during inundation limited by the concentration of toxic end-products of the anaerobic metabolic pathways.

### 11.3.4 Reproduction

Reproductive behaviour of most species is oriented towards the aquatic phase (Revilla 1981; Worbes 1986; Ziburski 1990, 1991). The majority of species flower and fruit during or at the end of the inundation. Seeds with hydrochor distribution are supplied with special aerated tissues and are able to float for several days (*Pseudobombax munguba*) or months (*Aldina latifolia*). Fruits with high specific weights (e.g., *Astrocaryum jauari*) sink to the bottom and have a high tolerance for anoxic conditions. Moreover submersion breaks dormancy in this species and supports the germination at the beginning of the following terrestrial phase. Few species possess anemochor dispersal like *Triplaris surinamensis*, fruiting during the terrestrial phase, and *Salix humboldtiana* fruiting the entire year. Other dispersal agents are birds, mammals and iguanas.

Fruits are essential in the diet of the Amazonian ichthyofauna (Sect. 20.2). At least 100 fish species eat fruits from várzea and igapó trees (Goulding 1983). The role of ichthyocory for the dispersal of seeds is con-

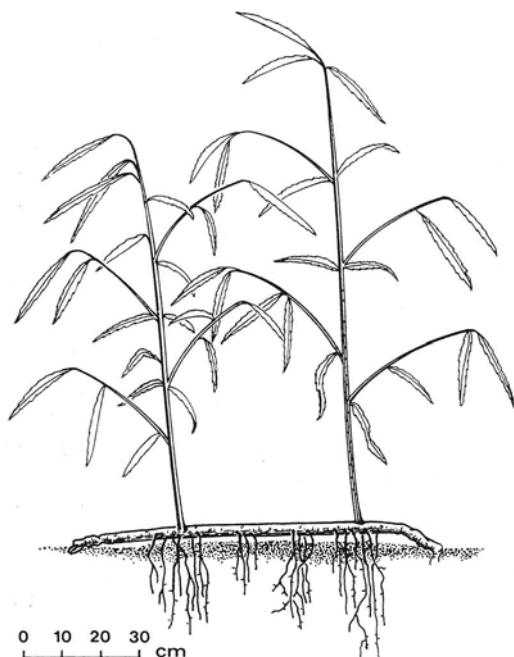
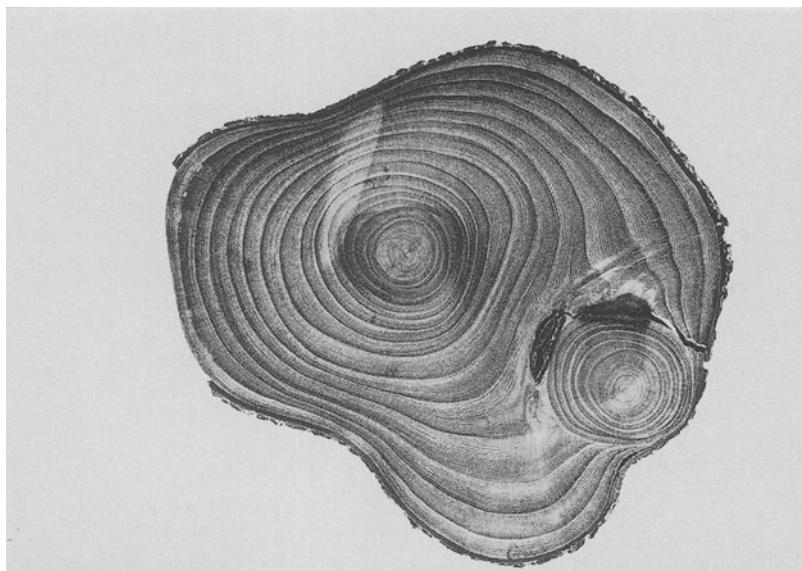


Fig. 11.16. Vegetative propagation of *Salix humboldtiana*, Salicaceae through parts of broken stems at a sand bank downstream of the Ilha de Marchantaria

troversial. Gottsberger (1978) and Goulding (1983) propose that flowering plant groups are dependent on fishes for seed dispersal and that there is a coevolutionary relationship between fish and tree species in the flood-plains. According to Ziburski (1991), only a few species with heavy fruits or with fruits which must be opened for the germination of the seeds (e.g., *Crescentia amazonica*) are dependent on ichthyochory. In general, ichthyochory seems to be less important because seed dispersal by more than one agent is very frequent.

Vegetative propagation plays an important role in those species which form monospecific stands. The lower branches of *Eugenia inundata* often become rooted. In young stands of *Salix humboldtiana* the lateral shoots of fallen trees become transformed into several orthotropic axes with independent newly formed root systems (Fig. 11.16). Vegetative propagation is of advantage in environments where establishment of seedlings is impeded by sedimentation (*Salix*) or anoxic soil conditions (*Eugenia*).

Many species are able to develop stump sprouts, e.g., *Crataeva benthamii*, *Piranhea trifoliata*, *Tabebuia barbata* and *Triplaris surinamensis*, indicated by stem disks with more than one center (Fig. 11.17). Stem discs with signs of stump sprouting were frequently found in forests at the margins of Ilha de Marchantaria, indicating an anthropogenic deforestation.



**Fig. 11.17.** Stem disk of the lower part of a *Tabebuia barbata*, Bignonoaceae tree from the margins of the Ilha de Marchantaria. The two centers indicate overwhelmed stump sprouts

### 11.3.5 Zonation

In the igapó, trees can apparently persist at lower sites (21 m) than in the várzea (Ferreira 1991). Schlüter (1989) suggests that there is a higher photon flux in the black water than in the white water. The leaves of some evergreen species in the igapó are photosynthetically active at a low level during submersion and that might be an advantage in tolerating flooding. Better oxygen conditions in black water habitats can also favour the occurrence of trees at lower sites (Sects. 4.4.3 and 20.5).

On an igapó site at Tarumá Mirim Ferreira (1991) found distinct variations in the distribution of tree species dependent on the elevation of sites and consequently along a flood level gradient. Besides generalistic species, such as *Malouetia fufuracea*, which occur along the entire flood gradient, other species show a centred distribution to a certain flood level (*Hevea spruceana* in the igapó at 23 m a.s.l.). Few species are restricted to extremely high (*Mora paraensis*, *Pentacletra macroloba*) or low elevations (*Symmeria paniculata*) exclusively.

Distribution patterns can be explained at least partially with reproduction biology and flood tolerance of the seedlings. Along the flood gradient in the igapó, *Swartzia polyphylla* has a low, *Mora paraensis* a high, and *Aldina latifolia* a mid-level distribution centre. Mortality of seedlings exposed to three months of flooding at 27 m a.s.l. was highest in *Mora paraensis* and lowest in *Swartzia polyphylla* (Ziburski 1990). A similar correlation between differences in distribution centre and mortality of seedlings can be made in the várzea for *Crataeva benthamii*, *Vitex cymosa* and *Pterocarpus amzonum* (Fig. 11.18).

A discussion on zonation and specific differences in flood tolerance must incorporate the fact that many tree species occupy a wide range along the flood gradient and that a large number of species from the várzea can also be found on terra firme sites with a definite dry season of several months (Kubitzki 1989). Generally an inundation results in reduced root growth and a reduced uptake of water and nutrients (Lee 1977, 1978). The water potential in the leaves is lowered. For many tree species inundation results ultimately in leaf fall because an insufficient amount of water can reach the crown (Crawford 1982).

Tree species which grow equally well on both very dry and periodically flooded sites are well known in the temperate zones (Ellenberg 1988) where survival is additionally a function of species tolerance to periodically low winter temperatures (e.g., *Quercus* spp.). One can assume that those widespread species found at all sites in tropical South America are not primarily adapted to flooding, but generally tolerant to seasonally poor growing conditions (Worbes 1985; Junk 1989; Adis 1992a).

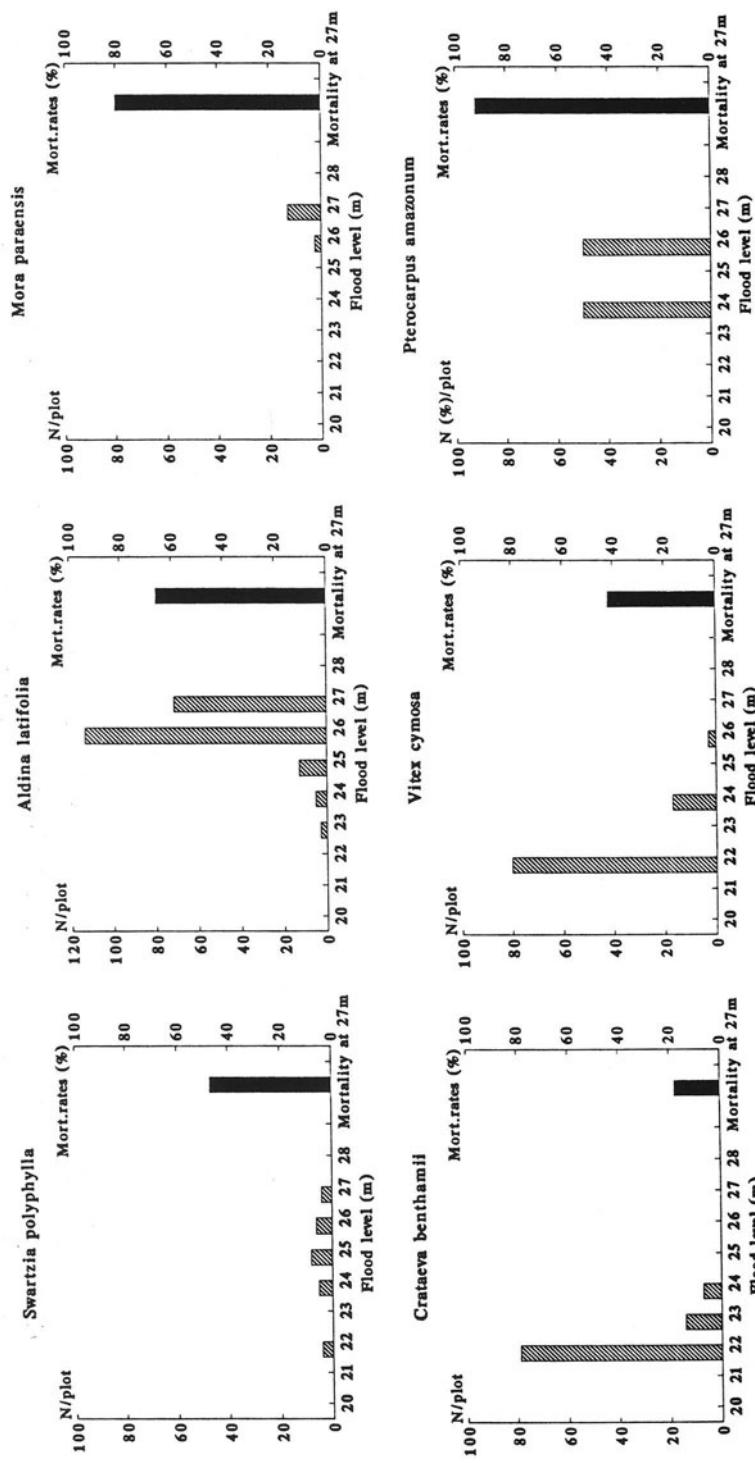


Fig. 11.18. Distribution of adult tree species (left y-axis) along the flood gradient (x-axis) and mortality of seedlings (right y-axis) during the submergence phase 1988 at 27 m a.s.l. of flood level. Species from igapó (above), from várzea (below), from várzea (below), from Ziburski (1990) and Ferreira (1991)

## 11.4 Biomass and Primary Production

Net primary production (NPP) of a forest is defined as the sum of the increase of wood biomass, the total below- and aboveground litter production and the losses by herbivory. In all forest ecosystems values of below-ground production and losses by herbivory are difficult to evaluate and rarely measured. In tropical forests the estimation of NPP is generally subjected to further specific difficulties, which were discussed in detail in Jordan (1983) and Whitmore (1984). Above all, the estimation of biomass increment is problematic because of the generally assumed absence of tree rings (Whitmore 1993), which in temperate zones are the basis for estimates of the wood increment. The majority of NPP calculations for tropical forests are based on leaf-fall measurements (Lieth and Whittaker 1975). In these cases NPP is estimated by multiplying leaf fall by a conversion factor of 2.5 (Murphy 1975).

Using tree-ring analyses of trees from várzea forests as described above we can calculate long-term biomass increase and, with measurements of the coarse (Martius 1989) and fine litter (Adis et al. 1979; Adis, unpubl. data), give a reliable figure of the aboveground NPP in the investigated várzea stands. In the igapó, the amount of fine litter fall and radial wood growth of the trees serves as an indicator for the NPP. All weight values in this section refer to dry weight.

### 11.4.1 Litter Production

Adis et al. (1979) measured litter production, including leaves, twigs, flowers and fruits, in the igapó at Tarumã Mirim and in four stands on the Ilha de Marchantaria using litter samples of 1 m<sup>2</sup> area over 1 year. In the same forests Meyer (1991) repeated the measurements during the emersion phase and found similar values. Within the várzea the litter fall varied from 7.8 tha<sup>-1</sup> year<sup>-1</sup>, in an early successional 12-year-old *Cecropia latiloba* stand, to 13.6 tha<sup>-1</sup> year<sup>-1</sup> in a mixed forest stand with an approximate age of 60 years (Table 11.3). The mean of four estimations is 10.3 tha<sup>-1</sup> year<sup>-1</sup>. The litter fall in the igapó is considerably lower with 6.7 tha<sup>-1</sup> year<sup>-1</sup>. At both sites leaves constitute about 80% of the total amount of litter fall.

A distinct seasonality of leaf fall is observable in várzea and igapó. At both sites the maximum leaf fall is at the end of the submersion phase from May until July (Fig. 11.19). In the várzea a second (lower) peak is found in November during the dry season, when the soils are partially

**Table 11.3.** Fractions of fine litter, total fine litter (n, 4 plots) and total nutrient storage of the uppermost 30 cm soil in selected Amazonian forest stands

Forest	Igapó <sup>a</sup>	TF Manaus <sup>a</sup>	TF Belém <sup>b</sup>	Várzea <sup>c</sup>
<i>Litter:</i>				
Leaves (%)	79	81	81	82
Twigs (%)	15	13	13	9.7
Fruits (%)	7	6	6	8.3
Total ( $\text{tha}^{-1} \text{a}^{-1}$ )	6.7	7.9	9.9	10.3
<i>Soil nutrients:</i>				
N ( $\text{kg ha}^{-1}$ )	4290 <sup>d</sup>	4263 <sup>e</sup>	–	3 350 <sup>d</sup>
P ( $\text{kg ha}^{-1}$ )	255 <sup>d</sup>	71 <sup>e</sup>	–	1 455 <sup>d</sup>
K ( $\text{kg ha}^{-1}$ )	2220 <sup>d</sup>	58 <sup>e</sup>	–	20 860 <sup>d</sup>
Na ( $\text{kg ha}^{-1}$ )	–	35 <sup>e</sup>	–	1 290 <sup>d</sup>

TF, Terra firme.

<sup>a</sup>Franken et al. (1979).

<sup>b</sup>Klinge (1977).

<sup>c</sup>Adis (unpubl.).

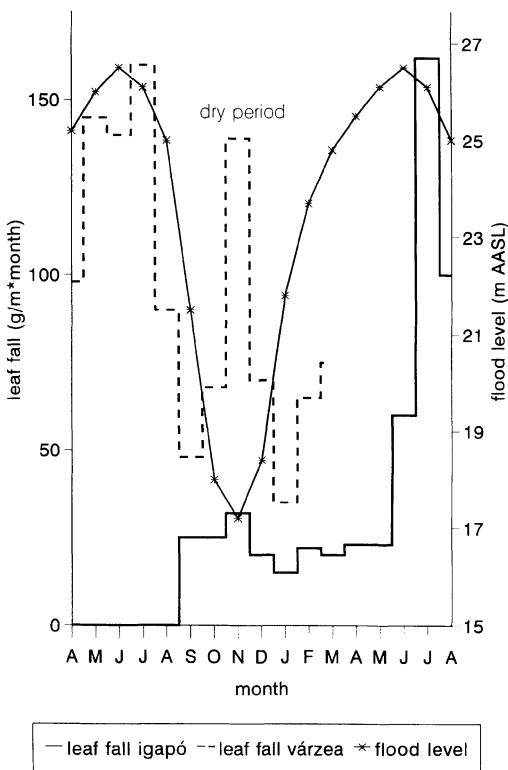
<sup>d</sup>Worbes (1986).

<sup>e</sup>Klinge (1975).

dried out to the wilting point for some weeks (Worbes 1986). The igapó trees in contrast to várzea trees have smaller and more sclerophyllous leaves (Klinge et al. 1983), which are less sensitive to water stress.

The annual litter fall in the várzea is within the range of the worldwide mean value of  $9.8 \text{ tha}^{-1}$ , which is taken from different tropical lowland forests given by Medina and Klinge (1983). Compared to other Amazonian forest stands várzea forests produce the highest and igapó forests the lowest amount of litter fall. The differences between the inundation forests in the amount of litter correlate with differences in the nutrient content of the soils (Table 11.3; Vitousek 1984). Igapó soils are poor and várzea soils are comparably rich in phosphorus (see Chap. 3). However, the terra firme soil is even poorer even though litter fall is higher than in the igapó, where the vegetation period is restricted by the floodings.

The amount of coarse litter fall (dead wood) was measured by Martius (1989) in different stands in the várzea on Ilha de Marchantaria. In the stand (V4) he measured  $6.6 \text{ tha}^{-1} \text{ year}^{-1}$  and in another stand at the Central Lake (V5)  $11.4 \text{ tha}^{-1} \text{ year}^{-1}$  of coarse litter (Sect. 12.2).

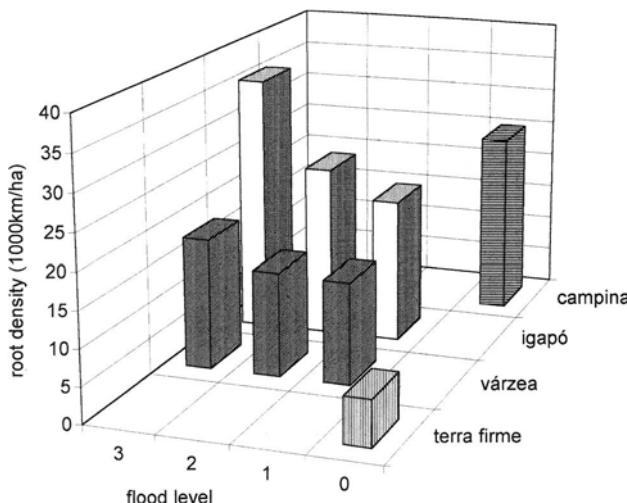


**Fig. 11.19.** Monthly leaf fall in the igapó in 1976 and 1977 from Adis et al. (1979), monthly leaf fall in the várzea in 1981 and 1982 adopted from Adis (unpubl. data) and pattern of flood level variation of Negro River

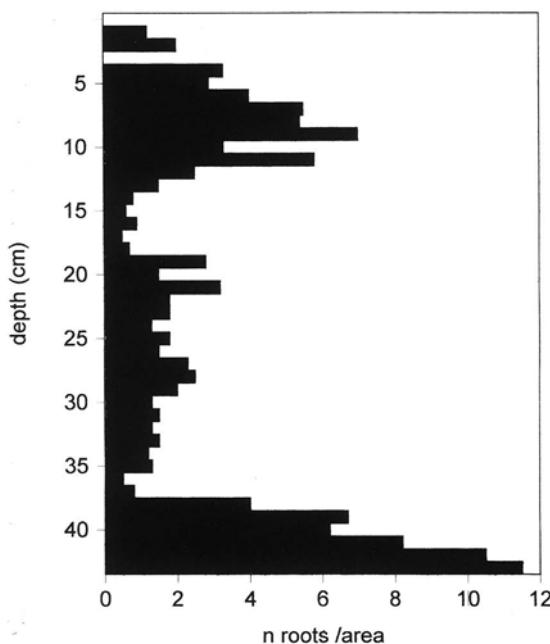
#### 11.4.2 Root Production

Meyer (1991) measured the root production in várzea and igapó stands with minirhizotrons (Taylor 1987) during the emersion phase down to a depth of 40 cm. The lengths and the densities of fine roots (<1.0 mm) were measured at the same sites on soil slides on a millimetre scale down to a depth of 80 mm. In both stands fine roots are concentrated in the humus soil profile directly beyond the litter layer. Depending on the duration of flooding on different sites the density of fine roots in the igapó was 1.4 to 2 times higher than in the várzea. The amount of fine roots increased with increasing length of inundation period from  $19.9$  to  $35.7 \text{ km } 10^3 \text{ ha}^{-1}$  in the igapó and from  $14.1$  to  $18 \text{ km } 10^3 \text{ ha}^{-1}$  in the várzea (Fig. 11.20).

A comparison of the lengths of fine roots in different Amazonian forest stands (Klinge 1973a) is shown in Fig. 11.20. The nutrient contents of



**Fig. 11.20.** Root density in  $\text{km ha}^{-1}$  in different Amazonian forest stands. The campina and the terra firme stands are never flooded (flood level 0) data from Klinge (1973). Length of inundation in the igapó: flood level 1, 80 days; flood level 2, 150 days; flood level 3, 175 days. Length of inundation in the várzea: flood level 1, 110 days; flood level 2, 180 days; flood level 3, 220 days

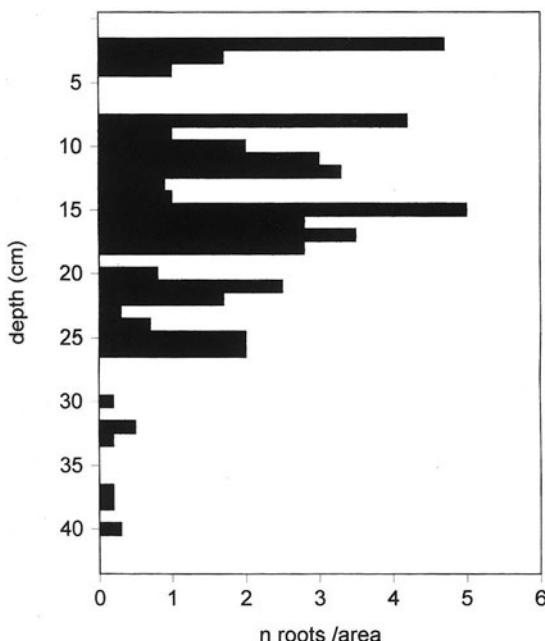


**Fig. 11.21.** Root production at different soil depths in the várzea measured with a minirhizotron. Unit of root production is number of newly formed roots per  $4\text{cm}^{-2}$  over 5 months

the soils are lowest in Campina on podsol, and increase from igapó, to terra firme to várzea (Klinge 1977; Worbes 1986). With respect to the increase of root biomass, this order is changed due to the influence of the inundation.

In general root production is higher in the várzea than in the igapó (Figs. 11.21, 11.22). High rates of production were observed in the upper horizon at both sites. In the várzea a second maximum occurred at a depth of 37 cm, where a sharp transition from clay to sand was observed (Worbes 1986).

The results show that root density and production depend strongly on nutrient content of the soil, soil type, and length of inundation. In the sandy soil horizons, with higher pore volumes (Worbes 1986), fine roots find better physical growth conditions than in denser clay soils. Stress factors, e.g., low nutrient supply and flooding, may stimulate the production of fine roots. A prolonged inundation means a short vegetation period for the trees. The activity of the roots is restricted during the submersion phase. At least at the beginning of the flood the reduced water and



**Fig. 11.22.** Root production in different soil depths in the igapó measured with a minirhizotron. Unit of root production is number of newly formed roots per  $4\text{ cm}^{-2}$  over 5 months

nutrient transport may be compensated by the production of a higher root biomass.

The inverse relationship between nutrient supply and root biomass production is observed in tropical forests as well as in forests of the temperate zones (Klinge and Herrera 1978; Keyes and Grier 1981; Scherfose 1990). The high root biomass on poor soils, as in the igapó forest, is explained by the need to optimize exploitation of very limited nutrient resources (Medina et al. 1977). The lower rates of root production in combination with a higher root density in the igapó indicates a longer life span for the roots in the igapó (Meyer 1991). Klinge et al. (1983) assumed a longer life span for the leaves of igapó trees. Both findings indicate a highly efficient use of the low nutrient resources in the igapó (Nadelhoffer et al. 1985).

#### 11.4.3 Wood Increment

The existence of annual rings in trees from inundation forests (Worbes 1984; Worbes and Junk 1989) allows us to apply dendrochronological methods for the estimation of wood increment. With this method we can make increment measurements over arbitrary time periods. In tropical forests the standard estimations of wood increments are for short periods of time and do not take into account growth changes caused by climatic variations or dynamic developments (Kira et al. 1967). The following calculations are based on the increment, i.e., each tree-ring width for every year of the entire life span of each tree. That is the longest possible measurement period.

Measurement of annual tree-ring widths over the complete life span of 203 trees show mean figures of  $3.5 \text{ mm year}^{-1}$  in the várzea and  $1.7 \text{ mm year}^{-1}$  in the igapó (Table 11.4). The influence of light on tree growth is shown in Fig. 11.23. Upper-storey trees have considerably higher increments than under-storey trees, which is typical of any forest community. A more detailed examination of the results from the várzea according to stands of different successional development shows a decrease in radial increment as stand age increases from  $9.9 \text{ mm year}^{-1}$  in a 20-year-old stand to  $1.7 \text{ mm year}^{-1}$  in a stand that is more than 200 years old. In most cases these values exceed those of other tropical forest investigations and were evaluated by repeated dbh measurements (Table 11.4). The values from igapó and from the two oldest várzea stands are of the same order of magnitude as those from a lowland humid forest in Venezuela (Veillon 1985). One reason for the high radial increment rates in the inundation forest is that these measurements include the growth of the trees during the

**Table 11.4.** Mean radial increments with extreme values in brackets of trees in different tropical forests

	Period of measurement (years)	Radial increments (mm a <sup>-1</sup> )
<b>Repeated dbh measurements</b>		
Natural Forest Sarawak <sup>a</sup> (n = 187)	1–4	0.7 (0.5–1.6)
Natural Forest <sup>a</sup> (1–2 years after Expl.) (n = 44)		2.0 (1.5–2.4)
Natural Forest <sup>a</sup> (3–4 years after Expl.) (n = 44)		1.1 (0.8–1.5)
Costa Rica, moist forest, <sup>b</sup> (n = 2010; BHD ≥ 10 cm)	13	1.3 (0.2–4.6)
Costa Rica, moist forest, <sup>b</sup> canopy		2.1 (0.5–4.6)
Costa Rica, moist forest, <sup>b</sup> subcanopy		0.9 (0.3–2.8)
Costa Rica, moist forest, <sup>b</sup> understory		0.5 (0.3–1.4)
Venezuela, woodland <sup>c</sup> (BHD ≥ 10 cm)	24	0.5
Venezuela, dry forest <sup>c</sup>		1.25
Venezuela, semidry forest <sup>c</sup>		1.75
Venezuela, moist forest <sup>c</sup>		2.25
Venezuela, Estado Barinas, seasonal forest <sup>c</sup>		1.8–2.55
Malaysia, Diptero.-forest, <sup>d</sup> (n = 3909; BHD ≥ 10 cm)	34	1.3 (0.4–2.5)
Malaysia, Diptero.-forest, <sup>d</sup> emergents		2.0 (1.5–2.5)
Malaysia, Diptero.-forest, <sup>d</sup> main canopy		1.1 (0.7–1.5)
Malaysia, Diptero.-forest, <sup>d</sup> understory		0.7 (0.4–1.1)
Panama, moist forest <sup>e</sup> (n = 3590; BHD ≥ 2.5 cm)	10	1.3 (0.1–5.8)
<b>Tree-ring measurements ≥5 cm<sup>f</sup></b>		
Brasil, Igapó (n = 45)		1.7 (0.8–3.1)
Brasil, Várzea (n = 158)		3.5 (0.7–12.3)
Venezuela, seasonal forest <sup>f</sup> (n = 56)		4.3 (0.9–12.5)
Brasil, Várzea: stand age 20 years (n = 9)		9.9 (4.7–12.3)
Brasil, Várzea: stand age 45 years (n = 49)		4.8 (2.4–10.1)
Brasil, Várzea: stand age 80 years (n = 80)		2.7 (0.7–7.6)
Brasil, Várzea: stand age >200 years (n = 20)		1.7 (0.7–2.6)

Own estimations on the base of tree ring analysis, others on the base of repeated dbh measurements.

<sup>a</sup> Primack et al. (1985), only Moraceae.

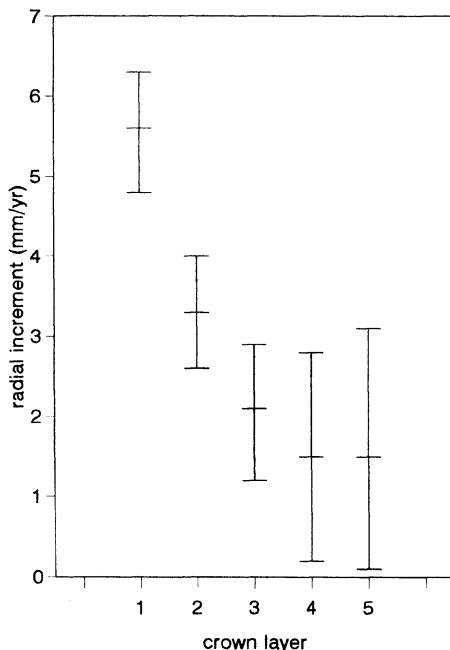
<sup>b</sup> Lieberman et al. (1985).

<sup>c</sup> Veillon (1985), 62 investigation areas.

<sup>d</sup> Manokaran and Kochummen (1987), only the 20 most important species.

<sup>e</sup> Lang and Knight (1983).

<sup>f</sup> Worbes (1994).



**Fig. 11.23.** Radial wood increment in mm (means and deviation) from 113 trees of the várzea (stand V5) in five crown layers from upper story (1) to understory (5). Further details of structural composition of this stand are given in Chapter 11

early life history, when the radial wood increments in young forest communities are higher than in older and differentiated stands. The assessment of data on radial growth rates should always take into consideration the successional stage and the structure of a forest stand.

Rates of radial increment are only relative figures with no direct relation to biomass production on a given area. Aboveground wood production was estimated by dividing the aboveground biomass by the ages of the stands (Worbes 1994). Aboveground biomass was measured by harvesting in the stands BIO1 and BIO2 (Klinge et al. 1996). In the other stands biomass for the stem of each tree was estimated from tree height, diameter at breast height and density of the wood. Ten percent of the result was added for the biomass of the branches and twigs (Ellenberg et al. 1986).

The calculation of wood production of individual trees (Worbes 1994) shows great variations between individuals of different crown layers but little variation between different species growing in the same stratum (Table 11.5). The mean wood production of the pioneer species *Pseudobombax munguba* ( $12 \text{ kg tree}^{-1} \text{ year}^{-1}$ ) is equal to the mean production of *Piranhea trifoliata*, a species of the mature forest. Together with

Table 11.5. Individual annual stem wood production with deviations and extreme values (min.-max.prod.) of different tree species from the várzea, with dimensions of the sample trees: height, radial increment, wood density, and number of samples (n)

	Height (m)	Radial incr. (mm a <sup>-1</sup> )	Wood density (g cm <sup>-3</sup> a <sup>-1</sup> )	Min. and max. prod. (kg a <sup>-1</sup> tree <sup>-1</sup> )	n	Mean production (kg a <sup>-1</sup> tree <sup>-1</sup> )
<i>Cecropia latiloba</i>	14-15	8.8-10.6	0.42-0.46	5.2-8.4	2	6.8 ± 2.3
<i>Crataeva benthamii</i>	4-16	2.9-5.3	0.39-0.48	0.2-3.8	4	1.9 ± 1.6
<i>Elaeoluma glabrescens</i>	20	2.7-3.4	0.56-0.59	7.6-10.8	2	9.2 ± 2.3
<i>Eschweilera albiflora</i>	17	1.5	0.75		1	5.0
<i>Eschweilera spec.</i>	20-25	3.3-4.8	0.50-0.55	15.1-19.7	2	17.4 ± 3.3
<i>Ilex inundata</i>	15-20	1.9-3.3	0.43		1	4.9 ± 0.9
<i>Laetia corymbulosa</i>	18-24	2.2-2.9	0.60-0.64	4.0-13.5	4	7.2 ± 4.4
<i>Luehea spec.</i>	22	3.9	0.57		1	15.3
<i>Luehea spec.</i>	18	2.5-3.3	0.37-0.42		1	3.0
<i>Macrolobium acaciifolium</i>	15-25	3.4-6.5	0.42-0.50	4.8-24.2	7	11.3 ± 6.8
<i>Mouriri guianensis</i>	17	2.7	0.82		1	6.6
<i>Myrciaria amazonica</i>	17-18	1.5	0.68-0.74		1	2.1
<i>Nectandra amazonum</i>	14-15	2.4-4.9	0.39-0.47	2.3-5.6	2	4.0 ± 2.3
<i>Piranhea trifoliata</i>	15-32	1.2-4.5	0.83-0.93	3.1-19.3	8	12.0 ± 5.5
<i>Pithecellobium inaequale</i>	10	1.8	0.62		1	1.6
<i>Pseudobombax munguba</i>	6-28	4.0-10.0	0.20-0.24	3.9-23.5	3	12.2 ± 10.1
<i>Pseudoxandra polyphleba</i>	8	1.9	0.51		1	0.7
<i>Psidium acutangulum</i>	4-18	0.7-1.6	0.80-0.85	0.1-4.0	2	2.1 ± 2.8
<i>Salix humboldtiana</i>	7-10	4.7-12.3	0.42-0.43	1.8-8.5	6	4.1 ± 2.4
<i>Sorocea duckei</i>	15	2.0	0.58		1	2.6
<i>Tabea bau barbata</i>	8-25	1.1-4.8	0.55-0.85	1.1-20.6	16	6.0 ± 5.4
<i>Trichilia singularis</i>	6	1.6	0.51		1	0.6
<i>Triplaris surinamensis</i>	26	4.2	0.62		1	14.1
<i>Vitex cymosa</i>	10-16	3.1-4.6	0.58-0.62	1.4-11.3	3	5.7 ± 5.1

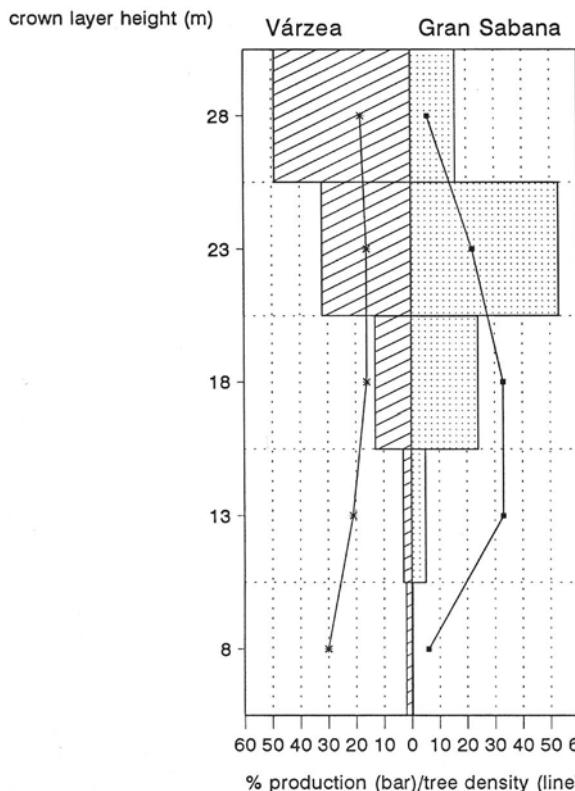


Fig. 11.24. Percentage of wood production and percentage of trees in different crown layers in the várzea stand V5. For comparison, on the right-hand side the corresponding figures for a disturbed stand of the Gran Sabana, Venezuela are documented. The Gran Sabana stand is characterized by crown damage to the trees so that even the third crown layer contributes a considerable proportion to total wood production. (Worbes 1994a,b)

structural data of tree density in all layers of stand (V5) on the Ilha de Marchantaria, values of individual wood production of trees from all crown layers allow the estimation of area-related figures of production. Separate estimations for five crown layers show that about 50% of the total wood production is caused by the individuals from the upper storey which comprise only 20% of the individuals in the stand (Fig. 11.24). On the other hand, 50% of the individuals grow in the two understoreys (up to 15 m height) but contribute less than 10% to the total amount of wood production. This is the result of decreasing radiation from the top to the forest floor as it is described by Kira and Yoda (1989) for a forest stand in Thailand.

The results of the area-related calculations document, in contrast to the behavior of the radial growth, an increase in biomass production with

**Table 11.6.** Aboveground biomass, total aboveground annual wood production in different forest types of the várzea (Worbes 1994a,b) and figures from literature (with extreme values). Detailed stand descriptions in Worbes et al. (1992)

	Biomass (tha <sup>-1</sup> )	Biomass increments (t a <sup>-1</sup> ha <sup>-1</sup> )
<b>Várzea:</b>		
Pionier (2 years old)	3	1.5
Pionier (4 years old)	14	3.4
Pionier (12 years old, BIO1)	98	8.1
Young secondary (44 years old, BIO2)	258	7.3
Late secondary (80 years old, V5):		
Gap	118	2.2
Most productive plot	470	8.6
Mean of 7 subplots	279	7.2
<b>Worldwide tropics:</b>		
Plantations <sup>a</sup> (15 means)		11.9 (4.9–27.5)
Natural forests <sup>a</sup> (10 means)		7.3 (4.9–12.4)

<sup>a</sup>Jordan (1983).

increasing age of the stands (Table 11.6). A two-year-old monospecific pioneer stand of *Salix humboldtiana* produces only 1.5 tha<sup>-1</sup> year<sup>-1</sup> wood. The wood increment increases to 8.1 tha<sup>-1</sup> year<sup>-1</sup> in a 12-year-old *Cecropia latiloba* stand. In the 80-year-old *Pseudobombax munguba* stand the amount of wood production decreases slightly to 7.2 t. This stand is a patchwork of relatively unproductive gaps (2.2 tha<sup>-1</sup> year<sup>-1</sup>) and highly productive plots with well-structured and differentiated tree stands (8.6 tha<sup>-1</sup> year<sup>-1</sup>).

These figures match closely the worldwide mean from ten investigations (Jordan 1983) of 7.3 tha<sup>-1</sup> year<sup>-1</sup>. This result confirms earlier findings (Jordan 1983; Medina and Klinge 1983) that wood production in tropical forests even under good nutrient conditions does not much exceed the wood production of temperate forests.

#### 11.4.4 Total Net Primary Production

The measurements of the aboveground wood production and of the coarse and fine litter production as given above were summarized to estimate the total aboveground primary production. For herbivory and for belowground production, estimates from the literature were added. Total NPP was calculated for a 40-year-old early secondary stand dominated by *Crataeva benthamii* (V4) and an 80-year-old late secondary stand domi-

**Table 11.7.** Aboveground NPP without losses from herbivory in the investigated várzea stands, in a rain forest in Thailand (Kira et al. 1964) and in a beech forest in the temperate zone. (Ellenberg et al. 1986)

Site	Fine litter	Dead wood	Wood increment	NPP
Várzea (V4, 40 years)	9.9	6.6	7.3	23.8
Várzea (V5, 80 years)	13.6	11.4	8.6	33.6
Rainforest, Thailand	12.0	13.3	3.1	28.4
Beech for., Germ. (120 years)	3.6	0.4	6.7	10.7

The age of the rain forest in Thailand was unknown.

Data for fine litter from Adis (unpubl. data).

All figures in  $\text{tha}^{-1}\text{year}^{-1}$ .

nated by *Pseudobombax munguba* (V5), which are described in Chapter 11. The total aboveground NPP, without losses due to herbivory, is  $23.8 \text{ tha}^{-1}\text{year}^{-1}$  in stand V4 and  $33.6 \text{ tha}^{-1}\text{year}^{-1}$  in the most productive plot of stand V5.

Grazing losses of the leaves vary between 2% in an oligotrophic tropical forest (Jordan and Uhl 1978) and 3–8% in tropical forests on fertile soil (Odum 1970). Estimations of root production in temperate forests vary from 10% (Ellenberg et al. 1986) to 170% (Reichle et al. 1973) of the aboveground wood production. Jordan and Escalante (1980) give a figure of 33% for a forest in San Carlos de Rio Negro, Venezuela. In the inundation forest it is very likely that the investment for root production is even higher than in non-flooded forests as pointed out above.

Adding a mean figure for grazing of 5% of the leaf production and a cautious estimation of 30% of the wood increment as root production, the total NPP of well-structured várzea forests varies between  $27 \text{ tha}^{-1}\text{year}^{-1}$  in stand V4 and  $36.9 \text{ tha}^{-1}\text{year}^{-1}$  in stand V5. Both figures considerably exceed the estimates of net primary production of other tropical forest stands (Table 11.7).

## 11.5 Discussion and Conclusions

The analysis of Neotropical forest vegetation, due to its great diversity, necessarily focuses on taxonomic inventories and descriptions. This work, based on the investigations of Martius et al. (1840–1869), is recently being edited for *Neotropical Flora* by Prance. The enormous quantity of taxonomical information led to theories on the evolution of neotropical plant species and in consequence to chronological explanations of

distribution patterns of the neotropical vegetation (Prance 1982; Kubitzki 1989).

A large-scale attempt is being made to classify the neotropical vegetation based on structural and physionomical differences of vegetation types linked with climatic, and partially with edaphic, variations (Holdridge 1966; Walter and Breckle 1991). Information on the phytosociological level of tropical forests and the linkage between the occurrence of plant communities and site conditions is relatively scarce. A great number of forestry inventories and the detailed knowledge of site factors of the vegetation of the Amazonian inundation forests allows us to make a phytosociological analysis on the basis of deterministic explanations.

### Flood Pulse

The most obvious growth factor in the inundation forests is the annual flooding defined by Junk et al. (1989) as flood pulse (Sect. 1.3). The predictable flood patterns lead to a distinct seasonality, which determines many growth patterns in the floodplains. To begin with, woody species rooting in the annually flooded soil have a periodic growth rhythm with a cambial dormancy during the aquatic phase. This is indicated by low cambial activity during flooding, the existence of annual rings in the wood, the existence of annual shoot growth and increased leaf fall during the aquatic phase. The concurrence between time series of the annually varying length of the flood-free period and tree-ring patterns shows that the main vegetation period is the terrestrial phase. This explains why reproductive behavior of tree and shrub species is oriented towards the flooding. Trees use the vegetation period for as long as possible for flowering, fruiting and the maturation of fruits. Many tree species of the várzea and the igapó start flowering during the aquatic phase, just as trees of the temperate zones flower as early as possible in the spring and trees of the tropical terra firme start flowering at the end of a dry phase (Alvim and Alvim 1978; Franco 1979). This example supports the view that flood pulse triggers all growth processes, as do low winter temperatures in the temperate zones and dry phases in tropical and subtropical regions.

As in habitats periodically influenced by other unfavorable climatic conditions, certain adaptations are required to tolerate the varying growth conditions. Since the maturity of fruits occurs during the inundation phase, fruits must have the ability to swim or to tolerate anoxic conditions on the bottom of the water body. Comparing fruits of closely related species from inundation forests and terra firme, Ziburski (1991) concluded that special buoyant tissues in fruits were developed secondarily.

The most important condition for woody species in the floodplains is the ability of the individual to tolerate the annual flooding. The flood tolerance is composed of two strategies. Cambial dormancy during the aquatic phase connected with deciduousness or sclerophyllic leaves in evergreen species reduces water consumption as far as possible. The shift of root metabolism from respiration to anoxic pathways enables living roots to survive until the beginning of the following terrestrial phase.

Different metabolic pathways result in differing levels of flood tolerance between species. In contrast to *Astrocaryum jauari*, Palmae, the dicotyledonous species *Macrolobium acaciifolium* is able to use the production of lactate and alanin as an energy supply during the aquatic phase. *Astrocaryum jauari* is restricted to sites of higher elevation and shorter inundations than *Macrolobium acaciifolium* (Piedade 1985; Ferreira 1992). Stress-avoiding systems (Crawford 1989) such as aerenchymas, lenticells and adventitious roots occur in some species but seem to be of minor importance under the long-lasting and high-rising floods in várzea and igapó.

Slopes on river banks cause a rapid change in duration of flooding and change site conditions over short distances. This, along with the aforementioned differences in flood tolerance of tree species, leads to a clear zonation of the forest vegetation.

## Soil Conditions

Plant communities in the Amazonian floodplains differ as the nutrient conditions of the soils differ. The concentration of nitrogen in the investigated soils is almost always the same, but there are great differences in P content (Chap. 3). Phosphorus seems to play an important role as a differentiating factor (Tilman 1982). This explains differences in species composition between várzea and igapó sites (cf. Schmidt 1973, 1976) as well as differences within the igapó between nutrient-poor white sand soil and the somewhat richer clay soil.

## Stand Dynamics

In tropical vegetation analyses an often neglected differentiating factor is the influence of the dynamic stage of a forest community. The basic problem is the assumed impossibility of dating the exact age of trees and forest stands, primarily due to the assumed absence of tree-rings in tropical trees (Whitmore 1990). Various indirect or time-consuming methods were tested, e.g., interviews with inhabitants (Uhl 1980) and estimation of mor-

tality rates (Lieberman et al. 1985), which led to vague information. Pure assumptions result in different datings with variations of 100% for the same stand depending on the author (Foster and Brokaw 1983; Lang and Knight 1983). Exact age dating by dendrochronological methods matches the definition of successional stages of forest communities (Worbes et al. 1992). The change in species composition over time incorporates change in structural elements, i.e., increasing biomass, decreasing population density and decreasing individual growth rates.

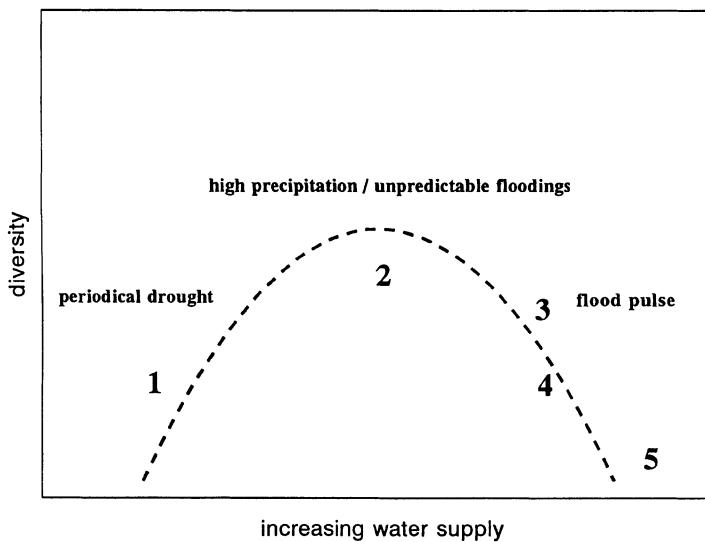
## Growth Factors and Diversity

The three differentiating factors in vegetation analysis of tropical plant communities are climate (in this case flood pulse), soil conditions and successional development. These factors lead to a better understanding of varying species composition, as discussed above, and of structural features, e.g., patterns of species richness.

The trends in the Amazonian floodplain forest are diversity, which increases in order from young to old stands, from the eutrophic várzea to more oligotrophic stands in the igapó and with decreasing flood stress (Ayres 1993). These findings can be explained using Grime's model of stress, competition and disturbance (Grime 1979) and can be linked with observations from non-flooded tropical forest communities (Gentry 1982; Ashton 1989). In Grime's model species diversity is low for sites with either high or low degrees of stress and disturbance. A high degree of disturbance and stress commonly occurs at the river margins of the Amazon. On sites often exposed to erosion and sedimentation, only monospecific (*Salix humboldtiana*) or tree communities with low species diversity are able to persist. A low degree of disturbance occurs in floodplain forests in the center of great islands and outside the main river channel where 106 species  $\text{ha}^{-1}$  were documented (Revilla 1991).

On non-flooded sites in Amazonia species richness increases from east to west, from 87 species  $\text{ha}^{-1}$  near Belém (Black et al. 1950) to over 179 species  $\text{ha}^{-1}$  near Manaus (Prance et al. 1976). Gentry (1982) explained species richness generally increases as precipitation increases. However, the increase in annual precipitation is correlated with a decrease in seasonality.

The flood pulse and periodic droughts can be interpreted as climatic stress factors, which are correlated with a depression of diversity. The effects of both factors on species richness are linked in Fig. 11.25. Drought occurs on sites with a deficit in precipitation, flood pulse occurs on sites with superfluous water. At the transition between the two habitat types



**Fig. 11.25.** Model of relative correlation between species diversity and water regime. The figures stand for forest inventories: 1 Terra firme, Belém (Black et al. 1950); 2 terra firme and floodplain, Napo River (Balslev et al. 1987); 3 Igapó, this work; 4 Várzea, this work; 5 low-lying shrub communities in the várzea. (Junk 1989)

either a high amount of precipitation throughout the year (at the left angle of the curve) or short and unpredictable floodings (at the right angle of the curve) are typical. Balslev et al. (1987) investigated a terra firme and an adjacent floodplain forest at the Napo River in Ecuador that fit the previously described conditions. Both forests show extremely high species diversity in comparison with terra firme sites with lower precipitation (Gentry 1982) or similar floodplain sites with a long-lasting flood pulse as in Central Amazonia.

The differences in species diversity of sites in igapó and várzea exposed to equal flood stress show the influence of nutrient supply in the soil. According to Tilman (1982), in tropical forests in Malaysia diversity is highest under moderate conditions, in the Amazonian floodplains these sites are in the igapó with clay soils. The above examples show that nutrient and climatic conditions of the site, as well as dynamic processes of the vegetation, must be considered for a comprehensive interpretation of the patterns of species composition and species diversity.

### Biomass Production

Total primary production of the várzea forest is high when compared with other tropical forests. The growth period of many species is concentrated

in a terrestrial phase of only about 200–250 days and often includes a period of drought stress of about four weeks. The impact of flood stress on tree growth in the várzea is compensated for by the input of nutrients during the floods. In the igapó, there is no nutrient input from the nutrient- and sediment-poor water of the Negro River. The igapó forest is very unproductive, as indicated by the low figures for litter fall and radial wood growth compared with figures from forest stands in San Carlos de Rio Negro (Medina and Klinge 1983).

The comparatively low wood production in comparison to the total NPP may be a disappointing result for those who expected to find a great potential for sustainable use and forestry in the tropical forest. The reason that tropical trees do not invest a greater proportion of the relatively high NPP in wood production is probably the high respiration loss from the sprout axis. A tree's stem and branches are not only dead organic matter, as they are often defined (Begon et al. 1990), but also a scaffold for the leaves. Their function in water transport and storage assimilation must be maintained through annual reproduction of the respiring cambial tissues. Total stem respiration in a tropical forest may be as much as  $19\text{tha}^{-1}\text{year}^{-1}$  (Medina and Klinge 1983). Therefore the costs for the maintenance of the wood biomass increases with weight. On the other hand the investment in "unproductive" wood tissue is the stabilizing factor of forest communities that are in competition with other highly productive plant communities, such as the perennial grass communities of the várzea. The conflict between developing a stabilized system and keeping down the costs for this system generally restrict the investment in wood production.

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