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Abstract

Twenty-eight years ago T.L. Erwin, J. Adis and G.G. Montgomery obtained about 50,000 arthropods by fogging the canopy with natural pyrethrum along transects in four forest types of Central Amazonia. A

first study of nearly 5,000 adult Coleoptera specimens indicated a low similarity of beetle species between forest types and a predominance of herbivores (Erwin 1983). This material has now been restudied to allow an ecological comparison in more detail.

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16.1 Introduction 7



Twenty-eight years ago T.L. Erwin, J. Adis and G.G. Montgomery obtained about 8
 50,000 arthropods by fogging the canopy with natural pyrethrum along transects in 9
 four forest types of Central Amazonia. A first study of nearly 5,000 adult Coleoptera 10
 specimens indicated a low similarity of beetle species between forest types and a 11
 predominance of herbivores (Erwin 1983). This material has now been restudied to 12
 allow an ecological comparison in more detail. 13

16.2 Material and Validity of Data 14

Coleoptera were obtained in 1979 from the canopy of a primary upland (terra firme) 15
 forest and of one inundation forest each in the blackwater (igapó), whitewater (várzea) 16
 and mixedwater (igapó & várzea) region during high water. All sites were within 70 km 17

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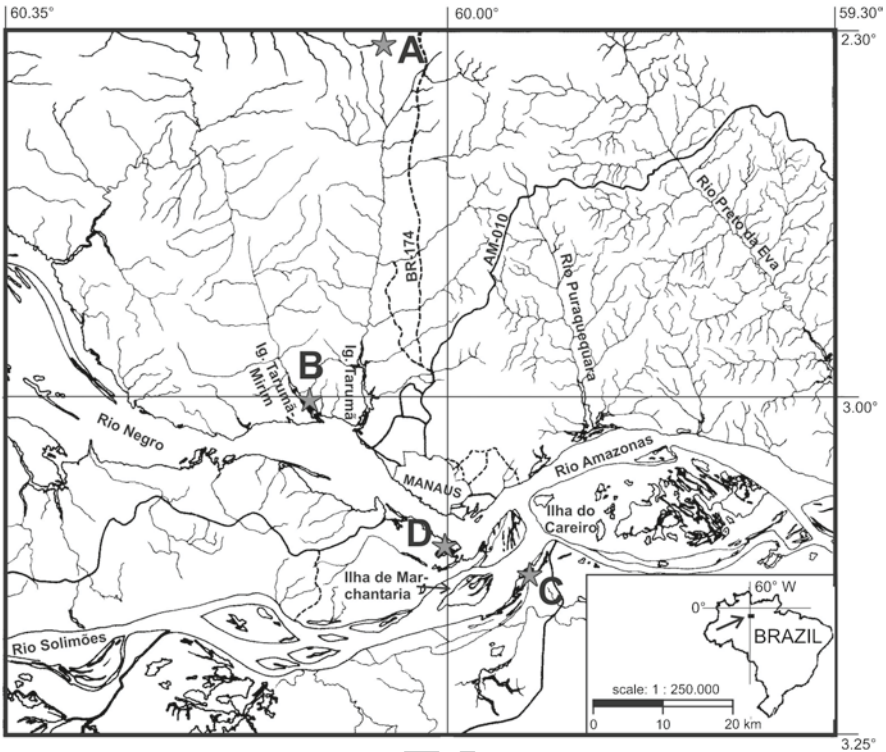


Fig. 16.1 Sampling sites at Manaus. (a) primary upland forest (terra firme; km 20 at ZF-2: 02°34'S, 60°06'W); (b) Blackwater inundation forest (igapó; Rio Taruma Mirim: 03°02'S, 60°17'W); (c) whitewater inundation forest (várzea; Ilha de Curari: 03°15', 59°49'W); (d) mixed-water inundation forest (igapó & várzea; Lago Janauari: 03°20'W, 60°17'W)

18 of Manaus (Fig. 16.1). Sampling procedures and information on sampling sites are
 19 given in Erwin (1983) and Adis (1981, 2002). The transect area of evaluated Coleoptera
 20 below the canopy represented 94.0 m² (48% of the total transect area sampled) in the
 21 upland forest, 75.8 m² (37%) in the mixedwater, 151.8 m² (60%) in the blackwater and
 22 32.4 m² (45%) in the whitewater forests (Table 16.1).

23 Of the total 4,845 adult Coleoptera specimens evaluated on morphospecies level
 24 by Erwin (1983), 74.4% (3,603 ind.) could be relocated in the material collection.
 25 Between 26.8% and 30.1% of specimens were missing from the inundation forests
 26 and 15.2% from the upland forest. For this reason, calculated abundance data in our
 27 study might be somewhat higher but patterns of abundances between forests did not
 28 change (Fig. 16.2).

29 Erwin (1983) assigned 1,060 species to their trophic level, which represented 795
 30 (74.4%) herbivore species, 145 (13.6%) predators, 100 (9.3%) scavengers (= saprophages)
 31 and 29 (2.7%) fungivores. Species numbers meanwhile increased in herbivores (+84),
 32 and predators (+2) but decreased in scavengers (-9). Of the original material, 83.5%
 33 of the herbivore species were included in our study, 43.5% of the predators and 48.0%
 34 of the scavengers. Fungivores were omitted.

Table 16.1 Characterization of the Coleoptera fauna evaluated from the canopy of four forest types in Central Amazonia

Parameters	Forests			
	Upland (94.0 m ²)	Blackwater (151.8 m ²)	Mixedwater (75.8 m ²)	Whitewater (32.4 m ²)
Number of individuals (N)	824	708	1.513	558
Number of species (S)	358	185	326	154
Individuals/species	2.3	3,8	4,6	3,6
Species/m ²	3.8	1,2	10,1	4,7
Singletons	232	102	173	85
Doubletons	55	26	55	24
Simpson diversity (D)	0.009	0.019	0.022	0.024
Shannon diversity (H)	5.298	4.471	4.668	4.278
Berger-Parker dominance	0.047	0.059	0.069	0.075
Evenness (E)	0.953	0.941	0.931	0.925

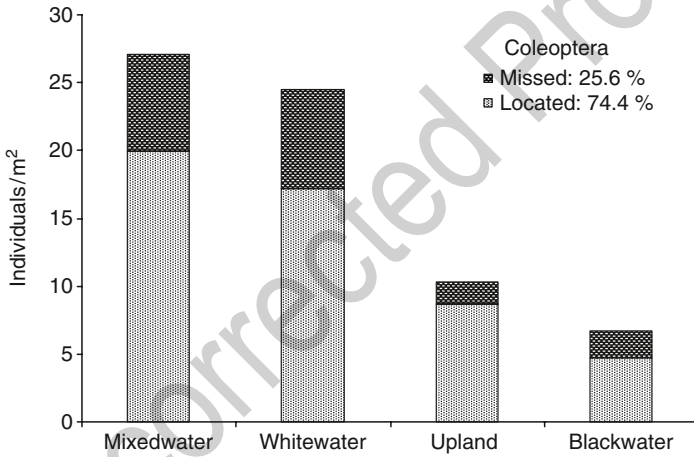


Fig. 16.2 Abundances of Coleoptera (ind./m²) evaluated by Erwin (1983) and in this study (*lower bars*) from the canopy of four forest types in Central Amazonia

Family and subfamily names used by Erwin (1983) have been maintained to enable comparisons. Changes in classification meanwhile occurred in Helodidae (=Scirtidae), Lagriidae (=Lagriinae: Tenebrionidae) and in several subfamilies of the Curculionidae (Anthonominae = Anthonomini; Apioninae = Apionidae; Attelabinae = Attelabidae: Attelabinae; Cholinae = Molytinae: Cholini; Cyliandrorhinae = Cyclominae; Eriirhininae = Eriirhinidae; Hylobinae = Molytinae: Hylobiini; Magdalinae = Mesoptillinae; Myrmecinae = Otidoccephalini; Prionomerinae = Molytinae: Camarotini and Piazorhini; Rhynchitinae = Attelabidae: Rhynchitinae; Rhynchophorinae = Dryophthoridae; Zygopinae = Conoderinae; see Alonso-Zarza and Lyal 1999).

Species richness was evaluated with the EstimateS Programme (version 7.5) of Colwell (2005). For determination of species similarity to Bray-Curtis, rarefaction

46 to Simberloff, and patchiness (Chi-square test) the Biodiversity Professional
 47 Programme (version 2) of Gage and McAleece (1979) was used. Magurran (1988)
 48 was followed to calculate diversity indices of Shannon (H) and Simpson (D) with
 49 log base e as well as the Berger-Parker dominance index and evenness.

50 **16.3 Results**

51 Adult Coleoptera represented 28.1% of the total arthropods evaluated by Erwin
 52 (1983) from the mixedwater inundation forest (96.8 arthropods/m²), 20.7% in the
 53 whitewater inundation forest (118.1 arthropods/m²), 17.6% in the blackwater inun-
 54 dation forest (38.1 arthropods/m²) and 13.1% in the upland forest (78.8 arthropods/m²).

55 The highest number of species was found in the upland forest (358 spp.) and the
 56 mixedwater inundation forest (326 spp.). Species number was considerably lower
 57 in the blackwater (185 spp.) and whitewater (154 spp.) inundation forests.
 58 Abundance was highest in the mixedwater (19.9 ind./m²; 4.6 ind./sp.) and whitewater
 59 (17.2 ind./m²; 3.6 ind./sp.) inundation forests and much lower in the upland forest
 60 (8.7 ind./m²; 3.8 ind./sp.) and the blackwater inundation forest (4.7 ind./m²; 2.3 ind./sp.)
 61 (Figs. 16.3 and 16.4; Table 16.1).

62 The rank-abundance curves (Whittaker plots) between Coleoptera specimens
 63 and species evaluated showed a low number of dominant species in all forest types
 64 (upland and mixedwater five spp. each, blackwater three spp., whitewater one sp.)
 65 (Fig. 16.4). The beetle fauna mostly consisted of rare species, with singletons and
 66 doubletons accounting for 69.1–80.2% in the four forests under study. On the
 67 upland, singletons represented 232 species (64.8% of the total catch), in the

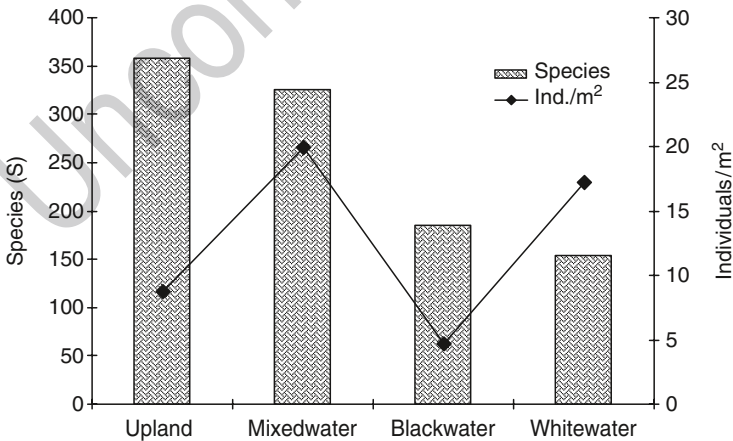


Fig. 16.3 Total number of species (S) and abundances (ind./m²) of Coleoptera evaluated from the canopy of four forest types in Central Amazonia

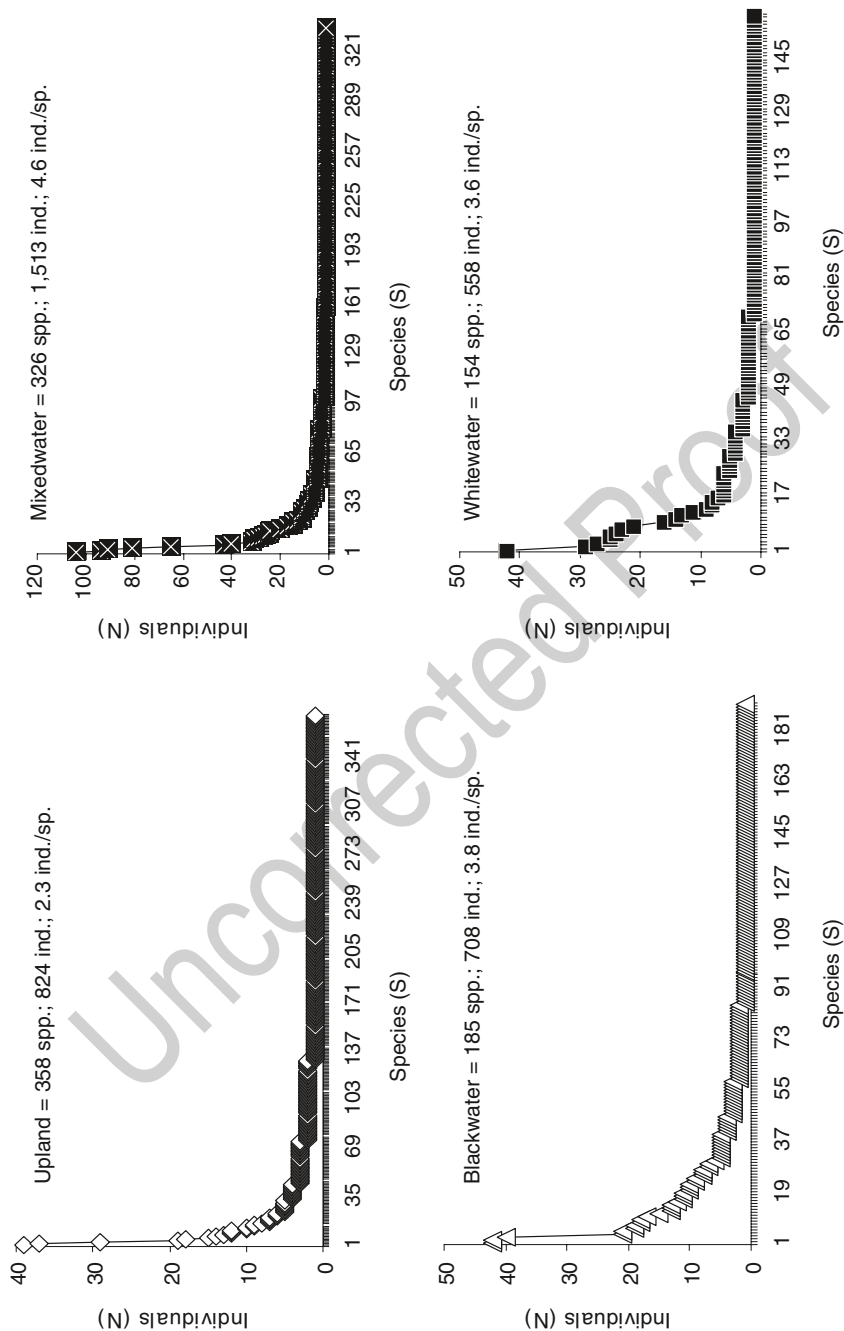


Fig. 16.4 Rank-abundance curves of Coleoptera specimens and species (N/S) evaluated from the canopy of four forest types in Central Amazonia

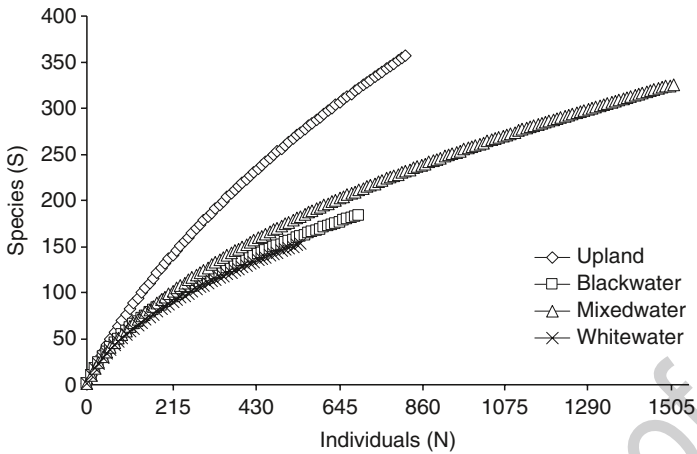


Fig. 16.5 Rarefaction curves of Coleoptera species and specimens (S/N) evaluated from the canopy of four forest types in Central Amazonia

68 mixedwater 173 species (53.1%), in the blackwater 102 species (55.1%) and in the
 69 whitewater 85 species (55.2%). On the upland and in the mixedwater, doubletons
 70 accounted for 55 species each (15.4% and 16.9% of the total catch, respectively),
 71 in the blackwater for 26 species (14.0%) and in the whitewater for 24 species
 72 (15.6%) (Table 16.1). This is mirrored in the rarefaction curves which indicate an
 73 increase of species with increasing number of individuals (Fig. 16.5).

74 Estimation of species richness for the mixedwater inundation forest suggests
 75 that, apart from the 326 species obtained, between 425.6 ± 31.7 (Bootstrap) and
 76 951.6 ± 96.7 (ICE) actually may occur on this sampling site and that 34.4–76.6%
 77 of all species had been sampled (Fig. 16.6).

78 On family level, the number of species and abundances (ind./m²) of herbivorous
 79 Curculionidae predominated in all forest types (Fig. 16.7). Highest values were
 80 recorded in the mixedwater (153 spp.; 101 ind./m²), followed by the upland
 81 (136 spp.; 31 ind./m²), the blackwater (80 spp.; 2.1 ind./m²) and the whitewater
 82 (60 spp.; 6.9 ind./m²). The herbivorous Chrysomelidae ranked second in all forests,
 83 with highest values recorded on the upland (85 spp.; 2.9 ind./m²), followed by the
 84 mixedwater (16 spp.; 3.1 ind./m²), the blackwater (36 spp.; 0.8 ind./m²) and the
 85 whitewater (14 spp.; 2.4 ind./m²). The herbivorous Anobiidae ranked third on
 86 the upland (18 spp.; 1.2 ind./m²), the saprophagous Tenebrionidae in the blackwater
 87 (18 spp.; 0.6 ind./m²) and the herbivorous Helodidae in the mixedwater (16 spp.;
 88 3.1 ind./m²) and whitewater (14 spp.; 3.4 ind./m²). Predominant subfamilies in the
 89 Curculionidae were Apioninae (124 spp.; 113 spp. in Erwin 1983) and
 90 Cryptorhynchinae (100 spp.; 91 spp. in Erwin 1983). Cholinae, Rhynchitinae and
 91 Rhynchophorinae only occurred on upland, Cylindrorhininae only in the mixedwater
 92 (Table 16.2). In the Chrysomelidae, predominance was recorded for
 93 Alticinae (73 spp.; 60 spp. in Erwin 1983) and Eumolpinae (61 spp.; 60 spp. in
 94 Erwin 1983). Hispininae only occurred in the mixedwater (Table 16.2).

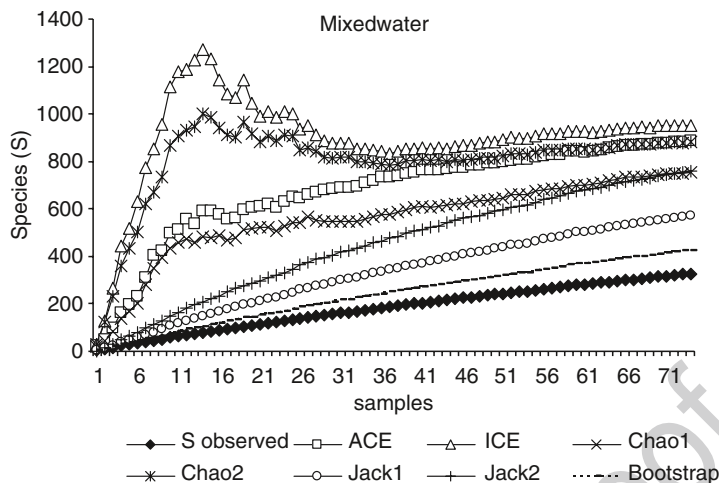


Fig. 16.6 Observed and calculated species richness for the Coleoptera evaluated from the canopy of a mixedwater inundation forest in Central Amazonia

Species similarity between the four forests was low (Fig. 16.8), indicating that each sampling site had a specific Coleoptera fauna. Lowest species similarity was found between the upland and inundation forests (blackwater 9.5%, mixedwater 4.9% and whitewater 3.3%). For this reason, the highest amount of site specific species was recorded in the upland forest (92.5%), followed by the blackwater (73.9%), mixedwater (72.7%) and whitewater (63.5%) inundation forests (Table 16.2). Highest species similarity was found between the mixedwater and whitewater inundation forest (21.6%) and between the mixedwater and blackwater inundation forest (11.1%). Nearly 85% of all species were restricted to one forest, 13.5% occurred in two forests, only 1.2% in three and 0.5% in four forests. However, percentages varied between families and subfamilies (Table 16.2).

In the mixedwater, occurrence of three dominant species from different families allowed an analysis of distribution. The evaluated material along three transects of *Eumolpinae* sp. #1, *Chrysomelidae* (n = 99), *Cryptorhynchinae* sp. #32, *Curculionidae* (n = 81) and sp. #4, *Helodidae* (n = 91) showed an aggregated distribution (Chi-square test: $p < 0.0001$) (Fig. 16.9).

16.4 Discussion

The reasons for the observed patterns are unknown and assumed to be ‘manifolded’. Each study site represents a distinct ecotype (cf. Adis 1997). The high presence of herbivore beetles certainly dominates detected traits. Dominance of *Curculionidae* and *Chrysomelidae* in both species richness and number of specimens seems to be typical for Amazonian forests (cf. Kirmse et al. 2003; Farrell and Erwin 1988). In

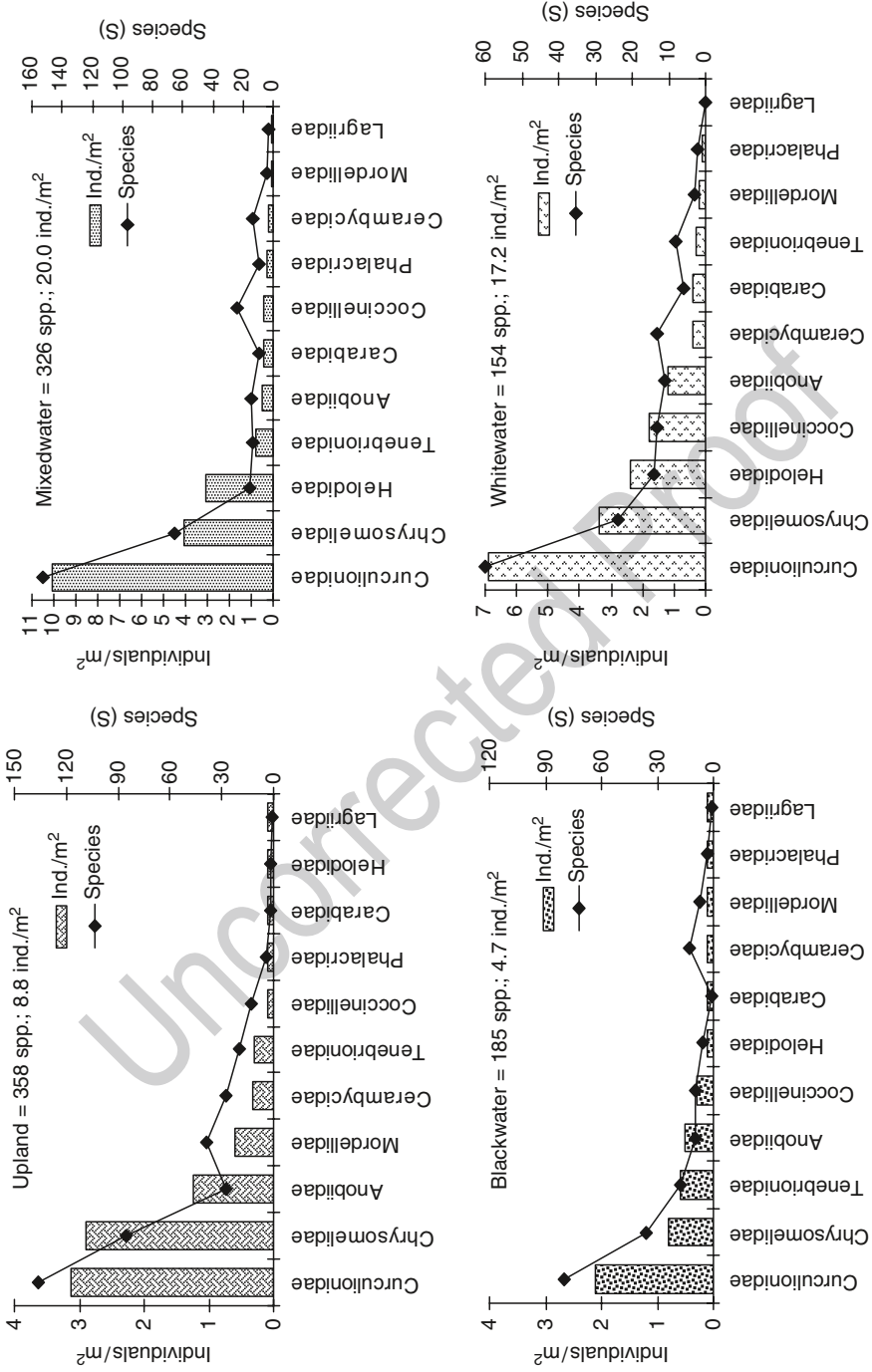


Fig. 16.7 Abundances (ind./m²) and number of species (S) of Coleoptera families evaluated from the canopy of four forest types in Central Amazonia

Table 16.2 Distribution of total Coleoptera species by families, subfamilies and trophic groups evaluated from the canopy of four forest types in Central Amazonia

		Only UL	Only BW	Only MW	Only WW	Restricted, one forest	Shared, two forests	Shared, three forests	Shared, four forests
	Σ spp.	(%) ^a				Σ spp. (%)			
t2.6	Herbivores (%) ^a	270 (92.5)	105 (73.9)	188 (72.7)	73 (63.5)	635 (84.8)	101 (13.5)	9 (1.2)	4 (0.5)
t2.7		(36.1)	(14.0)	(25.1)	(9.8)				
t2.8	Cerambycidae	26 (83.9)	12 (70.6)	10 (55.6)	11 (78.6)	59 (93.7)	3 (4.7)	1 (1.6)	-
t2.9	Lagritidae	1 (100.0)	1 (100.0)	3 (100.0)	-	5 (100.0)	-	-	-
t2.10	Curculionidae	120 (88.9)	58 (71.6)	112 (73.2)	36 (61.0)	325 (86.7)	48 (12.8)	2 (0.5)	-
t2.11	- Anthonominae	7 (87.5)	-	3 (60.0)	2 (100.0)	12 (85.7)	2 (14.3)	-	-
t2.12	- Apioninae	36 (92.3)	25 (96.2)	47 (82.5)	6 (46.2)	115 (92.0)	10 (8.0)	-	-
t2.13	- Attelabinae	2 (66.7)	-	-	-	2 (66.7)	1 (33.3)	-	-
t2.14	- Baridinae	2 (100.0)	2 (66.7)	8 (61.5)	2 (66.7)	14 (93.3)	1 (6.7)	-	-
t2.15	- Broadnose families (Entiminae)	4 (50.0)	-	3 (75.0)	-	7 (58.3)	5 (41.7)	-	-
t2.16	- Ceutorhynchinae	-	-	1 (50.0)	-	1 (50.0)	1 (50.0)	-	-
t2.17	- Cholinae	2 (100.0)	-	-	-	2 (100.0)	-	-	-
t2.18	- Cossoninae	1 (50.0)	-	-	-	1 (33.3)	2 (66.7)	-	-
t2.19	- Cryptorhynchinae	28 (87.5)	14 (70.0)	35 (79.5)	14 (77.8)	89 (89.0)	10 (10.0)	1 (1.0)	-
t2.20	- Cyliandrothinae	-	-	1 (100.0)	-	1 (100.0)	-	-	-
t2.21	- Eriirrhinae	2 (66.7)	-	-	1 (33.3)	3 (60.0)	2 (40.0)	-	-
t2.22	- Hylobiinae	8 (100.0)	4 (66.7)	3 (50.0)	1 (25.0)	15 (78.9)	3 (15.8)	1 (5.3)	-
t2.23	- Hyperinae	-	-	-	1 (100.0)	1 (50.00)	1 (50.0)	-	-
t2.24	- Magdalinae	3 (100.0)	-	-	1 (100.0)	4 (100.0)	-	-	-
t2.25	- Myrmecinae	6 (100.0)	2 (66.7)	2 (40.0)	-	10 (76.9)	3 (23.1)	-	-
t2.26	- Prionomerinae	-	-	4 (80.0)	2 (66.7)	6 (85.7)	1 (14.3)	-	-
t2.27	- Rhynchitinae	3 (100.0)	-	-	-	3 (100.0)	-	-	-
t2.28	- Rhynchohorinae	1 (100.0)	-	-	-	1 (100.0)	-	-	-

(continued)

Table 16.2 (continued)

	Only UL (%) ^a	Only BW	Only MW	Only WW	Restricted, one forest	Shared, two forests	Shared, three forests	Shared, four forests
Σ spp.	Σ spp. (%)				Σ spp. (%)			
Herbivores (%) ^a	270 (92.5)	188 (72.7)	73 (63.5)		635 (84.8)	101 (13.5)	9 (1.2)	4 (0.5)
- ychinea	2	-	-	-	0 (0.0)	2 (100.0)	-	-
- Zygotinae	14 (87.5)	4 (84.6)	4 (57.1)	6 (100.0)	35 (92.1)	3 (7.9)	-	-
- Nonidentifiable	1 (100.0)	-	1 (50.0)	-	3 (75.0)	1 (25.0)	-	-
Chrysomelidae	69 (81.2)	24 (66.7)	43 (66.2)	15 (60.0)	151 (84.8)	24 (13.5)	3 (1.7)	-
- Alticinae	21 (70.0)	12 (66.7)	21 (67.7)	6 (66.7)	60 (82.2)	11 (15.1)	2 (2.7)	-
- Cassidinae	2 (100.0)	-	-	1 (100.0)	3 (100.0)	-	-	-
- Chlamysinae	2 (100.0)	-	1 (100.0)	2 (100.0)	5 (100.0)	-	-	-
- Chrysomelidae	-	1 (50.0)	1 (100.0)	1 (100.0)	3 (75.0)	1 (25.0)	-	-
- Cryptocephalinae	12 (92.3)	1 (100.0)	7 (87.5)	1 (50.0)	21 (95.5)	1 (4.5)	-	-
- Eumolpinae	31 (88.6)	9 (75.0)	8 (44.4)	3 (33.3)	51 (83.6)	9 (14.8)	1 (1.6)	-
- Galerucinae	-	-	3 (75.00)	-	3 (60.0)	2 (40.0)	-	-
- Hispinae	-	-	1 (100.0)	-	1 (100.0)	-	-	-
- Lamprosomatinae	1 (100.0)	1 (100.0)	1 (100.0)	1 (100.0)	4 (100.0)	-	-	-
Helodidae	2 (100.0)	6 (100.0)	7 (43.8)	5 (35.7)	20 (69.0)	9 (31.0)	-	-
Mordellidae	33 (84.6)	2 (28.6)	3 (75.0)	1 (33.3)	39 (86.7)	5 (11.1)	1 (2.2)	-
Anobiidae	18 (64.3)	1 (10.0)	5 (33.3)	5 (45.5)	29 (69.1)	8 (19.0)	1 (2.4)	4 (9.5)
Phalacridae	1 (25.0)	1 (33.3)	5 (55.6)	-	7 (58.4)	4 (33.3)	1 (8.3)	-
Scavengers (= Saprophages)	18 (90.0)	11 (61.1)	4 (28.6)	5 (62.5)	38 (79.2)	8 (16.7)	2 (4.1)	-
(%) ^b	(37.5)	(22.9)	(8.3)	(10.4)	-	-	-	-
Tenebrionidae	18 (90.0)	11 (61.1)	4 (28.6)	5 (62.5)	38 (79.2)	8 (16.7)	2 (4.1)	-

Predators	64	10 (62.5)	6 (20.7)	25 (45.5)	13 (50.0)	54 (84.4)	7 (10.9)	2 (3.1)	1 (1.6)
(%) ^c	-	(19.6)	(11.8)	(35.3)	(17.6)	-	-	-	-
Carabidae	13	-	-	7 (22.6)	4 (30.8)	11 (84.6)	-	1 (7.7)	1 (7.7)
Coccinellidae	51	10 (76.9)	6 (60.0)	18 (75.0)	9 (69.2)	43 (84.3)	7 (13.7)	1 (2.0)	-
Total	860	299 (82.8)	121 (58.2)	218 (61.9)	91 (55.8)	727 (84.4)	116 (13.5)	13 (1.5)	5 (0.6)
(%) ^d	-	(34.8)	(14.1)	(25.3)	(10.6)	-	-	-	-

t2.29 ^aHerbivores (%)

t2.30 ^bScavengers (= Saprophages)(%)

t2.31 ^cPredators(%)

t2.32 ^dTotal(%)

t2.33 UL = upland forest, BW = blackwater forest, MW = mixedwater forest, WW = whitewater forest

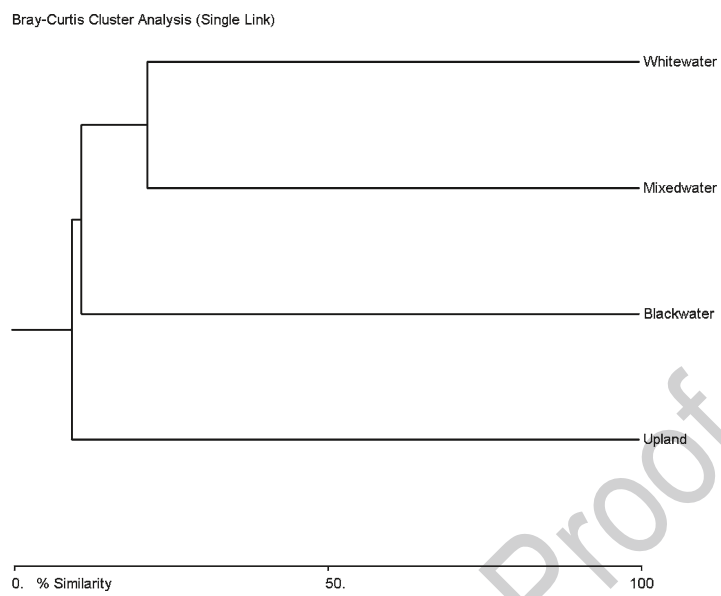


Fig. 16.8 Species similarity (Bray-Curtis; %) of Coleoptera between four forest types, evaluated from the canopy in Central Amazonia

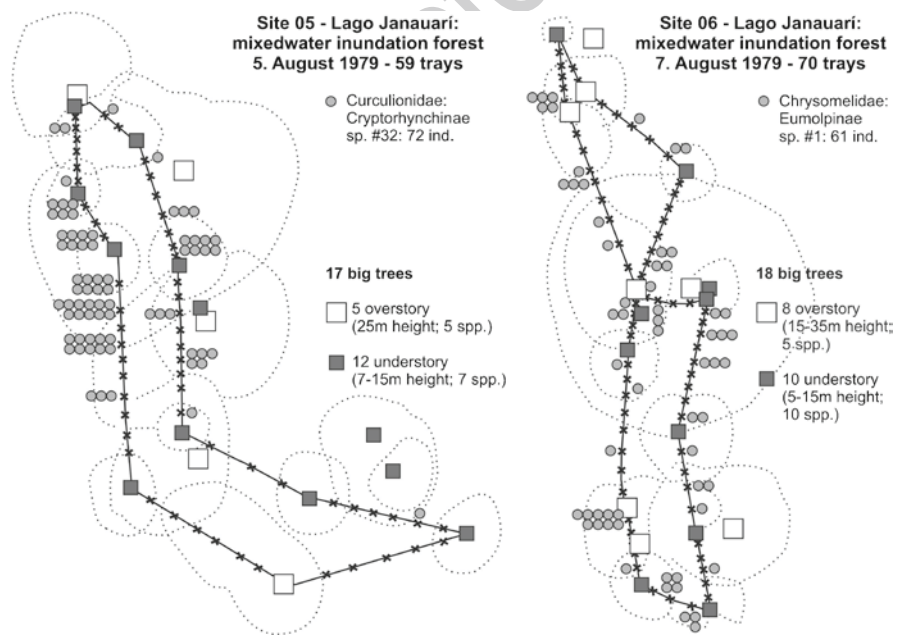


Fig. 16.9 Aggregated distribution of two dominant beetle species evaluated from the canopy of a mixedwater inundation forest in Central Amazonia along two selected transects

Central Amazonia, highest diversity and highest amount of site specific herbivore species on upland suggests a greater availability of food resources due to a higher number of tree species compared to inundation forests. In the vicinity of Manaus, up to 1,200 plant species (mostly trees) were reported from upland forests, up to 300 tree species from whitewater inundation forests and up to 200 tree species from blackwater inundation forests (Ribeiro et al. 1999; Worbes 1997). The low species similarity of herbivore beetles between upland and inundation forests is possibly mirrored in a low species similarity of tree species (Worbes 1997). Tree species between blackwater and whitewater inundation forests also differ greatly (Prance 1979) which could be one reason for their high amount of site specific beetle species. The vegetation in the mixedwater inundation forest represents an ecotone with characteristic tree species of the whitewater or/and blackwater region of Central Amazonia (Amaral et al. 1997). This might explain that in all inundation forests investigated the highest species number of beetles was obtained in the mixedwater but not that about 73% of its species were restricted to this forest type.

Inundation forests in Central Amazonia are covered by several meters of flood water for 5–7 months each year. The disturbance impact of this so-called flood pulse (Junk et al. 1989) can be another reason for the lower species diversity of beetles obtained in the black- and whitewater inundation forests compared to the non-flooded upland forest.

The rarefaction curves for the four forest types evaluated showed that a curve asymptote has not been reached. In Western Amazonia, 300–1,200 samples of 9 m² each were needed along transects in an Ecuadorian upland forest to ‘know’ the canopy/understory beetle fauna in a local area. The data base used had more than 15,000 beetles that were obtained during a three year period, seasonally, and represented 2,010 morphospecies (Erwin et al. 2005).

[AU2]

Aggregated distribution observed for some dominant herbivore beetle species in the mixedwater inundation forest suggests preference for certain tree species. Different quality of food resources, especially leaves that are rich in secondary compounds and digestion inhibitors (e.g. polyphenols, terpenoids) might be of importance (Downum et al. 2001; Janzen 1974, 2003). Higher beetle abundances (ind./m²) in the mixedwater and whitewater might indicate the availability of better food qualities, possibly due to better soil nutrient contents for plants compared to the blackwater inundation forest and the non-flooded upland forest (Furch 1997; Worbes 1997).

The canopy of each ecotype in Central Amazonia represents a discrete beetle guild. According to our data, local deforestation will result in the loss of many unique restricted beetle species. Comparative experimental studies on the food specificity of abundant herbivore species from different beetle families are mandatory in all ecotypes investigated, to obtain further insights in the traits observed.

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Abstract	<p>In Amazonian floodplain forests, the flood pulse results in an alternating aquatic and terrestrial phase per year. Consequentially, trees react with cambial dormancy, resulting in differing wood anatomical structures that appear as rings in the cross-section of the trees stem. Annual tree-ring patterns represent a reliable basis that can be used in various ways to gain information on historical growth rates, tree age, and past environmental conditions. In the following chapter, the anatomical background of the visibility of tree rings will be explained and an overview over the wood anatomy and tree-ring structures of the stem of many tree species in the igapó and várzea will be given. Most species in the várzea (77%) show well defined rings around the entire cross-section; most species in the igapó (60%) show distinct rings but they are not visible around the entire cross-section or are generally ill-defined; species with poor and barely visible boundaries originate from the igapó. Despite the large variability of tree rings from tropical regions, their annual nature could be proven for many tree species. This opens the possibility to widely apply tree-ring analytical studies in the tropics.</p>	
Keywords (separated by ',')	Ring structure - Tree ring analysis - Wood anatomy	

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Keywords Ring structure • Tree ring analysis • Wood anatomy 21

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22 17.1 Introduction

23 Trees all over the world face periodically unfavorable growing conditions and
24 consequentially respond with cambial dormancy due to the annual variation of
25 either precipitation (drought stress), temperature (frost) or flooding (water stress).
26 This results in the reduction of radial growth for days or months and in differing
27 wood anatomical structures that appear as rings in the cross-section of the tree
28 stems. Rings are annual, if the triggering climate factors, such as a dry period in
29 most parts of the tropics, occur once a year (Worbes 1995). Understanding the past
30 and current dynamics of the world's tropical rain forests is an important current
31 challenge for ecologists. Annual tree-ring patterns represent a reliable basis that can
32 be used in various ways to gain information on forest dynamics (Worbes et al. 1992;
33 Brienen and Zuidema 2006), tree ages (Worbes and Junk 1999) growth rates, [AU1]
34 climate reconstructions (Worbes 1999; Schöngart et al. 2004,) to estimate manage-
35 ment criteria (Schöngart this volume) and changes in the C-stocks of above-ground
36 coarse wood biomass (Schöngart et al. this volume a).

37 In Amazonian floodplain forests, flooding (lasting up to several months) and
38 water level fluctuations result in annually alternating aquatic and terrestrial phases.
39 During the aquatic phases of the soil, anoxic conditions hinder root respiration and
40 water uptake. This induces leaf shedding in many tree species (cf. Parolin et al. this
41 volume) followed by cambial dormancy (Schöngart et al. 2002). The reduction of [AU2]
42 growth at the end of the growing period leads in many species to a visible change
43 in the formation and differentiation of wood cells. In most obvious cases a clear
44 differentiation is possible into 'earlywood' cells, formed when the growing period
45 starts, and 'latewood' cells, formed later in or at the end of the growing period. The
46 first hint to the annual nature of these growth zones was given by Gessner (1968),
47 it was proven by means of radiocarbon dating (Worbes 1984) and is the basis for a
48 wide range of applications.

49 In the following chapter, an overview over the wood anatomy and tree-ring
50 structures of the stem of many tree species in the igapó and várzea will be given.
51 The described wood-anatomical structures are to be found in tree species through-
52 out the globe as well. Therefore this chapter is to exemplify the general character-
53 istics of tropical tree-ring structures.

54 Nomenclature follows APGII, authors of plant names are given in Table 17.1. In
55 the figures, wood structure is shown in the growing direction from the bottom-up,
56 arrows indicate tree-ring boundaries.

57 17.2 Anatomical Classification of Tree-Ring Structures

58 Macroscopically apparent growth structures become visible as rings in a cross-section
59 as light/dark zones or bands on sanded discs. Here, the anatomical background of
60 the visibility will be explained. In general, different colors within one growth zone

Table 17.1 Tree species in the várzea and the igapó with features in respect of tree-ring analysis: Distinctiveness of tree rings in the inner (in) and the outer (out) part of the stem disc expressed in '+' (good), '±' (visible) and '-' (poor)

	Family	Genus	Species	Author	Distinctiveness		Wood structure	Origin	
					In	Out			
t1.1	Annonaceae	<i>Amnona</i>	<i>sp.</i>	L.	+	+	A, B	várzea	
t1.2		<i>Duguetia</i>	<i>sp.</i>	A. St.-Hil.	+	+	0.33–0.39	A, B	várzea
t1.3	Apocynaceae	<i>Duguetia</i>	<i>uniflora</i>	Mart.	+	+	0.58	A	igapó
t1.4		<i>Guatteria</i>	<i>sp.</i>	Ruiz and Pav.	±	+		A, B	várzea
t1.5	Boraginaceae	<i>Pseudoxandra</i>	<i>polypheba</i>	(Diels) R.E.Fr.	+	+	0.51	A	várzea
t1.6		<i>Pseudoxandra</i>	<i>sp.</i>	R.E.Fr.	+	+		A, B	várzea
t1.7	Euphorbiaceae	<i>Anacampsa</i>	<i>riedelli</i>	(Müll. Arg.) Markgr.	-	-		A	igapó
t1.8		<i>Bonafousia</i>	<i>tetrastachya</i>	(H.B. and K.) Markgr.	±	-		A	várzea
t1.9	Aquifoliaceae	<i>Malouetia</i>	<i>furfuracea</i>	Benth. ex Müll. Arg.	-	-		?	igapó
t1.10		<i>Ilex</i>	<i>inundata</i>	Benth. ex Reissek	±	±	0.43	A (B)	várzea
t1.11	Bignoniaceae	<i>Crescentia</i>	<i>amazonica</i>	Ducke	+	+	0.41	A, B, C	várzea
t1.12		<i>Tabebuia</i>	<i>barbata</i>	(E. Mey.) Sandwith	±	+	0.76–1.0	A, B, C	igapó
t1.13	Boraginaceae	<i>Tabebuia</i>	<i>barbata</i>	(E. Mey.) Sandwith	+	+	0.53–0.85	A, B	várzea
t1.14		<i>Cordia</i>	<i>sp.</i>	L.	+	±	0.35–0.39	A	várzea
t1.15	Capparaceae	<i>Cratavea</i>	<i>bentharii</i>	Eichler	+/-	±	0.39–0.48	A, B	várzea
t1.16		<i>Chrysobalanus</i>	<i>sp.</i>	L.	-	-	0.95	C	igapó
t1.17	Clusiaceae	<i>Licania</i>	<i>heteromorpha</i>	Benth.	±	+	0.9	C	igapó
t1.18		<i>Licania</i>	<i>sp.</i>	Aubl.	-	±, -	0.78*	C	igapó
t1.19	Connaraceae	<i>Caratipa</i>	<i>parensis</i>	Huber	-	-	0.76	A, D	igapó
t1.20		<i>Garcinia</i>	<i>macrophylla</i>	Mart.	±	±	0.72*	A, C	várzea
t1.21	Euphorbiaceae	<i>Rourea</i>	<i>sp.</i>	Aubl.	+	+	0.65	A	várzea
t1.22		<i>Amanoa</i>	<i>oblongifolia</i>	Müll. Arg.	-	±	0.76	C	igapó
t1.23	Euphorbiaceae	<i>Hevea</i>	<i>guianensis</i>	Aubl.	+	+	0.4	A, B, C	igapó
t1.24		<i>Mabea</i>	<i>nitida</i>	Spruce ex Benth.	±	±	0.61	A, B	igapó
t1.25	Margaritaceae	<i>Margaritaria</i>	<i>nobilis</i>	L. f.	+	+	0.65	A, B	várzea
t1.26									

(continued)

Table 17.1 (continued)

Family	Genus	Species	Author	Distinctiveness		Density (g*cm ⁻³)	Wood structure	Origin
				In	Out			
Humiriaceae	<i>Piranhea</i>	<i>trifoliata</i>	Baill.	+	+/-	0.83–0.93	B, C	várzea
	<i>Humiriastrium</i>	<i>cuspidatum</i>	(Benth.) Cuatrec.	±	±		A	igapó
	<i>Vitex</i>	<i>cymosa</i>	Bert. ex Spreng.	+/-	+/-	0.58–0.59	A	várzea
Lauraceae	<i>Endlicheria</i>	<i>aranciflora</i>	(Meisn.) Mez and C.K. Allen	+	+	0.63–0.82	A	igapó
Lecythidaceae	<i>Nectandra</i>	<i>amazonum</i>	Nees	+	+	0.39–0.47	A	várzea
	<i>Eschweilera</i>	<i>albiflora</i>	Miers	±	±	0.75	C	várzea
	<i>Eschweilera</i>	<i>sp.I</i>	Mart. ex DC.	+	+	0.55–0.67	C	várzea
	<i>Eschweilera</i>	<i>sp.II</i>	Mart. ex DC.	±	+	0.71–0.91*	C	igapó
	<i>Eschweilera</i>	<i>sp.III</i>	Mart. ex DC.	±	±	0.71–0.91*	A, C	igapó
	<i>Jugastrum</i>	<i>sp.</i>	Miers	+	+	0.71	C	igapó
	<i>Aldina</i>	<i>latifolia</i>	Benth.	-	-		A	igapó
	<i>Macrobolobium</i>	<i>acacifolium</i>	Benth.	±	+	0.42–0.49	A, B	várzea
	<i>Macrobolobium</i>	<i>acacifolium</i>	Benth.	±	+		A, B	igapó
	<i>Parkia</i>	<i>auriculata</i>	Spruce ex Benth,	+	+	0.65	A, B	igapó
<i>Poecilanthè</i>	<i>amazonica</i>	(Ducke) Ducke	±	+	0.94	A, B	igapó	
<i>Pterocarpus</i>	<i>amazonum</i>	(Benth.) Amshoff	+	+	0.33	A, B, C	várzea	
<i>Swartzia</i>	<i>argentea</i>	Spruce ex Benth,	±	+		B, C	igapó	
<i>Swartzia</i>	<i>laevicarpa</i>	Amshoff	±	+	0.56–0.64	A, B, C	igapó	
<i>Swartzia</i>	<i>macrocarpa</i>	Spruce ex Benth,	±	±	1.02*	B, C	igapó	
<i>Swartzia</i>	<i>polypphylla</i>	DC.	±	+	0.56	A, B, C	igapó	
<i>Swartzia</i>	<i>sp.I</i>	Schreb.	-	±	1.02*	B	igapó	
<i>Swartzia</i>	<i>sp.II</i>	Schreb.	±	±	0.99	A,B,C	várzea	
<i>Swartzia</i>	<i>sp.III</i>	Schreb.	+	+	1.02*	A, B, C	várzea	
<i>Tachigali</i>	<i>sp.</i>	Aubl.	+	+	0.7	A	igapó	
<i>Vatairea</i>	<i>guianensis</i>	Aubl.	+	+	0.75	A	várzea	
<i>Zygia</i>	<i>inaequalis</i>	Pittier	+	±	0.62	A, B	várzea	

Linaceae	<i>Roucheira</i>	<i>sp.</i>	Planch.				0.82	A	igapó
Malvaceae	<i>Pseudobombax</i>	<i>munguba</i>	(Mart. and Zucc.) Dugand	±	±	±	0.21–0.26	A, D	várzea
	<i>Luehea</i>	<i>sp.</i>	Willd.	+	+	+	0.37–0.57	A	várzea
Melastomataceae	<i>Mollia</i>	<i>sp.</i>	Mart.	±, +	±, +			A	várzea
Meliaceae	<i>Mouriri</i>	<i>guyanensis</i>	Aubl.	±	±		0.82	A	várzea
	<i>Trichilia</i>	<i>singularis</i>	C.DC.	+	+		0.51	A	várzea
Moraceae	<i>Sorocea</i>	<i>duckei</i>	W.C. Burger	+	±		0.58	C	várzea
Myrtaceae	<i>Calythranthes</i>	<i>spruceana</i>	O. Berg	±	±		0.68–0.74	A	várzea
	<i>Myrciaria</i>	<i>amazonica</i>	O. Berg	±	±		0.75	A/B, C	várzea
	<i>Myrtaceae</i>	<i>sp.</i>	Juss.	±, -	±, -		0.80–0.84	A	igapó
	<i>Psidium</i>	<i>acutangulum</i>	DC.	±	±		0.55–0.62	A(B, C)	várzea
Polygonaceae	<i>Triplaris</i>	<i>surinamensis</i>	Cham.	±	+		0.52	A, D	igapó
Rubiaceae	<i>Ferdinandusa</i>	<i>paraensis</i>	Ducke	-	-			A	várzea
Rutaceae	<i>Zanthoxylum</i>	<i>compactum</i>	(Huber ex de Albuquerque) Waterman	±	±				
Salicaceae	<i>Casearia</i>	<i>sp.</i>	Jacq.	±	±		0.62	A, D	igapó
	<i>Laetia</i>	<i>corymbulosa</i>	Spruce ex Benth.	±	±		0.61–0.64	A, D	várzea
	<i>Laetia</i>	<i>suaveolens</i>	Benth.	+	±		0.74	A	igapó
	<i>Salix</i>	<i>martiana</i>	Leyb.	±	±		0.42–0.43	A	várzea
Sapindaceae	<i>Matayba</i>	<i>macrolepis</i>	Radlk.	+	+			A	várzea
	<i>Matayba</i>	<i>steinbachii</i>	Melch.	±	±		0.59–0.62	A	várzea
Sapotaceae	<i>Elaeoluma</i>	<i>glabrescens</i>	(Mart. and± Eichl. Ex Miq.) Aubrév.	±	±		0.56–0.59	A, C	várzea
	<i>Pouteria</i>	<i>glomerata</i>	(Miq.) Radlk.	±	±		0.75	C	várzea
	<i>Pouteria</i>	<i>elegans</i>	(A. DC.) Baehni.	±	±		0.82	C	igapó
Urticaceae	<i>Cecropia</i>	<i>latiloba</i>	Miq.	+	±		0.46	A, B	várzea
	<i>Cecropia</i>	<i>sp.</i>	Loefl.	+	±		0.48	A	várzea

(continued)

Table 17.1 (continued)

Family	Genus	Species	Author	Distinctiveness		Wood structure	Origin
				In	Out		
Violaceae	<i>Amphirrhox</i>	<i>surinamensis</i>	Eickl.	-	-	A	igapó
	<i>Erisma</i>	<i>calcaratum</i>	Warm.	±	±	C	igapó

t1.29 Wood structure in respect of tree-ring delimitation: A = density variation, B = marginal parenchyma band, C = pattern of concurring parenchyma and fibre
t1.30 tissue and D = variation of vessel size and density. Combinations of A – D occur frequently. Density data marked with * originate from the Wood Density
t1.31 Database for spp. of the respective genus (<http://www.worldagroforestrycentre.org/sea/Products/AFDbases/WD/Index.htm>)

can be traced back to the variation in wood density, where the dark zones show a higher density, which is attributed to fibre cells with shortened radial diameters and thickened walls. This is clearly visible in coniferous wood (Schweingruber 2001), but also in several broad-leaf families in the tropics. The high diversity of tropical woody species however is reflected in a high diversity of growth-zones structures, formed as a composition of different vessel, fibre and parenchyma characteristics. These can be ordered into almost 40 different classes (Carlquist 1988). Nevertheless, for a more applicable system, the authors follow Coster (1927, 1928) and reduce the number of classes to four basic tree-ring types (Worbes 1985):

A most common is a tree-ring boundary consisting of one or several rows of fibres with shortened radial diameter and thickened walls (Fig. 17.1), resulting in density variations. This type can be found in almost all the investigated plant families.

B Also common, especially in the Fabaceae, are boundaries with uni- or multi-rowed marginal bands of axial parenchyma cells, often filled with substances, of a very light appearance (Fig. 17.2).

C In several species, periodically recurring parenchyma and fibre bands of different widths result in a certain pattern delineating the boundary of the tree ring (Fig. 17.3). For Sapotaceae, Lecythidaceae and Moraceae in particular, a broad band of fibre cells marks the beginning of the ring. Adjacent to this, bands of parenchyma alternate with bands of fibres, usually becoming narrower toward the end of a ring.

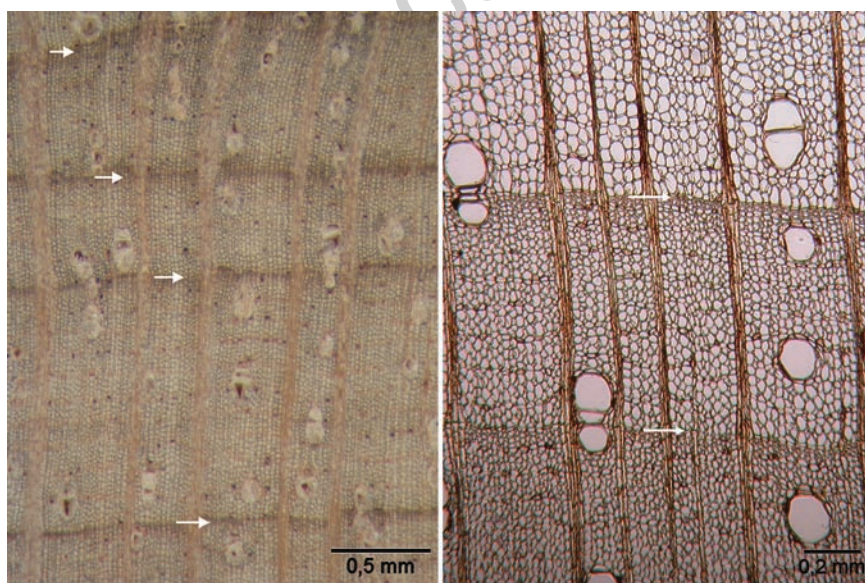


Fig. 17.1 Tree-ring type A, density variations in the wood structure of *Annona* sp., Annonaceae, in the várzea: (left) macroscopic and (right) microscopic cross-section

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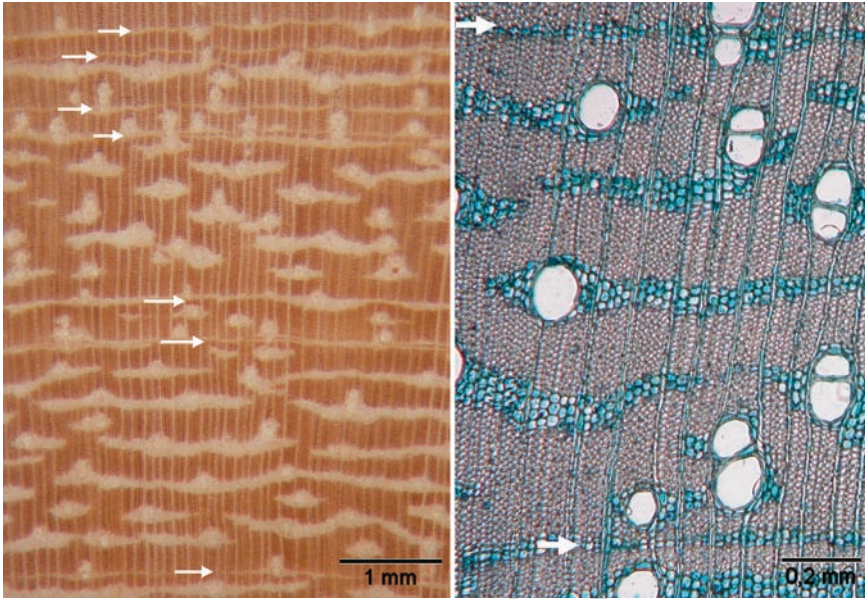


Fig. 17.2 Tree-ring type B, marginal parenchyma band in the wood structure of *Swartzia argentea*, Fabaceae, in the igapó, (left) macroscopic and (right) microscopic cross-section

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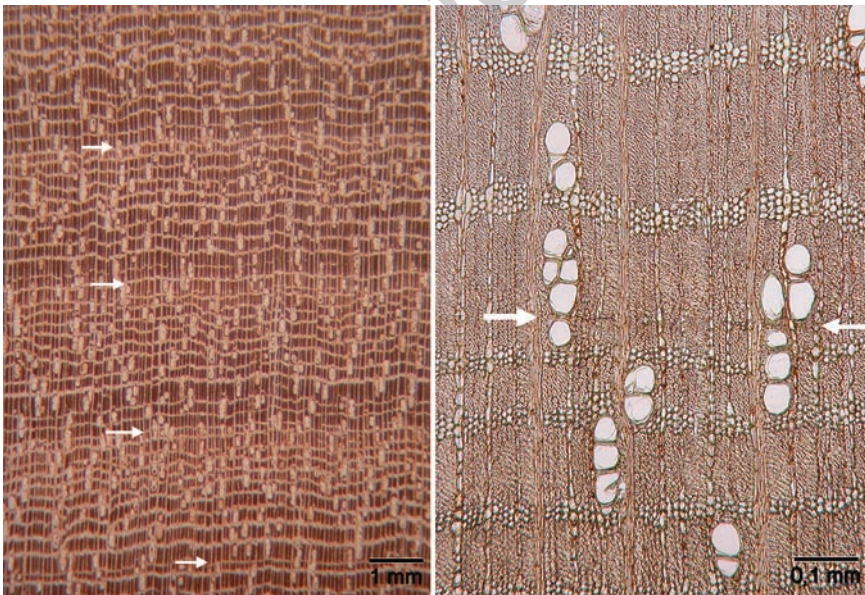
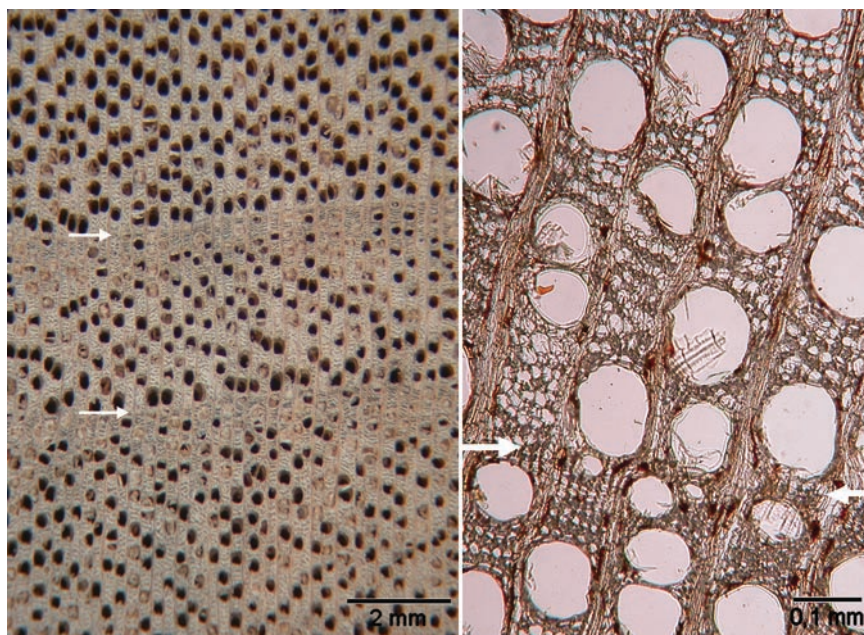


Fig. 17.3 Tree-ring type C, patterns of parenchyma and fibre bands, in the wood structure of *Pouteria glomerata*, Sapotaceae, in the várzea, (left) macroscopic and (right) microscopic cross-section



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Fig. 17.4 Tree-ring type D, variation in vessel density/size in the wood structure of *Pseudobombax munguba*, Bombacaceae, in the várzea, (left) macroscopic and (right) microscopic cross-section

D Often described for temperate tree species, but also occurring in tropical species, this type is characterized by varying frequency and diameter of vessels within a ring (Fig. 17.4). Often, this type is characterized by many and/or large vessels at the beginning of the ring, but other species show the largest vessels in the middle of the ring.

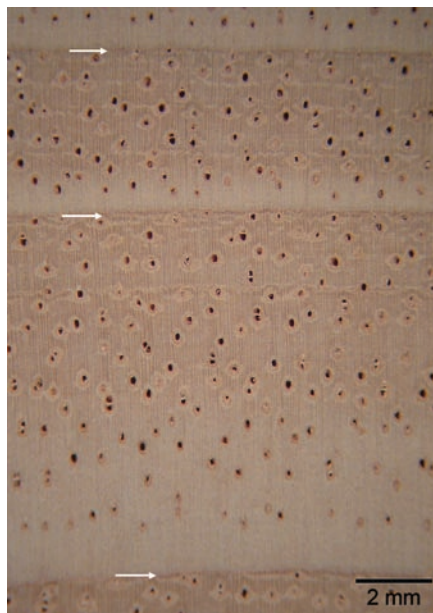
The characteristics described in A–D often occur in various combinations. Thereby combinations can co-occur within the same ring. An example is given by the rings of an individual of *Macrolobium acaciifolium* (Fig. 17.5) which combines three ring characteristics: The variation of cell wall thickness and cell lumen diameter results in a clear shift from light earlywood to dark latewood, the variation in vessel size and density from few small vessels at the beginning of the ring merge to frequent large vessels toward the end of the ring. Finally, a light terminal parenchyma band highlights the boundary. In other cases, different rings within the same individual can show extreme dissimilar characteristics. In an individual of *Salix martiana* (Fig. 17.6) for instance, two consecutive rings show a complete different appearance: The first ring is delineated only by a multi-rowed band of latewood fibres, while the second ring is characterized by the variation of vessel size and frequency, i.e. a broad band of many large vessels at the beginning of the ring.

To use growth patterns for tree-ring studies, a successful determination of tree-ring boundaries throughout a sample is required. To detect all boundaries within a sample, it is therefore essential to consider changes in the general pattern of the

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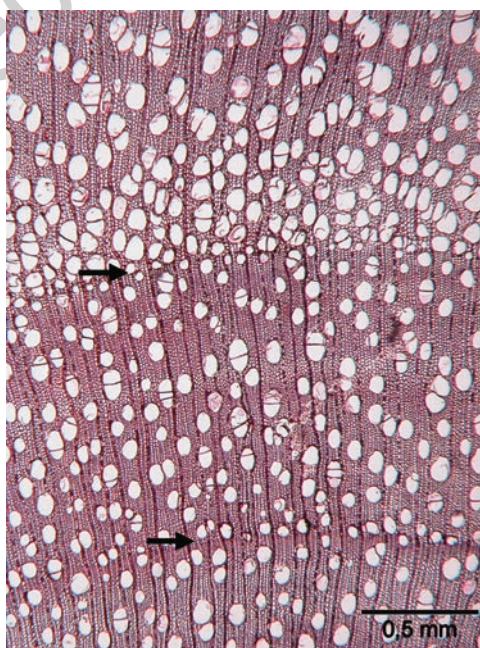
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Fig. 17.5 Tree-ring boundaries of *Macrolobium acaciifolium*, Fabaceae, in the várzea showing a combination of tree-ring types A, B and C in the same rings



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Fig. 17.6 Differing tree-ring boundaries of *Salix martiana*, Salicaceae, in the várzea showing variations in cell wall thickness (Type A) in one ring (*below*) and variations in vessel density/size (Type D) in a consecutive ring



growth structure rather than searching for a single specific character delineating a tree ring. 104
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17.3 Macroscopical Variability of the Visibility of Rings within Species and Individuals of Trees in the Igapó and Várzea 106
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In a study on structural and other adaptations to long-term flooding by trees in the igapó and várzea (Worbes 1985), cross-sections from almost all tree species of test plots were taken. The analysis was done with respect to the presence and formation of growth rings and showed that all tree species investigated have well-defined growth rings, that can be ascribed to one or more of the before characterized growth-rings types A–D (cf. Table 17.1). However, numerous examples show that even distinct tree-ring boundaries underly a broad variability within a species and among individuals: Sometimes ring boundaries are ill-defined near the center of the disc, whereas they are quite distinct in the outer region near the bark (cf. Table 17.1). Some species form clear ring boundaries in their juvenile stage, later forming either ill-defined rings or narrow rings of very few or single cell rows, that can hardly be distinguished. 108
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In certain taxa (e.g. Annonaceae) tree species tend to form wedging rings meaning that tree rings merge due to a failure of cambial activity at certain positions of the stem (Fig. 17.7). An explanation for wedging rings is, for example, a changing light saturation due to changing competition pressure by surrounding trees. This probably leads to differences in the local supply of carbohydrates, water, mineral elements and phytohormones (Dünisch et al. 1999). In tree species showing wedging rings, the correct identification of ring boundaries at a single radius is impossible but requires the analysis of stem discs. Nevertheless, within a tree 120
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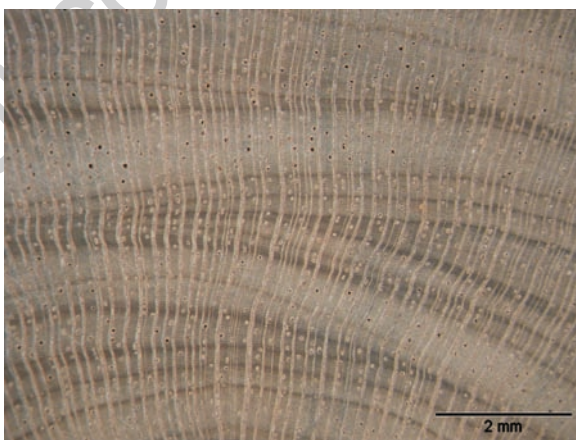


Fig. 17.7 Section of a disc of *Duguetia uniflora*, Annonaceae, in the igapó showing multiple wedging rings on various positions of the disc

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128 species, individuals with clear concentric rings may occur as well as those with
129 frequently wedging rings. Within a stem disc, rings may tend to wedge only in outer
130 parts, when the tree starts to form buttresses (Fig. 17.8).

131 In other species, the identification of tree rings is more difficult, because bound-
132 aries may tend to gradually disappear or break-off (Fig. 17.9). Finally, various
133 species show generally ill-defined boundaries, especially under high magnification
134 (Fig. 17.10).

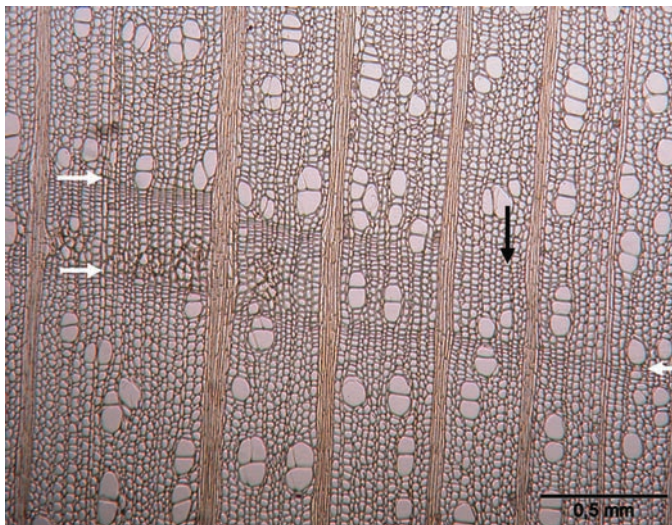
135 Various species of a family such as Euphorbiaceae, Lecythidaceae or Malvaceae
136 show different characteristics as regards the distinctiveness of tree-ring boundaries.
137 Species of other families (e.g. Lauraceae) show generally rather distinct growth
138 rings. The most diverse formation occurs within the genus *Swartzia*, although most
139 frequent are observations with wedging or disappearing rings. This genus forms
140 defined tree-ring boundaries in general (Fig. 17.2) but these are not evident over the
141 entire cross section. For many families no concentration in certain categories was
142 noted on the basis of the available wood samples. Three tendencies could be
143 observed: most species in the várzea (77%) show well-defined rings around the
144 entire cross-section; most species in the igapó (60%) show rings that are not visible
145 around the entire cross section or are generally ill-defined; species with poor and
146 barely visible boundaries originate from the igapó.

147 In general, both floodplain forests produce trees with ring structures suitable for
148 tree-ring analytical studies. Continuous as well as abrupt fluctuations of endoge-
149 nous and exogenous factors result in structural changes of the wood anatomy and

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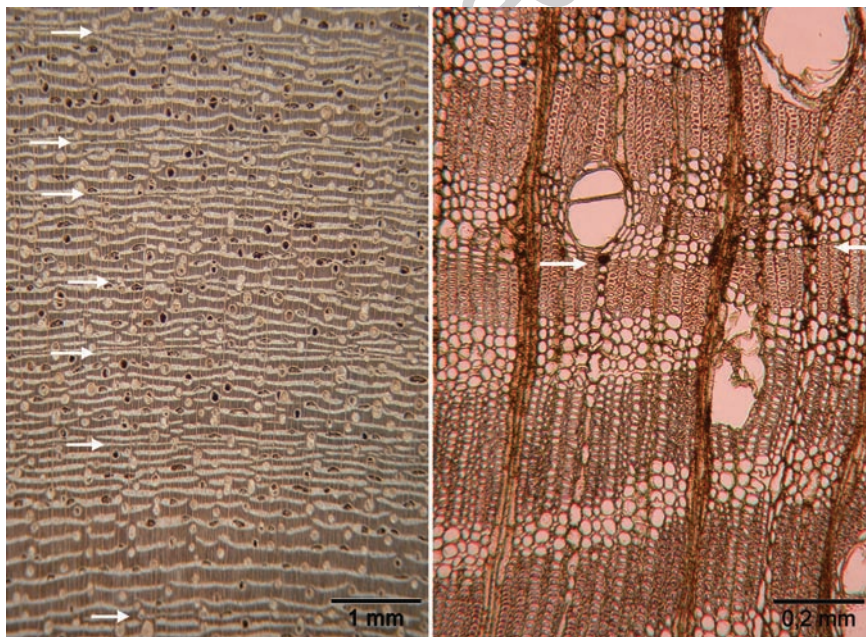


Fig. 17.8 Disc of *Swartzia polyphylla*, Fabaceae, in the igapó showing wedging rings in the outer part due to the formation of buttresses



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Fig. 17.9 Break-off of a tree-ring boundary in an individual of *Ilex inundata*, Aquifoliaceae, in the várzea. On the left site two, on the right site only one tree-ring boundaries are visible (white arrows), the black arrow roughly indicates the area where the boundary is not visible anymore



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Fig. 17.10 Wood structure of *Erismacalcaratum*, Vochysiaceae, in the igapó showing generally ill-defined ring boundaries, (left) macroscopic and (right) microscopic cross-section; with increasing magnification the boundaries become more difficult to detect

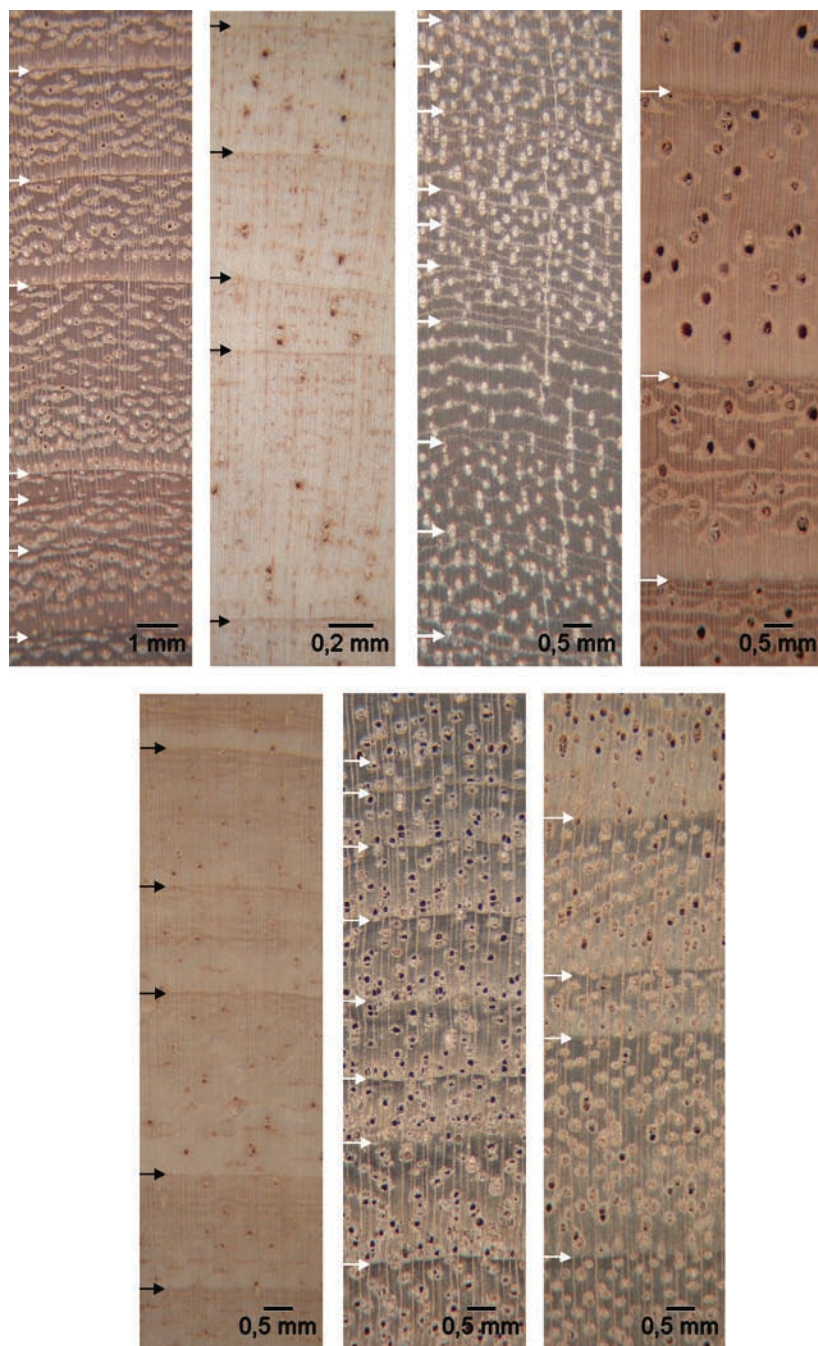
150 changing tree-ring widths. In dendrochronological studies abrupt changes are of
 151 special interest, as these can be used to date and analyse the impact of certain
 152 incidents, such as extreme climatic events or suppression and release effects
 153 (Schöngart et al. 2004; Brienen et al. 2006). [AU3]

154 17.4 Structure and Ecological Function of Xylem Elements 155 in Growth Zones

156 Little is known about the relation between ecological function and anatomical
 157 structure of wood. The majority of the wood anatomical literature deals with the
 158 taxonomic differentiation and seldom offers ecological explanations for differences
 159 in structure. In xylem, vessels, fibres and parenchyma accommodate hydraulic
 160 conductivity, stability, and storage, respectively. Well documented is only the
 161 relation between vessel dimensions and water supply (Baas 1990). At a rough geo-
 162 graphical scale, there is a trend that species with small vessels are linked with dry
 163 climate conditions, having safety margins against air embolism in dry periods. In
 164 many species of floodplain trees vessel size tends to decrease towards the end of
 165 the growth zones. This could be a hint for increasing water stress towards the begin-
 166 ning of flooding, when the water conduction from roots to leaves is inhibited by
 167 oxygen deficiency in the soil (Worbes 1997).

168 Large variations occur in the share of parenchyma and fibres, suggesting large
 169 variation in storage capacities and mechanical stability. In different species of
 170 growth zone type C (cf. *Macrolobium acaciifolium* in Fig. 17.11) the absence of
 171 parenchyma and vessels in a broad band of fibres in the earlywood is obvious. This
 172 band is followed by a mixture of parenchyma, vessels and fibre wood in specifically
 173 dependent variations. Fink (1982) as well as Dünisch and Puls (2003) observed in
 174 different tropical tree species that starch is predominantly stored in axial paren-
 175 chyma and soluble carbohydrates are mobilized at the beginning of the growing
 176 period in support of the formation of new leaves and secondary xylem before the
 177 new foliage produces carbohydrates through photosynthesis. That means, that the
 178 observed pattern in distribution of axial parenchyma and fibres is not random, but
 179 reflects clearly the mechanisms of carbohydrate storage and mobilization as a func-
 180 tion of specific phenological behaviour triggered by the dominating and limiting
 181 external growth factor. The composition of the xylem, in general, exhibits large
 182 variations within and between trees. The image analytical comparison of two
 183 individuals of *Tabebuia barbata* from the várzea and the igapó, respectively,
 184 showed that also nutrient availability affects the relative share of parenchyma and
 185 fibres: The individual from the igapó showed smaller radial increments (1.17 mm)

→
Fig. 17.11 (continued) Euphorbiaceae, igapó; *Piranhea trifoliata*, Euphorbiaceae, várzea;
Macrolobium acaciifolium, Fabaceae, várzea; *Pterocarpus amazonum*, Fabaceae, várzea,
Endlicheria arunciflora, Lauraceae, igapó and *Nectandra amazonum*, Lauraceae, várzea



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Fig. 17.11 Wood structure of tree species with distinct and continuous tree-rings boundaries: (from left above to right below) *Tabebuia barbarti*, Bignoniaceae, várzea; *Hevea guianensis*,

186 compared to the várzea tree (1.43 mm) and therefore invested more capacity in
187 storage and mobilization by forming a large amount of axial (34.81%) and radial
188 (11.23%) parenchyma compared to fibre cells (46.23%). That may help a tree to
189 survive periods of low resource levels and thereby compensate low nutrient
190 availability in the igapó. Given that fibre cells are the major costs of making xylem,
191 it is not astonishing that the individual from the nutrient rich várzea can invest most
192 in fibre cells (53.38%) and, as there is less need, fewer in axial (28%) and radial
193 (7.96%) parenchyma.

194 17.5 How to Measure Growth Dynamics in Tropical Trees

195 Despite the importance of basic data for the evaluation of growth and life history of
196 old-growth tropical forests there is a lack of information about wood growth rates
197 and ages of trees. Several traditional methods exist for this purpose, bearing different
198 limitations and problems.

199 Traditional methods of age determination are direct radiocarbon measurements of
200 the oldest parts of a tree, the center of the trunk base (a), calculations from repeated
201 diameter measurements (b) and the prediction of longevity from mortality rates (c).

202 (a) The advantage of radiocarbon dating is its independence from other metric
203 approaches. Its limitation is the restriction to time periods before 1640. Later the
204 'Suess effect' hinders an exact determination. Due to the varying ^{14}C content of
205 the atmosphere for the period between 1640 and 1950 up to five possible ages
206 can be related to one radiocarbon age. Nevertheless tree ages from this period are
207 published frequently, either with the oldest calibrated age of a series (Chambers
208 et al. 1998), or with a more conservative but nevertheless questionable approach,
209 the center of several possible calibrated ages (Viera et al. 2005).

210 (b) Growth trajectories based on short-term measurements give relative reliable
211 results when many individuals of different size classes are regarded and included
212 into the calculation (Clark and Clark 1999). Overestimations of ages are the con-
213 sequence, if lowest growth rates are combined with highest tree diameters
214 (Lieberman et al. 1985), while the calculation with highest observed growth rates
215 lead to assumed tree ages not older than 500–600 years (Laurance et al. 2004).

216 (c) A pure mathematical approach is the age calculation on the base of mortality
217 rates of a tree species population (Condit et al 1995), which never was validated
218 by other independent techniques.

219 Tree-ring analysis in tropical trees is not a new approach, but seldom used for
220 applied purposes in the tropics. The annual nature of tropical tree rings is proven
221 since the beginning of the twentieth century (Coster 1927). However the huge
222 diversity of tree species, wood structures and site conditions together with the still
223 living paradigm that tropical trees never have annual rings, makes it necessary to
224 prove the wood-growth periodicity of trees at many different sites. Again there are
225 a number of different techniques which are described below:

Phenological observations give a first indication if an external climate factor influences the growth rhythm of a tree; especially in combination with dendrometer measurements of short-term trunk increments (Schöngart et al 2002).

Cambial wounding developed by Mariaux (1967) provides exact information on the rhythm of wood formation. The cambium is injured in a small “window” of some square centimeters either mechanically by incision or chemically by injection. The wounds are covered by callus tissue in the consecutive years and remain as artificial and exactly datable scar in the wood.

Another artificial marking is the radiocarbon dating of individual growth zones based on the nuclear weapon effect (Worbes and Junk 1989). The growth periodicity can be proven by counting the number of rings between the radiocarbon dated ring and the youngest ring under the bark. The method is valid for the time between 1950 and today, when the radiocarbon content of the atmosphere doubled until 1963 as the consequence of the bomb explosions and decreased after the test ban treaty.

The dating of tree rings is also possible on the base of fire scars or tree rings with notable properties that differentiate from adjacent rings (pointer years) with exogenous factors such as fire or extreme climatic events (Worbes 1999). Unfortunately, this requires available long time records of such events, which is an obstacle in most tropical regions.

The successful correlation of tree-ring time series with climate records also indicate the existence of annual tree rings. Meanwhile this was carried out for many different tropical habitats reaching from floodplains (Schöngart and Junk 2007), over lowland forests (Brienen and Zuidema 2005) to very dry sites (Fichtler et al. 2004) enabling climate reconstructions for more than 500 years (Therrell et al. 2006). An overview on techniques and additional examples is given in Worbes (2002).

17.6 Discussion and Conclusions

Despite the large variability of tree rings from tropical regions, the existence of their annual nature could be proven for many tree species and is generally known since more than 100 years (overview in Worbes 2002). To ensure the successful application of dendrochronological studies a detailed knowledge of wood-anatomical structures and the variability of growth zones is required. In studies on time series analysis it is essential to start with species, known to be suitable for tree-ring analysis or with complete stem discs. Working with discs allows following the course of individual growth zones over the entire cross section and results in a reliable, correctly dated, reference data set to cross-date additional segments or cores. The use of concurring sections with distinguishable rings situated on different radii allows the exact counting of the trees age and even ring-width measurements in samples showing frequently wedging rings. After an initial classification of the tree-ring structure from disc samples, additional samples can be taken with an increment corer. In climatological studies, special carefulness should be paid

267 to the inner parts of the stem (juvenile wood) as young trees in the tropics usually
268 are influenced by strong competition and may show a different response to growth
269 limiting factors compared to mature trees.

270 Notwithstanding all the potential difficulties many species from the várzea and
271 igapó form distinct and continuous annual rings, suitable for tree-ring analysis.
272 Excellent examples for that are species from the genera *Tabebuia*, *Hevea*, *Piranhea*,
273 *Macarobium*, *Pterocarpus*, *Endlichera* or *Nectandra* (cf. Table 17.1 and Fig. 17.11).

274 On this basis and under consideration of the above mentioned variations and
275 peculiarities of the anatomical structures, tree-ring analysis can be used for a wide
276 range of applications. Thereby special interest should be paid to gain realistic incre-
277 ment data for the implementation of sustainable management plans, reliable proxy
278 data for tropical climate reconstruction and real tree ages for understanding forest
279 and population dynamics. An example is the reconstruction of the Southern
280 Oscillation Effect (ENSO) with tree-ring data for the nineteenth century using the
281 tree species *Piranhea trifoliata* in the várzea (Schöngart et al. 2004). An important
282 discussion of academic interest as well as in the frame of carbon sequestration is
283 the question of the maximum age of tropical tree species. In a review of recent lit-
284 erature on forest dynamics and carbon fluxes, the maximum age reported for the
285 oldest tropical forest trees was found to increase rapidly among successive studies
286 (Worbes and Junk 1999). These studies calculate or model the maximum age of
287 tropical trees and tend to overestimate considerably (Condit et al. 1995), with the
288 focus on the oldest theoretically possible age (Laurance et al. 2004).

289 In a Central Amazonian forest, however, three individual trees were reported to
290 be between 900 and 1,400 years old (Chambers et al. 1998). Those findings are
291 clear outliers to all other findings from tropical forests. They were based on single
292 samples from each tree and single radiocarbon estimations, without any corroborat-
293 ing data or replicated analyses. An analysis with radiocarbon dating confirmed by
294 tree-ring counting in a forest in Costa Rica resulted in 530 years for a large
295 *Hymenolobium mesoamericanum* with very dense wood (Fichtler et al. 2003), what
296 is an indicator for slow growth and high age. Other tree-ring based studies confirm
297 400–500 years as maximum age for tall growing timber species (Worbes and Junk
298 1999; Brienen and Zuidema 2006). This shows that the age of tropical trees does
299 not exceed principally that from temperate zone broad leaf species (Loehle 1988).

300 All of the above described aspects of wood and tree-ring formation are not lim-
301 ited to Amazonian floodplain forests, but of general nature for tropical trees. The
302 results stimulated tropical tree-ring analysis as a whole in the last 20 years and
303 helped to overcome the old paradigm that tropical trees do not form annual rings.

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AU2	Please fix a or b for Parolin et al. this volume here and in the following citation sin the text	
AU3	Please include Brienen et al. 2006 in the ref. list.	

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Abstract	Tropical rainforests play a major role in the global carbon budget, accounting for 32–36% of the terrestrial net primary production (NPP) (Mellilo et al. 1993; Clark 2004). They are a dynamic reservoir of carbon (C), but also a source of C-emissions to the atmosphere in regions undergoing deforestation (Houghton et al. 2000; Schimel et al. 2001). The rapid ongoing changes in the atmospheric concentration of CO ₂ and other greenhouse gases together with global climate change are likely to affect carbon cycling of tropical forests substantially.	

Chapter 18 1
Biomass and Net Primary Production 2
of Central Amazonian Floodplain Forests 3

Jochen Schöngart, Florian Wittmann, and Martin Worbes 4

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18.1 Introduction 5

Tropical rainforests play a major role in the global carbon budget, accounting for 32–36% of the terrestrial net primary production (NPP) (Mellilo et al. 1993; Clark 2004). They are a dynamic reservoir of carbon (C), but also a source of C-emissions to the atmosphere in regions undergoing deforestation (Houghton et al. 2000; Schimel et al. 2001). The rapid ongoing changes in the atmospheric concentration of CO₂ and other greenhouse gases together with global climate change are likely to affect carbon cycling of tropical forests substantially.

The Amazon basin contains the world’s largest tropical rainforest and thus plays a crucial role in the global carbon cycle. The total carbon in aboveground live forest biomass (AGLB) of the Amazon basin is estimated to be 93 ± 23 Pg C (Petagram = 10¹⁵ g or 10⁹ t) for an area of 5.76 × 10⁶ km² (Malhi et al. 2006). Based on more than 500 plot data and remote-sensing techniques, Saatchi et al.

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18 (2007) estimated a lower AGLB in the Amazon basin to be in the range of 59–73
 19 Pg C for an area of 5.46×10^6 km². Floodplain forests comprise in this estimation
 20 an area of 328,825 km², with a total AGLB of 3.25 Pg C.

21 There are two main types of floodplains along the large rivers in the Amazon
 22 basin which are distinguished by the characteristics of the flood-water and their
 23 flooding regime: the nutrient-poor igapó and the nutrient-rich várzea (Sioli 1954; [AU1]
 24 Prance 1979; Junk 1993). So far, the majority of studies have focused on biomasses
 25 and NPP of terra firme forests. In this chapter, we summarize the existing knowledge
 26 on biomass and the compounds that contribute to the NPP in floodplain forests.

27 18.2 Fine Litterfall

28 The most frequently measured component of NPP is fine litterfall (Clark et al.
 29 2001); however, in many studies it is not clearly stated what comprises fine litter-
 30 fall, especially with respect to the wood fraction (bark, branches, twigs). Data on
 31 litterfall for Amazonian floodplain forests are available for the tidal várzea flood-
 32 plains in eastern Amazonia (Cattanio et al. 2004), the central Amazonian várzea [AU2]
 33 and igapó (Adis et al. 1979; Franken et al. 1979; Worbes 1997), and the Peruvian
 34 várzea (Nebel et al. 2001a).

35 During November 2002 and October 2003, fine litterfall (defined here as com-
 36 prising leaves, fruits, flowers, and twigs up to 2 cm diameter) in permanent sample
 37 plots of late successional stages of low- and high-várzea forests was monitored in
 38 the Mamirauá Sustainable Development Reserve (MSDR) (Queiroz and Peralta,
 39 this volume). Low várzea forests establish where the annual water column averages
 40 heights of more than 3 m, whereas high-várzea forests establish where it averages
 41 <3 m (Wittmann et al. 2002a,b; Wittmann et al. this volume). In both forests, ten
 42 quadratic traps, each with a surface of 1 m², were randomly distributed over a 1-ha
 43 area and litter was collected every two weeks. The various components of the litter
 44 were then separated and dry mass was determined after 72 h of drying at 75°C.
 45 Monthly litterfall was correlated with monthly water-level fluctuations (data:
 46 Mamirauá Institute for Sustainable Development, IDSM) and precipitation data of
 47 Tefé (National Institute of Meteorology, INMET).

48 Total litter fall in the low várzea was 6.39 Mg ha⁻¹ year⁻¹ (Megagram = 10⁶ g)
 49 and in the high várzea 6.84 Mg ha⁻¹ year⁻¹ (Table 18.1). The difference in the

t1.1 **Table 18.1** Annual fine litterfall in late successional stages of a low and high várzea of the MSDR
 t1.2 (units in Mg ha⁻¹ year⁻¹). A *t*-test indicates no differences in litterfall between the two forest
 t1.3 types

t1.4 (Mg ha ⁻¹ year ⁻¹)	Low várzea	High várzea	<i>t</i> -value (p)
t1.5 Leaves	4.76	5.21	24 (n.s.)
t1.6 Other litter	1.62	1.62	0.98 (n.s.)
t1.7 Total litter	6.39	6.84	0.74 (n.s.)

t1.8 n.s. – not significant

annual dry mass of litterfall between the two forest types was not significant. The portion of leaves of the total fine litterfall was 74.5% and 76.2% in the low and high várzea, respectively, which is in the same range as reported for other floodplain and non-flooded forests (Worbes 1997; Clark et al. 2001). Litterfall in the Amazonian floodplains shows a strong seasonality (Adis et al. 1979; Franken et al. 1979; Ayres 1993; Worbes 1997; Schöngart et al. 2002; Haugaasen and Peres 2005; Moreira 2006) (Fig. 18.1), but the seasonal variation of litterfall differs between the low and high várzea. In the low várzea, litterfall peaks in April, at the beginning of the aquatic phase, when rainfall reaches its maximum. This explains the significant correlation between litterfall and precipitation in the low várzea (Table 18.2). In the high várzea, litterfall reaches maximum rates around November, at the end of the dry season, but no correlation between litterfall and rainfall variability or water-level fluctuations could be demonstrated in the high várzea.

Litterfall in Peruvian late successional várzea floodplain forests (6.9–7.1 Mg ha⁻¹ year⁻¹) was in the same range as in the central Amazonian mature floodplain forests, while young successional stages of central Amazonia had much higher litterfall, with a range of 7.8–13.7 Mg ha⁻¹ year⁻¹ (Table 18.3). A higher value was also reported for an eastern Amazonian late secondary stage, with annual litterfall of 13.8 Mg ha⁻¹ year⁻¹ (Cattanio et al. 2004). Litterfall in late successional stages of the nutrient-poor black-water igapó in central Amazonia is 6.7 Mg ha⁻¹ year⁻¹ (Adis et al. 1979) and 6.8 Mg ha⁻¹ year⁻¹ in the clear-water igapó of the Araguaia-Tocantins basin (Moreira 2006), which lies in the range of the late successional stages of the várzea forests. In the terra firme forests of central (7.5 ± 0.6 Mg ha⁻¹ year⁻¹) and eastern (8.8 ± 2.1 Mg ha⁻¹ year⁻¹) Amazonia, annual litterfall is higher than in late successional floodplain forests, but lower than in young successional stages. The litterfall data from 31 non-flooded late-phase forests in the tropics with a mean value of 6.4 ± 2.8 Mg ha⁻¹ year⁻¹ are rather similar to late successional floodplain forests (Clark et al. 2001).

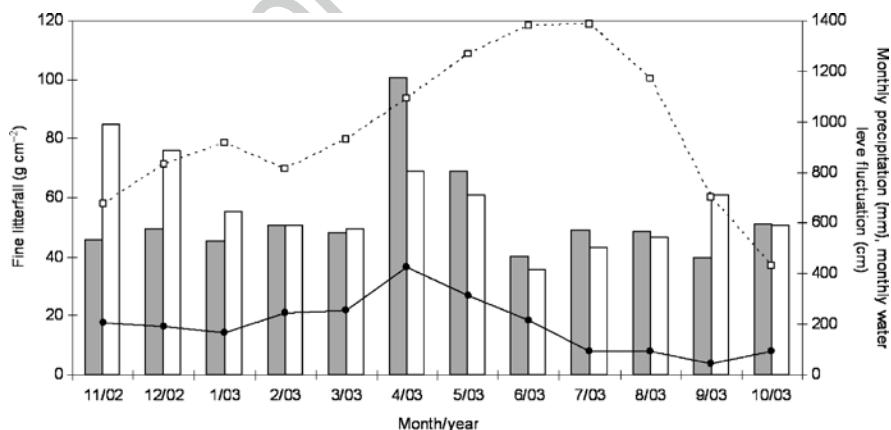


Fig. 18.1 Total fine litterfall in the low (grey bars) and high (white bars) várzea from November 2002 to October 2003 with respect to monthly rainfall (black line) (Data: INMET for Tefé-AM) and monthly water-level fluctuations of the Japurá River (dotted line) (Data: IDSM)

Table 18.2 Correlations between fine litterfall and external factors (precipitation, water-level fluctuation) in late successional stages of a low and high várzea in the MSDR

Correlation coefficient <i>r</i>	Low várzea		High várzea		Total litter	Total litter
	Leaves	Other litter	Leaves	Other litter		
Precipitation	0.61 (p < 0.05)	0.67 (p < 0.05)	0.05 (n.s.)	0.46 (n.s.)	0.79 (p < 0.01)	0.27 (n.s.)
Water level	0.13 (n.s.)	0.53 (n.s.)	0.23 (n.s.)	0.51 (n.s.)	0.31 (n.s.)	0.40 (n.s.)

t2.1

t2.2

t2.3

t2.4

t2.5

t2.6

Table 18.3 Comparison of fine litterfall data between the Amazonian floodplains of different successional development and nutrient status (várzea, igapó) as well as non-flooded up-land (terra firme) forests

Forest type	Litterfall (Mg ha ⁻¹ year ⁻¹)	Source
Várzea		
Eastern Amazonia (tidal várzea, late secondary succession)	13.8	Cattanio et al. (2004)
Central Amazonia, low várzea (12-year-old stand)	7.8	Worbes (1997)
Central Amazonia, low várzea (60-year-old stand)	13.7	Worbes (1997)
Central Amazonia, low várzea (late successional stage)	6.4	This study
Central Amazonia, high várzea (late successional stage)	6.8	This study
Peru, high várzea (late successional stage)	7.0 ± 0.4	Nebel et al. (2001a)
Peru, low várzea (late successional stage)	7.1 ± 0.4	Nebel et al. (2001a)
Peru, chavascal (late successional stage)	6.9 ± 0.3	Nebel et al. (2001a)
Igapó		
Central Amazon (late successional stage, black-water)	6.7	Adis et al. (1979)
Eastern Amazon (late successional stage, clear-water)	6.8 ± 0.4	Moreira (2006)
Terra firme		
Central Amazonia (pristine forests) (n = 6)	7.5 ± 0.6	Klinge and Rodrigues (1968); Klinge et al. (1975); Franken et al. (1979); Silva (1984); Luizão (1989)
Eastern Amazonia (pristine forests) (n = 2)	8.8 ± 2.1	Klinge (1978a); Silva (1982)
Worldwide tropics		
Pristine forests (n = 31)	6.4 ± 2.8	Clark et al. (2001)

18.3 Root Biomass

Only few data on root biomass and root increment are available for floodplain forests. We measured root biomass and distribution by examining the contents of holes of 2 × 2 m area and 90 cm deep that were dug in 1-ha permanent sample plots of late successional stages in a low-várzea stand and in a high-várzea stand of the MSDR (Wittmann et al. 2002b). All roots were sampled, grouped according to diameter classes (0–1.5, 1.5–3.0, 3.0–5.0, 5.0–10.0, 10.0–20.0, and 20.0–40.0 cm), and oven-dried at a temperature of 75°C for 72 h. Total root biomass was higher in the low várzea (8.5 Mg ha⁻¹) than in the high várzea (7.5 Mg ha⁻¹) (Table 18.4). Of the total root biomass, 89% (low várzea) and 95% (high várzea) was concentrated in the soil layer 0–30 cm (Fig. 18.2). Root mass in the lower diameter classes (<10 cm) was higher in the high várzea forest compared to the low várzea forest, while in the upper root diameter classes (>10 cm) the low várzea forest indicate more belowground root biomass. However, these figures were much lower than those

t4.1 **Table 18.4** Root biomass of várzea floodplain forests in eastern and central Amazonia compared
 t4.2 to that of mangroves as well as secondary and old-growth forests of the neotropical terra firme

t4.3	Forest type	Root biomass (Mg ha ⁻¹)	Source
t4.5	Várzea		
t4.6	Eastern Amazonia (low tidal várzea, t4.7 late secondary succession)	40 ± 9.3 (1-m depth)	Cattanio et al. (2004)
t4.8	Eastern Amazonia (intermediate tidal t4.9 várzea, late secondary succession)	36 ± 8.1 (1-m depth)	Cattanio et al. (2004)
t4.10	Eastern Amazonia (high tidal várzea, t4.11 late secondary succession)	35 ± 4.8 (1-m depth)	Cattanio et al. (2004)
t4.12	Central Amazonia (low várzea, late t4.13 successional stage)	8.5 (0.9-m depth)	Wittmann (unpublished data) [AU3]
t4.14	Central Amazonia (high várzea, late t4.15 successional stage)	7.5 (0.9-m depth)	Wittmann (unpublished data)
t4.16	Mangrove		
t4.17	Taiwan	509.5 (1-m depth)	Komiyama et al. (1987)
t4.18	Terra firme		
t4.19	Puerto Rico (15–50 year-old secondary t4.20 forests)	10.9–12.5 (1.0-m depth)	Lugo (1992)
t4.21	Costa Rica (70-year-old secondary t4.22 forests)	15.6 (0.85-m depth)	Berish (1982)
t4.23	Venezuela (20-year-old secondary t4.24 forests)	15.2 (0.7-m depth)	Saldarriaga et al. (1988)
t4.25	Venezuela (30-year-old secondary t4.26 forests)	16.7 (0.7-m depth)	Saldarriaga et al. (1988)
t4.27	Venezuela (60-year-old secondary t4.28 forests)	42.0 (0.7-m depth)	Saldarriaga et al. (1988)
t4.29	Venezuela (80-year-old secondary t4.30 forests)	17.2 (0.7-m depth)	Saldarriaga et al. (1988)
t4.31	Venezuela, São Carlos (pristine forest)	132.0 (1.0-m depth)	Klinge and Herrera (1983)
t4.32	Venezuela, São Carlos (pristine forest)	55.6–60.9 (0.5-m depth)	Stark and Spratt (1977); Sanford (1989)
t4.33			
t4.34	Brazil, Manaus (pristine forest)	40.0 (0.5-m depth)	Klinge (1973)

91 reported by Cattanio et al. (2004), who determined root biomasses in 24 holes, each
 92 with an area of 100 cm² and a depth of 100 cm, in tidal várzea forests (eastern
 93 Amazonia) of topographically low, intermediate, and high sites. Total root biomass
 94 increased along the flood-gradient, from 35 ± 4.8 at high elevations to 36 ± 8.1 Mg
 95 ha⁻¹ at intermediate elevations and 40 ± 9.3 Mg ha⁻¹ at low elevations (Table 18.4).
 96 At all elevations, thick-root biomass (>2 mm diameter) and fine-root biomass
 97 decreased with increasing soil depth (Fig. 18.3). Worbes (1997) also found that root
 98 density increased along the flood gradient for central Amazonian várzea and igapó
 99 forests. Root density increased in the igapó from 19.9 × 10³ km ha⁻¹ at elevations
 100 flooded on average for 80 days to 35.7 × 10³ km ha⁻¹ at elevations inundated for 175
 101 days mean aquatic phase. In the várzea, root density increases along the flood-gra-
 102 dient from 14.1 × 10³ km ha⁻¹ (110 days mean aquatic phase) to 18.0 × 10³ km ha⁻¹
 103 (220 days mean aquatic phase). The higher root densities in the igapó may be related

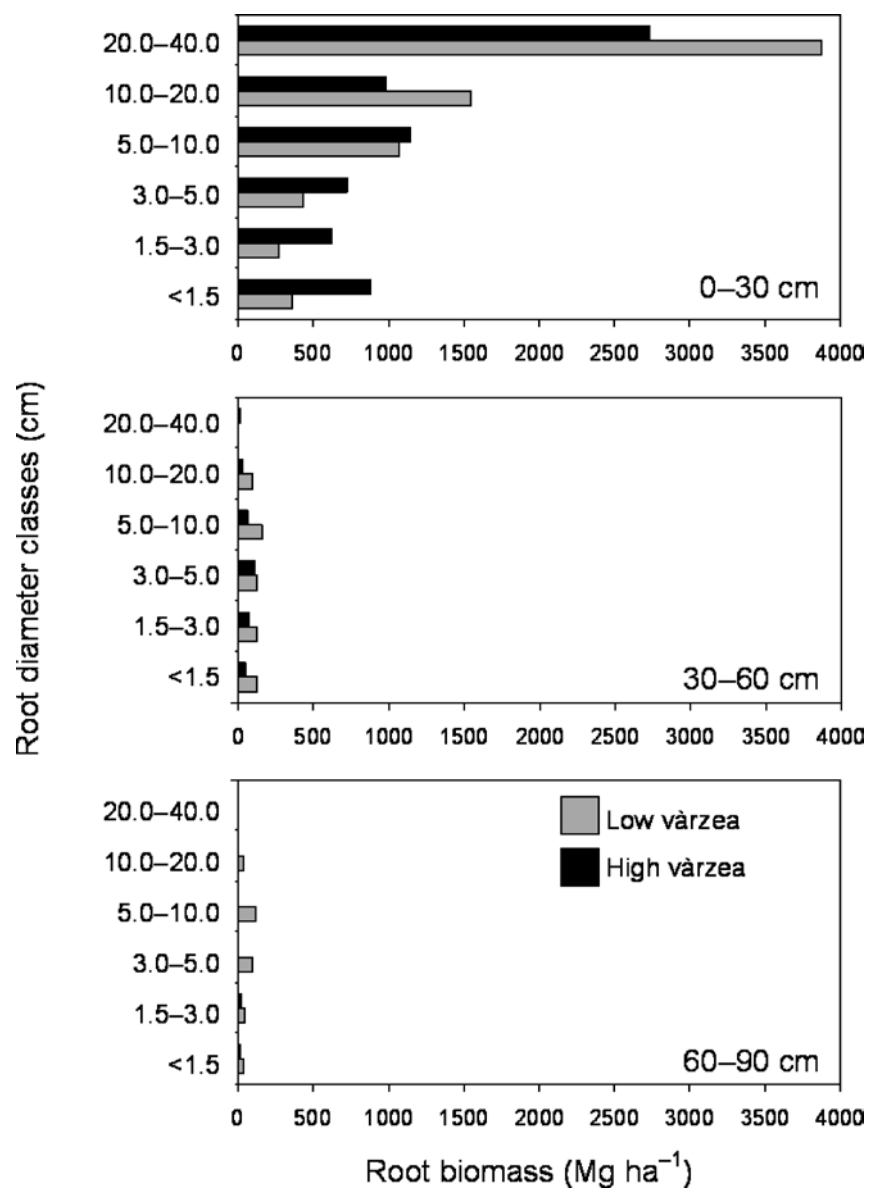


Fig. 18.2 Root biomass classified to different root diameter classes for soil layers 0–30, 30–60 and 60–90 cm in the low and high várzea of central Amazonia

to the lower nutrient content of igapó soils compared to várzea soils (Meyer et al. 104
this volume). 105

The rate of root growth is higher in the várzea than in the igapó, as indicated by the 106
formation of new fine roots (<1.0 mm diameter) per 4 cm² measured with a minirizotrons 107
over a period of 5 months during the terrestrial phase (Meyer 1991). In the igapó, 108

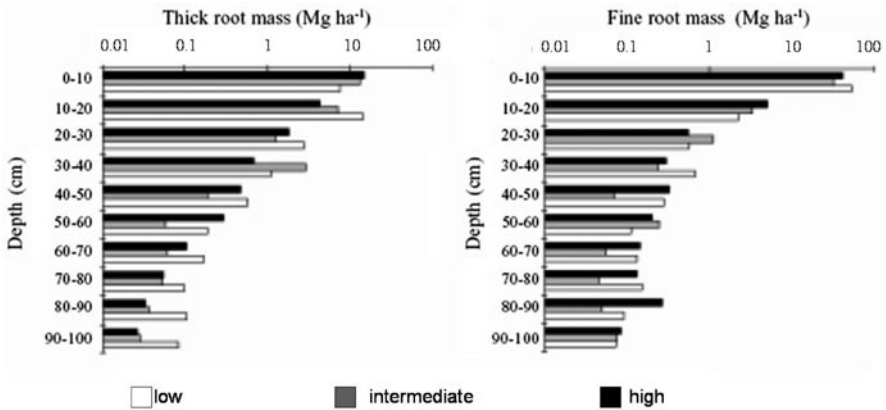


Fig. 18.3 Thick root biomass (>2 mm diameter) and fine root biomass (<2 mm diameter) in tidal várzea floodplains of different topographical elevations, classified by 10 cm soil layers (Cattanio et al. 2004)

109 fine-root production is mainly concentrated in the 0–20-cm soil layer. In the várzea
 110 root production is highest in the upper soil layer (0–15 cm) with a second maximum at
 111 a soil depth of about 40 cm, at the transition between clay and sand (Worbes 1997;
 112 Meyer et al. this volume). All studies in the floodplain forests indicate increasing root
 113 biomasses and root densities with increasing length of the inundation period. This can
 114 be explained by the reduced period of root activity, which is mainly restricted to the
 115 terrestrial phase. A high root density is necessary for sufficient nutrient and water
 116 uptake during the relatively short growing period (Meyer et al. this volume).

117 In 15–80 year-old secondary forests of Central America and Venezuela, root
 118 biomass values range from 10.9 to 42.0 Mg ha⁻¹ (Berish 1982; Saldarriaga et al.
 119 1988; Lugo 1992), which is similar to the values in floodplain forests of the tidal
 120 várzea (Table 18.4). In mature stages of pristine forests on neotropical terra firme,
 121 root biomass may be even higher than in floodplain forests, with roots reaching soil
 122 depths of up to 18 m (Nepstad et al. 1994). It can be assumed that, due to regular
 123 flooding, root depth in the floodplains is limited by anoxic conditions, resulting in
 124 belowground biomasses that are lower than those in the non-flooded terra firme.

125 18.4 Wood Density

126 Wood specific density (in g cm⁻³) is a crucial key parameter for estimates of above-
 127 ground coarse live wood biomass (AGWB) and an important data for assessments
 128 of C-stocks and predictions of potential C-sequestration can be derived (Ketterings
 129 et al. 2001; Baker et al. 2004b; Chave et al. 2004, 2005). Wood density is also
 130 generally recognized as a reliable index of dead-wood decomposition (Martius
 131 1992) and wood quality (Yao 1970) because of strong correlations with wood's

anatomical features, mechanical properties, and pulp yield (a.o., Panshin and De Zeeuw 1980) as well as a dendroclimatic proxy (Schweingruber 1996).

Wood density is conventionally determined by the oven dry mass (105°C) and related to the fresh volume of the wood sample (Chave et al. 2005), as it has been done for all data presented in this chapter. Specific wood densities of tropical tree species range from 0.14 to 1.29 g cm⁻³ (Brown 1997; Fearnside 1997; ter Steege 2000). From the Amazonian floodplains measurements are available for more than 200 tree species of the nutrient-poor igapó and nutrient-rich várzea (Martius 1992; Worbes et al. 1992, 1995, 2001; Worbes 1994, 1996, 1997; Parolin et al. 1998; Parolin and Worbes 2000; Parolin 2002b; Schöngart 2003; Schöngart et al. 2005; Wittmann et al. 2006b; Wittmann and Oliveira-Wittmann, this volume). The absolutely lowest wood densities known for a tree species of the floodplain forests are 0.144 g cm⁻³, for *Pseudobombax munguba* in the várzea (Martius 1992), and 0.126 g cm⁻³, for *Malouetia* sp. in the igapó (Schöngart unpublished data). These values are in the same range as the density of balsa wood (*Ochroma* sp.), the lightest wood known, with 0.130 g cm⁻³ (Bosshard 1984). The highest wood density described in the igapó is 1.00 g cm⁻³, for *Tabebuia barbata* (Worbes 1994), while in late successional várzea forests it is 1.11 g cm⁻³, for Myrtaceae sp. (Schöngart 2003). In terra firme forests, wood densities are even higher with 1.21 g cm⁻³, for *Astronium urundeuva* (Fearnside 1997), and 1.29 g cm⁻³, for *Swartzia bannia* (ter Steege 2000). Between tree species, wood densities differ by 794% in the igapó, 771% in the várzea, and almost 1,000% in the terra firme. This large variation in the wood densities of tree species indicates different growth conditions and adaptations which apply to light-demanding pioneer species at one end and to shade-tolerant late successional species at the other end of range (Budowski 1961; Swaine and Whitmore 1988; Worbes 1996; Parolin 2002b; Wittmann et al. 2006b). This is important to consider when estimating AGWB (Baker et al. 2004b; Chave et al. 2005; Malhi et al. 2006).

Many external (nutrient supply, interannual variation of climatic conditions, flood duration) and internal (wood anatomical features, incorporation of chemical substances in heartwood) factors determine the specific wood densities of floodplain species. Most tropical trees show density gradients from heartwood to sapwood (Wiemann and Williamson 1989; Fearnside 1997). This is also observable in trees from the várzea floodplains. In *P. munguba*, for instance, heartwood is denser than sapwood (0.22 versus 0.17–0.18 g cm⁻³) (Martius 1992). In the várzea, wood density increases by about 12% from bark to pith for 57 climax species (Wittmann et al. 2006b). In pioneer tree species, the increase in wood density from bark to pith is even higher, about 35% (Parolin 2002b). This increase of specific wood density with increasing tree diameter can be explained by the incorporation of mineral salts and chemical substances (terpenes, essential oils, tannins, flavonoids, aldehydes, alcohols, and coloured pigments) during the formation of heartwood to protect the wood against the attacks of predatory organisms such as fungi, insects, and wood destroying organisms (Wagenführ 1989). Wood-anatomical features (fibre length and diameter, percentage of parenchyma and vessels) also lead to different wood densities. Pioneer tree species such as *Salix martiana* and *P. munguba* have low

[AU4]

177 fibre contents and high vessel areas (>30%) (Worbes 1996); these result in low
178 wood densities of 0.39 and 0.23 g cm⁻³, respectively (Schöngart 2003). Late
179 successional tree species such as *Piranhea trifoliata* (0.91 g cm⁻³) and *T. barbata*
180 (0.75 g cm⁻³) have high wood densities due to their high fibre content (ca. 40%),
181 thick cell walls, incorporation of numerous secondary substances, and relatively
182 low vessel areas (<15%) (Worbes 1996).

183 In the várzea, mean wood density and standard deviation increase along the suc-
184 cessional gradient (Worbes et al. 1992), from 0.30 ± 0.05 g cm⁻³ in a 6-year-old
185 monospecific pioneer stand formed by *Cecropia latiloba* (Schöngart unpublished
186 data) to 0.70 ± 0.20 g cm⁻³ in a 240-year-old late successional stage containing 111
187 tree species ha⁻¹ (Schöngart 2003) (Table 18.5). This difference can be explained
188 by the substitution of pioneer tree species with low wood densities by late suc-
189 cessional tree species with high wood densities along the successional gradient
190 (Worbes et al. 1992). Low-density wood permits high radial increment rates, while
191 high-density wood results in low increment rates. Thus, mean radial increment cor-
192 relates negatively with wood density (Worbes 1996). Based on this relationship,
193 Schöngart (2003) developed a non-linear regression model that predicts mean
194 radial increments of várzea tree species by wood density (ρ) ($R^2 = 0.50$, $p < 0.01$)
195 (Fig. 18.4). This approach allows age to be estimated on the basis of the tree diam-
196 eter d as measured in the field and wood density ρ ($age = d/2 \times 1.3763 \rho^{-1.2735}$).

197 One of the external factors determining wood density is interannual climate
198 variation, as has been described for tree species growing in temperate and
199 boreal zones (e.g., Schweingruber 1996). Worbes et al. (1995) used densitometry
200 (Schweingruber et al. 1978) to show a significant relationship between the non-
201 flooded period (vegetation period) and the maximum wood densities (latewood
202 density) of the igapó species *Swartzia laeviscarpa* ($r = 0.54$, $p < 0.05$) and of the
203 várzea species *Pseudoxandra polyphleba* ($r = 0.55$, $p < 0.05$). It should also be
204 noted that nutrient supply and light conditions result in different wood densities.
205 Parolin et al. (1998) found that the wood densities of *Nectandra amazonum* and
206 *T. barbata* were significantly higher in the nutrient-poor igapó than in young
207 successional stages of the nutrient-rich várzea. The authors ascribed these differ-
208 ences to the lower increment rates of igapó species (Worbes 1997), which lead to
209 higher wood densities and act as a special adaptation to the low nutrient content in
210 the igapó (Parolin and Ferreira 1998). However, the comparison of wood density in
211 trees of the same species but growing in different environments, i.e., young suc-
212 cessional stages in the várzea and old-growth forests in the igapó, is problematic.
213 Within the floodplain forests of the várzea, the diameter increment rates of
214 *T. barbata* at the same tree age are about twice as high in young successional stages
215 as in the late successional stage (Worbes et al. 2001), which can be explained by
216 the larger amounts of relative photosynthetic active radiation (rPAR) in the young
217 successional stage (Wittmann and Junk 2003) (Fig. 18.5). *T. barbata* has a signifi-
218 cantly lower wood density in young successional stages than in old-growth forests
219 with stand ages over 200 years, as indicated by a t -value of 4.59 ($p < 0.001$).
220 No difference in the density of wood of same ages was found in *T. barbata*
221 trees which grew under similar flooding regimes in old-growth forests of the

Table 18.5 Average and range of wood density in different forests types of the nutrient-poor black-water floodplain forests (igapó) and the nutrient-rich white-water floodplain forests (várzea), with respect to location, flood height, stand age, and number of species (*samples*) analyzed

	Source	Forest type/location	Flood height (m)	Stand age (years)	Species (samples)	Wood density (g cm ⁻³)
t5.4						
t5.5						
t5.6	Várzea					
t5.7	Martius (1992)	Lower Solimões River	4.00–5.50	20–40	13 (53)	0.49 (0.24–0.72)
t5.8	Parolin et al. (1998)	Lower Solimões River	Varying	40–50	30 (177)	0.53 (0.22–0.87)
t5.9	Schöngart (unpublished data)	MSDR	6.00	6	1 (104)	0.30 (0.19–0.43)
t5.10	Schöngart (2003)	MSDR	3.36	7	4 (38)	0.32 (0.21–0.54)
t5.11	Schöngart (2003)	MSDR	3.47	19	15 (104)	0.35 (0.19–0.68)
t5.12	Schöngart (2003)	MSDR	4.65	52	17 (110)	0.42 (0.18–0.82)
t5.13	Schöngart (2003)	MSDR	4.14	125	77 (459)	0.60 (0.22–1.10)
t5.14	Schöngart (2003)	MSDR	4.28	180	51 (133)	0.63 (0.30–1.11)
t5.15	Schöngart (2003)	MSDR	3.36	240	34 (54)	0.70 (0.23–1.01)
t5.16	Wittmann et al. (2006b)	MSDR	4.10	Late succession	30 (90)	0.62 (0.29–0.86)
t5.17	Wittmann et al. (2006b)	MSDR	2.20	Late succession	30 (90)	0.57 (0.33–0.79)
t5.18	Igapó					
t5.19	Schöngart (unpublished data)	Middle Negro River (Barcelos)	4.50	20	3 (30)	0.22 (0.14–0.34)
t5.20						
t5.21	Schöngart (unpublished data)	JNP	6.55	Late succession	7 (56)	0.60 (0.27–0.84)
t5.22	Schöngart (unpublished data)	JNP	4.10	Late succession	13 (65)	0.61 (0.29–0.97)
t5.23	Schöngart (unpublished data)	JNP	1.90	Late succession	14 (48)	0.67 (0.44–0.92)
t5.24	Parolin and Ferreira (1998)	JNP/Tarumã mirim (Manaus)	Varying	Late succession	35 (206)	0.68 (0.40–0.86)
t5.25						
t5.26	Parolin and Worbes (2000)	JNP	Varying	Late succession	27 (114)	0.67 (0.35–0.87)

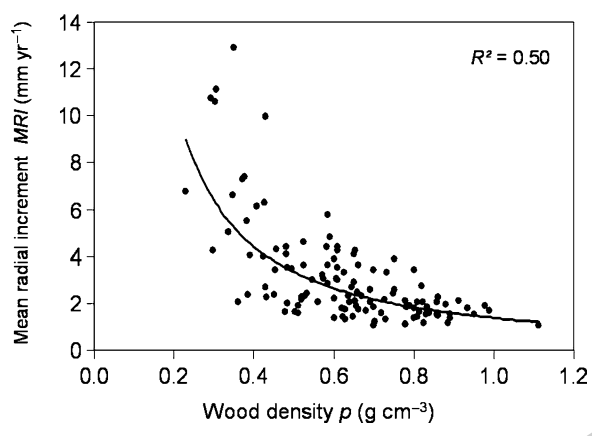


Fig. 18.4 Relationship between wood density and mean radial increment rates of 117 tree species in the várzea floodplain forests of central Amazonia (Schöngart 2003)

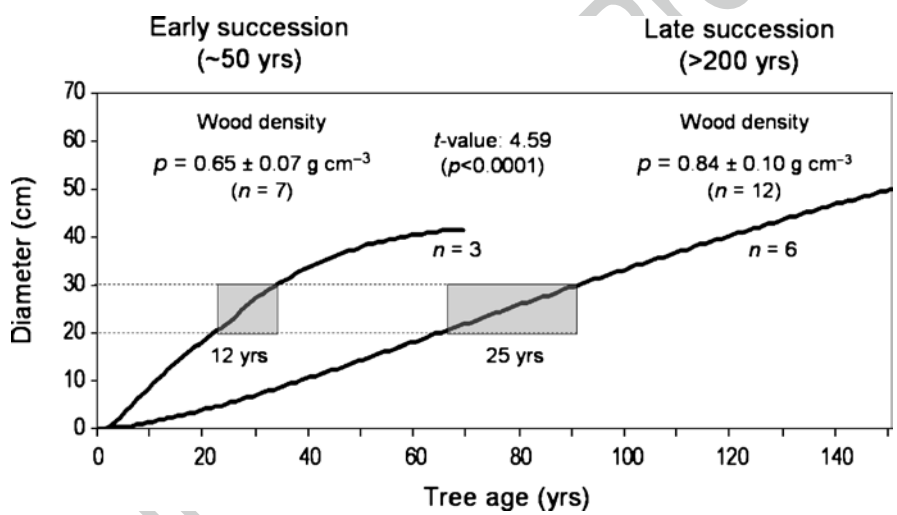


Fig. 18.5 Differences in the wood densities of *Tabebuia barbata* with fast growth rates in young successional stages and slow growth rates in a late successional stage. The grey boxes indicate the mean passage time to surpass a diameter class of 20–30 cm (Worbes 1994; Worbes et al. 2001; Schöngart 2003)

222 várzea ($0.80 \pm 0.08 \text{ g cm}^{-3}$, $n = 20$) and the igapó ($0.83 \pm 0.08 \text{ g cm}^{-3}$, $n = 20$)
 223 (Fonseca Júnior 2007). For other tree species, however, this is not the case.

224 Schöngart et al. (2005) reported that the wood densities of emergent trees of
 225 *Macaranga acaciifolium* with similar diameters and growing under the same
 226 flooding conditions in old-growth forests were significantly lower in the igapó
 227 ($0.39 \pm 0.03 \text{ g cm}^{-3}$, $n = 20$) than in the várzea ($0.45 \pm 0.03 \text{ g cm}^{-3}$, $n = 20$)
 228 ($t = 5.01$, $p < 0.001$). Despite its lower wood densities, the maximum tree age of

M. acaciifolium is significantly higher in the igapó (502 years) than in the várzea (183 years). An explanation for the lower wood density in the igapó might be the higher percentage of parenchymal tissue, which has a lower density that allows for the storage of assimilated carbohydrates (Schöngart et al. 2005). During the aquatic phase, these compounds are dissimilated by anaerobic metabolism (Schlüter 1989; Piedade et al. this volume) and thus provide energy for leaf-exchange, flowering, and fruiting, which is carried out by *M. acaciifolium* in both floodplain systems during the aquatic phase (Ferreira 1991; Ziburski 1991; Worbes 1996; Schöngart et al. 2002; Parolin et al. this volume c). To store the same amount of assimilated carbohydrates, a species needs a higher proportion of parenchymal tissue in the smaller tree rings formed in the wood of trees growing in the igapó than in the wider tree rings of those occurring in the várzea. This difference is most likely compensated by the incorporation of chemical substances into the wood, which allows the tree to protect itself against the attack of xylophagous pathogens – a basic condition for the tree to reach ages >500 years (Loehle 1988).

It seems that no general conclusions can be made regarding whether the wood density of a tree species is higher in the igapó or in the várzea. A comparison of species occurring in both floodplain systems indicated higher wood densities in the igapó than in the várzea for *Mabea nitida*, *Pouteria elegans*, and *Couepia paraensis*, whereas the opposite was true for *M. acaciifolium*. Other species, such as *Crudia amazonica*, *Hevea spruceana*, *T. barbata*, and *Vatairea guianensis*, showed no differences in wood densities between the floodplain systems (Parolin et al. 1998; Schöngart et al. 2005; Fonseca Júnior 2007). Parolin and Ferreira (1998) concluded that wood densities of tree species are higher in the igapó due to the absence of pioneer species. During an excursion in November 2005 in the igapó floodplains near Barcelos at the middle Negro River, we studied homogeneous pioneer stands with a canopy height of about 10 m and a stand age of about 20 years, as indicated by ring-counting on stem disks. The mean wood density of the dominating species, *Malouetia* sp. indet., *Duguetia* sp. indet., and *Sapotaceae* sp. indet., was 0.14 ± 0.01 , 0.16 ± 0.03 , and 0.34 ± 0.04 g cm⁻³, respectively.

These recent findings raise new questions regarding the adaptations of tree species, especially those in the nutrient-poor igapó. Thus, further studies should analyze the wood chemical compounds of tree species, primarily those with low wood densities. A comparison of mean wood densities in stands of similar age or successional development between the várzea, igapó, and terra firme did not reveal significant differences. Pioneer stands of about 20 years in the igapó have a mean wood density of 0.22 ± 0.09 g cm⁻³, which is even lower than that of early secondary stages with similar stand age in the várzea (mean wood density 0.30–0.35 g cm⁻³) (Schöngart 2003). Late successional stages of floodplain forests at lower elevations in both systems have similar mean wood densities in the várzea (0.57–0.70 g cm⁻³) and in the igapó (0.61–0.68 g cm⁻³) (Table 18.5). The mean wood density of ten pristine terra firme stands in central Amazonia is 0.66 g cm⁻³ (Fearnside 1997; Baker et al. 2004b) which agrees pretty well with the pantropical average for pristine lowland forest (Brown 1997). However, comparisons of the wood densities from tree species in the várzea, igapó, and terra firme yielded statistically

t6.1 **Table 18.6** Differences between the means and standard deviations of wood densities ρ of the
 t6.2 várzea, igapó, and terra firme as determined by *t*-tests

t6.3	Forest type	Number of tree species	ρ (g cm ⁻³)	<i>t</i> -test	<i>t</i> -value
t6.5	Várzea (<i>v</i>) ^a	170	0.60 ± 0.15	<i>v</i> versus <i>i</i>	$t = -2.86, p < 0.01$
t6.6	Igapó (<i>i</i>) ^b	73	0.66 ± 0.17	<i>v</i> versus <i>tf</i>	$t = -3.39, p < 0.001$
t6.7	Terra firme (<i>tf</i>) ^c	696	0.65 ± 0.19	<i>i</i> versus <i>tf</i>	$t = 0.58, p = 0.28$

t6.8 ^aData from Martius (1992); Worbes et al. (1995); Worbes (1996); Parolin and Ferreira (1998);
 t6.9 Schöngart (2003); (Wittmann et al. 2006b)

t6.10 ^bData from Worbes (1994); Parolin et al. (1998); Parolin (2002b); Schöngart (unpublished data)

t6.11 ^cData from Brown (1997); Fearnside (1997); ter Steege (2000); Baker et al. (2004b)

274 significantly lower wood densities in the várzea than in the igapó and terra firme
 275 (Table 18.6). Várzea floodplain forests are highly dynamic ecosystems character-
 276 ized by intense sedimentation and erosion processes that annually create large new
 277 areas where pioneers start the primary succession (Worbes et al. 1992; Wittmann
 278 et al. 2002a,b, 2004). In igapó and terra firme forests, these processes depend on
 279 opportunities at much smaller spatial scales, such as the formation of small to
 280 medium gaps caused by lightning, microburst of wind, disease, pest or age-related
 281 mortality; catastrophic destruction over large areas, common in some other forest
 282 formations, are rare. Due to such intensely dynamic processes, the proportion of
 283 pioneer tree species of the total species pool is much higher in the várzea than in
 284 the igapó and the terra firme, which explains the lower mean wood density of
 285 várzea tree species compared to those of the igapó and terra firme.

286 18.5 Aboveground Coarse Wood Biomass (AGWB)

287 The AGWB of tropical forests is the long-term carbon pool of the vegetative part
 288 of the tree, which has the capacity to store large amounts of carbon (Malhi et al.
 289 2004). This aspect has increased the number of studies monitoring changes in
 290 AGWB as for instance in more than 227 permanent sample plots in the Amazon
 291 basin within the RAINFOR program (Amazon Forest Inventory Network) (Peacock
 292 et al. 2007). The aims of these studies include obtaining data on C-sequestration
 293 and its relation to environmental parameters and responses to climate change
 294 (Malhi et al. 2006). However, most of the studies in the Amazon basin have been
 295 carried out in terra firme forests (Phillips et al. 1998, 2002, 2008; Laurance et al.
 296 1999; Bernoux et al. 2001; Chambers et al. 2001; Chave et al. 2001; Keller et al.
 297 2001; Baker et al. 2004a; Malhi et al. 2004, 2006; Saatchi et al. 2007). Regarding
 298 floodplain forests, there are only a few estimates for várzea forests; specifically,
 299 those of different successional stages with ages up to 80 years in the central
 300 Amazon (Klinge et al. 1996; Worbes 1997; Piedade et al. 2001), and those with
 301 unknown stand ages in western Amazonia (Nebel et al. 2001a; Baker et al. 2004a;
 302 Malhi et al. 2004, 2006; Saatchi et al. 2007).

In this section we examine the different allometric models used to predict AGWB in várzea floodplain forests along the successional gradient, from early secondary stages established on recently deposited sand bars along the river margins to late successional stages (Wittmann et al. this volume). The annual change in the AGWB was estimated by growth models based on tree-ring analyses relating age, diameter, and tree height of dominating tree species. This represents a new approach in tropical forest research. Our field data were extrapolated to a regional scale (MSDR) by remote-sensing techniques. The function of the AGWB in the várzea floodplains as a significant measure of C-sink is discussed with respect to data from terra firme forests.

The várzea floodplains of the focal area of the MSDR (Queiroz and Peralta this volume), located in the Amazonas State of Brazil, 550 km west from Manaus, at the confluence of the Solimões and Japurá Rivers (02°48'–02°54' S, 64°53'–65°03' W), were studied. AGWB values were estimated for five different, almost undisturbed successional stages, with stands varying between 7 and 240 years of age, exposed to an average flood period of 140–174 days per year (Schöngart 2003). The climate in the study areas is characterized by a mean daily temperature of 26.9°C and annual precipitation of almost 3,000 mm, with a distinct dry season from July to October (Schöngart et al. 2005). Four 1-ha plots in várzea forests were established in the focal area of the MSDR and all trees >10 cm diameter at breast height (d = 130 cm height) were enumerated by measuring d (in the case of buttresses the diameter was recorded above them) the x -, y - coordinates, and total tree height (h). Additionally, a circular plot of 500 m² was established in a young pioneer stage on a recently formed sand bar at the Japurá River. First estimates of AGWB in black-water floodplain forests have been performed in November 2004 in the Jaú National-Park (JNP) (01°54'–01°57' S, 61°27'–61°31' W) in plots of 25 × 25 m (625 m²) located in three old-growth forests along the flood-gradient. The low, medium, and high elevations are flooded by a mean water column of 6.55, 4.10, and 1.90 m, respectively. Total tree height, d and wood density for every tree >10 cm d were determined. Stand parameters of five different successional stages in the várzea (MSDR) and of three mature forests along the flood-gradient in the igapó (JNP) are presented in Table 18.7.

So far, allometric models specific for floodplain forests have not been described. Therefore, to predict AGWB, we used allometric models developed for tropical forests and consisting of large data sets of harvested trees from one stand (Chambers et al. 2001) or of data obtained from many forest types of different tropical regions (Brown et al. 1989; Overman et al. 1994; Chave et al. 2005). These allometric models transform forest inventory data into estimates of AGWB by employing regression models with independent variables. We estimated the AGWB (in kg) for every tree by diameter at breast height (d , in cm), specific wood density (ρ , in g cm⁻³ after drying at a temperature of 105°C for 72 h), and total tree height (h , in m) using seven allometric models (Table 18.8). In allometric model (1), produced by Cannell (1984), basal area, derived from the measured d , is multiplied with tree height, wood density, and a fixed form factor of 0.6, assuming taper does not change as the trees become larger (Chave et al. 2005). This model was used to predict AGWB in Peruvian várzea forests (Nebel et al. 2001a) and in successional stages in central

Table 18.7 Stand parameters of different successional stages in the várzea floodplain (MSDR) and three pristine forests in the igapó (JNP) at different topographical levels (trees with diameter ≥ 10 cm)

t7.1 t7.2	Parameter	Unit	Várzea (MSDR)						Igapó (JNP)			
			Young pioneer	Early secondary	Late secondary	Intermediate	Late succession	Low elevation	Middle elevation	High elevation		
t7.4	Plot size	ha	0.05	1	1	1	1	1	0.0625	0.0625	0.0625	0.0625
t7.5	Mean flood height	m	3.36	3.47	4.65	4.14	3.36	3.36	6.55	4.10	4.10	1.90
t7.6	Stand age	years	7	20	50	125	240	240	>200	>200	>200	>200
t7.8	Tree density	trees ha ⁻¹	1220	838	487	504	462	462	896	1040	1040	784
t7.9	Tree species	ha ⁻¹ (plot ⁻¹)	(4)	30	45	87	111	111	(7)	(12)	(12)	(14)
t7.10	Mean diameter	cm	13.8 ± 2.8	18.7 ± 8.4	31.4 ± 16.3	22.3 ± 13.1	22.9 ± 14.9	22.9 ± 14.9	15.3 ± 7.4	22.0 ± 9.8	22.0 ± 9.8	18.2 ± 9.3
t7.11	± sd											
t7.12	Mean tree height	m	7.3 ± 1.9	13.6 ± 3.0	19.8 ± 5.3	16.4 ± 5.4	15.8 ± 6.1	15.8 ± 6.1	10.0	17.3 ± 3.5	17.3 ± 3.5	16.8 ± 3.7
t7.13	± sd											
t7.14	Basal area	m ² ha ⁻¹	13.8	30.5	50.5	26.9	27.3	27.3	20.3	47.8	47.8	27.7
t7.15	Volume*	m ³ ha ⁻¹	69	302	683	342	342	342	127	554	554	331
t7.16	Mean wood density	g cm ⁻³	0.32 (0.21–0.54)	0.35 (0.19–0.68)	0.42 (0.18–0.82)	0.60 (0.22–1.10)	0.70 (0.23–1.01)	0.70 (0.23–1.01)	0.60 (0.27–0.84)	0.61 (0.29–0.97)	0.61 (0.29–0.97)	0.67 (0.44–0.92)
t7.17	(min-max)											
t7.18												

Table 18.8 Allometric models to transform forest inventory data into predictions of aboveground coarse wood biomass (AGWB) by diameter at breast height (d , in cm), specific wood density (ρ , in g cm^{-3} after drying at a temperature of 105°C for 72 h), and total tree height (h , in m)

Allometric model	Source	
1. $AGWB = F \times \rho \times h \times \pi \times (d/2)^2$	Cannell (1984)	t8.1
2. $AGWB = 0.112 \times (\rho \times h \times d^2)^{0.916}$	Chave et al. (2005)	t8.2
3. $AGWB = 0.0509 \times \rho \times h \times d^2$	Chave et al. (2005)	t8.3
4. $AGWB = \rho \times \exp(-0.667 + 1.784\ln(d) + 0.207(\ln(d))^2 - 0.0208(\ln(d))^3)$	Chave et al. (2005)	t8.4
5. $AGWB = \rho \times \exp(-1.499 + 2.148\ln(d) + 0.207(\ln(d))^2 - 0.0208(\ln(d))^3)$	Chave et al. (2005)	t8.5
6. $AGWB = \rho/0.67 \times \exp(0.33(\ln(d)) + 0.933(\ln(d^2)) - 0.122(\ln(d))^3) - 0.37$	Baker et al. (2004a)	t8.6
7. $AGWB = 0.044 \times (d^2 \times h)^{0.9719}$	Brown et al. (1989)	t8.7

Amazonia (Worbes 1997; Schöngart 2003). Chave et al. (2005), referring to a data set of 2,410 harvested trees from tropical regions in America, Africa, and Asia, established allometric models for different forest types using two (d , ρ) or three (d , ρ , h) independent variables. Models (2) and (4) were established for dry forests with severe seasonality, where plants suffer serious water stress for >5 months, as it occurs during the aquatic phase in the floodplain forests. Models (3) and (5) were developed for moist forests with annual precipitation of 1,500–3,000 mm, which is in the range of the annual precipitation of the MSDR and the JNP. Thus, allometric models (2)–(5) were deemed adequate to estimate the AGWB of the várzea forests in our study region. Allometric equation (18.6) was developed by Chambers et al. (2001) for terra firme forests in the region of Manaus (BIONTE project), based on data from 315 trees with a mean wood density of 0.67 g cm^{-3} (Baker et al. 2004b). For estimates of AGWB in floodplain forests, the equation was modified by Baker et al. (2004a) to incorporate a simple multiplication factor ($\rho/0.67$) that accounts for variations in wood density (Malhi et al. 2004). Brown et al. (1989) developed model (7) for AGWB estimates in tropical old-growth forests.

Estimates of AGWB in the central Amazonian floodplain forests differed considerably depending on the forest type and the allometric model used to transform the forest inventory data into predictions of AGWB (Table 18.8). Minimum and maximum predictions of AGWB within a forest type ranged from 176% to 257% in the várzea and from 172% to 226% in the igapó (Table 18.9), which led to the question: What is the most realistic prediction of AGWB? The conversion of forest inventory data to AGWB estimates can produce large errors due to variations in height, crown architecture, wood density between forest types and tree species depending on edaphic, climatic, and hydrological conditions as well as on the successional stage (Ketterings et al. 2001; Ometto et al. 2005) and perhaps ecotype-related variations. The most important predictors for the AGWB of a tree are, in decreasing order, d , ρ , h , and forest type (Chave et al. 2005). Models (1)–(3), which use the first three predictors, showed good congruence in predictions of AGWB in all stands. The allometric equation of Brown et al. (1989), using only d and h as independent parameters, produced much higher AGWBs especially for young successional stages. The mean wood density of the trees used for developing allometric model (7) was $0.59 \pm 0.16 \text{ g cm}^{-3}$ (Brown 1997) but a considerably lower value was

19.1 **Table 18.9** Prediction of the AGWBs of five different successional stages in the
 19.2 várzea floodplain and three pristine forests in the igapó using allometric equa-
 19.3 tions (18.1–18.7) (Table 18.7) (for description, see text)

19.4 Várzea	(1)	(2)	(3)	(4)	(5)	(6)	(7)
19.5 <i>Young pioneer</i>							
19.6 Mg ha ⁻¹	15	21	16	25	26	33	35
19.7 Mg m ⁻² basal area	1.1	1.5	1.2	1.8	1.9	2.4	2.6
19.8 <i>Early secondary</i>							
19.9 Mg ha ⁻¹	108	127	117	102	128	171	217
19.10 Mg m ⁻² basal area	3.5	4.2	3.8	3.4	4.2	5.6	7.1
19.11 <i>Late secondary</i>							
19.12 Mg ha ⁻¹	249	264	269	183	266	340	471
19.13 Mg m ⁻² basal area	4.9	5.2	5.3	3.6	5.3	6.7	9.3
19.14 <i>Intermediate</i>							
19.15 Mg ha ⁻¹	222	228	240	169	240	305	239
19.16 Mg m ⁻² basal area	8.3	8.5	8.9	6.3	8.9	11.3	8.9
19.17 <i>Late succession</i>							
19.18 Mg ha ⁻¹	233	233	251	174	257	307	253
19.19 Mg m ⁻² basal area	8.5	8.5	9.2	6.4	9.4	11.2	9.3
19.20 Igapó	(1)	(2)	(3)	(4)	(5)	(6)	(7)
19.21 <i>Low</i>							
19.22 Mg ha ⁻¹	68	85	74	99	115	155	94
19.23 Mg m ⁻² basal area	1.7	2.1	1.8	2.4	2.8	3.8	2.3
19.24 <i>Medium</i>							
19.25 Mg ha ⁻¹	333	362	360	272	356	485	393
19.26 Mg m ⁻² basal area	7.0	7.6	7.5	5.7	7.5	10.1	8.2
19.27 <i>High</i>							
19.28 Mg ha ⁻¹	240	257	259	188	246	324	235
19.29 Mg m ⁻² basal area	8.7	9.3	9.4	6.8	8.9	11.7	8.5

381 determined for the young pioneer and secondary stages (0.32–0.42 g cm⁻³;
 382 Table 18.7). Model (7), applied to describe a late secondary stage (50-year-old
 383 stand), produced particularly large errors due to the dominance in the canopy of
 384 low-density wood species, such as *P. munguba* ($\rho = 0.23 \pm 0.04$ g cm⁻³), *Luehea*
 385 *cymulosa* ($\rho = 0.38 \pm 0.04$ g cm⁻³), and *Ilex inundata* ($\rho = 0.39 \pm 0.03$ g cm⁻³).
 386 These three species together comprised 66–69% (172–187 Mg ha⁻¹) of these
 387 stands' AGWBs as estimated by models (1)–(3). The AGWB predicted by model
 388 (7) for these three species was twofold higher and accounted for 81% of the stand's
 389 AGWB. Estimations of AGWB generated by model (7) for stands >100 years old
 390 were similar to those produced by models (1)–(3), because of the similar mean
 391 wood densities of the successional stages. We therefore concluded that allometric
 392 models, which do not use ρ as a predictor, are biased towards errors in estimating
 393 the AGWB, due to the large variations in mean wood densities, especially of emergent
 394 trees, within and between stands. Baker et al. (2004a) and Malhi et al. (2004, 2006)
 395 used allometric equation (18.6) to estimate the AGWB of western Amazonian
 396 floodplain forests. Tree height, however, is not included in regression model (6),
 397 resulting in much higher predictions of AGWB in all stands than obtained with

models (1)–(3), because tree heights differ considerably between floodplain forests and terra firme forests. Differences in tree heights between young successional stages in the várzea and terra firme forests are about 30–40 m and 10–15 m between old-growth floodplain forests and terra firme forests (Schöngart 2003). It is obvious that forests with higher canopies are capable of greater C-storage than forests with lower canopies. Thus, predictions derived from model (6) were assumed to be biased towards overestimating AGWB. Our results therefore indicate that realistic estimates of AGWB can be achieved only with regression models that use d , ρ , and h as predictors, especially when these estimates are made for new forest types. Therefore, in the assessed successional stages, we considered only those predictions of AGWB that were based on models (1)–(3) calculating a mean value and standard deviation of these three estimates.

For the 7-year-old young pioneer stage, the models predicted an AGWB of 15–21 Mg ha⁻¹, which accumulated with increasing stand age to 249–269 Mg ha⁻¹ for the 50-year-old late secondary stage. For old-growth forests, the models estimated AGWBs varying from 222–240 Mg ha⁻¹ in the 125-year-old stand to 233–251 Mg ha⁻¹ for the 240-year-old late successional stage (Table 18.9). These predictions are in the same range as estimates of AGWB in the Manaus region for 2–80-year-old successional stages in the várzea, as determined by allometric model (1) (Worbes 1997; Piedade et al. 2001) (Table 18.10). Estimated AGWBs of central Amazonian várzea forests were significantly correlated with stand age, as indicated

Table 18.10 Comparison of basal area, AGWB and AGWB per unit basal area for várzea floodplain forests in the Amazon basin

Várzea	Basal area m ² ha ⁻¹	AGWB Mg ha ⁻¹	AGWB/Basal area Mg m ⁻²
Eastern Amazonia ^a			
$n = 4$	32.0 ± 10.3	193 ± 18	6.4 ± 1.7
Central Amazonia (Manaus) ^b			
Pioneer (2-year)		3	
Pioneer (4-year)		14	
Pioneer (12-year)		98	
Early secondary (44-year)		258	
Late secondary (80-year)		279	
Central Amazonia (MSDR)			
Pioneer (7-year)	13.8	18 ± 3	1.3 ± 0.2
Early secondary (20-year)	30.5	117 ± 9	3.8 ± 0.3
Late secondary (50-year)	50.5	261 ± 10	5.2 ± 0.2
Intermediate (120-year)	26.9	230 ± 9	8.5 ± 0.3
Late succession (240-year)	27.3	239 ± 11	8.8 ± 0.4
Western Amazonia ^c			
Late succession ($n = 15$)	27.2 ± 3.7	270 ± 40	10.1 ± 0.6

^aData from Almeida et al. (2004) of four 1-ha stands in the eastern Amazonian várzea

^bData from Worbes (1997)

^cData from Malhi et al. (2006) based on forest inventories in várzea forests of 1–1.1 ha in Bolivia, Ecuador and Peru

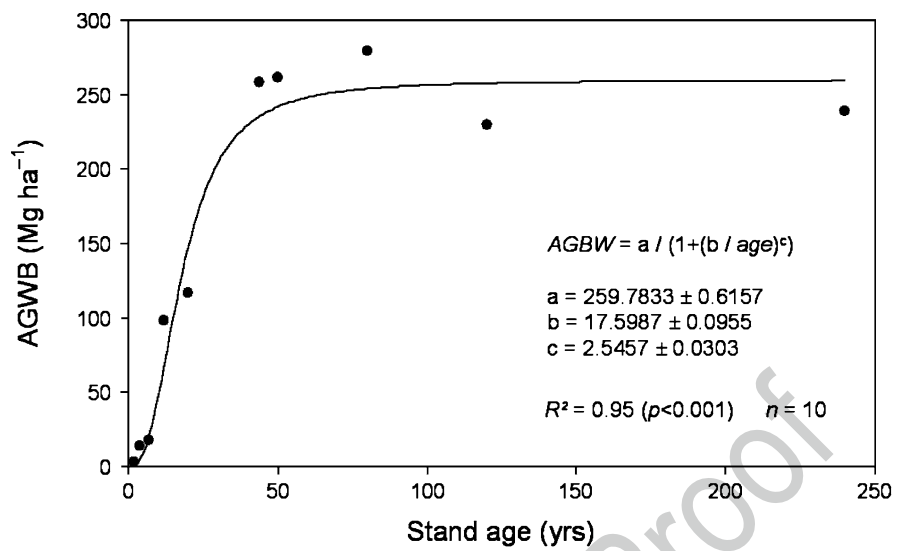


Fig. 18.6 Relationship between accumulated aboveground wood biomass (AGWB) and stand age along a successional gradient in the central Amazonian várzea

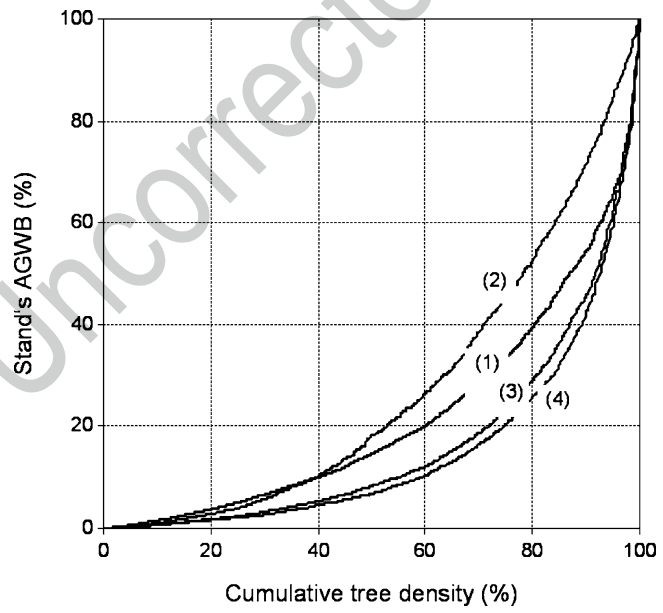


Fig. 18.7 Distribution of AGWB with respect to relative abundance in four 1-ha stands of varying stand age. 1 – 20-year-old early secondary stage, 2 – 50-year-old late secondary stage, 3 – 120-year-old intermediate stage, 4 – 240-year-old late successional stage

in Fig. 18.6 by a non-linear regression model explaining 95% of the variability between AGWB and age. The model follows the universal biological growth trend with a strong increase in AGWB during the first 50–80 years of successional development, reaching 250 Mg ha⁻¹, but afterwards no increase in AGWB can be observed. Along the successional gradient, the AGWB became concentrated on a smaller number of emergent trees (Fig. 18.7). In the 20-year-old successional stage in the MSDR, 20% of the biggest trees comprised 60% of the estimated AGWB, while in stands >100 years old, trees of that size comprised 71–74% of the total stand's AGWB. In the four successional stages, 60% of the smaller trees in the understorey comprised not more than 10–26% of the total AGWB.

Our findings indicate much lower AGWBs for várzea forests than early estimates by Junk (1985), who reported an AGWB of 400 Mg ha⁻¹ for floodplain forests. The AGWBs (trees 10 cm *d*) of várzea floodplain forests in different regions of the Amazon basin are indicated in Table 18.10. Almeida et al. (2004) estimated that the AGWB of four 1-ha várzea forests (tress 10 cm *d*) in the eastern Amazon basin in the range of 171–215 Mg ha⁻¹, however, no information was provided on flood height and stand ages, nor how AGWB was determined. The western Amazonian várzea forests have the highest AGWB, 195–357 Mg ha⁻¹ (Malhi et al. 2006); however, this may be an overestimate due to the application of allometric model (6). Saatchi et al. (2007) reported a basin-wide estimate of 161.3 ± 101.7 Mg ha⁻¹, based on 40 plots of floodplain forests from Bolivia, Peru, Colombia, and Brazil, but these authors did not differentiate between nutrient status (igapó, várzea), successional stage, or flood height, leading to large variations of the AGWB as indicated by the high standard deviation.

In the igapó forests of the JNP, AGWB ranges from 68–74 Mg ha⁻¹ at low elevations, to 333–360 Mg ha⁻¹ at middle elevations, and 240–259 Mg ha⁻¹ at the highest elevations (Table 18.9). However, AGWB was estimated based on small plots of 625 m², which due to the disproportionate influence of big trees tend to yield overestimates of AGWB (Clark et al. 2001). Therefore, we related the estimated AGWB to 1 m² of the basal area, defined by Malhi et al. (2006) as the structural conversion factor (SCF). Along the flood-gradient, the SCF was found to increase considerably with decreasing flood height (Table 18.9). A comparison of the estimated SCF from old-growth floodplain forests, with a mean flood height of 4.10 m, indicated a slightly higher AGWB in the várzea (intermediate stage: 8.5 ± 0.3 Mg m⁻² basal area) than in the igapó (middle elevation: 7.4 ± 0.3 Mg m⁻² basal area). No data were available to compare the AGWBs between várzea and igapó for lower and higher elevations or for successional stages.

18.6 C-Sequestration in AGWB

The function of the Amazonian forests as a long-term carbon sink is controversially discussed in the literature. While the classic theory describes old-growth forests as steady-state ecosystems (climax) (Clements 1936; Whittaker 1953), studies based on repeated diameter measurements (Phillips et al. 1998, 2002, 2008; Baker et al. 2004a; Malhi et al. 2004) and eddy covariance data (Grace et al. 1995; Malhi et al.

460 1998) indicate that carbon stocks in Amazonian non-flooded upland forests (terra
 461 firme) have increased over the last decades, probably due to increasing atmospheric
 462 CO₂ concentrations. Other recent studies, however, showed that the increasing tem-
 463 perature and/or reduced soil moisture associated with the El Niño phenomenon
 464 (e.g., Tian et al. 1998; Cox et al. 2000; Clark et al. 2003) can make tropical forests
 465 net carbon sources. A basin-wide estimate indicated that the biomass of floodplain
 466 forests (153,000 km²) is a C-sink of, annually, 15×10^{12} g C (Grace and Malhi
 467 2002), corresponding to 0.98 Mg C ha⁻¹ year⁻¹. Baker et al. (2004a) estimated a net
 468 C-sequestration of 1.27 ± 1.27 Mg C ha⁻¹ year⁻¹ in three mature várzea forests of
 469 the western Amazon basin, observed during a 4–5-year period. We estimated
 470 annual C-sequestration in the AGWB along the entire successional gradient, from
 471 early secondary stages to old-growth forests in the MSDR. For these estimates, we
 472 applied growth models based on tree-ring analyses of the dominating tree species
 473 and species groups (Schöngart 2003). Our field data were extrapolated to a regional
 474 scale by remote-sensing techniques of Landsat TM image data (Wittmann et al.
 475 2002a,b). In the following, the function of the AGWB in the várzea floodplains as
 476 a C-sink is discussed, in the light of data from terra firme forests.

477 Based on over 28,800 ring-width measurements and 2,624 height measurements,
 478 we constructed 23 growth models for dominant tree species in the different succes-
 479 sional stages (Table 18.11, Fig. 18.8) to estimate the range of AGWBs along the life
 480 span of the trees (Schöngart 2003). Therefore, we modelled age-diameter
 481 relationships, which were fitted to a sigmoidal regression model according to the
 482 formula (Schöngart et al. 2007; Schöngart 2008):

$$483 \quad d = a / \left(1 + (b / age)^c \right) \quad (18.1)$$

484 From this model, the current (annual) diameter increments (*CDI*, in mm) for the
 485 studied tree species were derived. *CDI* is defined as the difference in the diameter
 486 *d* from year (*t-1*) to year (*t*) (Pretzsch 2001):

$$487 \quad CDI = d_t - d_{t-1} \quad (18.2)$$

488 For the same tree species, the relationship between tree height and diameter was
 489 modelled with a non-linear regression model (Nebel et al. 2001a; Schöngart 2008)
 490 (Fig. 18.8):

$$491 \quad h = d \times a / (d + b) \quad (18.3)$$

492 Substitution of the diameter variable in age-diameter relationship by the
 493 species-specific diameter-height relationship resulted in an estimate of cumula-
 494 tive height growth and height increment along the life-span of a tree. Tree
 495 species with similar tree heights, wood densities, and increment rates, such as
 496 *Cecropia* spp., *Licania* spp., Myrtaceae spp., and Leg.-Mimosioideae spp., were
 497 grouped together to increase the number of observations for growth modelling
 498 (Table 18.11). All growth models were based on significant age-diameter and
 499 diameter–height relationships.

Table 18.11 Growth models to estimate the accumulation of C-stocks and annual C-sequestration in AGWB for characteristic tree species and species groups (*underlined*) from different successional stages of central Amazonian floodplain forests. The models are based on wood density (mean and standard deviation) and significant age-diameter and diameter-height relationships, as indicated by the correlation coefficient *r* and the confidence-level *p*. The number of ring-width and height measurements is indicated for every tree species and species group

Tree species / -group	Age-diameter relationship				Diameter–height relationship				Wood density (g cm ⁻³)	
	<i>n</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>r</i> (<i>p</i>)	<i>n</i>	<i>a</i>	<i>b</i>		<i>r</i> (<i>p</i>)
Short-living pioneers										
t11.8 <i>Alchornea</i>	295	34.5512 ± 9.2112	6.7906 ± 2.1527	1.6089 ± 0.2229	0.90 (<0.001)	29	10.4556 ± 1.0660	3.0487 ± 1.6031	0.50 (<0.01)	0.33 ± 0.05
t11.9 <i>castaneifolia</i>										
t11.10 <i>Salix maritima</i>	90	51.0618 ± 18.3017	12.4897 ± 6.3191	1.3585 ± 0.2672	0.95 (<0.001)	11	12.3870 ± 1.299	5.4649 ± 2.0833	0.67 (<0.05)	0.39 ± 0.01
t11.11 <i>Cecropia spp.</i>	914	51.3725 ± 7.6154	15.1728 ± 3.4250	1.3396 ± 0.1288	0.81 (<0.001)	223	40.4367 ± 1.2784	29.1673 ± 1.4665	0.93 (<0.001)	0.30 ± 0.05
t11.12 <i>Cecropia latiloba</i>										
t11.13 <i>Cecropia membranacea</i>										
t11.14 <i>Cecropia sp.</i>										
t11.15 <i>Ficus insipida</i>	277	119.5742 ± 13.1913	18.4937 ± 3.3550	1.2997 ± 0.0788	0.82 (<0.001)	54	28.6667 ± 0.7424	16.1743 ± 1.3022	0.74 (<0.001)	0.39 ± 0.01
t11.16 <i>Nectandra amazonum</i>	588	38.1257 ± 8.4482	17.0721 ± 5.1163	1.3956 ± 0.1457	0.96 (<0.001)	160	33.0253 ± 1.1758	20.9225 ± 1.3735	0.89 (<0.001)	0.38 ± 0.03
t11.17 <i>Rhodostemonodaphne sp.</i>	346	52.3525 ± 37.3011	20.7981 ± 21.9496	1.2330 ± 0.3940	0.76 (<0.001)	64	29.7391 ± 1.3373	14.8990 ± 1.5194	0.89 (<0.001)	0.39 ± 0.06
t11.18 Long-living pioneers										
t11.19 <i>Pseudobombax munguba</i>	683	101.8435 ± 2.7307	44.2009 ± 2.0969	1.0507 ± 0.0127	0.83 (<0.001)	399	44.2589 ± 0.6661	42.6987 ± 1.1402	0.96 (<0.001)	0.23 ± 0.04
t11.20 <i>Luehea cymulosa</i>	1,349	86.5839 ± 7.9985	37.2305 ± 4.4048	1.5818 ± 0.0827	0.92 (<0.001)	338	46.0880 ± 0.7894	38.7428 ± 1.0514	0.91 (<0.001)	0.38 ± 0.04
t11.21 <i>Ilex inondata</i>	1,657	107.2910 ± 17.2131	55.8769 ± 6.7550	2.3162 ± 0.1282	0.95 (<0.001)	230	39.7600 ± 0.5244	24.8028 ± 0.7075	0.95 (<0.001)	0.39 ± 0.03
t11.22										
t11.23										
t11.24										
t11.25										
t11.26										
t11.27										
t11.28										
t11.29										
t11.30										

(continued)

Table 18.11 (continued)

Tree species / -group	Age-diameter relationship				Diameter–height relationship				Wood density (g cm ⁻³)	
	<i>n</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>r</i> (<i>p</i>)	<i>n</i>	<i>a</i>	<i>b</i>		<i>r</i> (<i>p</i>)
<i>Macarobium acacifolium</i>	521	137.5987 ± 9.2697	72.4934 ± 4.9681	1.8257 ± 0.0511	0.94 (<0.001)	18	32.0676 ± 1.8523	26.8365 ± 3.4760	0.85 (<0.001)	0.45 ± 0.03
Leg.-Mimosoideae	404	68.2018 ± 9.2628	34.3210 ± 4.1722	2.4826 ± 0.4428	0.83 (<0.01)	63	33.9638 ± 0.6674	15.7564 ± 0.8382	0.89 (<0.001)	0.58 ± 0.07 0.57 ± 0.05
<i>Albizia subdimidiata</i>										
<i>Inga cf. laterifolia</i>	719	135.7112 ± 12.1825	93.1059 ± 8.8556	1.9746 ± 0.1156	0.91 (<0.001)	49	39.3949 ± 0.9865	28.0887 ± 1.5729	0.96 (<0.001)	0.63 ± 0.04
Climax species (emergents)										
<i>Pouteria elegans</i>	1,101	121.1704 ± 18.3318	128.7794 ± 20.4456	1.8654 ± 0.1631	0.95 (<0.001)	43	30.8071 ± 0.8567	16.0890 ± 1.1890	0.95 (<0.001)	0.65 ± 0.13
<i>Eschweilera parvifolia</i>	1,697	129.0611 ± 17.0861	154.7658 ± 20.3358	1.7954 ± 0.0876	0.97 (<0.001)	60	41.7222 ± 0.9561	29.0724 ± 1.4189	0.91 (<0.001)	0.74 ± 0.07 0.72 ± 0.08
<i>Chrysophyllum argenteum</i>										
<i>Eschweilera albiflora</i>	2,078	156.3565 ± 39.7620	214.0361 ± 51.8604	1.7155 ± 0.1144	0.89 (<0.001)	49	40.5848 ± 1.7031	32.4352 ± 2.4191	0.93 (<0.001)	0.83 ± 0.07
<i>Tabebuia barbata</i>	1,187	125.8597 ± 10.7838	199.1537 ± 19.7898	1.4775 ± 0.0401	0.79 (<0.001)	24	32.6267 ± 0.9274	15.6984 ± 1.3845	0.98 (<0.001)	0.87 ± 0.12
<i>Piranhea trifoliata</i>	4,757	129.3670 ± 7.9906	197.8906 ± 16.7651	1.3795 ± 0.0399	0.88 (<0.001)	60	40.9838 ± 0.8856	26.0373 ± 1.2283	0.87 (<0.001)	0.94 ± 0.07
Climax species (understorey)										
<i>Oxandra riedeliana</i>	2,872	70.7002 ± 7.1419	80.2651 ± 11.8156	1.4935 ± 0.0931	0.88 (<0.001)	123	39.8997 ± 1.5936	26.5367 ± 1.8491	0.87 (<0.001)	0.47 ± 0.06
<i>Mabea nitida</i>	1,265	99.5568 ± 47.3068	263.7226 ± 188.0593	1.0319 ± 0.1032	0.88 (<0.001)	79	25.8096 ± 0.7010	9.9601 ± 0.7382	0.83 (<0.001)	0.59 ± 0.07
<i>Duroia duckei</i>	1,048	64.0335 ± 9.0689	89.8719 ± 22.6634	1.1774 ± 0.1119	0.91 (<0.001)	115	29.2212 ± 0.7247	15.0565 ± 0.8710	0.91 (<0.001)	0.69 ± 0.06

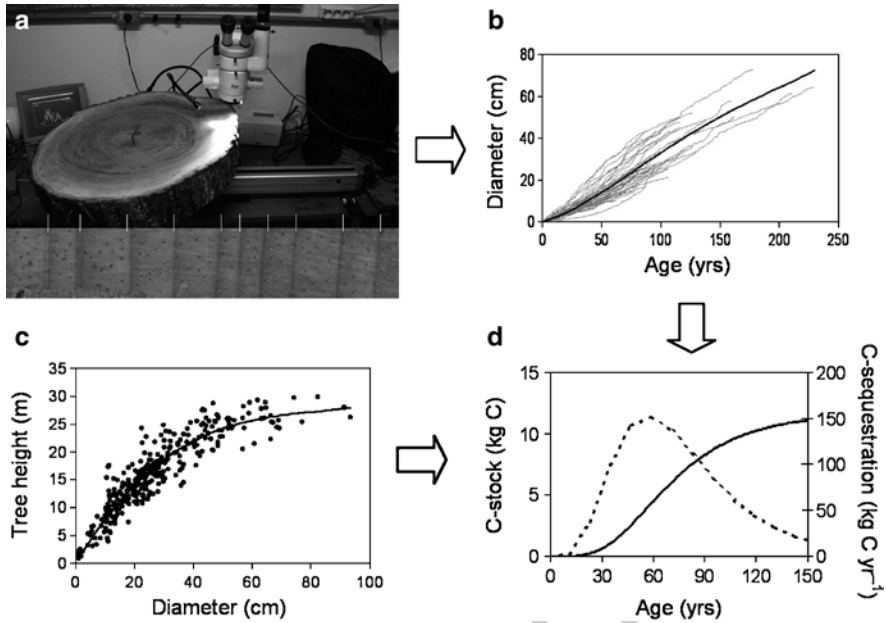


Fig. 18.8 Growth modelling based on tree-ring analyses: (a) Annual tree rings were analyzed on wood samples and ring-width was measured with a digital linear table (LINTAB) to (b) construct cumulative diameter growth curves for individual trees (*grey curves*) and a mean curve (*black curve*) for a tree species. (c) Relationship between diameter and tree height fitted to a non-linear regression model. (d) When models (b) and (c) are combined by allometric models (Table 18.7), the C-stock in the AGWB (*black line*) can be estimated for the entire life span of the tree species. From this model, C-sequestration is derived as the annual change in the C-stock of the AGWB (*dotted line*)

500 With these models, AGWB was estimated for every year by allometric equations
 501 (18.1)–(18.3), using diameter, tree height, and wood density. We estimated the
 502 C-content of AGWB to be 50% for slow-growing tree species in mature forests
 503 (Clark et al. 2001; Malhi et al. 2004) and 45% for fast-growing tree species of
 504 young successional stages. The wood of this latter group is characterized by fewer
 505 stable carbon compounds (e.g., lignin) than are found in densewood tree species
 506 (Elias and Potvin 2003). To estimate the carbon sequestration of a tree (kg year^{-1}),
 507 the difference between the C-stock in the AGWB of the year of the stand inventory
 508 (t) and that of the year before ($t-1$) was determined by the estimated diameter and
 509 height increments. The mean residence time of carbon in the AGWB (C-turnover)
 510 was calculated as the ratio C-storage/C-sequestration (Malhi et al. 2004).

511 Four distinct growth patterns corresponding to the successional stages were
 512 distinguished among the analyzed tree species (Fig. 18.9). Short-living pioneers,
 513 such as *Cecropia* spp., *Alchornea castaneifolia*, and *Nectandra amazonum*, which
 514 dominate the young successional stages (young pioneer stage, early secondary
 515 stage), rapidly accumulate carbon in the AGWB, but their total C-storage is low due
 516 to their short life spans. Long-living pioneer tree species, such as *L. cymulosa* and
 517 *P. munguba*, which are typical of late secondary stages, reach high levels of

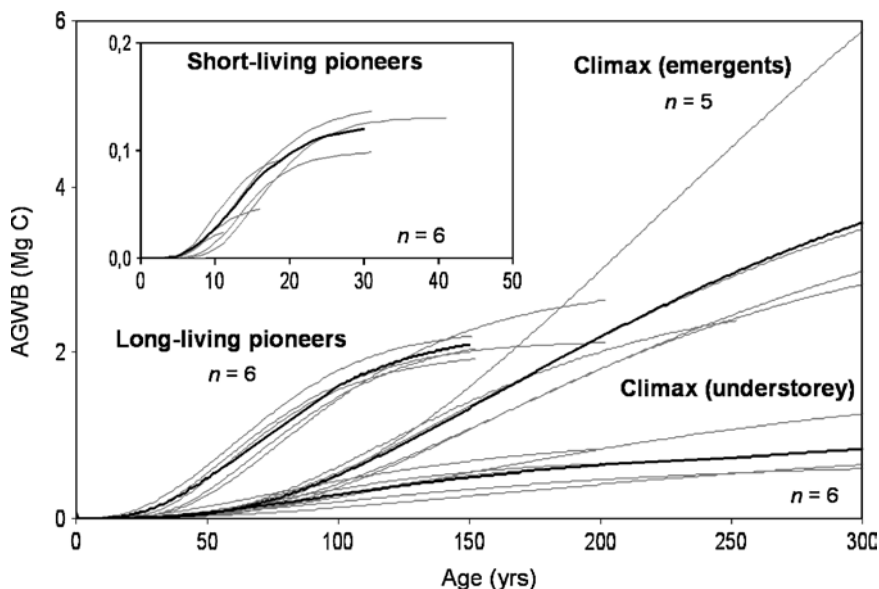


Fig. 18.9 Growth models of 23 tree species grouped according to growth type with respect to the accumulation of carbon in the AGWB. For every type, a mean growth curve is indicated (black line)

C-storage, up to 2 Mg C tree⁻¹, during their life spans. C-storage in the AGWB of emergent climax species (*P. trifoliata*, *Eschweilera* spp.) dominating the intermediate and late successional stages increases slowly during the 200–400-year life-span of these trees, but eventually exceeds the cumulative C-stocks of the long-living pioneers. The AGWB during the life span of understorey species such as Myrtaceae spp. is low. These growth models were used to estimate C-sequestration in AGWB according to allometric equations (18.1)–(18.3) for all trees in the young pioneer stage, 90.2% of the individuals in the 20-year-old early secondary stage, 59.1% of all trees in the 50-year-old late secondary stage, 65.5% of all trees in the 125-year-old intermediate stage, and 52.6% of all individuals in the 240-year-old late successional stage. For the remaining trees, C-sequestration was estimated by the ratio between C-stock and C-sequestration, since all models indicated significant relationships between these two parameters ($p < 0.01$).

Along the chronosequence, C-storage in the AGWB increases during the first 50 years to 117.4 ± 4.7 Mg C ha⁻¹ in the late secondary stage (Fig. 18.10). In light of the standard deviation of the C-stocks in the AGWB of the intermediate (115.0 ± 4.6 Mg C ha⁻¹) and climax (119.5 ± 5.3 Mg C ha⁻¹) stages, these values do not indicate increasing C-stocks in AGWB with increasing stand age. C-sequestration in the AGWB reaches its maximum in the 20-year-old early secondary stage (8.45 ± 0.49 Mg C ha⁻¹ year⁻¹) and declines more than threefold along the successional gradients. Mean residence time of carbon in the AGWB increased with increasing stand age, from 2.8 ± 0.1 years for the 7-year-old stand to 43.8 ± 0.1 years in the climax stage.

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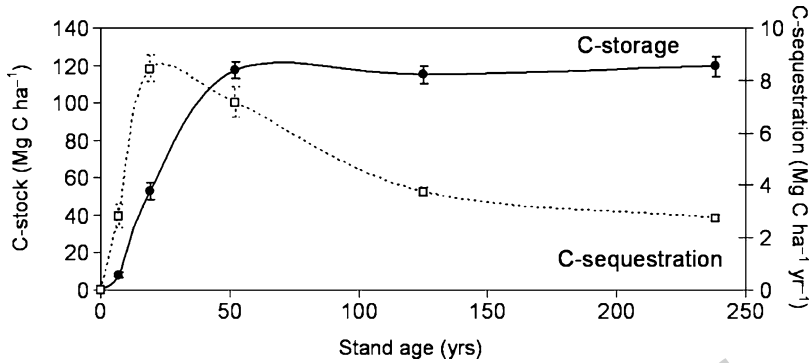


Fig. 18.10 Carbon stock (*black line*) and carbon sequestration (*dotted line*) in the AGWB along the successional gradient estimated by allometric equations (18.1–18.3)

541 Our results of C-storage in AGWB were much lower than those reported in other
 542 studies of nutrient-poor floodplain forests (igapó of clear-water rivers, Malhi et al.
 543 2004) and of terra firme forests in central Amazonia (Chambers et al. 2001), the
 544 neotropics (Malhi et al. 2004), and the tropics worldwide (Clark et al. 2001).
 545 Our estimates of annual C-sequestration in the AGWB of várzea forests were lower
 546 than those of Nebel et al. (2001a) but similar to those of Malhi et al. (2004). Both
 547 studies were based on repeated diameter measurements in the várzeas of Peru and
 548 Bolivia (Table 18.12). In general, C-sequestration rates are lower in igapó forests
 549 and terra firme than in várzea forests. This can be traced to the better nutrient status
 550 of alluvial soils in the várzea (Furch 1997, 2000), which leads to higher diameter
 551 growth rates of várzea tree species than of igapó and terra firme tree species
 552 (Worbes 1997; Schöngart et al. 2005; Fonseca Júnior 2007).

553 Differences in canopy surface structure (canopy height, average and variation of
 554 crown sizes, aerodynamic roughness features) lead to different spectra in the RGB-
 555 scale of satellite images (Landsat TM, bands 3, 4, and 5) and permit the classifica-
 556 tion of forested areas in the MSDR into young pioneer and early secondary stages
 557 (coverage of 21,648 ha), late secondary stages (coverage of 71,094 ha), and climax
 558 stages (coverage of 92,004 ha) (Wittmann et al. 2002b). Up-scaling of the field data
 559 on C-storage and C-sequestration in the AGWB for different successional stages by
 560 multiplying those values with the estimated specific forest coverage resulted in a
 561 total C-storage of 19.8×10^6 Mg C and a total C-sequestration of 0.93×10^6 Mg C
 562 year⁻¹ for the focal area of the MSDR, comprising 184,746 ha (Table 18.13).
 563 C-stocks in the AGWB of terra firme forests for an area of the same size as the
 564 forested focal area of the MSDR are 136–151% higher than in the várzea floodplain
 565 forests, based on the data of Chambers et al. (2001), Clark et al. (2001), and Malhi
 566 et al. (2004) (Table 18.13). C-sequestration in the AGWB of terra firme forests,
 567 however, is only 41–53% of that in the várzea. High C-storages and low
 568 C-sequestration rates in the AGWB of terra firme forests result in low C-turnover
 569 rates of 56–80 years. In the várzea floodplain forests, the mean C-turnover rate
 570 (mean residence time of C) in the AGWB is only 25.9 years.

Our results characterize várzea floodplain forests as highly dynamic ecosystems with high C-sequestration rates but low mean carbon residence time in the AGWB. After 50 years of primary succession, C-stocks of the AGWB did not increase (Fig. 18.10), indicating that losses of carbon through dynamic processes (e.g., tree fall)

Table 18.12 Comparison of C-storage and C-sequestration in AGWB for different forest types in the Amazon basin (várzea, igapó, and terra firme) and the tropics worldwide. Each of the studies considered trees with diameter ≥ 10 cm. C-sequestration was estimated by tree-ring analyses (this study) and repeated diameter measurements in long-term research plots (other studies)

Source	C-storage (Mg C ha ⁻¹)	C-sequestration (Mg C ha ⁻¹ year ⁻¹)		C-turnover (years)
		Mean (minimum–maximum)	Mean (minimum–maximum)	
Várzea (white-water floodplain forests)				
This study (stand ages 7–240 years) (<i>n</i> = 5)	82.5 (7.9–119.5)	4.98 (2.73–8.45)	20 (3–44)	
[AU6] Nebel et al. (2001) (<i>n</i> = 9)	198.4 (172.5–243.5)	7.43 (5.93–8.38)	27 (23–29)	
Malhi et al. (2004) (soil class 7) (<i>n</i> = 4)	124.4 (107.8–137.4)	4.56 (2.63–5.43)	29 (24–41)	
Igapó (clear-water floodplain forests)				
Malhi et al. (2004) (soil class 7) (<i>n</i> = 2)	213.2 (169.1–257.3)	2.94 (2.45–3.43)	72 (69–75)	
Terra firme (upland forests)				
Central Amazonia (Chambers et al. 2001) (<i>n</i> = 21)	162.1 (116.0–195.5)	2.06 (1.60–3.05)	80 (61–108)	
Neotropics (Malhi et al. 2004) (soil class 1–4, <i>n</i> = 61)	146.3 (55.8–308.9)	2.66 (1.53–4.12)	57 (30–157)	
Pantropics (Clark et al. 2001) (<i>n</i> = 39, <i>n</i> = 18)	139.0 (22.5–324.5)	1.90 (0.30–3.80)	56 (26–106)	

Table 18.13 Up-scaling of field data on C-storage and C-sequestration in the AGWB for different successional stages according to forest coverage, as estimated by remote-sensing data for a focal area of the MSDR (Wittmann et al. 2002b). The data are compared with estimates for C-storage and C-sequestration in the AGWB of terra firme forests (Data from Chambers et al. 2001; Clark et al. 2001; Malhi et al. 2004) of equivalent forest area

Forest type	Land cover (ha)	C-storage		C-sequestration	
		(Mg C ha ⁻¹)	(10 ⁶ Mg C)	(Mg C ha ⁻¹ year ⁻¹)	(10 ⁶ Mg C year ⁻¹)
Young pioneer stages	21,648	30.4	0.7	5.63	0.12
Early secondary stages	71,094	117.4	8.3	7.17	0.51
Late successional stages	92,004	117.2	10.8	3.23	0.30
Total	184,746		19.8		0.93
Terra firme					
Chambers et al. (2001)	184,746		29.9 ± 3.4		0.38 ± 0.06
Clark et al. (2001)	184,746		29.1 ± 8.1		0.45 ± 0.13
Malhi et al. (2004)	184,746		27.0 ± 8.5		0.49 ± 0.10

575 are in the same range as annual C-sequestration. Old-growth forests with stand ages
 576 >100 years have already reached equilibrium (steady state). Therefore, net
 577 C-sequestration in the AGWB in the várzea only occurs during the first 50–80 years
 578 of primary succession on newly deposited alluvial soils, reaching a maximum of
 579 approximately $5.31 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ after about 17 years (Fig. 18.11). This observa-
 580 tion is congruent with studies of forest recovery following complete clearance by
 581 humans for agricultural purposes (secondary succession), which have shown that bio-
 582 mass approaches old-growth values after 80–100 years (Saldarriaga 1987; Fearnside
 583 and Guimarães 1996; Alves et al. 1997; Guariguata and Ostertag 2001; Vargas et al.
 584 2008). Increasing stocks of AGWB in floodplain forests in the range of $0.62 \text{ Mg C ha}^{-1}$
 585 year^{-1} and $1.16 \pm 0.39 \text{ Mg C ha}^{-1} \text{ year}^{-1}$, reported by Phillips et al. (2008) and Baker
 586 et al. (2004a), respectively, were not confirmed by our data and might have been the
 587 result of overestimates of C-stocks and, consequently, of C-sequestration. Large
 588 C-stocks of AGWB are also lost through natural forest destruction caused by the lateral
 589 erosion and channel migration of rivers (Salo et al. 1986). Thus, net C-sequestration in
 590 AGWB during the first decades of primary succession may balance C-release from
 591 AGWB through natural forest destruction in the várzea, since the total forest cover in
 592 the várzea floodplains does not change over time (Fig. 18.12). Peixoto (2007) studied
 593 losses and gains of floodplains by erosion and sedimentation along the main channel
 594 of the Solimões and Japurá Rivers in the MSDR from 1984 to 2005 applying remote
 595 sensing techniques. During this period the floodplains lost 5.57% and gained 6.85% of
 596 its area resulting in net area increase of 1.27% corresponding to 3,300 ha or in average
 597 157 ha year^{-1} .

598 We found significant correlations between C-sequestration in the AGWB and the
 599 structural parameters of the stand. The AGWB per m^2 basal area is linearly nega-
 600 tively correlated with C-sequestration (Malhi et al. 2006) ($r = 0.99$, $p < 0.01$). Our
 601 results showed that increasing AGWB m^{-2} basal area led to decreasing C-sequestration
 602 in the AGWB (Fig. 18.13). C-sequestration was also negatively correlated with
 603 crown coverage ($\text{m}^2 \text{ ha}^{-1}$). Increasing crown coverage along the successional

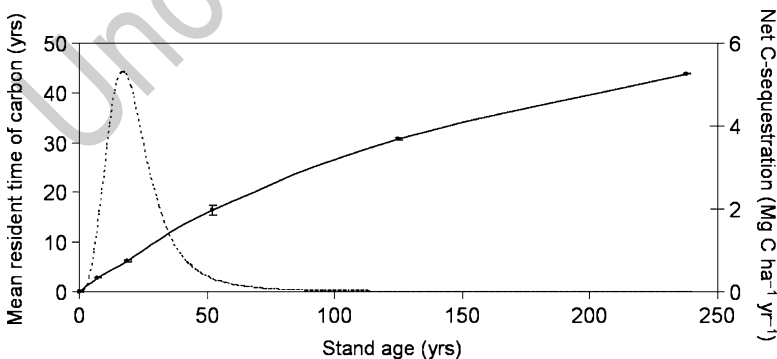


Fig. 18.11 Net carbon sequestration (*black line*) and mean residence time of carbon (ratio C-storage/C-sequestration) (*dotted line*) in the AGWB along the successional gradient estimated by allometric equations (18.1–18.3)

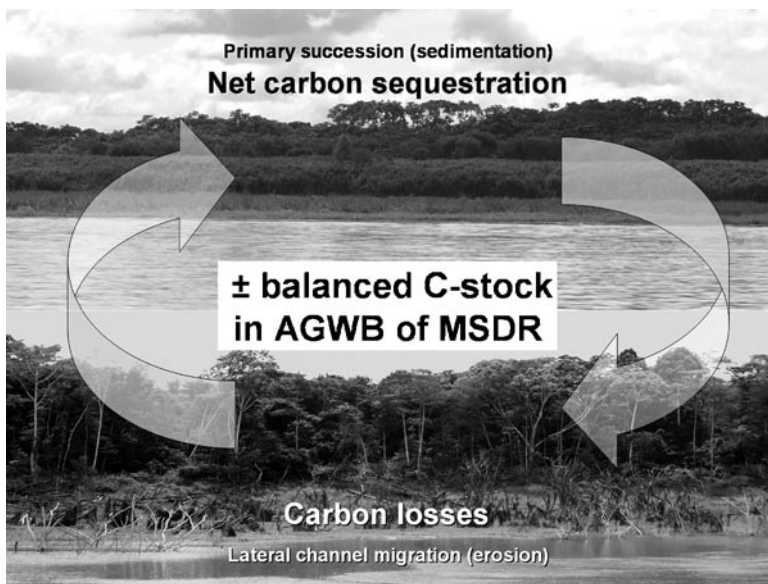


Fig. 18.12 In the várzea forest ecosystem net carbon sequestration in the AGWB occurs during the first 50–80 years of primary succession, which establishes on new deposited soils. On the other side C-stocks of AGWB get lost as a consequence of natural forest destruction caused by lateral erosion and channel migration of the rivers. The total C-stock in the AGWB in the whole várzea forest ecosystem may be almost balanced, since the total forest cover does not change considerably

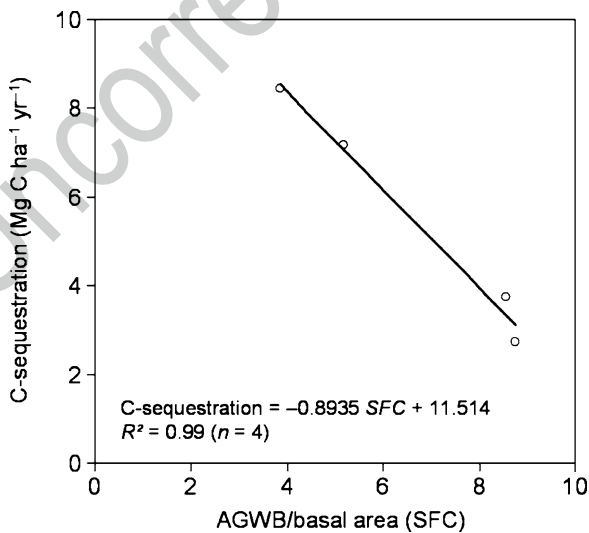


Fig. 18.13 Carbon sequestration as a function of accumulated AGWB per unit basal area, the structural conversion factor (SCF) (Malhi et al. 2006)

604 development (Schöngart 2003) corresponded to decreasing C-sequestration rates
 605 (Fig. 18.14). Surprisingly, C-sequestration in AGWB dropped along the successional
 606 gradient by almost 70% from the 20 year-old secondary stage to the 240 year-old
 607 stand. This strong decrease in C-sequestration can be explained by changes in species
 608 composition and in vertical canopy structure with increasing stand age. Along the
 609 successional gradient, tree height, individual crown size, and crown coverage per
 610 hectare increase (Terborgh and Petren 1991; Wittmann et al. 2002b; Schöngart
 611 2003). In the 7-year-old young pioneer stage examined in this study, only 71% of the
 612 area was covered by tree crowns, compared to 245% of the area of the 240-year-old
 613 late successional stage (Table 18.14). This corresponds to a decline of the *rPAR*
 614 measured above the forest floor, from about 31% *rPAR* in the 7-year old young pio-
 615 neer stage to 4.6% *rPAR* in the late successional stage (Wittmann and Junk 2003).
 616 Despite the much higher crown coverage, the late successional stage absorbs only
 617 25% more light than the young successional stages. In young successional stages,
 618 about 90% of tree crowns are exposed to sunlight compared to only about 40% in
 619 the late successional stage (Wittmann et al. 2002b; Schöngart 2003). Pioneer tree
 620 species forming the canopies of young successional stages have much higher net
 621 photosynthetic rates than climax tree species or understorey species (Table 18.15).
 622 The high crown areas in the lower and middle height classes of the canopy in the late
 623 successional stage exposed to low *rPAR* have low photosynthetic rates, but relatively
 624 high respiration rates to maintain important physiological processes (Horna 2002;
 625 Horna et al. this volume; Parolin et al. this volume a). This leads to lower
 626 C-sequestration in old-growth forests than in young successional stages.

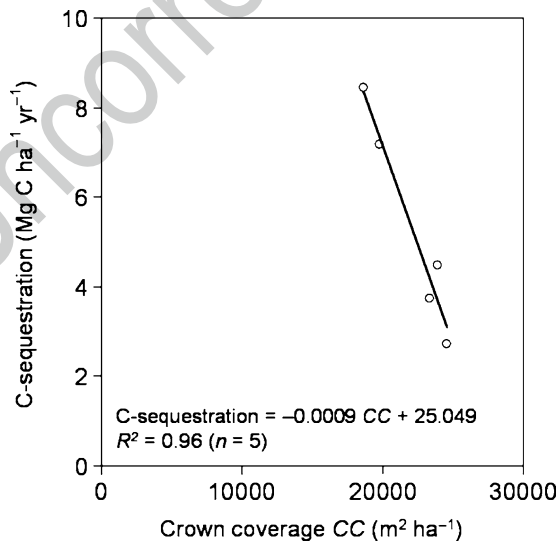


Fig. 18.14 Carbon sequestration in AGWB as a function of total crown area

Table 18.14 Crown coverage (Schöngart 2003) and photosynthetic active radiation (rPAR) on the forest floor (Wittmann and Junk 2003) of different successional stages in the central Amazonian várzea

Successional stage	Characteristic tree species	rPAR (%)	Crown coverage (%)
Young pioneer stage	<i>Alchornea, Salix</i>	31.0	70.8
Early secondary stage	<i>Cecropia, Nectandra</i>	19.4	186.9
Late secondary stage	<i>Pseudobombax, Luehea</i>	6.6	198.2
Late successional stage	<i>Piranhea, Tabebuia, Sloanea</i>	4.6	245.4

Table 18.15 Maximum photosynthetic and respiration rates of pioneers and late successional tree species (emergents, understorey) (After Medina and Klinge 1983)

Species group	Photosynthetic rate (mg CO ₂ dm ⁻² h ⁻¹)	Respiration rate (mg CO ₂ dm ⁻² h ⁻¹)	Net photosynthetic rate ^a
Pioneers (n = 4 species)	22.7 (21–26)	1.2 (0.9–1.9)	21.5
Climax (emergents) (n = 13 species)	12.0 (6–24)	1.31 (0.8–4.0)	10.7
Climax (understorey) (n = 3 species)	2.6 (1.8–3.4)	0.23 (0.1–0.3)	2.4

^aNet photosynthetic rate = gross photosynthetic rate-respiration (Jordan 1983)

18.7 Net Primary Production (NPP)

Information on NPP is needed for the development of realistic regional and global carbon budgets, to evaluate eddy covariance measurements in tropical forests, and to project how these forests respond to climatic changes (Clark et al. 2001). The NPP of a plant community is the difference between total photosynthesis (gross primary production) and total plant respiration (Jordan 1983; Medina and Klinge 1983); however, in the field, it is difficult to determine NPP according to this definition. An alternative definition of the NPP of an ecosystem is the total amount of carbon fixed from the atmosphere for the biochemical synthesis of new organic matter per unit time (Chambers et al. 2001; Roy et al. 2001). This includes the amount of new organic material retained by plants at the end of the time interval (e.g., wood biomass increment) and organic material that has been either produced or lost by the plant within the time interval (e.g., litterfall) (Clark et al. 2001). In forests, above-ground biomass increment, fine litterfall, aboveground losses through consumers (herbivory), emissions of biogenic volatile organic compounds (VOCs), and losses of leached organic compounds (Malhi et al. 2004) comprise the aboveground NPP (ANPP). The belowground NPP (BNPP) is the total net increment of root biomass, dead coarse and fine roots, root losses to consumers, root exudates, carbohydrates delivered to the mycorrhizal or nodule system, and net increase in stores of non-structural carbohydrates (Clark et al. 2001). ANPP and BNPP are expressed as biomass units (g or Mg) per unit soil area (meter or hectare) and time (year) (Medina and Klinge 1983). NPP can be partitioned into the long-lived (wood) and

649 the short-lived (leaves, fine roots) carbon pool (Malhi et al. 2004). However, at
650 some field sites, realistic data are available only for aboveground biomass increment
651 and fine litterfall (Clark et al. 2001; Malhi et al. 2004), while other components of the
652 ANPP and BNPP of tropical forests are lacking, insufficient or based on assump-
653 tions. Another problem is that most studies have no consistent methodology for
654 calculating aboveground biomass increment and litterfall, which complicates com-
655 parisons between the NPPs of tropical forests and between forest ecosystems of
656 other climates.

657 The ANPP of central Amazonian várzea floodplain forests was estimated by
658 Worbes (1997). The value for 40–80-year-old successional stages near Manaus was
659 23.8–33.6 Mg ha⁻¹ (11.9–16.8 Mg C ha⁻¹). For old-growth forests along the flood-
660 gradient in the Peruvian várzea, Nebel et al. (2001a) reported an ANPP of 20.8 Mg
661 ha⁻¹ (10.4 Mg C ha⁻¹) in the high várzea and 25.6 Mg ha⁻¹ (12.8 Mg C ha⁻¹) in the
662 low várzea. However, methods of the two studies differed. Nebel et al. (2001a)
663 estimated ANPP by the sum of the current biomass increment (derived from
664 repeated diameter measurements during a 4-year period) and litterfall (including
665 branches), while the estimate of Worbes (1997) was derived from the sum of fine
666 litterfall (excluding branches), mean wood biomass increment, and dead wood. The
667 latter method is problematic for two reasons. First, mean wood biomass increment
668 was determined by total AGBW divided by stand age (Piedade et al. 2001), which
669 is not equivalent to current AGBW production, derived by repeated diameter mea-
670 surements or tree-ring analysis (Schöngart 2003). Second, for the estimate of
671 ANPP, either dead wood (highly uncertain due to annually, periodically and epi-
672 sodically varying mortality, varying decomposition rates between tree species) or
673 annual wood increment should be accounted, but not both (Nebel et al. 2001a).
674 Dead wood can only be an estimate of wood biomass increments of forests that are
675 in a steady state, which is not the case for young successional stages. Nebel et al.
676 (2001a) predicted AGBW by estimated height, which, for the same forest type,
677 were much higher than our measured tree heights. Repeated diameter measure-
678 ments over short periods are problematic because of the imprecision in these mea-
679 surements (Chave et al. 2004) as well as climate-induced growth anomalies
680 (Clark and Clark 1994). The years 1993–1997 were characterized mainly by El
681 Niño conditions and probably higher increment rates in várzea forests than in other
682 years (Schöngart et al. 2004, 2005). Thus, the predictions of ANPP from Nebel
683 et al. (2001a) may be biased towards overestimate.

684 Table 18.16 presents estimates of ANPP for three studied successional stages in
685 várzea floodplain forests in the MSDR (Schöngart 2003) based on wood biomass
686 increments and fine litterfall. Herbivory was estimated to be 10% of the litterfall,
687 assuming that litterfall is made up, on average, of ~75% leaves (cf. Worbes 1997)
688 and that 12% of this material is lost through herbivory (Clark et al. 2001). To
689 account for additional losses through fruit and seed consumption, sap-sucking, and
690 nectar-feeding by animals, we estimated total aboveground herbivory losses to be
691 120% of the leaf herbivory. VOCs, mainly isoprene and monoterpenes (Kesselmeier
692 et al. 2002), were accounted for by the addition of 0.62 Mg ha⁻¹ year⁻¹ (Guenther
693 et al. 1995). The ANPP was 28.2 Mg ha⁻¹ year⁻¹ in a 20-year-old successional stage,

31.8 Mg ha⁻¹ year⁻¹ in a 50-year-old successional stage, and 13.3 Mg ha⁻¹ year⁻¹ in a 240-year-old late successional stage. Estimates of total NPP—including BNPP, which was estimated as 20–120% of ANPP (Clark et al. 2001) – are highly uncertain. Young successional stages of the central Amazonian várzea have the highest ANPPs among tropical forests (Table 18.17). Their ANPPs exceed those of secondary forests and pine and mahogany plantation forests in Puerto Rico, quoted by Brown and Lugo (1992), if similar stand ages are compared. The estimated ANPP of old-growth forests in the várzea is in the upper range of the ANPP of 38-old-growth forests in the terra firme (mean of 5.6 Mg C ha⁻¹ year⁻¹) (Clark et al. 2001).

VOC emissions must be considered as a substantial loss of carbon to the atmosphere. However, data on VOC emissions are insufficient due to the variability in the emission patterns of plant species and vegetation types as well as the number

Table 18.16 Estimates of ANPP as the sum of aboveground wood biomass production (AGWBP), fine litterfall (including twigs, but excluding branches), losses to consumers (herbivory), and volatile organic compounds (VOCs) for different successional stages in the várzea. All data are expressed in Mg ha⁻¹ year⁻¹. Numbers in bold are reported, numbers in brackets are estimated (see text for details)

Stand age (years)	AGWBP	Fine litterfall	Herbivory	VOCs	ANPP
20	18.8	7.8 ^a	(1.0)	(0.6)	(28.2)
50	15.9	13.6 ^b	(1.7)	(0.6)	(31.8)
240	5.5	6.4 ^c	(0.8)	(0.6)	(13.3)

^aData from Adis et al. (1979) for a 12-year-old successional stage (After Worbes 1997)

^bData from Adis et al. (1979) for a ~60-year-old successional stage (After Worbes 1997)

^cThis study

Table 18.17 Comparison of estimated ANPPs of central Amazonian floodplain forests, pantropical old growth forests (Clark et al. 2001), secondary forests, and forest plantations (Brown and Lugo 1992). All numbers are expressed in Mg C ha⁻¹ year⁻¹ (carbon is 50% of dry biomass; Clark et al. 2001), numbers in bold are reported, numbers in brackets are estimated

	AGWBP	Fine litterfall	Herbivory	VOCs	ANPP
Floodplain forests (várzea)					
20 years	8.5	3.9	(0.5)	(0.3)	(13.5)
50 years	7.2	6.8	(0.8)	(0.3)	(15.1)
240 years	2.7	3.2	(0.4)	(0.3)	(6.6)
Old-growth forests terra firme (pantropics) ^a					
<i>n</i> = 38	0.3–3.0	0.9–6.0	(0.1–1.1)	(0.2–0.3)	(1.4–9.9)
Plantation forests (Puerto Rico) ^b					
<i>Pinus</i> (19 years)	1.1	6.8	(0.8)	(0.3)	(9.1)
<i>Swietenia</i> (17 years)	3.3	5.6	(0.7)	(0.3)	(9.9)
<i>Swietenia</i> (40 years)	4.2	6.3	(0.8)	(0.3)	(11.5)
Secondary forests (Puerto Rico) ^a					
3–8 years (<i>n</i> = 1)	1.5	2.7	(0.3)	(0.3)	(4.8)
15–30 years (<i>n</i> = 2)	0.6–1.6	3.6–4.0	(0.4–0.5)	(0.3)	(5.4–6.0)
>50 years (<i>n</i> = 1)	1.3	5.3	(0.7)	(0.3)	(7.5)

^aData for NPP from Brown and Lugo (1992)

^bData for NPP from Clark et al. (2001)

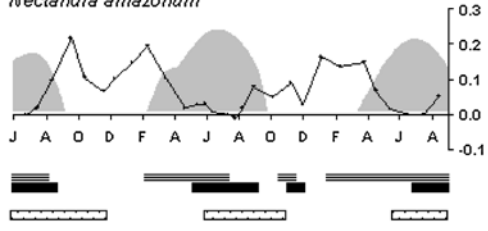
706 and amount of the different VOC species. Kesselmeier et al. (2002) reported that
707 3.4–27% of the net ecosystem production (NEP = NPP – heterotrophic respiration)
708 of tropical forests is released in the form of VOCs. Emissions of isoprenoids
709 (isoprenenes, monoterpenes) account for up to 2% of the NPP, but much higher
710 values of 15–50% are reached under special conditions (Harley et al. 1999).
711 Especially during the aquatic phase, which in the central Amazonian floodplain
712 forests can last up to 270 days year⁻¹ at the lowest elevations (Junk 1989), other
713 organic C-compounds, such as ethanol and acetaldehyde, are emitted in response to
714 the anoxic conditions of the areas surrounding the roots (Rottenberger 2003).
715 Branch enclosure under greenhouse experimental conditions in which four different
716 floodplain tree species were examined indicated a pronounced diurnal pattern in
717 ethanol and acetaldehyde emissions, with maximum amounts released during the
718 morning. This pattern was interpreted as arising from ethanol accumulation in the
719 roots at night (Schlüter and Furch 1992), when the stomata are closed, and an emis-
720 sion as soon as the stomata open, due to the light-induced transpiration stream.
721 Differences between ethanol and acetaldehyde emissions among tree species also
722 have been observed (Parolin et al. 2004). With this background, the Amazonian
723 floodplain forests are of special interest because of the potential change in the emission
724 levels in response to root anoxia, and may have even higher ANPPs than indicated.

725 18.8 Climate–Growth Relationships

726 For several tree species in the central Amazonian floodplains there is a negative
727 correlation between the monthly increment rates and the mean water level
728 (Schöngart et al. 2002). During the first half of the aquatic phase, diameter incre-
729 ment decreases to zero, indicating a cambial dormancy of at least 2 months during
730 the flooding period, ultimately leading to the formation of the tree ring (Worbes and
731 Fichtler this volume) (Fig. 18.15). Diameter growth starts again immediately after
732 the flushing of new leaves and diameter increment rates remain high during the
733 terrestrial phase. The sum of monthly increment rates during the vegetation period
734 accounts for the width of the annual tree ring. Ring-width indices correlate significantly
735 with the length of the terrestrial phase, as shown for *T. barbata* (Worbes 1989;
736 Fonseca Júnior 2007), *P. trifoliata* (Schöngart et al. 2004), and *M. acaciifolium*
737 (Schöngart et al. 2005). Thus, the yearly oscillation in ring width captures the inter-
738 annual variation in the length of the terrestrial phase (Fig. 18.16). During El Niño
739 years, basin-wide negative rainfall anomalies generally occur, leading to a weak-
740 ened flood-pulse (Schöngart and Junk 2007) and an extension of the terrestrial
741 phase (Schöngart et al. 2004). Trees in the central Amazonian floodplains respond
742 to these anomalies by a significant increase in growth, as indicated in Table 18.18.
743 In the adjacent non-flooded terra firme forests, however, tree growth is correlated
744 with precipitation patterns (Worbes 1999; Dünisch et al. 2003; Brienen and
745 Zuidema 2005). Tree-ring chronologies of *Cariniana micrantha* and *Eschweilera*
746 spp. from central Amazonian terra firme forests correlate significantly with rainfall

I. Evergreen tree species

Nectandra amazonum



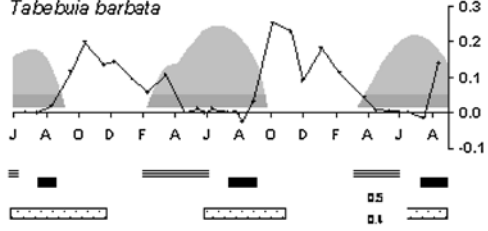
II. Brevi-deciduous tree species

Macrolobium acaciifolium



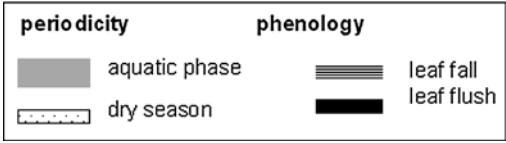
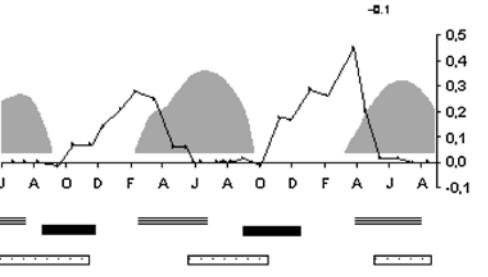
III. Deciduous tree species

Tabebuia barbata



IV. Stem-succulent tree species

Pseudobombax munguba



Monthly diameter increment (cm)

Fig. 18.15 Phenology and monthly variations in stem diameter increment derived from dendrometer measurements in a central Amazonian white-water floodplain forest for different ecotypes. The results are shown in relation to the flooded period and the dry season for the study period between June 1998 and August 2000 (Schöngart et al. 2002)

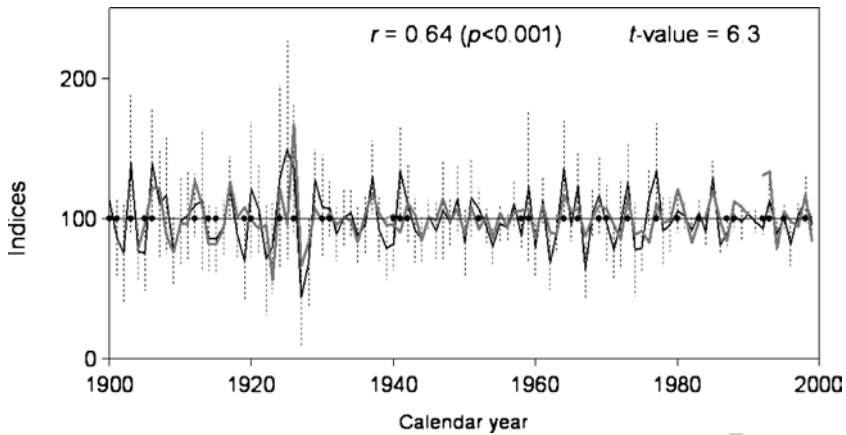


Fig. 18.16 Indexed ring-width chronology ($n = 10$ stem discs) of *Piranhea trifoliata* (black curve) and indexed time series of the duration of the non-flooded period (grey curve) derived from the daily recorded water level at the port of Manaus. The correlation between the two curves is significant. Vertical lines indicate error bars; black points represent El Niño events (Schöngart et al. 2004)

t18.1 **Table 18.18** Tree-ring chronologies from terra firme and floodplain forests in central Amazonia,
t18.2 indicating differences in ring-width indices between El Niño years and other years, as determined
t18.3 by t -test.

t18.4	Ring-width index	<i>El Niño</i> -years	Other years	t -value
t18.5	Terra firme			
t18.6	1871–2002	$n = 44$	$n = 88$	
t18.7	<i>Eschweilera</i> spp. ^a	95.0 ± 16.1	100.6 ± 19.4	$-1.77 (p < 0.05)$
t18.8	<i>Cariniana micrantha</i> ^b	93.5 ± 18.8	102.3 ± 16.6	$-2.68 (p < 0.01)$
t18.9	Várzea			
t18.10	1871–1999	$n = 43$	$n = 85$	
t18.11	<i>Piranhea trifoliata</i> ^c	104.2 ± 8.3	97.2 ± 8.9	$4.26 (p < 0.001)$
t18.12	1871–2003	$n = 44$	$n = 89$	
t18.13	<i>Macrobium</i>	106.7 ± 34.9	95.0 ± 32.2	$1.85 (p < 0.05)$
t18.14	<i>acaciifolium</i> ^d			
t18.15	Igapó			
t18.16	1871–2003	$n = 44$	$n = 89$	
t18.17	<i>M. acaciifolium</i> ^d	107.4 ± 32.3	96.0 ± 35.8	$1.81 (p < 0.05)$

t18.18 ^aData from M. Sack (unpublished)

t18.19 ^bData from Funck (2004)

t18.20 ^cData from Schöngart et al. (2004)

t18.21 ^dData from Schöngart et al. (2005)

747 patterns (data: INMET for Manaus). A t -test indicated significantly lower ring-width
748 indices during El Niño years than during other years and the opposite tree-ring pattern
749 in the floodplain forests (Table 18.18).

750 The opposing climate-growth relationship between terra firme and várzea is
751 important in the context of the interannual variation of carbon sequestration in the
752 AGWB of adjacent Amazonian forests. The drier and warmer climate conditions
753 during an El Niño cause a decrease in soil moisture in terra firme forests and thus

reduced photosynthesis, increased heterotrophic respiration rates, and a lower NPP (Tian et al. 1998). Therefore, most parts of terra firme forests act as carbon sources during an El Niño event, as suggested by biogeochemical models (Prentice and Lloyd 1998; Foley et al. 2002). Floodplain forests, however, sequester part of the climate-induced carbon emissions of terra firme forests (Schöngart et al. 2004). Nonetheless, it is difficult to quantify these variations in the floodplain forests because of the following reasons:

- Phenological ecotypes in central Amazonian floodplain forests (Parolin et al. this volume c), such as evergreen, brevi-deciduous, deciduous, and stem-succulent tree species, exhibit different climate-growth relationships (Schöngart et al. 2002). Diameter growth of deciduous and brevi-deciduous tree species responds to water-level fluctuations, while that of evergreen species shows significant correlations with rainfall variability and water level. In stem-succulent tree species such as *P. munguba* there is a strong relationship between monthly diameter increment and rainfall variations, but not with water-level fluctuations. This tree species alone comprises up to 22% of the total importance-value-index and accounts for about 39% of C-sequestration in the highly productive late secondary stages (Schöngart 2003).
- Differences in the growth rhythms of floodplain and terra firme tree species in central Amazonia arise from a 2–3-month displacement in the temporal occurrences of the terrestrial phase (vegetation period in the floodplains) and the rainy season (vegetation period in the terra firme) (Schöngart et al. 2002). In other regions of the Amazon basin, displacement of the vegetation periods between the floodplain and terra firme may be shorter or longer depending on the temporal occurrence of the flood pulse. In the western Amazon basin, for instance, the displacement in the vegetation period between floodplains and terra firme is almost zero and the growth rhythms of ecotypes in the two systems may be synchronous. Thus, an opposite reaction to climate anomalies in tree growth between várzea and terra firme tree species might be less evident.
- In central Amazonian floodplains, the El Niño signal is stronger at middle elevations than at lower or higher elevations (Schöngart and Junk 2007). The tree-ring chronology of *P. trifoliata*, established from trees growing at middle elevations (Schöngart et al. 2004), indicates a stronger El Niño signal than the chronology of *M. acaciifolium*, developed from trees growing at low elevations (Schöngart et al. 2005). No information on climate-growth relationships is available for tree species of high-várzea forests. However, own phenological observations and the monitoring of fine litterfall during the year (Fig. 18.1) indicate that several species of the ecosystem are triggered by rainfall variability.
- Realistic estimates of C-stocks and C-sequestration in the AGWB are only available for successional stages with no or low anthropogenic disturbances in várzea forests of central Amazonia (Schöngart 2003). Estimates for secondary forests of different stand ages, species composition, and geographical regions as well as estimates for different forest types in the black-water and clear-water igapó are lacking.

798 **18.9 Conclusions and Outlook**

799 Earlier studies in the Amazonian floodplain forests were restricted to areas close to
800 Manaus. The várzea forests in this region suffered from transformations into areas
801 used for agriculture and pastures as well as forest exploitation. After agricultural
802 activities were abandoned, secondary forests became established in these areas, with
803 a high proportion of pioneer tree species. These forests served as references for stud-
804 ies on species richness and composition, forest structure, wood density, diameter
805 increment, ecophysiology, phenology, germination, regeneration, and productivity
806 (increment, litterfall) and accumulative production (AGWB) in which várzea forests
807 and old-growth black-water forests along the lower Negro River (*Tarumã mirim*)
808 were compared. However, due to differences in successional development, these
809 comparisons were problematic and often resulted in wrong hypotheses due to the
810 lack of data for old-growth várzea forests. The data presented in this chapter for old-
811 growth forests in the várzea, however, provide several new insights:

- 812 • Fine litterfall in mature forests of the várzea and igapó does not differ signifi-
813 cantly. Young successional stages have higher litterfall rates than old-growth
814 forests in the várzea.
- 815 • Shallower rooting depths in floodplain forests lead to lower root biomasses than
816 in terra firme forests.
- 817 • No differences in the wood density between old-growth forests in the várzea and
818 igapó were found. The wood densities of old-growth floodplain forests are in the
819 range of those of mature terra firme forests.
- 820 • Biomasses in the floodplain forests are lower than indicated by earlier estimates
821 or measurements. C-stocks in the AGWB are much lower than in terra firme
822 forests.
- 823 • Tree-ring analysis indicates that biomass productions in younger successional
824 stages are much higher than indicated in earlier studies. By contrast, biomass
825 production of old-growth forests in the várzea was found to be lower.
- 826 • New estimates of the ANPP for várzea forests of different successional develop-
827 ment showed that young successional stages, which have an ANPP of 31.8 Mg
828 ha⁻¹ year⁻¹, are among the most productive tropical forests worldwide. The NPPs
829 of old-growth várzea forest is in the range of terra firme forests. The database
830 for estimates of BNPP is insufficient.

831 Results obtained as part of the Large-Scale Biosphere-Atmosphere Experiment in
832 Amazonia (LBA) have contributed to controversial discussions about the function
833 of tropical forests as significant long-term carbon sinks (a.o., Grace et al. 1995;
834 Malhi et al. 1998, 2004; Phillips et al. 1998, 2008; Clark 2002; Grace and Malhi
835 2002; Richey et al. 2002; Saleska et al. 2003; Ometto et al. 2005). Our results char-
836 acterize várzea floodplain forests as highly dynamic ecosystems with low AGWB
837 and high NPP, but also indicate variations of NPP and biomass for stands of differ-
838 ent successional stages. Stand age is an important predictor and parameter for
839 estimates of the components contributing to NPP, but in most studies no information
840 regarding stand ages is provided (Clark et al. 2001; Malhi et al. 2004, 2006) due to

uncertainties and methodological problems in estimating tree ages (Worbes and Junk 1999; Worbes and Fichtler this volume). Maximum tree ages in the terra firme, estimated by mean diameter increment rates derived from repeated diameter measurements (Laurance et al. 2004) or radiocarbon-dating (Chambers et al. 1998; Viera et al. 2005), may be as high as 1,380–1,870 years, while dendrochronological determinations have suggested that the maximum age of trees in the terra firme is not more than 600–700 years (Worbes and Junk 1999; Fichtler et al. 2003; Brienen and Zuidema 2005; Worbes and Fichtler this volume). The lack of data on tree ages and stand ages in the terra firme complicates the comparison of NPP data from permanent sample plots.

Due to the increasing CO₂ concentration in the atmosphere (IPCC 2007), many studies based on long-term tree data of forest plots (Phillips et al. 1998; Chambers et al. 2001; Baker et al. 2004a; Malhi et al. 2004) and eddy covariance studies (Grace et al. 1995; Malhi et al. 1998) have suggested that C-uptake is stimulated in Amazonian old-growth forests. Initial determinations were made by eddy-covariance measurements to estimate NEP, defined as the difference between the amount of organic carbon fixed by photosynthesis in an ecosystem and total ecosystem respiration. These measurements, made from towers, of vertical CO₂ fluxes indicated that Amazonian terra firme forests serve as large carbon sinks of 1.0–5.9 Mg C ha⁻¹ year⁻¹ (Grace et al. 1995; Malhi et al. 1998) or 0.5–3.0 Pg C year⁻¹ for the Amazon basin (Saleska et al. 2003), which would explain parts of the large missing terrestrial carbon sink in the global carbon budget (Schimel et al. 2001). These data are much higher than estimates of C-uptake of 0.1–1.2 Mg C ha⁻¹ year⁻¹, which were derived from permanent observation plots (Phillips et al. 1998, 2008; Baker et al. 2004a). However, the sum of instantaneous CO₂ fluxes at the measurement towers does not always provide a realistic estimate of NEP. During the night, low air turbulence often causes insufficient mixing of CO₂ from canopy respiration, and CO₂ is probably lost due to drainage of air currents along topographical depressions (*baixios*) and thus is not measured at the towers (Ometto et al. 2005). Water availability limits tree growth, especially in El Niño years, when large regions of the Amazonian terra firme experience low rainfall (Tian et al. 1998; Foley et al. 2002). Estimates of the net ecosystem exchange in old-growth terra firme forests depend strongly on the climate conditions during the measurement. NEP estimates by eddy covariance methods over a 3-0year period in the Tapajós region (Saleska et al. 2003) indicated an annual C-loss of 1.3 Mg C ha⁻¹ year⁻¹. Surprisingly, carbon was lost during the wet season and gained during the dry season, contrary to the seasonal cycle of tree growth. There is a huge variety of different forest types in different successional developments and they grow under different climatic, hydrologic, and edaphic conditions across the Amazon basin. The database on stand ages, AGWB, and components of NPP for the Amazonian forest ecosystems is still insufficient due to methodological problems and to the scarcity of temporal and spatial scales to estimate basin-wide C-budgets and their interannual changes as a function of climate variations. This holds true especially for the floodplain forests. Another aspect that is not considered in biogeochemical models or measurements of gas fluxes or the accumulation of carbon in vegetation for the Amazon basin is the difference in the interannual variation of C-sequestration between floodplain and terra firme forest ecosystems, as determined by tree-ring analysis.

887 Many studies have shown that sea surface temperatures (SSTs) in the tropical
888 Pacific basin and tropical North Atlantic influence water-level fluctuations and
889 discharge in the catchments of the Amazon rivers (Richey et al. 1989; Marengo
890 1992; Whetton and Rutherford 1994; Adis and Latif 1996; Amarasekera et al.
891 1997; Marengo et al. 1998, 2008; Coe et al. 2002; Foley et al. 2002; Aalto et al.
892 2003; Schöngart et al. 2004; Ronchail et al. 2005; Harris et al. 2008). The El Niño-
893 Southern Oscillation (ENSO) causes large-scale precipitation anomalies in the
894 Amazon basin (Sombroek 2001), which results in high flood-levels of the Amazon
895 River during La Niña events (cold ENSO phases) and low flood-levels during El
896 Niño events (warm ENSO phases) (Schöngart and Junk 2007).

897 Two future scenarios with opposite trends may impact the flooding patterns of
898 central Amazonia and thus affect tree growth. The first is that runoff and river dis-
899 charge generally increase when natural vegetation (especially forest) is removed
900 (Foley et al. 2005). In the light of future land-use scenarios for the Brazilian
901 Amazon region (Soares-Filho et al. 2006), this will strongly impact the floodplain
902 forests along the Madeira, Tapajós, Xingú, Tocantins, and Araguaia Rivers. For
903 instance, the Tocantins River basin in Brazil showed a 25% increase in river dis-
904 charge between 1960 and 1995, coincident with expanding agriculture in the catch-
905 ment area, but no major change in precipitation (Costa et al. 2003). The second
906 trend is a decrease in inundation length driven by increasing temperatures and CO₂
907 concentrations (Foley et al. 2002). The models of Costa and Foley (2002) predict a
908 basin-wide decrease of precipitation and an increase in temperature as effects of
909 deforestation, doubled CO₂ concentrations, and interactions between these pro-
910 cesses. A temperature increase in the Amazon basin may exacerbate drought effects
911 by accelerated evaporation (White et al. 1999). Severe droughts in terra firme for-
912 ests provoked by El Niños such in 1925/1926 and 1997/1998 (Sternberg 1988;
913 Sombroek 2001; Williams et al. 2005) caused CO₂ releases over large areas of
914 Amazonian non-flooded terra firme forests (Prentice and Lloyd 1998; Foley et al.
915 2002) and increased the fire risk of these forests in areas experiencing high rates of
916 selective logging and fragmentation (Nepstad et al. 1999). Large-scale fires, pas-
917 tures, agriculture, and commercial logging all release huge amounts of greenhouse
918 gases to the atmosphere (Laurance et al. 2001; Cochrane 2003; Asner et al. 2005),
919 which feed back and accelerate climate changes (IPCC 2007) and probably increase
920 the strength of the ENSO (Timmermann et al. 1999). The predicted increase in
921 SSTs in the tropical Pacific and Atlantic (IPCC 2007) will probably lead to
922 increased drought probability for the future (Malhi et al. 2008; Nepstad et al. 2008)
923 and generally lower floods in the central Amazonian floodplain forests (Schöngart
924 and Junk 2007; Marengo et al. 2008) and will probably affect forest dynamics and
925 the carbon cycle in the AGWB of floodplain forests.

Author Queries

Chapter No.: 18 0001170107

Queries	Details Required	Author's Response
AU1	Please fix a or b for Sioli 1954 here and in the following citations in the text.	
AU2	Please include Cattanio et al. 2004 in the ref. list.	
AU3	Please provide the Year for Wittmann Unpubl. data	
AU4	Please provide author initials and year for unpublished data.	
AU5	Please signify the meaning of * in Table 18.7.	
AU6	Please fix a or b for Nebel et al. 2001.	

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Abstraction	<p>Amazonian floodplain trees are used for a variety of purposes (i.e. Le Cointe 1922; Phillips et al. 1994; Parolin 2000; Kvist and Nebel 2001; Kvist et al. 2001; Bentes-Gama et al. 2002; Schöngart 2003), but there is little information about the commercial importance of the different tree species. Easy access to floodplain forests combined with the low cost of timber harvesting, processing, and transport led to the overexploitation of many floodplain trees soon after the intense immigrations associated with the rubber boom (1850–1920) and continuing as the search for natural rubber extended from the vicinity of the city of Belém, near the Amazon estuary, to equatorial areas further west (Santos 1980). A second, major wave of immigration waves marked the second, smaller rubber boom, during World War II (1939–1945), when many cities and settlements were established in the Amazon basin, and the population of existing settlements, such as Belém, Santarém, Manaus, Tefé, and Iquitos, grew exponentially. The overwhelming proportion of these settlements is located along or close to Amazonian white-water rivers.</p>	

Chapter 19 1
Use of Amazonian Floodplain Trees 2

Florian Wittmann and Astrid de Oliveira Wittmann 3

Contents

19.1 Introduction..... 000
 19.2 Non-Timber Forest Products..... 000
 19.3 Timber Products..... 000
 19.4 Conclusions..... 000

19.1 Introduction 4

[AU1] Amazonian floodplain trees are used for a variety of purposes (i.e. Le Cointe 1922; 5
 Phillips et al. 1994; Parolin 2000; Kvist and Nebel 2001; Kvist et al. 2001; Bentes- 6
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 Manaus, Tefé, and Iquitos, grew exponentially. The overwhelming proportion of 17
 these settlements is located along or close to Amazonian white-water rivers. 18

[AU2] In general, floodplain inhabitants have preserved an intimate knowledge of the flood- 19
 plain environment and its resources (e.g., Hiraoka 1992; Padoch 1988; Junk et al. 2000) 20

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21 such that the management of crops and trees is adapted to the environment (Ohly
22 2000b; De Jong 2001). Most information about the use of forest resources in
23 Ecuador, Peru, Colombia, Bolivia, and the Guyanas originates from the Amerindian
24 population. However, the majority of floodplain inhabitants in Brazilian Amazonia
25 are descendants of colonists and their use of forest resources may differ substan-
26 tially from that of the Amerindian population.

27 This chapter provides an overview of the use of Amazonian floodplain trees,
28 with respect to non-timber forest products and timber. The number of useful species
29 among the 186 common várzea tree species within the Amazon basin was investi-
30 gated, and the most important use categories were determined. It should be noted
31 that, as our data originated from a variety of sources (herbaria, literature, the
32 Internet), it was not possible to verify each one its origin, Amerindian or colonial.
33 Instead, this chapter presents results from a botanical point of view, without distin-
34 guishing between uses by different ethnic groups.

35 19.2 Non-Timber Forest Products

36 Many Amazonian floodplain trees provide non-timber forest products (NTFPs).
37 These comprise “all biological materials other than timber which are extracted from
38 forests for human use” (NTFP 2007). Peters et al. (1989) investigated the economic
39 potential of NTFPs compared to the value of standing timber from a 1-ha inventory
40 in terra firme near Iquitos, Peru. These authors identified 72 species (26.6% of the
41 total) and 350 individuals (41.6% of the total) that had market value in Iquitos. The
42 net present value (NPV) of fruits and latex was US\$6,330.00, and that of timber
43 US\$6,820.00. In an investigation of NTFPs from three 1-ha plots in Ecuador, two
44 located in the terra firme and one located in the várzea, Grimes et al. (1994) found
45 that the NPV of the terra firme plots averaged about US\$2,800.00 each, and that of
46 the várzea plot US\$1,257.00. These values must be considered cautiously, because
47 the NTFPs of floodplains depend on the forest type, especially with respect to stand
48 age and location along the flooding gradient (Kvist et al. 2001). Furthermore, the
49 values are subject to strong seasonal and spatial differences, i.e., the development
50 of economic cycles (Crook and Clapp 1998) and the distance to the markets
51 (Bennett 2002). The examples show, however, that the economic potential of
52 NTFPs from floodplains can be comparable to that of timber and should therefore
53 be addressed. In addition, their role as a buffer in times of food shortage makes
54 NTFPs a critical component in the food security of rural populations (Lipper
55 2000).

56 In várzea forests, quantitative inventories of the ratio species pool/useful species
57 range from 48% to 87% of all tree species. In a floristic inventory comprising 7.5
58 ha of várzea forests, Pinedo-Vásquez et al. (1990) reported that floodplain inhabit-
59 ants in northern Peru use 60.1% of all tree species present. In a quantitative ethno-
60 botanical investigation of terra firme and floodplain (várzea) forests along the
61 Manú and Madre de Dios Rivers in southeastern Peru, Phillips et al. (1994) found

that 94% of all stems present in forest inventories totaling an area of 6.1 ha were 62
 useful to the inhabitants. Contrary to the findings of Grimes et al. (1994), the 63
 authors noted that floodplain forests are more useful than other forest types, mostly 64
 due to their importance as sources of construction materials and food. About 80% 65
 of forest plant products were of subsistence value (not sold) for floodplain inhabitants, 66
 whereas about 20% were of commercial value. The authors also concluded that 67
 forests, especially those of the floodplain, are endangered through intense defores- 68
 tation and overexploitation. 69

In data originating from nine permanent 1-ha sample plots in alluvial forests at 70
 the Ucayali River, near Jenaro Herrera in Peru, Kvist et al. (2001) evaluated the use 71
 of várzea tree species by 12 households during a 1-year period. The authors found 72
 that, of 321 tree species present in the plots (Nebel et al. 2001), 156 (48.6%) were 73
 used for 43 different purposes. Of the NTFPs, the products with the greatest eco- 74
 nomic potential were edible fruits, in particular the commercially used palm fruits 75
 of *Mauritia flexuosa*, *Euterpe precatória*, and *Oenocarpus bataua*. Other NTFPs 76
 described included fire wood, tree cortex for tying and braiding, palm hearts, fruits 77
 used as fish bait, fishing poisons, vessels and containers, and phytomedical products 78
 for the treatment of different diseases. In a study of the ethnobotany of Amerindian 79
 and colonial communities along forests of the upper Nangaritza river (white-water) 80
 in southeast Ecuador, Luna (2004) stated that, of the 135 useful plant species (trees, 81
 shrubs, lianas, and herbaceous plants), the majority were trees that provided edible 82
 fruits (36.3% of the total), followed by timber trees (24.4% of the total), phyto- 83
 medical extracts from trees (21.5% of the total), and trees used for multiple pur- 84
 poses (14.8% of the total). 85

Reyes-García et al. (2006) calculated the practical, cultural, economic, and total 86
 values of 114 plant species within the Tsimane territory, located at the foothills of 87
 the Andes in the department of Beni, Bolivian Amazon (“gallery forests” along 88
 white-water rivers, and terra firme). The highest total values were obtained from 89
 firewood, followed by trees providing fruits, trees providing “tools” (mortars, grinding 90
 boards, food containers, mats, storage boxes, brooms, bows, arrows, weaving materials), 91
 trees providing “other” products (uses that usually take place outside the house- 92
 holds e.g., canoe building), and trees providing medical products. 93

We compiled information on the use of 186 common várzea tree species (*sensu* 94
 Wittmann et al. 2006, Table 19.1) within the Amazon basin, based on information 95
 from: (a) herbaria (mainly the Instituto Nacional de Pesquisas da Amazonia 96
 (INPA), Manaus, Brazil; Missouri Botanical Garden (MBG), USA; New York 97
 Botanical Garden (NYBG), USA, Royal Botanical Gardens, Kew, Great Britain) 98
 and (b) the literature (i.e., Phillips and Gentry 1993; Phillips et al. 1994; Kvist et al. 99
 2001; Worbes et al. (2001); Schöngart (2003); Reyes-García et al. 2006), or more 100
 specialized literature about the chemical constituents of plants (see Table 19.3). 101
 Only those trees usually cut as a whole for use (roundwood, house and boat con- 102
 struction, floating houses, carpentry, panelling, floors, sleepers, instrument shafts, 103
 plywood, etc.) were considered as timber species. Other uses were considered to 104
 provide NTFPs (medical uses, edible fruits, fish baits, fishing and hunting poisons, 105
 palm hearts, firewood, manufacture of oars, fishing rods, arrows and bows, resins, 106

[AU3]

[AU4]

Table 19.1 List of the 186 investigated tree species from Amazonian várzea and the quantitatively most important use categories. For more detailed use categories, see Tables 19.3 and 19.4. The data originated from information provided in herbaria (mainly Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; Missouri Botanical Garden (MOBOT), USA; New York Botanical Garden (NYBG), USA; Royal Botanical Garden Kew, Great Britain); and information provided in the literature (see text)

t1.5 t1.6	Family	Species	No known use								
			NTFPs								
t1.7			Phytomedical	Edible fruits	Fish bait	Ornamental tree	Handicrafts	Other	Timber		
t1.8	Anacardiaceae	<i>Spondias lutea</i> L.									
t1.9	Annonaceae	<i>Annona hypoglauca</i> Mart.	x	x				x	x		
t1.10		<i>Annona hypoglauca</i> Mart.		x							
t1.11		<i>Annona tenuipes</i> R.E.Fries							x		
t1.12		<i>Duguetia quitarensis</i> Benth.						x			
t1.13		<i>Duguetia quitarensis</i> Benth.							x		
t1.14		<i>Duguetia quitarensis</i> Benth.						x			
t1.15		<i>Duguetia quitarensis</i> Benth.							x		
t1.16		<i>Duguetia spixiana</i> Mart.							x		
t1.17		<i>Guatteria inundata</i> Mart.						x			
t1.18		<i>Guatteria inundata</i> Mart.									
t1.19		<i>Oxandra riedeliana</i> R.E.Fries							x		
t1.20		<i>Oxandra riedeliana</i> R.E.Fries							x		
t1.21		<i>Unonopsis floribunda</i> Diels									
t1.22		<i>Unonopsis floribunda</i> Diels		x							
t1.23		<i>Unonopsis guatterioides</i> (A.DC.) R.E.Fries	x						x		
t1.24		<i>Unonopsis guatterioides</i> (A.DC.) R.E.Fries									
t1.25		<i>Xylopia calophylla</i> R.E.Fries							x		
t1.26		<i>Xylopia calophylla</i> R.E.Fries						x			
t1.27	Apocynaceae	<i>Aspidosperma rigidum</i> Rusby							x		
t1.28		<i>Aspidosperma rigidum</i> Rusby	x								
t1.29		<i>Himantanthus sucuba</i> (Spruce ex Müll. Arg.) Woodson	x								
t1.30		<i>Himantanthus sucuba</i> (Spruce ex Müll. Arg.) Woodson									
t1.31		<i>Himantanthus sucuba</i> (Spruce ex Müll. Arg.) Woodson									

Table 19.1 (continued)

Family	Species	No known use	NTFPs	Timber
	<i>Tabebuia barbata</i> (E.Mey) Sandwith		x	x
	<i>Tabebuia serratifolia</i> (Vahl) G.Nicholson		x	x
Boraginaceae	<i>Cordia nodosa</i> Lam.	x		
Brassicaceae	<i>Crataeva benthamii</i> Eichler			x
Burseraceae	<i>Protium strumosum</i> Daly	x		
Caryocaraceae	<i>Caryocar microcarpum</i> Ducke		x	x
Chrysobalanaceae	<i>Couepia chrysocalyx</i> (Poepp.) Benth. ex Hook f.	x		
	<i>Couepia paraensis</i> (Mart. and Zucc.) Hook f.		x	
	<i>Licania apetalata</i> (E.Mey) Fritsch			x
	<i>Licania brittoniana</i> Fritsch	x		
	<i>Licania heteromorpha</i> Benth.		x	x
	<i>Licania longistyla</i> (Hook f.) Fritsch		x	
	<i>Parinari excelsa</i> Sabine			x
	<i>Tapura juruana</i> (Ule) Rizzini	x	x	

Clusiaceae	<i>Calophyllum brasiliense</i> Camb.	x				x
	<i>Caraipa punctulata</i> Ducke				x	x
	<i>Clusia panapanari</i> (Aubl.) Choisy	x				
	<i>Garcinia brasiliensis</i> Mart.	x		x		x
	<i>Garcinia madruno</i> (Kunth) Hammel				x	
	<i>Tovomitia umbellata</i> Benth.	x				
	<i>Vismia baccifera</i> (L.) Triana and Planch.				x	x
	<i>Vismia macrophylla</i> Kunth			x		
Combretaceae	<i>Buchenavia oxycarpa</i> (Mart.) Eichler					x
	<i>Terminalia dichotoma</i> G.Mey.					x
Elaeocarpaceae	<i>Sloanea floribunda</i> Spruce ex Benth.	x				
	<i>Sloanea terniflora</i> (Sessé and Moc. ex DC.) Standl.					x
Erythroxylaceae	<i>Erythroxylum</i> <i>capplerianum</i> Peyr.					x

Table 19.1 (continued)

Family	Species	No known use	NTFPs	Timber
Euphorbiaceae	<i>Erythroxylum tucuricense</i>	x		
	Plowman			
	<i>Alchornea castaneifolia</i> (Humb. and Bonpl.) A.Juss.		x	
	<i>Alchornea discolor</i> Poepp.			x
	<i>Dioscorea brasiliensis</i>	x		
	Klotzsch			
	<i>Hevea brasiliensis</i> (Willd. ex A.Juss.) Müll.Arg.			x
	<i>Hevea pauciflora</i> (Spruce ex Benth.) Müll.Arg.			x
	<i>Hevea spruceana</i> (Benth.) Müll.Arg.			x
	<i>Hura crepitans</i> L.			x
	<i>Mabea nitida</i> Spruce ex Benth.			x
	<i>Piranhea trifoliata</i> Baill.			
	<i>Sapium glandulosum</i> (L.) Morong			x
Lauraceae	<i>Aniba affinis</i> (Meisn.) Mez.	x		
	<i>Aniba hostmanniana</i> (Nees) Mez.			x

<i>Aniba megaphylla</i> Mez.	x			
<i>Aniba riparia</i> (Nees) Mez.		x		
<i>Endlicheria anomala</i> (Nees) Mez.				x
<i>Endlicheria formosa</i> A.C.Sm.				x
<i>Licaria armenitaca</i> (Nees) Kosterm.				x
<i>Nectandra amazonum</i> Nees				x
<i>Nectandra hihua</i> (Ruiz. and Pav.) Rohwer	x			
<i>Ocotea aciphylla</i> (Nees) Mez.				x
<i>Ocotea cymbarum</i> Kunth	x		x	
<i>Couroupita subsessilis</i> Pilg.	x		x	
<i>Eschweilera albiflora</i> (DC.) Diers				x
<i>Eschweilera ovalifolia</i> (DC.) Nied				x
Lecythidaceae				

(continued)

Table 19.1 (continued)

Family	Species	No known use	NTFPs	Timber
	<i>Eschweilera parviflora</i> Mart. ex DC.			x
	<i>Gustavia augusta</i> L.		x	
	<i>Gustavia poeppigiana</i> O.Berg	x		
	<i>Lecythis pisonis</i> Camb.			x
Fabaceae:	<i>Acosmium nitens</i> (Vogel) Yakovlev			x
Caesalpinioidae	<i>Campsiandra comosa</i> Benth.	x		
	<i>Cassia leiandra</i> Benth.	x	x	
	<i>Copaifera officinalis</i> (Jacq.) L.	x		x
	<i>Crudia amazonica</i> Spruce ex Benth.			
	<i>Cynometra bauhiniifolia</i> Benth.	x		
	<i>Macrolobium acaciifolium</i> (Benth.) Benth.			x
	<i>Macrolobium bifolium</i> (Aubl.) Pers.			x
	<i>Schizolobium amazonicum</i> Huber ex Ducke			x
	<i>Senna bacillaris</i> (L.f.) H.S. Irwin and Barneby	x		

	<i>Senna reticulata</i>	x
	(Willd.) H.S.Irwin and Barneby	
	<i>Tachigali venusta</i>	x
	Dwyer	
Fabaceae:	<i>Acacia lorentensis</i>	x
Mimosoideae	J.F.Macbr.	
	<i>Albizia subdimidiata</i>	x
	(Splitg.) Barn. and Grimes	
	<i>Hydrochorea corymbosa</i>	x
	(Rich.)Barn. and Grimes	
	<i>Inga cinnamomea</i>	x
	Spruce ex Benth.	
	<i>Inga disticha</i> Benth.	x
	<i>Inga obidensis</i> Ducke	x
	<i>Inga pilosula</i> (Rich.) J.F.Macbr.	x
	<i>Inga punctata</i> Willd.	x
	<i>Inga splendens</i> Willd.	x
	<i>Pseudoptadenia suaveolens</i> (Miq.) Grimes	x

(continued)

Table 19.1 (continued)

Family	Species	No known use	NTFPs	Timber
Fabaceae: Papilionoideae	<i>Stryphnodendron guianense</i> (Aubl.) Benth.	x		
	<i>Zygia cataractae</i> (Kunth) L.Rico		x	
	<i>Zygia latifolia</i> (L.) Fawcett and Rendle	x		
	<i>Clitoria amazonum</i> Mart. ex Benth.	x		
	<i>Erythrina fusca</i> Lour.		x	x
	<i>Etaballia dubia</i> (Kunth) Rudd.			x
	<i>Lecointea amazonica</i> Ducke			x
	<i>Ormosia macrocalyx</i> Ducke			
	<i>Paramachaerium ormosioides</i> (Ducke) Ducke			x
	<i>Platymiscium ulei</i> Harms			
	<i>Pterocarpus amazonum</i> (Mart. ex Benth.) Ams.			x
	<i>Vatairea guianensis</i> Aubl.		x	x
	Malpighiaceae	<i>Byrsonima japurensis</i> A.Juss.		

Malvaceae	<i>Glandonia macrocarpa</i> Griseb.	x														x
	<i>Apeiba glabra</i> Aubl.															x
	<i>Ceiba pentandra</i> (L.) Gaertn.															x
	<i>Guazuma ulmifolia</i> Lam.															x
	<i>Herrania mariae</i> (Mart.) Decne ex Goudot															x
	<i>Luehea cymulosa</i> Spruce ex Benth.															x
	<i>Pachira insignis</i> (Sw.) Sw. ex Savigny															x
	<i>Pseudobombax munguba</i> (Mart. and Zucc.) Dug.															x
	<i>Sterculia apetala</i> (Jacq.) H.Karst															x
	<i>Theobroma cacao</i> L.															x
	<i>Mouriri acutiflora</i> Naudin															x
	<i>Mouriri grandiflora</i> DC.															x
	<i>Cedrela odorata</i> L.															x
	<i>Guarea guidonia</i> (L.) Sleumer															x
<i>Trichilia lecointei</i> Ducke															x	
Melastomataceae																x
Meliaceae																x

(continued)

Table 19.1 (continued)

Family	Species	No known use	NTFPs	Timber
Moraceae	<i>Batocarpus amazonicus</i> (Ducke) Fosberg			x
	<i>Ficus antheleminitica</i> Mart.		x	x
	<i>Ficus amazonica</i> (Miq.) Miq.	x		
	<i>Ficus casapiensis</i> Dugand	x		
	<i>Ficus guianensis</i> Desv. ex Ham.			x
	<i>Ficus matthewsii</i> Standl.	x		
	<i>Helicostylis scabra</i> (J.F.Macbr.) C.C.Berg			x
	<i>Maclura tinctoria</i> (L.) D.Don. ex Steud.		x	x
	<i>Maquira calophylla</i> (Poepp. and Endl.) C.C.Berg		x	
	<i>Maquira coriacea</i> (H.Karst) C.C.Berg		x	x
	<i>Sorocea duckei</i> W.C.Burger	x		
Myristicaceae	<i>Virola calophylla</i> (Spruce) Warb.		x	
	<i>Virola mollissima</i> (Poepp. Ex A.DC.) Warb.	x		x

	<i>Virola surinamensis</i> (Roll. Ex Roebb.) Warb.	x				x	
Myrsinaceae	<i>Cybianthus spicatus</i> (Kunth) G. Agostini	x					x
Myrtaceae	<i>Calythranthes multiflora</i> O. Berg		x				
	<i>Eugenia inundata</i> DC.	x					
	<i>Eugenia ochrophloea</i> Diels	x					
	<i>Myrciaria dubia</i> (Kunth) Mc Vaugh		x				
	<i>Psidium acutangulum</i> DC.		x				
Nyctaginaceae	<i>Neea aequinosa</i> Sattndl. <i>Neea spruceana</i> Heimerl	x					x
Ochnaceae	<i>Quiina rhytidopus</i> Tul.	x					
Olacaceae	<i>Heisteria acuminata</i> (Humb. and Bonpl.) Engl.			x			x
	<i>Minquartia guianensis</i> Aubl.					x	
Polygonaceae	<i>Symmeria paniculata</i> Benth.						
	<i>Triplaris dugandii</i> Brandbyge				x		

(continued)

Table 19.1 (continued)

Family	Species	No known use	NTFPs	Timber
Rubiaceae	<i>Triplaris surinamensis</i> Cham.			x
	<i>Alibertia edulis</i> (Rich.) A. Rich ex DC.		x	
	<i>Bothriospora corymbosa</i> (Benth.) Hook.f.	x		
	<i>Calycohyllum spruceanum</i> (Benth.) Hook.f. ex K.Schum.		x	x
	<i>Duroia duckei</i> Huber	x		
	<i>Genipa americana</i> L.		x	x
	<i>Zanthoxylum compactum</i> (Huber ex Albuq.) P.G. Waterman	x		
	<i>Banara guianensis</i> Aubl.	x		
	<i>Casearia aculeata</i> Jacq.	x		
	<i>Homalium guianense</i> (Aubl.) Oken	x		
Salicaceae	<i>Laetia corymbulosa</i> Spruce ex Benth.		x	x
	<i>Salix maritima</i> Leyb.		x	
	<i>Xylosma bentharii</i> (Tul.) Triana and Planch.	x		
	<i>Chrysophyllum argenteum</i> Jacq.			x

t2.1 fuels, fragrances, pigments, phytocosmetics, hedges, tying, braiding, roof
 t2.2 construction, vessels, etc.). The results indicated that 135 tree species (72.6%) are
 t2.3 useful to floodplain inhabitants and/or extractors (Table 19.2). This amount is well
 t2.4 within the range of data from the previously described ethnobotanical inventories.
 t2.5

t2.1 **Table 19.2** Use categories of the 186 investigated tree species from the Amazonian várzea (for
 t2.2 category definition, see text). The data originated from information provided in herbaria (mainly
 t2.3 Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; Missouri Botanical Garden
 t2.4 (MOBOT), USA; New York Botanical Garden (NYBG), USA; Royal Botanical Garden Kew,
 t2.5 Great Britain); and information provided in the literature (see text)

t2.6		No. of species	
t2.7		used	(%)
t2.8	Useful species (from 186 species)	135	72.58
t2.9	Used for a single purpose (from 135 species)	49	36.29
t2.10	Used for multiple purposes (from 135 species)	86	63.71
t2.11	Non timber forest products-NTFP (from 186 species)	98	52.69
t2.12	Phytomedical products	43	23.12
t2.13	Edible fruits	31	16.66
t2.14	Ornamental tree	13	6.99
t2.15	Fish bait	11	5.91
t2.16	Handicraft	9	4.84
t2.17	Tying and braiding	5	2.69
t2.18	Fishing and hunting poison	4	2.15
t2.19	Firewood	4	2.15
t2.20	Rubber	4	2.15
t2.21	Fragrances and cosmetics	4	2.15
t2.22	Oil, fuel, resin	4	2.15
t2.23	Dyes, pigments	3	1.61
t2.24	Containers, vessels	3	1.61
t2.25	Arrows, bows, arrow heads, fishing rods	3	1.61
t2.26	Oars	2	1.07
t2.27	Roof construction	2	1.07
t2.28	Palm-heart extraction	2	1.07
t2.29	Stuffing material	2	1.07
t2.30	Insect repellent	2	1.07
t2.31	Living hedges	2	1.07
t2.32	Bark coal (i.e., in the manufacture of ceramics)	1	0.54
t2.33	Boat sealant	1	0.54
t2.34	Timber products (from 186 species)	78	41.94
t2.35	House construction	63	33.87
t2.36	Carpentry	22	11.83
t2.37	Furniture	21	11.29
t2.38	Boat and canoe construction, floating houses	20	10.75
t2.39	Plywood	18	9.68
t2.40	Heavy construction and sleepers	16	8.60
t2.41	Floors and panels	15	8.06
t2.42	Fences	9	4.84
t2.43	Tools (i.e., instrument shafts, handles)	7	3.76

Forty-nine of these useful species (36.3%) are employed for a single purpose, but most are used for multiple purposes. Ninety-eight tree species yield NTFPs. The quantitative most important fraction of NTFP is medical products (43 species), for which most of the species are used for different purposes: anti-inflammatory and anti-rheumatic (13 species), anti-pyretic (nine species), anti-fungal (eight species), anti-helminthic (five species), muscle-relaxant effects (five species), or more specialized (i.e. diarrhea, leishmaniasis, expectorant, narcotic, antibiotic, anti-viral, anti-malarial, analgesic, antiseptic, stimulant, anti-depressive, and anxiolytic effects) (Table 19.3). Furthermore, ten tree species produce compounds with anti-cancer and cytotoxic effects, although information could not be obtained as to how many of these species are traditionally used for those purposes. Sources describing the actual and potential use of phytochemical extracts from várzea tree species are listed in Table 19.3.

Thirty-one species provide edible fruits (Table 19.1), most which are rarely consumed by the region's inhabitants. In Brazilian Amazonia, the palm fruits of *Mauritia flexuosa*, *Euterpe precatoria*, and *Oenocarpus bataua* seem to have the strongest commercial importance, followed by fruits of a few dicots such as *Theobroma cacao*, *Genipa americana*, and *Spondias mombin*. Other fruit species with local importance in Brazilian Amazonia include *Garcinia brasiliensis*, *Cassia leiandra*, and, because of its elevated vitamin C content, especially *Myrciaria dubia* (Justi et al. 2000). There are, however, other introduced fruit species that naturally are found in non-flooded (sometimes pan-tropical) environments but that are cultivated by floodplain inhabitants in home gardens (Gutjahr 1996; Junk et al. 2000). These tree species, e.g. *Mangifera indica* L. (mango), *Eugenia malaccensis* L. (jambo), *Artocarpus altilis* (Parkinson) Fosberg (breadfruit), *Cocos nucifera* L. (coconut), *Psidium guajava* L. (guava), *Carica papaya* L. (papaya), and *Averrhoa carambola* L. (carambola) can be of economic importance to households located in the vicinity of markets. The introduced species are moderately tolerant to seasonal inundations and therefore can be cultivated at high-várzea sites.

Our investigation further indicated 11 tree species that are reported to provide fruits commonly used as fish bait, i.e., *Alchornea discolor*, *Crataeva benthamii*, *Ilex inundata*, *Mabea nitida*, and *Symmeria paniculata*. As ichthyochory is particularly common in low-várzea trees (i.e. Goulding 1983; Ziburski 1991), many more species may be useful for this purpose. Kvist et al. (2001) noted that nearly two thirds of all species available in a 3-ha inventory of low-várzea (tahuampa) forests in Peru were, according to the inhabitants, able to attract fish. The authors further stated that fishermen usually spend more time within the low várzea and thus are aware of the fruits eaten by fish in this forest type. In our study, all species described to be useful as fish bait are species of the low várzea (Table 19.1).

Other NTFPs each derived from a few or even a single tree species, are quantitatively less important (Table 19.2). These uses may be locally of some economic importance, such as palm – heart extraction in the Peruvian Amazon (mostly *E. precatoria*) and in the Brazilian Amazon (mostly *E. oleracea*, but also *Astrocaryum jauari* along the upper Negro River, Piedade et al. 2006), or the extraction of fruit fibers (kapok) from *Ceiba pentandra* and *Pseudobombax munguba*,

Table 19.3 Actual and potential phytomedical uses of 43 tree species from the Amazonian várzea. Note that not all species are traditionally used, even when information about their chemical constituents and potential activities is available (Source H = Information provided by herbaria (mainly Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; Missouri Botanical Garden (MOBOT), USA; New York Botanical Garden (NYBG), USA; Royal Botanical Garden Kew, Great Britain)

Species	Phyto-medical use								Source	
	1	2	3	4	5	6	7	8		
t3.5										
t3.6	x								Anti-viral, analgesic	H; Dunstan et al. (1997); Barros (2004); Hiruma-Lima et al. (2006)
t3.7									Anti-depressive, Anxiolytic	H; Sousa et al. (2004)
t3.8										
t3.9										
t3.10			x							H
t3.11								x		H; Pretto et al. (2004)
t3.12										H
t3.13										H
t3.14										H; Martins et al. (2003)
t3.15										H; Lima et al. (2003)
t3.16										H
t3.17										Herforth et al. (2003)
t3.18										H
t3.19										Payne (1991)
t3.20										H
t3.21										H
t3.22										Gonçalves et al. (2005)
t3.23										Oga et al. (1981)
t3.24										Compresse et al. (2003); Seigler (2005)
t3.25										De Souza et al. (2001)
t3.26										Kraus et al. (1998)
t3.27										H; De Miranda et al. (2000)
t3.28										Beutler et al. (2000)
t3.29										Braca et al. (2000)

t3.30	<i>Maclura tinctoria</i> (L.) D. Don ex Steud.	x			Anti-viral	El-Sohly et al. (1999); Groweiss et al. (2000)
t3.31						
t3.32	<i>Malouetia tamaquarina</i> (Aubl.) A. DC.	x		x		Suffredini et al. (2002)
t3.33	<i>Maquira calophylla</i> (Poepp. and Endl.) C.C. Berg	x				Rovinski et al. (1987)
t3.34	<i>Maquira coriacea</i> (H. Karst) C.C. Berg				Anti-plasmodial	Mitaine-Offer et al. (2001)
t3.35	<i>Ocotea cymbarum</i> Kunth	x		x		H
t3.36	<i>Pourouma guianensis</i> Aubl.				Anti-leishmaniosis	H; Torres-Santos et al. (2004)
t3.37	<i>Salix maritima</i> Leyb.	x				H
t3.38	<i>Senna bacillaris</i> (L. f.) H. S. Irwin & Barneby			x		Mabberley (1997)
t3.39	<i>Simaba multiflora</i> A. Juss.	x			Anti-malarial	Moretti et al. (1986); Cabral et al. (1993)
t3.40	<i>Spondias lutea</i> L.	x				Kvist et al. (2001)
t3.41	<i>Tabebuia barbata</i> (E. Mey.) Sandwith			x		De Saizarbitoria et al. (1997)
t3.42	<i>Tabebuia serratifolia</i> (Vahl) G. Nicholson	x		x	Anti-Leishmaniosis	Duke and Vázquez (1994)
t3.43	<i>Tabernaemontana markgrafiana</i> J. F. Macbr.	x		x	Disinfectant	Nielsen et al. (1994)
t3.44	<i>Tabernaemontana siphilitica</i> (L.f.) Leeuwenb.	x		x		H
t3.45	<i>Theobroma cacao</i> L.			x	Stimulant, antiseptic	Leung (1980)
t3.46						
t3.47	<i>Unonopsis floribunda</i> Diels				Diarrhea	H
t3.48	<i>Vatairea guianensis</i> Aubl.	x			Anti-mycotic	H
t3.49	<i>Virola calophylla</i> (Spruce) Warb.					H
t3.50	<i>Virola surinamensis</i> (Rol. ex Rottb.) Warb.			x	Anti-malarial	Lopes et al. (1999)
t3.51	<i>Vismia macrophylla</i> Kunth	x		x		H; Lopez et al. (2001); Hussein et al. (2003)
t3.52						
t3.53	<i>Vitex cymosa</i> Bert. ex Spreng.				Analgesic	H

t3.54 1 – anti-inflammatory and anti-rheumatic effects, 2 – anti-cancer and cytotoxic effects, 3 – anti-pyretic effects, 4 – anti-fungal effects, 5 – anti-helminthic effects, 6 – muscle-relaxant effects, 7 – expectorant effects, and 8 – narcotic effects

t3.55

156 which were commercially harvested until the mid-1900s for stuffing material and the
157 manufacture of lifejackets. Some species provide resins or latex that are traditionally
158 used as fishing and hunting poisons (*Caryocar microcarpum*, *Hura crepitans*,
159 *Maquira coriacea* and *Sapium glandulosum*, see also Cannon et al. 2004), while
160 others are particularly preferred as firewood (*Alibertia edulis* and *Calycophyllum*
161 *spruceanum*, Kvist et al. 2001). Seeds from nine tree species are used for the manu-
162 facture of handicrafts sold in many Amazonian cities (e.g., *Attalea phalerata*, *Cedrela*
163 *odorata*, *Crescentia amazonica*, *Malouetia tamaquarina* and *Ormosia macrocalyx*).
164 Due to their high flexibility, shoots from *Alchornea discolor* and buttresses from
165 *Duguetia quitarensis* and *Lecointea amazonica* are used for the manufacture of
166 arrows, bows, and fishing rods, whereas wood originating from buttresses of
167 *Aspidosperma rigidum* is preferred for the manufacture of oars. Fruit from the gener-
168 era *Crescentia* and *Lecythis* are used as containers and are found in nearly all house-
169 holds located along Amazonian rivers. Resins from *Calycophyllum spruceanum* and
170 *Caraipa punctulata* are commonly used as insect repellents. The leaves of most of
171 the palm species from the Amazonian floodplains provide roofing and braiding
172 (Henderson et al. 1995), whereas the bark of *Eschweilera parvifolia*, *Genipa ameri-*
173 *cana*, and some genera of Annonaceae (mostly *Guatteria* and *Oxandra*) is used for
174 cordage and technical tying. Resin from the high-várzea species *Licania heteromor-*
175 *pha* is used by the inhabitants of many Amazonian cities as a boat sealant.

176 One modern use of tree species that is rarely mentioned in literature is as ornamental
177 trees. These are of increasing importance because municipalities are interested in
178 improving the quality of life of city inhabitants by cultivating trees that reduce solar
179 radiation, improve air quality, and are visually attractive, i.e., by producing large
180 and colorful flowers. Ornamental trees are, optimally, fast-growing species that are
181 resistant to stressful conditions, such as seasonal drought, soil compaction, and
182 elevated anthropogenic gas imissions, while negative properties, such as the devel-
183 opment of large buttresses, massive leaf shedding, and the production of large
184 fruits, are not desired. We identified 13 central Amazonian várzea tree species that
185 are used as ornamental trees in Brazilian cities (Table 19.1). Some of these tree
186 species, including *Vitex cymosa*, *Ficus guianensis* and *Ceiba pentandra*, are widely
187 distributed throughout the neotropics, while others, e.g., *Cassia leiandra* and
188 *Pterocarpus amazonum*, have restricted distribution patterns in the Amazonian
189 várzea. Fast-growing and light-demanding várzea species, such as *Pseudobombax*
190 *munguba* and *Triplaris surinamensis*, were recently planted along the devastated
191 banks of small rivers (igarapés) in the city of Manaus (Secretaria Municipal do
[AU] 192 Meio Ambiente (SEMMA), Manaus; personal communication).

193 19.3 Timber Products

194 Although the area covered by floodplain forests is smaller than the accounted for
195 by Amazonian terra firme, about 70–75% of the wood exploited in Amazonia
196 before the mid-1970s originated from the floodplains (Ros-Tonen 1993;

Bentes-Gama et al. 2002). During the late 1970s, the creation of settlements and roads, especially in the southern part of the basin, led to the intensification of timber harvest in the terra firme such that the importance of wood from the floodplains declined. According to estimations of the IBAMA, roundwood production in the Amazonian floodplains in the year 1999 amounted to 3 million cubic metres year⁻¹, which is about 10% of the total roundwood production within the 'Amazônia Legal'. Wood production in floodplains thus contributes US\$120 million to the Amazonian gross product and currently directly generates about 30,000 jobs (IBAMA 2000; Bentes-Gama et al. 2002).

Approximately 350 tree species of the Amazon basin are used as timber resource and 34% of them occur in the floodplains (Martini et al. 1998). Many floodplain tree species provide timber for house and boat construction as well as for tools, handles, carpentry, furniture, and plywood. Some of these timber species are commercially exploited for regional, national, and even international timber markets (Klenke and Ohly 1993; Higuchi et al. 1994). Commercial exploitation within floodplain forests is concentrated on comparatively few tree species. In the floodplain forests of Peru and the Amazon State, Brazil, 69–90% of the total timber exploited involves only seven to nine tree species (Klenke and Ohly 1993).

In central Amazonia, the timber industry and timber export are mainly in the cities of Manaus and Itacoatiara, where *Mil Madeireira Ltda.* and *Gethal-Amazonas S.A.* together account for the export of about 3,50,000 m³ of timber year⁻¹ (Worbes et al. 2001). The timber species most highly valued for export are especially those with comparatively high wood densities (wood specific gravity (WSG) >0.6–0.65 g cm⁻³, Worbes et al. 2001; Schöngart 2003), such as *Cedrela odorata* and *Calophyllum brasiliense*, and the low-density wood species (WSG <0.6–0.65 g cm⁻³) *Virola* spp. (Macedo and Anderson 1993). Recently, the exploitation of low-density wood species has become important, particularly because of the expanding plywood industry in Belém and Manaus (Worbes et al. 2001). Albernaz and Ayres (1999) estimated that low-density wood species amounted to 60–70% of the total timber exploited in Amazonian floodplains. The most frequently exploited plywood species are *Ceiba pentandra*, *Hura crepitans*, *Virola surinamensis*, and *Schizolobium amazonicum* (Brienza-Junior et al. 1991; Albernaz and Ayres 1999; Worbes et al. 2001).

Most of the várzea timber species occur exclusively in the high várzea (48 species), five species occur in both high-várzea and low-várzea forests, and 24 timber species have restricted distribution patterns in the low várzea. High-density wood species mostly occur in high-várzea forests (Wittmann and Junk 2003, see also Table 19.4), which cover only 10–15% of the várzea landscape (Wittmann et al. 2002). The high várzea is, however, the area where inhabitants prefer to settle and where the conversion of forests into agricultural areas and pastures is therefore concentrated. High-density wood species of the high várzea are those with low natural abundances (Nebel et al. 2001; Wittmann et al. 2004). In addition, these species need a relatively long period to reach maturity and to develop stems of exploitable diameters and heights. Deforestation and overexploitation already have led to significant reductions of species populations, especially in eastern Amazonia and in the central and western part of Brazilian Amazonia, in the vicinities of the

t4.31	<i>Duguetia spixiana</i> Mart.	x							x	ISDM; Phillips et al. (1994); Kvist et al. (2001)
t4.32										
t4.33	<i>Endlicheria anomala</i> (Nees) Mez.	x	x	0.48	x				x	ISDM
t4.34	<i>Endlicheria formosa</i> A.C. Sm.	x	x	-	x					Phillips et al. (1994); Luna (2004)
t4.35	<i>Erythrina fusca</i> Lour.	x	x	0.31-0.33	x	x				ISDM
t4.36	<i>Eschweilera albiflora</i> (DC.) Diers	x	x	0.66-0.83					x	ISDM
t4.37	<i>Eschweilera ovalifolia</i> (DC.) Nied	x	x	-	x	x				ISDM
t4.38	<i>Eriaballia dubia</i> (Kunth) Rudd.	x	x	0.62-0.66	x					ISDM
t4.39	<i>Euterpe precatoria</i> Mart.			-	x					ISDM; Henderson et al. (1995); Kvist et al. (2001)
t4.40										
t4.41	<i>Ficus anihelminica</i> Rich. ex DC.	x		0.35-0.38					x	ISDM; Phillips et al. (1994)
t4.42	<i>Garcinia brasiliensis</i> Mart.		x	0.58-0.64	x					ISDM
t4.43	<i>Genipa americana</i> L.	x	x	0.57-0.66	x	x	x	x	x	ISDM; Kvist et al. (2001)
t4.44	<i>Guarea guidonia</i> (L.) Sleumer	x	x	0.53	x				x	ISDM; Phillips et al. (1994)
t4.45	<i>Guazuma ulmifolia</i> Lam.	x	x	0.49-0.52	x				x	ISDM
t4.46	<i>Heisteria acuminata</i> (Humb. & Bonpl.)		x	-	x					ISDM; Phillips et al. (1994)
t4.47	Engl.									
t4.48	<i>Hevea brasiliensis</i> Müll. Arg.	x	x	0.52-0.64	x				x	Worbes et al. (2001)
t4.49	<i>Hura crepitans</i> L.	x	x	0.36-0.42	x	x	x	x	x	ISDM; Phillips et al. (1994); Albermaz and Ayres (1999); Kvist et al. (2001)
t4.50										
t4.51	<i>Laeitia corymbulosa</i> Spruce ex Benth.	x		0.61-0.67	x					Kvist et al. (2001)
t4.52	<i>Lecointea amazonica</i> Ducke	x	x	0.97-1.03	x				x	ISDM; Kvist et al. (2001)
t4.53	<i>Lecythis pisonis</i> Camb.	x	x	0.84	x				x	ISDM
t4.54	<i>Licania apetala</i> (E. Mey.) Fritsch	x	x	0.64-0.78	x					ISDM; Kvist et al. (2001)
t4.55	<i>Licaria armeniaca</i> (Nees) Kosterm.	x	x	0.44-0.51	x				x	ISDM; Phillips et al. (1994); Kvist et al. (2001)
t4.56										
t4.57	<i>Luehea cymulosa</i> Spruce ex Benth.	x		0.38-0.48	x				x	ISDM; Worbes et al. (2001)
t4.58	<i>Maclura tinctoria</i> (L.) D. Don. ex Steud.	x	x	0.69-0.73	x				x	ISDM
t4.59	<i>Macrobolium acacifolium</i> (Benth.) Benth.	x	x	0.43-0.49	x				x	ISDM; Worbes (1997); Kvist et al. (2001); Santos et al. (2004)
t4.60										

(continued)

Table 19.4 (Continued)

Species	Occurrence		WSG (g cm ⁻³)	Use category									Source	
	LV	HV		1	2	3	4	5	6	7	8	9		
<i>Macrolebium bifolium</i> (Aubl.) Pers.	x	x	0.46	x									x	ISDM
<i>Maquira coriacea</i> (H. Karst) C.C. Berg	x	x	0.45–0.49	x	x	x	x						x	ISDM; Kvist et al. (2001), Worbes et al. (2001)
<i>Minquartia guianensis</i> Aubl.	x	x	0.76–0.88	x		x								ISDM; Silva (1977); Phillips et al. (1994); Kvist et al. (2001); Santos et al. (2004)
<i>Mouriri acutiflora</i> Naudin	x	x	0.77–0.82	x										ISDM
<i>Mouriri grandiflora</i> DC.	x	x	–	x										Kvist et al. (2001)
<i>Nectandra amazonum</i> Nees	x	x	0.38–0.47	x										ISDM
<i>Ocotea aciphylla</i> (Nees) Mez.	x	x	0.58–0.63	x										ISDM; Marques (2001)
<i>Ocotea cymbarum</i> Kunth	x	x	0.58–0.62	x	x	x	x	x	x	x			x	ISDM; Albernaz and Ayres (1999); Worbes et al. (2001)
<i>Oxandra riedeliana</i> R. E. Fries	x	x	0.47–0.51	x										ISDM; Phillips et al. (1994)
<i>Pachira insignis</i> (Sw.) Sw. ex Savigny	x	x	0.43–0.47	x									x	Phillips et al. (1994)
<i>Paramacherium ormosioides</i> (Ducke) Ducke	x	x	0.37–0.42	x							x			ISDM
<i>Parinari excelsa</i> Sabine	x	x	0.64–0.68	x	x	x	x							ISDM; Worbes et al. (2001)
<i>Piranhea trifoliata</i> Baill.	x	x	0.86–0.94	x	x	x	x							ISDM; Worbes et al. (1992)
<i>Platymiscium ulei</i> Harms	x	x	0.73–0.77	x	x	x	x	x	x					ISDM; Silva (1977); Worbes et al. (2001)
<i>Pouteria procera</i> (Mart.) T. D. Penn.	x	x	0.65–0.73	x										ISDM; Phillips et al. (1994); Kvist et al. (2001)
<i>Pseudobombax munguba</i> (Mart. & Zucc.) Dug.	x	x	0.21–0.29	x									x	ISDM
<i>Pseudoptadenia suaveolens</i> (Miq.) J.W. Gr.	x	x	0.59	x									x	ISDM; Phillips et al. (1994)
<i>Pterocarpus amazonum</i> (Mart. ex Benth.) Amsh.	x	x	0.33–0.38	x	x									Phillips et al. (1994); Santos et al. (2004)

<i>Schizolobium amazonicum</i> Huber ex Ducke	x	0.58–0.64	x	x	ISDM; Brienza-Junior et al. (1991)
<i>Sloanea terniflora</i> (Sessé & Moc.) Standl.	x	0.63–0.71	x	x	ISDM; Phillips et al. (1994)
<i>Spondias lutea</i> L.	x	0.31–0.41	x	x	Worbes et al. (2001); Santos et al. (2004)
<i>Sterculia apetala</i> (Jacq.) H. Karst	x	0.33–0.36	x	x	ISDM; Worbes et al. (2001)
<i>Tabebuia barbata</i> (E. Mey) Sandwith	x	0.65–0.79	x	x	ISDM; Albermaz and Ayres (1999)
<i>Tabebuia serratifolia</i> (Vahl) G. Nicholson	x	0.87–1.01	x	x	ISDM
<i>Terminalia dichotoma</i> G. Mey.	x	0.64–0.68	x	x	ISDM
<i>Trichilia lecointei</i> Ducke	x	0.70–0.88	x	x	ISDM
<i>Triplaris surinamensis</i> Cham.	x	0.51–0.63	x	x	Worbes et al. (2001)
<i>Unonopsis guatterioides</i> (A. DC.) R.E. Fries	x	0.42–0.48	x	x	ISDM; Worbes et al. (2001)
<i>Vatairea guianensis</i> Aubl.	x	0.70–0.75	x	x	ISDM; Worbes et al. (2001)
<i>Virola calophylla</i> (Spruce) Warb.	x	0.48–0.64	x	x	ISDM; Phillips et al. (1994)
<i>Virola surinamensis</i> (Rol. ex Rottb.) Warb.	x	0.37–0.42	x	x	ISDM; Phillips et al. (1994); Anderson et al. (1999); Worbes et al. (2001); Santos et al. (2004)
<i>Vismia baccifera</i> (L.) Triana and Planch.	x	0.54–0.60	x	x	ISDM
<i>Vitex cymosa</i> Bert. ex Spreng.	x	0.56–0.59	x	x	ISDM
<i>Vochysia guianensis</i> Aubl.	x	0.40–0.65	x	x	ISDM
<i>Xylopia calophylla</i> R.E. Fries	x	0.33–0.37	x	x	ISDM; Phillips et al. (1994)

242 cities Itacoatiara, Manaus, and Tefé. While deforestation is concentrated around
243 settlements along the main river channels, timber exploitation occurs also in more
244 isolated areas, because roundwood is transported to the sawmills by rafting during
245 high-water periods, when the cost of transport is less than that incurred by trucks
246 hauling timber from the uplands (Higuchi et al. 1994; Barros and Uhl 1999;
247 Albernaz and Ayres 1999). The overexploitation of comparatively few commer-
248 cially used tree species in some regions along the Solimões, Madeira, Purús, and
249 Japurá Rivers already has led to their substitution by alternative species on the local
250 timber markets, such as the substitution of the high-density wood species *Cedrela*
251 *odorata* and *Platymiscium ulei* by *Ocotea cymbarum*, *Calycophyllum spruceanum*,
252 and *Piranhea trifoliata*, and the substitution of the low-density wood species *Ceiba*
253 *pentandra* and *Virola* spp. by *Sterculia apetala*, *Ficus anthelmintica*, and *Couroupita*
254 *subsessilis* (Ayres 1993; Worbes et al. 2001; Schöngart 2003).

255 Specific information about the uses of timber species by floodplain inhabitants
256 is scarce, but several authors reported that the most important use of floodplain
257 timber is house and boat construction (Phillips et al. 1994; Kvist et al. 2001; Luna
258 2004). Using literature data describing the mechanical characteristics of wood,
259 Worbes et al. (2001) and Schöngart (2003) investigated the actual and potential use
260 of timber trees originating from Amazonian floodplains. The investigation about
261 the use of 186 common central Amazonian várzea tree species indicate that less tree
262 species are used for timber (78 species, 41.9%) than for NTFPs (Table 19.2, but
263 note that the large majority of timber species also provide NTFPs). We separated
264 the fate of timber into nine categories with respect to its use: home construction,
265 heavy construction and sleepers, boat and canoe construction (including round-
266 wood for houseboats), carpentry, furniture, flooring and panels, plywood, tools
267 (e.g., instrument shafts), and fences (Table 19.2). The results showed that most
268 timber trees are used for multiple purposes (Table 19.4). Quantitatively, the cate-
269 gory containing the most species was house construction (63 species), followed by
270 carpentry (22 species), furniture (21 species), and boat, houseboat, and canoe con-
271 struction (20 species, e.g., *Apeiba glabra*, *Buchenavia oxycarpa*, and *Hura crepi-*
272 *tans*). Eighteen tree species are commercially harvested for plywood (among the
273 most important: *Hura crepitans*, *Ceiba pentandra*, *Ocotea cymbarum*, *Couroupita*
274 *subsessilis*, *Schizolobium amazonicum*, *Sterculia apetala*, and *Maquira coriacea*,
275 Table 19.4), some of them representing species with no or only little commercial
276 values for local inhabitants. Such species include *Ficus anthelmintica* and
277 *Pseudopiptadenia suaveolens* (but note that the former provides NTFPs, Table 19.3).

278 During the last several years, the price of central Amazonian várzea timber has
279 consistently increased, from US\$7.90–11.40 m⁻³ (low-density wood) and US\$15.20 m⁻³
280 (high-density wood) in the year 2003 to approximately US\$17.50 m⁻³ and 31.00 m⁻³
281 in the year 2007 (Forest Management Programme Mamirauá, Schöngart et al. this
282 volume). Based on the normative regulations established by the IBAMA (mini-
283 mum logging diameter of 45 cm, cutting cycle of 25 years, and a maximum yield
284 of 5 trees ha⁻¹), the NPV from selectively logged várzea timber thus actually ranges
285 between US\$13.80 and 51.36 ha⁻¹ year⁻¹. Unfortunately, we have no comparable
286 data for the NPV of NTFPs.

19.4 Conclusions

287

The multiple options for the use of Amazonian floodplain trees demonstrate that these forests are not only an important source of natural resources and income for the overwhelming part of the Amazonian population, but they already represent useful resources for the human population as a whole. Of particular interest is the rapidly increasing knowledge on the phytomedical potential of tropical tree species and it is certain that still-unknown resources will contribute to the treatment of many human diseases. There exists, however, a gap in ethnobotanical inventories, especially in the Brazilian Amazon, where the largest part of the Amazonian floodplain forests is located. Filling in these gaps would provide crucial support for conservation planning and the need for sustainable management programs within the Brazilian Amazon.

While the NPV of timber depends on the regional, national, and international timber markets, and thus can easily be quantified, much remains to be learned about the economic value of NTFPs. The value of some NTFPs to the local inhabitants may be indirect and thus difficult to measure, as is the case for non-edible fruits used as fish bait, or for resins used as hunting poisons. Additionally, the NPVs of phytomedical and phytocosmetical products are mostly unknown and/or undervalued by extractors, thus depriving inhabitants of a fair economic return.

Although there are some promising pilot projects that involve local communities in the extraction of oils and resins for the manufacture of biofuel, fragrances, and phytocosmetics within the Brazilian Amazon (i.e., projects within the framework of the internationally founded program Provárzea/IBAMA), the importance of NTFPs from Amazonian floodplains is still under-represented in sustainable forest management planning. Moreover, the inclusion of such products in these plans may be accompanied by conflicts of interest because logging alters the physical components of primary forests (forest structure and species composition) (Shanley et al. 2002; Menton 2003), and many of the logged timber species provide NTFPs. We are of the opinion, however, that these conflicts can be minimized when forest management is based on scientific data and reliable cost-benefit analyses. Communally sustainable forest management that includes both logging and NTFPs could maximize the economic profit available to the floodplain inhabitants, thereby contributing to the conservation of floodplain forests and their ecologic integrity.

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Abstract	<p>The science inspired awareness of the need to preserve and conserve tropical forests within the framework of protection of local and regional habitat and climate, plant and animal species and biodiversity, genetic resources and local livelihood gradually evolved over the past centuries until the issue has become one of the most important ecological and social challenges of our times. For centuries, the Amazonian floodplains have been used and settled by a human population of high density that carried out agriculture, pasture, fishing and hunting, as well as the extraction of timber, wood and non-wood forest products (NWFPs). Consequently, floodplain forests are one of the most stressed and threatened forest ecosystems in the Amazon. They are endangered by their conversion to agriculture and pasture as well by commercial exploitation by an expanding timber and plywood industry (Higuchi et al. 1994; Uhl et al. 1998).</p>	

Chapter 20 1
Traditional Timber Harvesting in the Central 2
Amazonian Floodplains 3

Jochen Schöngart, Rosanademiranda Rocha, and Helder L. Queiroz 4

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20.1 Introduction 5

The science inspired awareness of the need to preserve and conserve tropical forests within the framework of protection of local and regional habitat and climate, plant and animal species and biodiversity, genetic resources and local livelihood gradually evolved over the past centuries until the issue has become one of the most important ecological and social challenges of our times. For centuries, the Amazonian floodplains have been used and settled by a human population of high density that carried out agriculture, pasture, fishing and hunting, as well as the extraction of timber, wood and non-wood forest products (NWFPs). Consequently, floodplain forests are one of the most stressed and threatened forest ecosystems in the Amazon. They are endangered by their conversion to agriculture and pasture as well by commercial exploitation by an expanding timber and plywood industry (Higuchi et al. 1994; Uhl et al. 1998).

These unique forest ecosystems sustain manifold ecological processes, functions and services of importance to people, such as regulating parts of the hydrological

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20 cycle and reducing the energy of water and erosion. Moreover, floodplain forests
21 are habitats for highly adapted plant and animal species, many of them endemic to
22 the várzea. They also represent important sinks and sources for biogeochemical
23 cycles (Piedade et al. 2001; Schöngart et al. this volume b) and are an important
24 food source for many fish species, which in turn are the primary protein base for
25 the local human population (Junk et al. 1997, 2007). In this context, sustainable
26 management of tropical forests offers promise to safeguard the socio-ecologically
27 important multiple functions and services of forest ecosystems and to guarantee the
28 use of natural resources for the growing population in Amazonia. In this chapter the
29 traditional timber extraction in the Amazonian várzea and the socio-economic
30 improvements it provides to the local population are described and discussed as an
31 example of community forest management as practiced in the Mamirauá Sustainable
32 Development Reserve (MSDR) (Queiroz and Peralta this volume).

33 20.2 Traditional Commercial Timber Harvesting 34 in Amazonian Floodplain Forests

35 Parallel to the decline of timber stocks in Southeast Asia and within Brazil's south-
36 ern region and coastal rainforests (*Mata Atlântica*), the Amazon basin with its
37 immense forest resources has acquired increasing importance as source of tropical
38 timber (Veríssimo et al. 1992). Prior to the 1980s, almost all logging was in the form
39 of "river scratching" in floodplain forests adjacent to the major rivers, mainly in
40 eastern Amazonia. The rivers served as easy access for the loggers and transport
41 route for timber for more than three centuries (Anderson et al. 1999; Fortini et al. [AU1]
42 2006). Many tree species from floodplain forests were and still are utilized for non-
43 timber products, such as resins, oils, palm hearts, edible fruits, textile fibres, tannins,
44 kapok, and medicinal purposes (Kvist et al. 2001; Wittmann and Oliveira Wittmann
45 this volume). With the beginning of the rubber boom, in the mid-nineteenth cen-
46 tury, logging increased in floodplain forests. Extracted fuelwood provided an energy
47 supply both for steamboats and for the vulcanization of latex (*Hevea brasiliensis*),
48 thereby sustaining the growing population of Manaus (Ohly 2000b; Parolin 2000). [AU2]

49 With the opening up of the Amazon basin following the construction of a road
50 network from central Brazil into the Amazon basin, projects that were initiated at
51 the end of the 1960s (Kohlhepp 1989), recorded roundwood production in Amazonia
52 increased from 4 million cubic meters in 1975 (Carvalho 1998) to 27.5 million
53 cubic meters in 1997 (Nepstad et al. 1999) and was 26.6–49.8 million cubic meters
54 year⁻¹ during the period 2000–2002 (Asner et al. 2005), mainly occurring in non-
55 flooded upland forests (terra firme). Today centres of logging are situated at the
56 expanding frontiers of the "arch of deforestation", comprising the states of Pará,
57 Mato Grosso, Rondônia and Acre (Nepstad et al. 1999). Together they account for
58 more than 75% of the total deforestation taking place in the Brazilian Amazon
59 (*Amazônia Legal*) with about 5 million square kilometers (INPE 2006).

60 In the western Amazon basin of Brazil and Peru, access to terra firme forests is
61 restricted due to the absence of a road network. Still, 60–90% of the local and

regional markets are provided with timber obtained from the floodplain forests (Kvist and Nebel 2001; Worbes et al. 2001). Lima et al. (2005) reported that, in the year 2000, 74.6% of the timber for the plywood and veneer industries in the Amazon state originated from the várzea. Deforestation in the Amazonas state remains relatively low (less than 3%, INPE 2006), but is concentrated along the river margins. About 33.8% of the total deforestation in Amazonas state occurs in the floodplains, with increasing deforestation rates reported from 1997 to 2004 (Affonso et al. 2007).

20.2.1 Timber Species

About 350 tree species in the Amazon basin are currently used for timber production (Martini et al. 1998); of these timber species, 34% also occur in the várzea. They can be classified as low-density tree species (*madeira branca*), which float due to their relatively low wood density ($<0.60 \text{ g cmP}^{-3\text{P}}$), and high-density tree species (*madeira pesada*), with wood densities above $0.60 \text{ g cmP}^{-3\text{P}}$ (Schöngart 2003). The latter group is mainly used for house, ship and boat construction as well as furniture, while low-density woods are mainly processed as plywood and veneers (Albernaz and Ayres 1999; Kvist et al. 2001; Worbes et al. 2001; Wittmann and Oliveira Wittmann this volume). Most commercial tree species occur in high-várzea forests (Worbes et al. 2001), flooded to a height of less than 3 m above forest floor per year and covering only 8–10% of the Central Amazonian várzea (Wittmann et al. 2002b). Many timber species in the várzea forests occur in high tree densities, because the species richness of trees in várzea floodplain forests is much lower than in adjacent terra firme forests (Nebel et al. 2001d; Wittmann et al. 2006a, Wittmann et al. this volume). Forest inventories in várzeas along the lower Solimões and the upper and lower Juruá, Madeira, and Purus Rivers (Bruce 2001) recorded between 9.1 and 12.4 trees $\text{haP}^{-1\text{P}}$ above the diameter cutting limit (DCL) of 45 cm (Table 20.1). Similarly, in várzea forests along the middle Solimões River (MSDR), Brampton (2001) found 12.2 trees $\text{haP}^{-1\text{P}}$ above the DCL of 45 cm at forest inventories of more than 342 ha (Fig. 20.1). In the tidal várzea, Fortini et al. (2006) reported 51–104 individuals $\text{haP}^{-1\text{P}}$ of commercial tree species with diameters above 30 cm. Among the most abundant low-density timber species in the Brazilian várzea are *Hura crepitans*, *Couroupita subsessilis*, *Maquira coriacea*, and *Virola* spp. The most abundant high-density timbers are *Manilkara* sp., *Pouteria* spp., *Calycophyllum spruceanum*, *Ocotea cymbarum*, and *Piranhea trifoliata*. In forest inventories of Peruvian várzeas, Nebel et al. (2001e) determined 44–89 trees $\text{haP}^{-1\text{P}}$ of timber species ($>10 \text{ cm}$), with a basal area of $2.6\text{--}10.0 \text{ mP}^{2\text{P}}$ $\text{haP}^{-1\text{P}}$ and a volume of $59\text{--}240 \text{ mP}^{3\text{P}}$ $\text{haP}^{-1\text{P}}$. In young successional stages of várzea forests in the MSDR 14–103 trees passed over the DCL of 45 cm comprising commercial stem volumes of up to $191 \text{ mP}^3 \text{ haP}^{-1}$ (Schöngart 2003). These large stockings of commercial timbers on easily accessible terrain make várzea forests attractive for commercial timber extraction.

Commercial exploitations in the várzea of the central and western Amazon basin are concentrated on only a few timber species, mostly low-density species for the

t1.1 **Table 20.1** Density (trees haP^{-1P}) of timber species (diameter at breast height >45 cm) in 27 forest
t1.2 inventories in the state of Amazonas (Bruce 2001)

t1.3		Middle	Upper	Middle		
t1.4	Timber species with diameter	Solimões	Juruá	Juruá	Madeira	Purus
t1.5	>45 cm	River	River	River	River	River
t1.6	Forest inventory (ha)	6	8	5	6	2
t1.7	High-density tree species					
t1.8	<i>Manilkara</i> spp.	0.9	2.4	1.2	0.6	2.0
t1.9	<i>Pouteria</i> sp.	1.6	2.3	1.5	0.7	1.4
t1.10	<i>Calycophyllum spruceanum</i>	1.8	1.3	0.6	1.4	0.2
t1.11	<i>Calophyllum brasiliense</i>	0.6	0.1	0.2		
t1.12	<i>Copaifera</i> sp.	0.3	0.1	0.6		0.4
t1.13	<i>Piranhea trifoliata</i>	0.5			0.8	1.3
t1.14	<i>Vatairea guianensis</i>	0.6			0.7	0.4
t1.15	<i>Carapa guianensis</i>		0.1	0.4		0.2
t1.16	<i>Guarea</i> sp.	0.7				
t1.17	<i>Ocotea cymbarum</i>			0.1		
t1.18	Subtotal	7.0	6.3	4.6	4.2	5.9
t1.19		(57%)	(51%)	(43%)	(46%)	(58%)
t1.20	Low-density tree species					
t1.21	<i>Hura crepitans</i>	2.0	1.6	2.3	0.8	1.5
t1.22	<i>Virola</i> sp.	0.9	1.7	1.3	1.7	0.8
t1.23	<i>Maquira coriacea</i>	2.1		0.9	1.0	1.0
t1.24	<i>Ceiba pentandra</i>	0.2	1.0	0.5	0.3	0.6
t1.25	<i>Ficus insipida</i>		0.8	0.2	0.7	0.2
t1.26	<i>Macrolobium acaciifolium</i>		1.0	0.2		0.2
t1.27	<i>Couroupita subsessilis</i>			0.7		
t1.28	<i>Sterculia elata</i>				0.4	
t1.29	Subtotal	5.2	5.1	6.1	4.9	4.3
		(43%)	(49%)	(57%)	(54%)	(42%)
t1.30	Total	12.2	12.4	10.7	9.1	10.2

104 plywood and veneer industries (Lima et al. 2005). The low-density species
105 *H. crepitans*, *M. coriacea*, *C. pentandra*, and *Virola* spp. together with the high-
106 density species *Manilkara* sp., *C. odorata*, *O. cymbarum*, *C. spruceanum*,
107 *Calophyllum brasiliense*, and *Copaifera* sp. comprise 70–90% of the total timber
108 exploitation (Table 20.2). These intensive exploitations of a few tree species, car-
109 ried out without knowledge of their growth rates, population structures, and regen-
110 eration processes, have locally exhausted merchantable stocks and caused the
111 disappearance of some timber species from local and regional markets within only
112 a few decades (Ayres 1993; Higuchi et al. 1994; Worbes et al. 2001; Lima et al.
113 2005). Many of these unsustainable timber extractions include also trees with diam-
114 eters below the 45 cm DCL (Albernaz and Ayres 1999; Anderson et al. 1999),
115 which accelerates the degradation of species population structure. Macedo and
116 Anderson (1993) report wood extraction of 145 m³ haP^{-1P} of *Virola surinamensis* in
117 inundation forests of the Preto River at the Marajó Island representing 90% of the
118 original *Virola*-population and 56% of the entire floodplain forest growing stock.

[AU3]

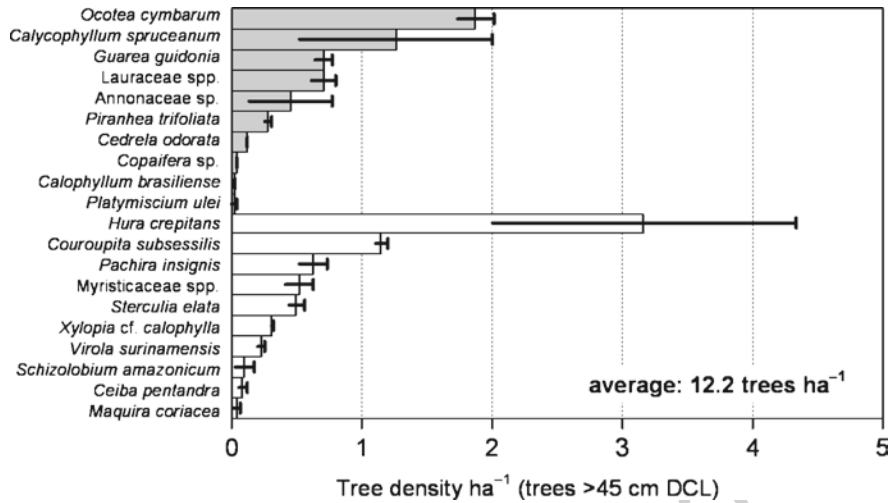


Fig. 20.1 Tree density of high-density (grey bars) and low-density (white bars) tree species above the diameter cutting limit (DCL) of 45 cm in várzea forests of the Mamirauá Sustainable Development Reserve (MSDR) (mean and standard deviation of two inventories with a total area of 342.9 ha) (Data: Brampton 2001)

The high-density timber species *C. odorata* and *Platymiscium ulei* have been heavily exploited during the 1970s at the middle Solimões River (Ayres 1993) and meanwhile replaced in the markets by *O. cymbarum*, *C. spruceanum* and *P. trifoliata* (Brampton 2001). Within three decades the timber growing stocks of the low-density species *C. pentandra* and *V. surinamensis* decreased dramatically in the várzeas of the Amazonas state causing their substitution by species with similar wood characteristics such as *H. crepitans*, *M. coriacea*, *C. subsessilis* and *Sterculia elata* (Ayres 1993; Albernaz and Ayres 1999; Worbes et al. 2001; Lima et al. 2005) (Fig. 20.2).

20.2.2 Logging, Skidding, and Transport

Logging in the floodplain forests generally starts with increasing water level at the end of the terrestrial phase but is sometimes also carried out when the forests are already flooded (Fig. 20.3) (Albernaz and Ayres 1999). Logs only can be removed from the forest if water floods the harvested area. Sinkable high-density woods, such as *C. spruceanum* and *P. trifoliata*, are tied together with floats (*boiás*) for skidding and transport. The floats are trunks of species with low wood densities, such as *H. crepitans*, *Apeiba* spp., *Sapium hippomane*, *Luehea cymulosa*, *Hevea spruceana*, and *Pseudobombax munguba*. The logs are skidded out of the forests, drifted to assembly points, usually lakes, and tied together in large log rafts with up

Table 2.0.2 Timber exploitation in the western Amazon basin (Brazil, Peru) (Schöngart 2003)

t2.1	Source	Gethal S.A. (unpublished)	Albermaz and Ayres (1999)	Kvist and Nebel (2001)	Ucayali (Peru)
t2.2	Location	Madeira, Jurua, Purus Rivers	MMSDR Japurá/Solimões Rivers	Loreto (Peru)	
t2.3	Year	1990s	1993/1994	1996	1996
t2.4	Category	Roundwood ^{IP}	Roundwood ^{IP}	Roundwood	Lumber
t2.5	Unit	Volume	Logs	Volume	Volume
t2.6	High-density tree species	mP ^{IP} yearP ^{-IP} (%)	mP ^{IP} yearP ^{-IP} (%)	mP ^{IP} yearP ^{-IP} (%)	mP ^{IP} yearP ^{-IP} (%)
t2.7	Manilkara sp.	12.9	86	27,154	25,670
t2.8	Cedrela odorata	0.3	589	8,295 ^{EP}	19,686 ^{EP}
t2.9	Ocotea cymbarum	4.8	61	28,482	47,966
t2.10	Copaifera spp.	28.1	1,259		
t2.11	Sum				
t2.12	Low-density tree species				
t2.13	Hura crepitans	18.5	1,765	3,191	26,719
t2.14	Maquira coriacea	11.7	274	5,031	
t2.15	Ceiba pentandra	8.1	469	60,323	3,426
t2.16	Virola spp.	2.9	872	27,884	17,247
t2.17	Sum	41.0	3,380	96,429	47,392
t2.18	Other timber species	30.9	539	36,392	28,089
t2.19	Total	100	5,178	173,183	123,447

P^{IP}Sum of four concessions (Manicoré, Humaitá, Itamarati und Lábrea)

t2.23 P^{IP}Average of the exploitations in the years 1993 and 1994

t2.24 P^{IP}Copaifera paupera (Herzog) Dwyer

t2.25



Fig. 20.2 The low-density timber species *Ceiba pentandra* (left) has been heavily exploited since the 1980s and has been almost substituted by *Sterculia elata* (right) and other low-density tree species of the Amazonian várzea forests (Photos: Jochen Schöngart)



Fig. 20.3 Logging, skidding and transport in the várzea forests. (a) Trees are harvested at the end of the terrestrial phase or (b) when the forests are already flooded. (c) Skidding only can be performed during the aquatic phase. Logs of sinkable high-density trees must be tied between floats of low-density trees (*boiá*) for skidding. (d) Logs are concentrated in lakes or channels and bound together for their transport to sawmills and plywood factories (Photos: PMFC/Mamirauá Institute for Sustainable Development, IDSMD)

138 to several thousand cubic meters and sold to sawmills and plywood factories
139 (Higuchi et al. 1994; Albernaz and Ayres 1999).

140 Costs for logging are lower in the floodplain forests (US\$6.73 mP^{-3P}) as in the
141 non-flooded terra firme forests (US\$14.32 mP^{-3P}) due to the easier access and lower
142 energy costs (Barros and Uhl 1997). Costs for transport on a distance of 100 km
143 amount to US\$0.90 mP^{-3P} for the river by rafts and US\$30.00 mP^{-3P} by track on the
144 road (Barros and Uhl 1999). The low costs for logging, skidding and transport in
145 the floodplains enables logging in forests which are hundreds of kilometres away
146 from sawmills and plywood factories. Plywood industries in Manaus and Itacoatiara
147 already have concessions along the Madeira, Purus, Juruá and upper Solimões
148 Rivers (Worbes et al. 2001). On terra firme the costs for transport by timber lorries
149 on roads is higher and will continue to increase, as the distances increase by moving
150 the exploitation frontier (Nepstad et al. 1999). Thus, in the future increasing pres-
151 sure may be expected for the floodplain forests, especially in the western Amazon
152 basin (Barros and Uhl 1997; Uhl et al. 1998).

153 Wastage and losses during logging, skidding, and transport in tropical forests
154 are normally high and can reach up to, or exceed 50% of the total merchantable
155 volume actually cut (Bruenig 1998; Sist et al. 1998). Johns et al. (1996) docu-
156 mented in the terra firme of eastern Amazonia that for every felled tree another 16
157 individuals with diameters >10 cm are damaged. Veríssimo et al. (1992, 1995)
158 reported an even higher number, 27–31 damaged trees (diameter >10 cm) for every
159 harvested tree by logging 6.4 trees haP^{-1P} on average. For floodplain forests,
160 although no information is available, the damages may well be of the same order of
161 magnitude, since yields of 36–78 mP^{3P} haP^{-1P} (Worbes et al. 2001) are in the same
162 range as those in the terra firme of central Amazonia (35–84 mP^{3P} haP^{-1P}, Worbes
163 et al. 2001) and eastern Amazonia (18–62 mP^{3P} haP^{-1P}, Veríssimo et al. 1992).
164 Another problem, which is specific to the floodplain forests, is the skidding of the
165 logs, which can only be done after sufficient flooding. If this is not the case, the
166 losses of logged timber are high because low-density wood starts to rot and is
167 attacked by pathogens (insects, fungi) (Martius 1989) until flooding finally reaches
168 the harvested area (Albernaz and Ayres 1999). However, the damage to regenerating
169 and remaining trees by water-borne skidding in floodplain forests might be lower
170 than that caused by mechanical skidding with heavy machinery in terra firme forests
171 (Fortini et al. 2006).

172 20.2.3 Marketing and Wood Prices

173 The traditional marketing of timber in the floodplain forests is practiced in various
174 ways (Albernaz and Ayres 1999). Traders (*padrão*) often operate as middle man
175 in the area where they customarily trade, often barter, with local riparian commu-
176 nities for natural products, buying at low prices against selling at high prices. This
177 form of trading is common for local populations living far away from regional
178 markets. In other cases, the local people receive an advance in form of food, daily

necessities and equipment to extract forest products, which is later, cleared against the lowly fixed value of the NWFP and timber (*aviamento*) (Hummel 1994; Queiroz and Peralta this volume). In some cases, local people even lease their areas to outsiders for a rental, a share in the extracted logs, plus goods and/or services. Rarely will sawmill and veneer and plywood factory owners visit the floodplain areas to buy logs directly from local communities. The majority of these timber extractions and sales are not authorized by environmental agencies such as IBAMA (Brazilian Institute of Environment and Renewable Natural Resources) and IPAAM (Institute of Environmental Protection of the Amazonas State). There is a risk of fines or embargoes or need for preventive action which subdues the log prices offered and paid to the local inhabitants by the middle men (Albernaz and Ayres 1999).

Generally, high-density timber commands higher roundwood prices than low-density timbers (Albernaz and Ayres 1996; Brampton 2001). Higuchi et al. (1994) reported a price of US\$10.00 mP^{-3P} for *H. crepitans*, US\$20.00 mP^{-3P} for *M. coriacea*, and US\$35.00 mP^{-3P} for *C. pentandra* in 1993 at sawmills and plywood factories. Bentes-Gama et al. (2002) indicated timber prices in the várzea of the Amazonian estuary of R\$30.00 (US\$ 16.39) per log for *V. surinamensis* and *C. subsessilis*, R\$32.00 (US\$ 17.49) per log for *Hymenea oblongifolia* and R\$40.00 (US\$21.86) per log for *C. odorata* in 2000 (US\$1.00 = R\$1.83).

20.3 Community Forest Management in the Mamirauá Reserve

Customary timber and NWFP harvesting by native communities under Native Customary Law of forest usufruct has over millennia be on a whole sustainable. Commercial timber and NWFP in the Amazonian várzea has long and traditionally been unsustainable, mostly illegal, and predatory (Ayres 1993; Higuchi et al. 1994; Hummel 1994; Albernaz and Ayres 1999; Anderson et al. 1999). The increasing timber extraction in várzea forests and the competition between forest management and other land-use options (agriculture, pasture, settlement) thus requires strategies to guarantee the long-term conservation of várzea floodplain forests as an ecological and economic resource.

In this context, participative community forest management and forest management of small private properties (up to 500 ha) have gained increasing acceptance in recent years (Amaral and Amaral Neto 2005). These types of forest-management strategies have been implemented within the framework of large development programs, such as PPG7-Projects Pro-Manejo and Pro-Várzea, executed by IBAMA, and projects of other national and international governmental institutions and NGOs. In the state of Amazonas exists more than 450 operational forest management plans for the sustainable management of small-scale private properties and community forests, mainly in várzea floodplains along the Solimões, Amazonas, Juruá, and Madeira Rivers (IEB 2007).

220 Similar concepts of participatory communal forest management in várzea
221 floodplains are also pursued in the MSDR at the confluence of the Solimões and
222 the Japurá Rivers, approximately 70 km northwest of the city of Tefé, in the Central
223 Amazon (Queiroz and Peralta, this volume). The MSDR comprises 11,240 km² of
224 várzea floodplains. The reserve was the first conservation unit in the Brazilian
225 várzea, established in 1990 as an Amazonas State Ecological Station and trans-
226 formed into a Sustainable Development Reserve in 1996 by the State's Governor as
227 a new category of conservation unit in Brazil (Queiroz and Peralta this volume).
228 Together with the Amanã Sustainable Development Reserve, Jaú National Park,
229 and the Anavilhanas Biological Reserve, the MSDR forms the "Central Amazon
230 Conservation Complex" with a total area of about 6 million hectares. This region
231 was declared a world natural heritage site by UNSECO in the year 2000 and recog-
232 nition was extended in 2003 (Ayres et al. 2005). Since 1992, numerous community-
233 based management projects have been initiated in the focal area of the MSDR
234 (2,600 km²) based on socio-economic and biological-ecological studies of fishery,
235 agriculture, agro-forestry, eco-tourism, and forestry (Sociedade Civil Mamiarauá
236 1996; Ayres et al. 1998; Queiroz and Peralta this volume).

237 The community forest management program *Manejo Florestal Comunitário*
238 (MFC) was established in 1998 and operated the first time in 2000. Since then, more
239 than 30 cooperatives (*associação comunitária*) set up to perform controlled timber
240 extractions have been founded within the focal area of the MSDR. Timber harvesting
241 permission requires a management plan (Forest Code No. 4.711, 15 September
242 1965) authorized by environmental agencies (Schöngart 2003) and based on a forest
243 inventory, which considers in the MSDR all trees of timber species >20 cm diameter
244 in the areas selected for harvest. The maximum area allocated for sustainable timber
245 and wood harvesting is 500 ha per cooperative. Within this area, a polycyclic
246 harvesting system (Lamprecht 1989; Dawkins and Philip 1998; Whitmore 1993) in
247 the sense of a Selection Silvicultural Management System (Wyatt-Smith 1995;
248 Bruenig 1998), adapted from the CELOS system in Surinam (de Graaf et al. 2003),
249 is permitted. The aim is to keep an all-ages stand through selective tree cuttings at
250 shorter intervals (felling cycle) and by establishing a DCL. The felling cycle defines
251 the interval in years between successive timber harvests in the same coupe area. Due
252 to the harvest of only a few selected trees above the established DCL, the uneven-age
253 structure of the forest is maintained by the establishment of seedlings on the ground
254 in small gaps and saplings in the understorey. To achieve a more or less constant
255 annual harvest, the total area for forest management is divided into several blocks of
256 similar size and growing stock quality corresponding to the number of years of the
257 felling cycle. Thus far, forest management in the MSDR applies a DCL of 45 cm, a
258 felling cycle of 25 years, and a maximum yield of 5 trees ha⁻¹p⁻¹, including floats.
259 Furthermore, 10% of the emerging A-storey trees (Richards 1996) of commercial
260 species, as a rule above the DCL, must remain in the forest to improve the chances
261 for regeneration of timber species (Pires 2004).

262 The management rules and principles are based on laws and normative instructions
263 (IN) established by the IBAMA (Schöngart 2003; Schöngart et al. 2007) but also
264 on decisions made by the local people involved (Sociedade Civil Mamiarauá 1996;

Queiroz and Peralta this volume). Timber species potentially or actually threatened 265
 by extinction, such as *C. brasiliense*, *C. odorata*, *C. pentandra*, *P. ulei*, *V. surinamensis*, 266
 and *Xylopia frutescens*, are excluded from the list of commercial species and totally 267
 protected (Worbes et al. 2001). The recently established IN no°5, from 11 December 268
 2006 (IBAMA), enables modified management options. Felling cycles are 25–35 269
 years and periodic yields limited to 30 m³ haP⁻¹P (full yield modality) or alternatively 270
 10 m³ haP⁻¹P every 10 years (low yield modality). In várzea forests yields can 271
 exceed 10 m³ haP⁻¹P yearP⁻¹P, but must be restricted to three harvested trees haP⁻¹P. 272
 The establishment of species-specific DCLs that take into account ecological and 273
 technical criteria has also been mandated. If this information is not available for a 274
 commercial timber species, a common DCL of 50 cm is applied. 275

Economic activities in the várzea, such as agriculture, fishery, and timber extrac- 276
 tion, and consequently the income they, are synchronically associated with water- 277
 level fluctuations. Fishing is possible during low-water levels, when fish stocks are 278
 concentrated in the remaining water bodies (Fig. 20.4). Agriculture is practiced 279
 during the terrestrial phase on higher elevations, where flooding is shortened and 280
 crops have enough time to mature and ripen (Junk et al. this volume a). Forestry 281
 activities are mainly restricted to the aquatic phase, when the forests can easily be 282
 accessed and transport costs are low (Barros and Uhl 1995; Albernaz and Ayres 283
 1999). In the MSDR, 70% of the annual income is derived from fishery, about 20% 284
 from agriculture (mainly cassava), and only 5% from timber extraction (Sociedade 285
 Civil Mamirauá 1996). For domestic households, this leads to high incomes during 286
 the terrestrial phase and low incomes during the flooded period (Fig. 20.4). 287

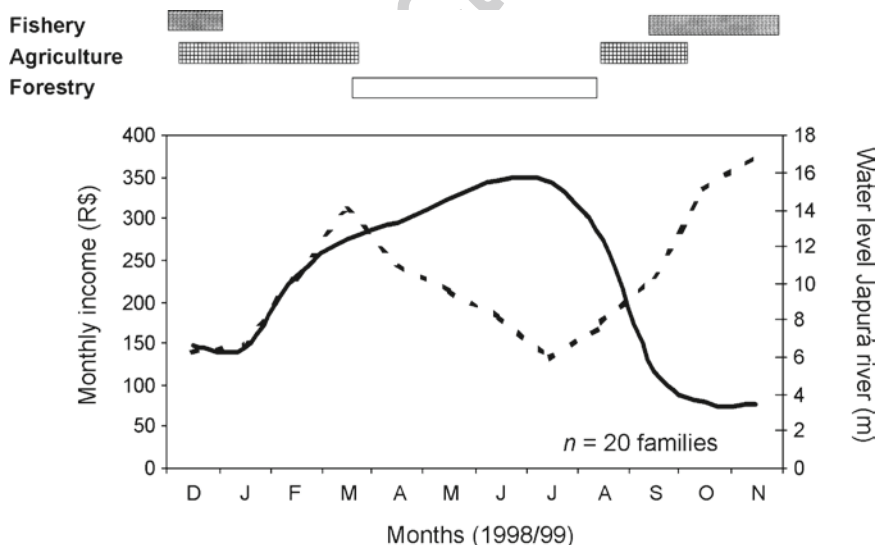


Fig. 20.4 Performance of economic activities in the várzea and average monthly income (dotted line) of 20 households in the MSDR in relation to water-level fluctuations of the Japurá River (black line) (Data: Sociedade Civil Mamirauá 1996; Albernaz and Ayres 1999; Mamirauá Institute for Sustainable Development IDSM)

288 In spite of the small financial share in household income, the controlled
 289 community-based forest management is making a welcome contribution to the
 290 meagre budgets of households in the Amazonian várzea, especially when the
 291 monthly income is seasonally very low (Queiroz and Peralta this volume). As timber
 292 harvesting and selling is authorized by environmental agencies the wood and timber
 293 prices (per meter cube) are several times higher than those obtained in unauthorized,
 294 illegal operations (Table 20.3). Roundwood prices are given in Brazilian Reais (R\$)

t3.1 **Table 20.3** Wood prices (roundwood) paid for illegal forest exploitation in 1994 and legal wood
 t3.2 extraction in 2004 in the várzea of the Solimões River (Data: Albernaz and Ayres 1996; Mamirauá
 t3.3 Institute for Sustainable Development, IDS/MFC; Secretary for Environment and Sustainable
 t3.4 Development of the Amazonas State, SDS/AM). Roundwood prices are indicated in Brazilian
 t3.5 Reais (R\$) due to the strong variation in the exchange rate with US Dollars (US\$)

t3.6 (R\$ mP ^{-3P})	Middle Solimões (MSDR)	Middle Solimões (MSDR)	Upper Solimões
t3.7 Period/year	1994	2004	
t3.8	Illegal	Legal	
t3.9 <i>Low-density tree species</i>	exploitation	management	
t3.10 Assacú (<i>Hura crepitans</i>)	1.45–5.00 ^{aP} 0.75–2.50 ^b	28.00	40.00
t3.11 Muiratinga (<i>Maquira coriacea</i>)	3.30–10.30 ^{aP} 1.75–5.15 ^{bP}	36.00	80.00
t3.12 Sumaúma (<i>Ceiba pentandra</i>)	3.30–10.30 ^{aP} 1.75–5.15 ^{bP}		50.00
t3.13 Macacarecuia (<i>Couroupita</i> t3.14 <i>subsessilis</i>)	1.20–3.00 ^{aP} 2.40–6.00 ^{bP}	28.00	
t3.15 Abiorana (<i>Pouteria</i> sp.), Arapari t3.16 (<i>Macrolobium acaciifolium</i>), t3.17 Faveira (<i>Vatairea guianensis</i>), t3.18 Tacacazeiro (<i>Sterculia elata</i>), t3.19 Ucuúba (<i>Virola</i> spp.), Paricarana t3.20 (<i>Schizolobium amazonicum</i>)		36.00	
t3.21 Caxinguba (<i>Ficus insipida</i>)		32.00	
t3.22 <i>High-density tree species</i>			
t3.23 Cedro (<i>Cedrela odorata</i>)			120.00
t3.24 Jacareúba (<i>Calophyllum brasiliense</i>)	4.23 ^b –8.45 ^{aP}		80.00
t3.25 Coração de negro (<i>Swartzia</i> sp.), t3.26 Gitó (<i>Guarea guidonia</i>), Louro t3.27 abacate (<i>Aniba guianensis</i>), Louro t3.28 amarelo (<i>Aniba riparia</i>), Louro t3.29 inamuí (<i>Ocotea cymbarum</i>), Louro t3.30 preto (<i>Licaria</i> sp.), Mulateiro t3.31 (<i>Calycophyllum spruceanum</i>), t3.32 Piranheira (<i>Piranhea trifoliata</i>), t3.33 Tanimbuca (<i>Terminalia dichotoma</i>)	4.23 ^{bP} –8.45 ^{aP}	48.00	

t3.39 ^aDiameter <50 cm

t3.40 ^bDiameter >50 cm (diameter measured at the smaller end of the log)

because of the presently very strong fluctuation of the US\$ exchange rate. In 2004 (US\$1.00 = R\$2.93), low-density woods were sold at the middle Solimões River (MSDR) for R\$28.00–36.00 mP^{-3P} (US\$9.55–12.28), at the upper Solimões River the wood prices are even higher, between R\$40.00 and 80.00 (US\$13.65–27.30) mP^{-3P}. From 1993 to 2007, wood prices of low-and high-density woods from the MSDR have increased ten to fifteen times (Fig. 20.5). In 2007, the price of sawn wood was even higher, between R\$130.00 (US\$ 61.91) mP^{-3P} for low-density timber and R\$170.00 (US\$80.95) mP^{-3P} for high-density timber, (US\$1.00 = R\$ 2.10) (data: Mamirauá Institute for Sustainable Development, IDSMM/MFC).

The annual income of a cooperative in the MSDR was calculated from data of three cooperative logging projects on kinds of timber species, number of logs, log volumes, and timber or wood prices (Tables 20.4–20.6). The income varied considerably between the three projects, from R\$ 27.75 (US\$ 13.21) haP^{-1P} to R\$ 102.72 (US\$ 48.91) haP^{-1P}. Causes are differences in the percentages of low-density and high-density woods. A larger proportion of low-density timber species results in higher incomes despite the lower prices per meter cube of low-density timbers, but their trunk and log dimensions are much larger than in high-density timber species. The annual income from a forest management area of 500 ha with a felling cycle of 25 years is then between R\$13.88(US\$6.61) and R\$51.36(US\$ 24.46) haP^{-1P} yearP^{-1P} or periodically between R\$277.60(US\$ 132.20) and R\$1,027.20(US\$489.14). In comparison, the total annual average income per family in the cooperative for the period 2000–2003 was R\$307.76–1,049.94 (US\$130.96–495.83) (Pires 2004).

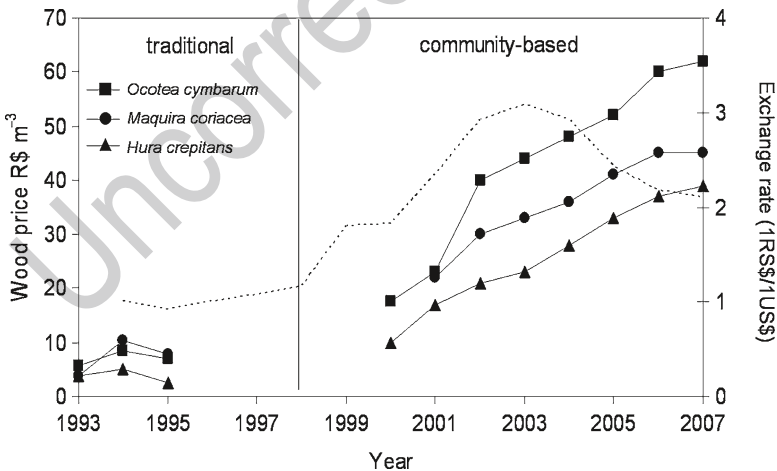


Fig. 20.5 Development of roundwood prices (R\$ mP^{-3P}) in the MSDR from 1993 to 2007 for the high-density tree species *Ocotea cymbarum* and low-density tree species *Maquira coriacea* and *Hura crepitans* (Data: Albernaz and Ayres 1996; Mamirauá Institute for Sustainable Development, IDSMM/MFC). The exchange rate between US\$ and R\$ is indicated for the period (dotted line) (Data: <http://www.exchangerate.com>)

t4.1 **Table 20.4** Timber extraction from community-based forest management of the 19.5-ha high
t4.2 várzea forest “Traíra Lake”, MSDR (Sector Tijuaca, community Nova Betel) (Data: Brampton
t4.3 2001, Mamirauá Institute for Sustainable Development, IDS/MFC)

t4.4			Trees	Volume	Wood price	Value
t4.5	Local name	Scientific name	haP ^{-1P}	(m ³ haP ^{-1P})	2007 (R\$ mP ^{-3P})	(R\$)
t4.6	<i>Low-density tree species</i>					
t4.7	Assacú	<i>Hura crepitans</i>	0.67	5.21	39.00	203.12
t4.8	Macacarecuia	<i>Couroupita subsessilis</i>	0.21	0.65	35.00	22.78
t4.9	Subtotal		0.88	5.86		225.90
t4.10	<i>High-density tree species</i>					
t4.11	Louro inamuí	<i>Ocotea cymbarum</i>	2.36	3.80	62.00	235.50
t4.12	Mulateiro	<i>Calycophyllum</i>	0.72	3.26	62.00	202.47
t4.13		<i>spruceanum</i>				
t4.14	Gitó	<i>Guarea guidonia</i>	0.26	0.30	62.00	18.47
t4.15	Piranheira	<i>Piranhea trifoliata</i>	0.15	0.19	62.00	11.48
t4.16	Subtotal		3.49	7.55		467.92
t4.17	<i>Floats</i>					
t4.18	Munguba	<i>Pseudobombax</i>	0.10	0.24		
t4.19		<i>munguba</i>				
t4.20	Bolacheira	<i>Apeiba</i> sp.	0.10	0.11		
t4.21	Subtotal		0.20	0.34		
t4.22	<i>Total</i>		4.57	13.75		693.82
t4.23		m ³ haP ^{-1P} yrP ^{-1P}		0.55	R\$ haP ^{-1P} yrP ^{-1P}	27.75

t5.1 **Table 20.5** Timber extraction of the community-based forest management in the MSDR of the
t5.2 9.0 ha high várzea forest “Redondo Lake” (Sector Tijuaca, community Nova Betel) (Data:
t5.3 Brampton 2001, Mamirauá Institute for Sustainable Development, IDS/MFC)

t5.4			Trees	Volume	Wood price	Value (R\$)
t5.5	Local name	Scientific name	haP ^{-1P}	(m ³ haP ^{-1P})	2007 (R\$ mP ^{-3P})	(R\$)
t5.6	<i>Low-density tree species</i>					
t5.7	Assacú	<i>Hura crepitans</i>	2.89	47.04	39.00	1,834.56
t5.8	Tacacazeiro	<i>Sterculia elata</i>	0.22	2.05	45.00	92.25
t5.9	Subtotal		3.11	49.09		1,926.81
t5.10	<i>High-density tree species</i>					
t5.11	Louro inamuí	<i>Ocotea cymbarum</i>	1.00	1.79	62.00	182.90
t5.12	Mulateiro	<i>Calycophyllum</i>	0.22	4.77	62.00	295.74
t5.13		<i>spruceanum</i>				
t5.14	Gitó	<i>Guarea guidonia</i>	0.22	2.95	62.00	110.98
t5.15	Piranheira	<i>Piranhea trifoliata</i>	0.11	0.83	62.00	51.46
t5.16	Subtotal		1.55	10.34		641.08
t5.17	<i>Floats</i>					
t5.18	Bolacheira	<i>Apeiba</i> sp.	0.33	1.38		
t5.19	Subtotal		0.33	1.38		
t5.20	<i>Total</i>		4.99	60.81		2,567.89
t5.21		m ³ haP ^{-1P} yrP ^{-1P}		2.43	R\$ haP ^{-1P} yrP ^{-1P}	102.72
t5.22						

Table 20.6 Timber extraction from community-based forest management of the 28.34-ha high várzea forest “Marajá”, MSDR (Sector Tijuaca, community Putiri) (Data: Mamirauá Institute for Sustainable Development, IDSM/MFC)

Local name	Scientific name	Trees haP ^{-1P}	Volume (m ³ haP ^{-1P})	Wood price 2007 (R\$ mP ^{-3P})	Value (R\$)
<i>Low-density tree species</i>					
Assacú	<i>Hura crepitans</i>	1.31	10.29	39.00	401.26
Arapari	<i>Macrolobium acaciifolium</i>	0.28	0.96	43.00	41.16
Macacarecuia	<i>Courouputa subsessilis</i>	0.10	0.97	35.00	33.83
Muiratinga	<i>Maquira coriacea</i>	0.10	0.40	45.00	17.78
Mungubarana	<i>Pachira insignis</i>	0.14	0.61	33.00	20.20
Paricarana	<i>Schizolobium amazonicum</i>	0.18	1.12	45.00	50.22
Seringa barriguda	<i>Hevea spruceana</i>	0.04	0.05	30.00	1.53
Tacacazeiro	<i>Sterculia elata</i>	0.18	1.71	45.00	77.01
Subtotal		2.33	16.11		642.99
<i>High-density tree species</i>					
Abiorana	<i>Pouteria</i> sp.	0.28	2.50	43.00	107.58
Perereca	<i>Dulacia candida</i>	0.04	0.14	62.00	8.60
Louro inamuí	<i>Ocotea cymbarum</i>	0.95	3.12	62.00	193.90
Louro preto	<i>Licaria</i> sp.	0.07	0.20	62.00	12.58
Louro abacate	<i>Aniba guianensis</i>	0.04	0.34	62.00	20.72
Louro amarelo	<i>Aniba riparia</i>	0.10	0.22	62.00	13.70
Gitó	<i>Guarea guidonia</i>	0.64	2.72	62.00	168.66
Mulateiro	<i>Calycophyllum sprucenaum</i>	0.07	0.35	62.00	21.80
Piranheira	<i>Piranhea trifoliata</i>	0.07	0.48	62.00	29.89
Tanimbuca	<i>Terminalia dichotoma</i>	0.18	0.80	62.00	49.61
Castanharana	<i>Eschweilera ovalifoila</i>	0.07	0.34	43.00	14.58
Faveira	<i>Vatairea guianensis</i>	0.10	0.34	43.00	14.56
Coração de negro	<i>Swartzia</i> sp.	0.07	0.16	62.00	10.01
Subtotal		2.67	11.71		666.19
Total		5.00	27.82		1,309.18
m ³ haP ^{-1P} yrP ^{-1P}			1.11	R\$ haP ^{-1P} yearP ^{-1P}	52.37

The socio-economic improvement of the community forest management system of the MSDR is shown in Table 20.7 comparing the period before (year 1993) and after (year 2003) its implementation. In 1993 about 300 people were involved in timber harvesting, extracting 6,897 trees with a total volume of 20,235 m³ (Albernaz and Ayres 1999). This corresponds to 23 trees in average per person with an average volume of 2.9 m³ per tree and 67.5 m³ per person. In 2003 about 98 persons were involved in the MFC with a total yield of 949 trees comprising a volume of 8,507 m³. The logging intensity declined considerably and in average a person yielded only 9.7 trees, but every tree had the threefold volume resulting in even a higher harvested volume (86.8 m³) per person as under uncontrolled conditions. The improvement of the management system and the increasing timber prices (Fig. 20.5)

t7.1 **Table 20.7** Comparison between the traditional timber harvesting in 1993 and the community
 t7.2 forest management (MFC) in 2003 in the MSDR (Data: Albernaz and Ayres 1999; Worbes et al.
 t7.3 2001; Mamirauá Institute for Sustainable Development, IDS/MFC)

t7.4	Traditional timber	Community forest
t7.5	harvesting	management
t7.6	1993	2003
t7.7	6,897 trees	949 trees
t7.8	20,235 m ³	8,507 m ³
t7.9	2.93 m ³	8.96 m ³
t7.10	300	98
t7.11	23.0 trees	9.7 trees
t7.12	67.5 m ³	86.8 m ³
t7.13	219.63	1,049.94

328 resulted in an almost fivefold higher income per person under controlled
 329 management conditions when compared to the traditional harvesting system.
 330 Additionally, training of the local communities by the technical staff of the MFC in
 331 performing forest inventories, logging, skidding, and marketing increases the effi-
 332 ciency of community forest management, limits damages to the remaining trees,
 333 and reduces the risks to human health (Pires 2004) and possibly will increase net
 334 returns. This kind of development renders community forest management a socially
 335 and economically important component of communal life, which contributes signifi-
 336 cantly to improving the financial situation, social coherence and welfare of riparian
 337 communities, especially noticeably during the aquatic phase, when fishing and
 338 agriculture are limited (Fig. 20.4).

339 20.4 Discussion and Conclusions

340 Persistent long-term success of forest management depends on a number of criteria:
 341 (1) the natural conditions of the forest ecosystem must support its use as a sus-
 342 tainably highly productive system; (2) the management concept has to be socially
 343 accepted by the local communities as well as compatible with public policies and
 344 forest legislation; and (3) there must be a thorough scientific data base for designing
 345 and monitoring ecologically and socio-economically viable sustainable forest man-
 346 agement and conservation, and the capability, if necessary, to adapt, adjust and test
 347 new management concepts and criteria with the ultimate aim to transform them into
 348 policies.

349 Generally, the conditions for sustainable and integrated forest management and
 350 conservation are more favourable in the várzea than in the terra firme, as the former
 351 consists of highly productive forest ecosystems (Schöngart et al. this volume b), has
 352 plenty of commercial timber species and timber harvesting is simple and costs are
 353 low (e.g., Barros and Uhl 1995, 1999). Rapid depletion of nutrient stocks in the
 354 soils after removal of large amounts of wood biomass, as reported for timber exploi-
 355 tation in Amazonian terra firme forests (Martinelli et al. 2000), is not a problem in

várzea forests. The annually regular sediment load deposits sufficient nutrients to maintain long-term fertility and utility of floodplain soils (Furch 1997, 2000). The total timber harvest is between 4.57 and 5 trees haP^{-1P} which yields 13.8–60.9 m³ haP^{-1P} per felling cycle or 0.55–2.37 m³ haP^{-1P} yearP^{-1P} (Tables 20.4–20.6). The productivity of várzea floodplain forests and its external inputs are sufficient to replace these amounts of annually extracted timber volumes, wood biomass, nutrients and soil organic matter. Várzea floodplain forests are thus among the most productive and manageable tropical forest ecosystems (Nebel et al. 2001a; Schöngart et al. this volumeb). Volume increments of mature várzea forests are in the range of 10.1–16.2 m³ haP^{-1P} yearP^{-1P}, and young successional stages have even higher annual volume increments of 43.7–51.9 m³ haP^{-1P} yearP^{-1P} (Schöngart 2003). Worbes et al. (2001) estimated that, under the management options practiced in the MSDR, the harvested wood biomass of the timber species (0.54 Mg haP^{-1P} yearP^{-1P}) more or less corresponds to the annual wood biomass production of timber (0.50 Mg haP^{-1P} yearP^{-1P}). At the stand level, the applied polycyclic system seems therefore ecologically sound (Worbes et al. 2001).

So far, most studies have promoted reduced-impact logging (RIL) as a model of sustainable forest management that limits soil disturbance by heavy equipment and reduces damages to residual trees (Dykstra and Heinrich 1996; Vidal et al. 1997, 2002; Gerwing 2002; Putz et al. 2008). The forest operations comprise fundamental activities, such as pre-harvest inventories and mapping of commercial tree species; pre-harvest planning of skid trails, roads, and patches; pre-harvest vine cutting; directional felling; efficient utilization of felled trunks; optimum widening of roads and skid trails with minimal ground disturbance; slash management; and personnel training. Many studies have indicated that RIL significantly lowers residual stand damage and soil disturbance, reduces logging wastage and losses, and are also less costly and more profitable than conventional ones, but naturally less cash-flow producing and profitable in the short run than resource-plundering timber mining (Johns et al. 1996; Bruenig 1998; Boltz et al. 2001; Holmes et al. 2002). These site, habitat and growing stock caring and preserving systems are crucial for the conservation of tropical forests as multiple-functional resource. However, the technical and logistic improvements of timber harvesting are not sufficient to promote sustainable management of timber resources unless they are integrated in a silvicultural management and conservation system which is solidly based on ecological information on the ages, lifetime growth rates, regeneration processes and life histories of the commercial and non-commercial tree species which structure and drive the forest ecosystem.

One of the biggest obstacles in the sustained management of tropical forests is obtaining reliable data on the growth of trees. This information is a prerequisite for determining harvesting volumes and felling cycles. Consequently, there is much scepticism about growth rates being used as the basis for managing many of the forests in the region because the established time and diameter limitations are estimations or simply conform to legal restrictions and are not derived from sound scientific data. Species-specific and site-specific management criteria based on wood growth data and structural analyses of natural stands in the tropics are quite

401 rare (Nebel et al. 2001b; Schwartz et al. 2002; Sokpon and Biaou 2002; Nebel and
402 Meilby 2005; Brienen and Zuidema 2006a,b, 2007; Schöngart et al. 2007; Schöngart
403 2008). Forest management in the várzea forests, as in the tropics and elsewhere
404 generally, needs a scientific database describing species-specific and site-specific growth
405 rates, tree ages, and regeneration processes to achieve sustainable timber resource
406 management.

407 For the várzea, the restrictions established in IN nº5 of IBAMA do not reflect
408 scientific data. By contrast, it is already a progress to use the best available data to
409 set tentatively felling cycles ranging from 10 to 35 years. The IN nº5 further
410 demands species-specific DCLs based on supporting studies of population structure
411 (diameter distribution), ecological aspects (reproduction, highest productivity) and
412 technical market demands (prices for different diameter classes, minimum diame-
413 ters for the various forms of timber processing, timber qualities for different uses,
414 and so on). Only by step-wise implemented rules and adaptive management can we
415 rationally approach and approximate sustainable management and conservation.
416 Nonetheless, we must be aware that hasty application of management criteria for
417 certain timber species remains a high-risk gamble as long as data on forest pro-
418 cesses, such as tree growth and natural regeneration, are inadequate. The genetic to
419 architectural forest population structure is likely to suffer, genetic resources decline
420 and species are lost, and the forest ecosystem becomes more vulnerable particularly
421 to the impacts of climate change. Therefore, immediate efforts are crucial to obtain
422 realistic estimations of tree age, increment rates, volume production, population
423 structure and regeneration processes of tree species growing under varying edaphic,
424 hydrologic, and climatic conditions, as shown by the concept on growth-oriented
425 logging (GOL) (Schöngart this volume). This and similar approaches that increase
426 the welfare of the involved local populations and maintain the ecosystem's multiple
427 services are the only way that the long-term ecological and socio-economic viability
428 of the management of timber resources can be safeguarded.

Author Queries

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AU3	Please fix if it is Anderson et al. 1999 a or b here and in further occurrences.	

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Abstract The conservation of tropical forests has become a huge challenge in our time in the background of global climate change and increasing human populations in developing countries associated with high deforestation rates. A promising way to conserve tropical forests is the development of sustainable management systems which guarantee the long-term use of natural resources such as timber and non-wood forest products (NWFP) and maintain the multiple ecological functions and services of the forests. But a great difficulty for a sustained management of tropical forests is obtaining reliable data on tree growth, which is a prerequisite for determining harvesting volumes and felling cycles. The long-term success of forest managements depends primarily on the sustainability of timber production, and thus on information about the growth rates and regeneration processes of commercial tree species (Boot and Gullison 1995; Brienen and Zuidema 2006a, b; Schöngart 2008).

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21.1 Introduction 6

[AU1] The conservation of tropical forests has become a huge challenge in our time in the 7
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For centuries the várzea floodplains has been settled and used, largely 19
 because of its easy accessibility, high soil fertility, and richness in natural 20
 resources (Junk 2000a). Most commercial tree species occur in high-várzea forests 21
 (Worbes et al. 2001) which become flooded to a height of annually less than 3 m 22
 above forest floor. These forests cover only 8–10% of the central Amazonian várzea 23

24 (Wittmann et al. 2002b) and are threatened by strong pressures to increase
25 timber logging and to converse large areas to pastures, agricultural lands, and
26 settlements. Another forest type, the low várzea, occur on about 40% of the
27 floodplains in central Amazonia, comprises fewer commercial tree species and
28 is inundated annually by a water column of 3–6 m above the ground (Wittmann
29 et al. 2002b). Due to its longer inundation period, the low várzea suffers less
30 conversion pressure, because the agriculturally permissive period is too short.
31 Forest management can be more readily performed on this forest type, since
32 flooding occurs regularly each year, thus guaranteeing access to harvested trees
33 for skidding and transport (Schöngart et al., this volume a). An increasing num-
34 ber of tree species of the low várzea forests is becoming commercialized; for
35 example, in the Peruvian várzea, tree species of the low várzea, such as
36 *Maclobium acaciifolium*, *Paramachaerium ormosioides*, and *Ficus insipida*,
37 already are exploited by the timber industry (Schöngart 2003). Martini et al.
38 (1998) pointed out the low-várzea tree species *Vatairea guianensis*, *Pseudobombax*
39 *munguba*, and *Pouteria elegans* as commercially important. High-density
40 species from the low várzea, including *Tabebuia barbata*, *Chrysophyllum*
41 *argenteum*, *Eschweilera albiflora*, and *Piranhea trifoliata*, as well as the wood
42 of some low-density species, such as *P. munguba* and *Luehea cymulosa*, are
43 harvested by local inhabitants (Brampton 2001; Kvist et al. 2001; Wittmann
44 et al. 2009; Wittmann and Oliveira-Wittmann, this volume) for substantial use.

45 The várzea is a dynamic landscape patchwork of water bodies, aquatic and
46 terrestrial macrophytes and forests as a result of erosion and sedimentation pro-
47 cesses (Salo et al. 1986; Irion et al. 1997; Kalliola et al. 1991; Worbes et al. 1992;
48 Schöngart et al. 2003; Wittmann et al. 2004; Wittmann et al., this volume). Primary
49 succession initiates at sites with high sedimentation rates, i.e., next to a river. Due
50 to geomorphological and environmental modifications, young pioneer stands (up to
51 20 years of age) are able to develop into early secondary stages (20–40 years old).
52 These are followed by late secondary (50–80 years old) and late successional stages
53 at higher elevated sites with relatively longstanding stable environmental condi-
54 tions, resulting in trees up to 400 years old (Wittmann et al. 2004; Wittmann et al.,
55 this volume). Along this successional gradient, the wood densities increase whereas
56 diameter increment rates decrease, reflecting the substitution of pioneer species by
57 those that are long-living and by climax species (Swaine and Whitmore 1988;
58 Worbes et al. 1992; Schöngart 2003; Schöngart et al., this volume b). With increas-
59 ing stand age, tree density declines and tree species richness increases, leading to
60 changes in the canopy architecture, i.e., increasing stand height and crown size and
61 decreasing crown number (Terborgh and Petren 1991; Wittmann et al. 2002b;
62 Schöngart et al. 2003) leading to changing optical and aerodynamic properties of
63 the canopy (Wittmann et al., this volume).

64 Most studies dealing with sustainable forest management in the várzea have
65 based their approach to sustainability on data describing species composition and
66 structure and on evaluation of the value of timber and NWFPS, for instance, in the
67 Amazon Estuary (Bentes-Gama et al. 2002; Gama et al. 2005a,b; Fortini et al.
68 2006). However, scientific reliable knowledge from scientific research about tree

ages, increment rates, and the regeneration processes occurring in the várzea floodplain is vague to provide suitable and adequate information for the planning and monitoring of sustainable forest management. Preliminary approaches to sustainable forest management of floodplain forests have been described for the Peruvian várzea and were developed based on socio-economic studies (Kvist and Nebel 2001), ethnobotany (Kvist et al. 2001), the structure and floristic composition of adult trees (Nebel et al. 2001a), regeneration (Nebel et al. 2001b), estimations of net primary production (Nebel et al. 2001c), and diameter and volume growth models of two commercial tree species (Nebel 2001; Nebel et al. 2001b).

Timber extraction in Amazonian forests requires a management plan based on legal regulations and normative instructions (IN) established by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA). The recently established IN nº5 (11 December 2006) defines diameter cutting limits (DCLs) and felling cycles (Schöngart et al., this volume a) for regular management plans with a felling cycle of 25–35 years and maximum yields of up to $30 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ or, alternatively, management plans with low yield intensities ($< 10 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) applying a shorter felling cycle of 10 years (in várzea yields can exceed $10 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$, but must be restricted to 3 harvested trees ha^{-1}). The IN nº5 requires the establishment of species-specific diameter cutting limits based on ecological and technical criteria, but if this information is not available for a timber species, a common DCL of 50 cm is applied.

Management concepts, which keep an all-ages stand by establishing a DCL and through selective tree cuttings at shorter intervals (felling cycle), are known as selective systems or polycyclic systems (Lamprecht 1989; Bruenig 1996). So far, most studies have promoted selective harvests in combination with reduced-impact logging (RIL) as a model of sustainable forest management (Dykstra and Heinrich 1996; Vidal et al. 1997, 2002; Gerwing 2002; Putz et al. 2008). Generally, RIL significantly lowers residual stand damage and soil disturbance, reduces logging wastage and losses, and is also less costly and more profitable than conventional ones, but naturally less cash-flow producing and profitable in the short run than resource-plundering timber mining (Bruenig 1996; Johns et al. 1996; Boltz et al. 2001; Holmes et al. 2002). These management systems are crucial for the conservation of tropical forests as multiple-functional resource. However, the technical and logistic improvements of timber harvesting are not sufficient to guarantee sustainable management of timber resources unless they are integrated in a silvicultural management and conservation system which is solidly based on ecological information on the ages, lifetime growth rates, regeneration processes and life histories of the commercial and non-commercial tree species which structure and drive the forest ecosystem.

The GOL concept (Growth-Oriented Logging) developed by Schöngart (2008) is an approach to the sustainable management of tropical timber resources in nutrient-rich central Amazonian várzea forests using species-specific DCLs, in term of an optimized minimum logging diameter (MLD), and felling cycles derived from growth models of 12 commercial tree species. Growth modeling is based on tree-rings, which are annually formed in the wood as a consequence of the annual flood-pulse (Worbes 1986, 1995; Schöngart et al. 2002, 2004, 2005; Worbes and

114 Fichtler, this volume). The derived management criteria are compared with
115 currently practised timber resource management in the central Amazonian várzea
116 (Schöngart et al., this volume a) and, together with data from population structure
117 of the studied tree species, new management concepts are developed. In this chap-
118 ter, the GOL concept is also extended to the nutrient-poor floodplains (igapó) to see
119 how the contrasting nutrient status (Furch 1997, 2000) affects diameter growth and
120 the derived management criteria of its commercial tree species.

121 21.2 Material and Methods

122 21.2.1 Tree-Ring Analysis and Growth Modeling

123 The várzea sites are situated in the Mamirauá Sustainable Development Reserve
124 (MSDR) described more in detail by Queiroz and Peralta (this volume). The study
125 sites of the igapó are located in the Amanã Sustainable Development Reserve (ASDR)
126 and upon the confluence of the Negro and Branco Rivers (Fig. 21.1). From 14 tree
127 species, 137 stem disks and 170 cores were been collected from emergent individuals

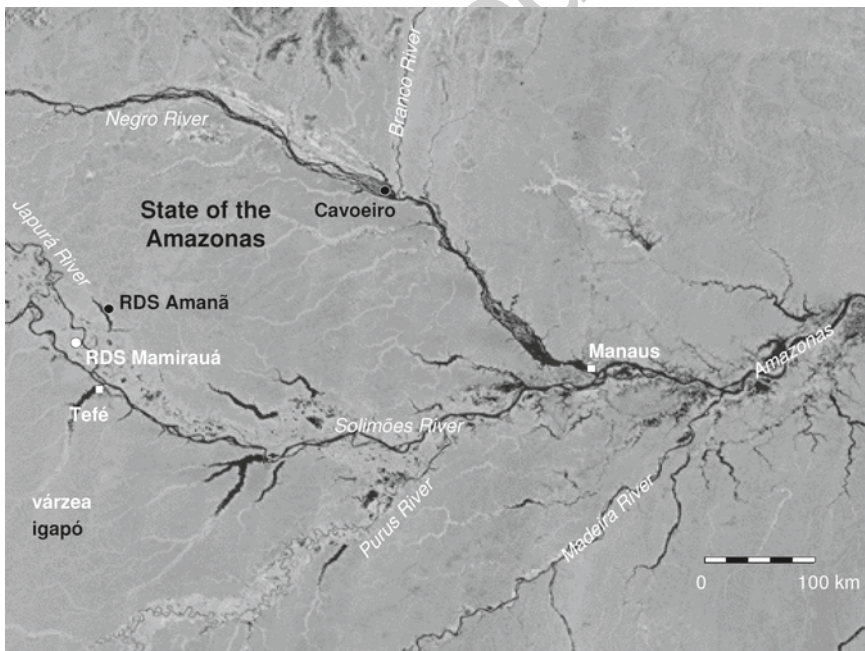


Fig. 21.1 Map of the Central Amazon region indicating study sites in the nutrient-poor black-water floodplains (igapó, black circles) and the nutrient-rich white-water floodplains (várzea, white circle)

for tree-ring analyses. In the MSDR wood samples were obtained from 12 tree species 128
 comprising *Ficus insipida* (Moraceae) in a 20-year-old early secondary stage 129
 (Schöngart et al. 2007) and from *Pseudobombax munguba*, *Luehea cymulosa* (both 130
 Malvaceae), *Ilex inundata* (Aquifoliaceae), *Macrolobium acaciifolium*, and *Albizia*
subdimidiata (both Fabaceae) in a 50-year-old late secondary stage. In the over 132
 100-year-old late successional stages *Tabebuia barbata* (Bignoniaceae), *Eschweilera*
albiflora (Lecythidaceae), *Piranhea trifoliata* (Euphorbiaceae), *Pouteria elegans*, 134
Chrysophyllum argenteum (both Sapotaceae), and *Sloanea terniflora* (Elaeocarpaceae) 135
 were sampled (Schöngart 2003). The study sites are located in the low várzea almost 136
 at the same elevation and are annually flooded between 120–150 days, by an average 137
 depth of 336–465 cm (Schöngart 2003). In the igapó wood samples were obtained in 138
 pristine floodplain forests from *M. acaciifolium* (RDSA) (Schöngart et al. 2005) and 139
Calophyllum brasiliense (Clusiaceae) (*Cavoeiro*). At both igapó sites the average 140
 water column passes over 6 m. The commercial tree species were classified using a 141
 threshold of about 0.60 g cm⁻³, into low-density (*madeira branca*) and high-density 142
 (*madeira pesada*) trees (Schöngart 2003; Schöngart et al. this volume a). 143

The wood samples were analyzed in the Dendrochronological Laboratory of the 144
 National Institute for Amazon Research (INPA) in Manaus. The cores were clued 145
 on wooden supports and polished together with the stem disks with sand paper of 146
 decreasing grain size from 40 to 600 grits and cleaned afterwards with compressed 147
 air. Tree rings were dated by their wood anatomical structure using a binocular. 148
 More details on wood anatomy and tree ring analysis were previously described 149
 (Schöngart et al. 2004, 2005, 2007; Worbes and Fichtler, this volume). Ring width 150
 was measured with a digital measuring device (LINTAB) to the nearest 0.01 mm 151
 supported with software for tree-ring measurement, analysis and presentation 152
 (TSAP-Win, Rinntech, Heidelberg, Germany). 153

Diameter growth of a tree species was modelled in two ways (Fig. 21.2). First, 154
 from different individuals of a tree species, the increment rates measured on the 155
 wood samples, from pith to bark, were accumulated to form individual growth 156
 curves related to the measured diameter (Brienen and Zuidema 2006a,b, 2007). The 157
 mean cumulative diameter growth curve described the relationship between tree 158
 age and diameter of a species (Stahle et al. 1999; Worbes et al. 2003; Schöngart 159
 et al. 2007). Second, tree ages determined by ring counting were related to the 160
 corresponding diameter *d* from several individuals of a species. Both age–diameter 161
 relationships were fitted to a sigmoidal function (Schöngart 2008): 162

$$d = a / (1 + (b / age)^c) \tag{21.1} \quad 163$$

Height growth of a tree species was estimated by combining the age-diameter rela- 164
 tionship and the relationship between diameter and tree height *h* measured in the 165
 field fitted to a non-linear regression model (Nebel 2001; Nebel et al. 2001a; 166
 Schöngart et al. 2007): 167

$$h = d \times a / (d + b) \tag{21.2} \quad 168$$

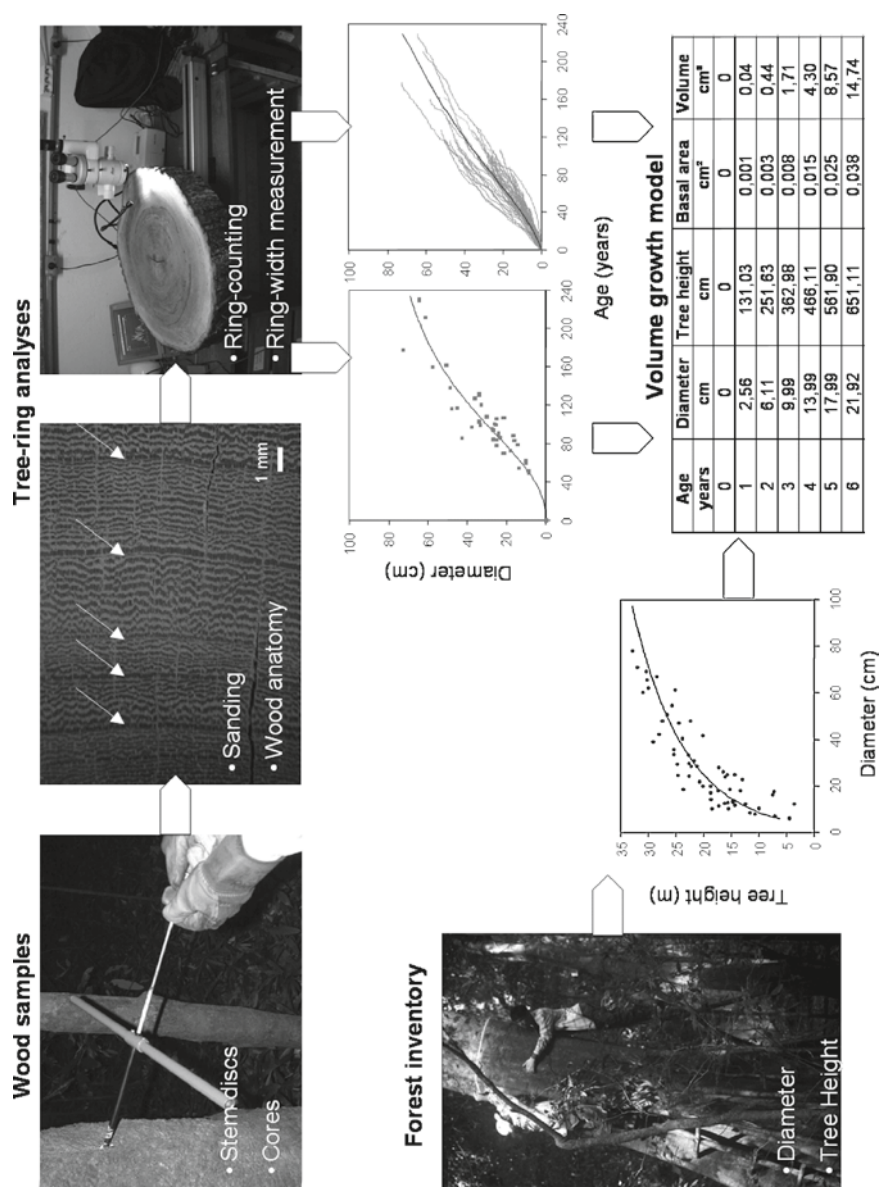


Fig. 21.2 Growth modelling based on tree-ring analysis: Wood samples (cores and stem disks) from a commercial tree species are collected in the field and prepared in the laboratory for tree-ring analysis (wood anatomy), ring-counting, and ring-width measurements. The data are used to construct age-diameter relationships by cumulative diameter growth curves or scatter plots fitted to non-linear (sigmoidal) regression models. Non-linear regression models describe the relationship of field data between diameter at breast height (d) and total tree height (h) of this species. With these regression models cumulative volume growth (V_t) can be estimated for every growth year, along the life-span of a tree by diameter (d), tree height (h) and a form factor (f) of 0.6 ($V_t = \pi \times (d/2)^2 \times h_t \times f$)

Thus, for every tree age over the lifespan of a species, the diameter and 169
 corresponding tree height can be derived. Cumulative volume growth was calcu- 170
 lated for every year by the basal area multiplied with the corresponding tree height 171
 and a common form factor of 0.6 (Cannell 1984): 172

$$V_t = \pi \times (d_t / 2)^2 \times h_t \times f \tag{21.3} \quad 173$$

Where V_t is the volume at age t ; d_t is the diameter at age t ; h_t is the tree height at 174
 age t , and f is the form factor (the ratio of tree volume to the volume of a cylinder 175
 with the same basal diameter and height). 176

21.2.2 Definition of Management Criteria 177

From the cumulative volume growth over the life span of a tree the current annual 178
 volume increment rate CAI_v and mean annual volume increment rate MAI_v were 179
 derived (Fig. 21.3) by the following equations (Schöngart 2008): 180

$$CAI_v = CGW_{V(t+1)} - CGW_{V(t)} \tag{21.4} \quad 181$$

$$MAI_v = \frac{CGW_{V(t)}}{t} \tag{21.5} \quad 182$$

Where CGW_v is the cumulative volume in different years t over the entire life span. 183

From the volume growth model and volume increment rates, criteria for a 184
 species-specific management were derived. The model in Fig. 21.3 indicates and 185
 increasing CAI_v with increasing diameter and age. To achieve an optimal volume 186
 production a tree should be harvested between the optimum of the CAI_v 187
 ($CAI_{v(max)}$) and the optimum of the MAI_v ($MAI_{v(max)}$). This time difference was 188
 defined as preferred period for harvest (Schöngart 2008). Harvests before the 189
 $CAI_{v(max)}$ and after $MAI_{v(max)}$ would lead to an inefficient use of the growth poten- 190
 tial of a tree species. The minimum logging diameter is defined as diameter at 191
 the age in the optimum of the CAI_v ($CAI_{v(max)}$) and can be derived by the specific 192
 age–diameter relationship (Schöngart et al. 2007). To estimate the felling cycle 193
 the mean time through 10-cm diameter classes until achieving the specific MLD 194
 was calculated (Schöngart 2008). This period represented the average time, 195
 which an individual needs to grow from one to the next diameter class of 10-cm 196
 intervals (Fig. 21.3): 197

$$Fellingcycle = age_{(MLD)} / MLD \times 10 \tag{21.5} \quad 198$$

The estimated felling cycles by mean passage times through 10-cm diameter 199
 classes can easily be transferred to the forest inventory data. 200

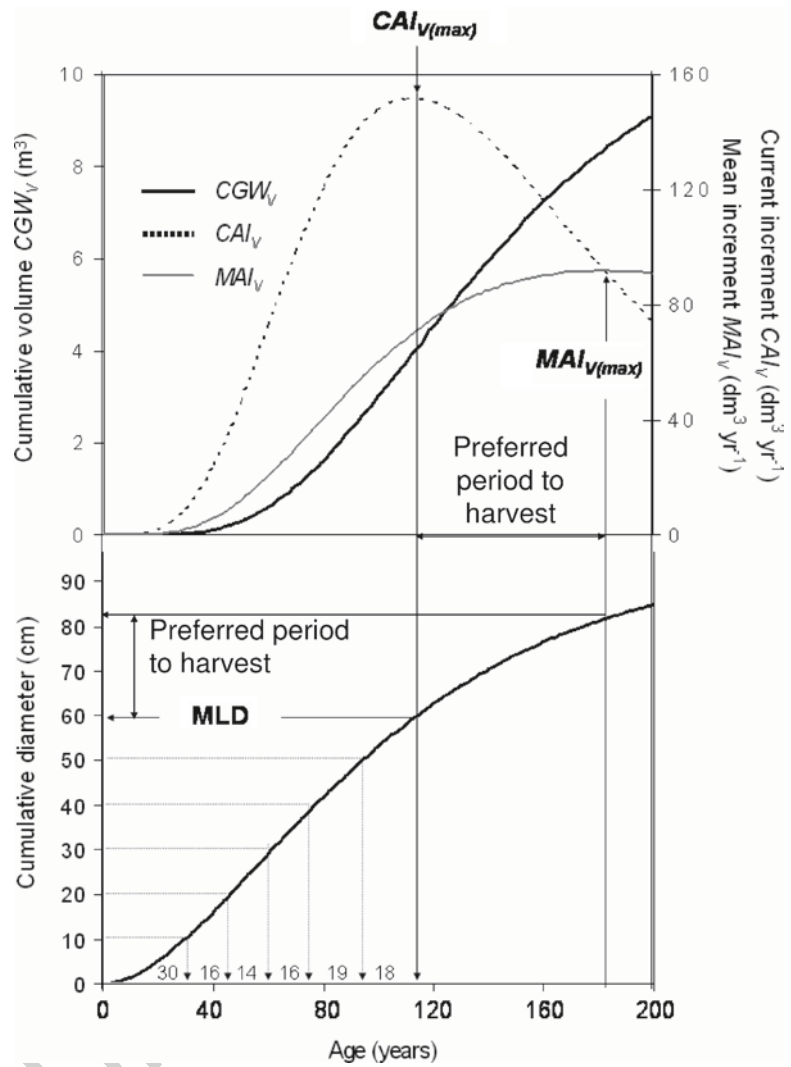


Fig. 21.3 Model of cumulative volume growth (CGW_v) for a tree species and the derived current (CAI_v) and mean (MAI_v) annual volume increment rates. The preferred period for harvest is between the maximum CAI_v and MAI_v . The diameter at the age of the maximum CAI_v is defined as the minimum logging diameter (MLD) (Schöngart 2008)

201 **21.3 Results**

202 **21.3.1 The Growth Model**

203 All growth models were based on significant relationships between age and
 204 diameter as well as diameter and height (Schöngart et al. 2007; Schöngart 2008;

Schöngart et al., this volume b). In the várzea, low-density timbers need periods of 15 years (*F. insipida*) to 67 years (*S. terniflora*) to surpass a DCL of 50 cm, defined by the IN n°5 from the IBAMA; high-density woods require between 106 years (*P. elegans*) and 151 years (*E. albiflora*) to reach this limit (Fig. 21.4). Under the same flooding regime, but contrasting nutrient status, the low-density tree species *M. acaciifolium* has significantly lower increment rates in the nutrient-poor igapó than in the nutrient-rich várzea (Fig. 21.5). In the várzea, *M. acaciifolium* species reaches a DCL of 50 cm in 54 years (Fig. 21.4), while in the igapó the same species needs 171 years (Fig. 21.6). *C. brasiliense* surpasses a DCL of 50 cm only after 261 years in the igapó floodplains.

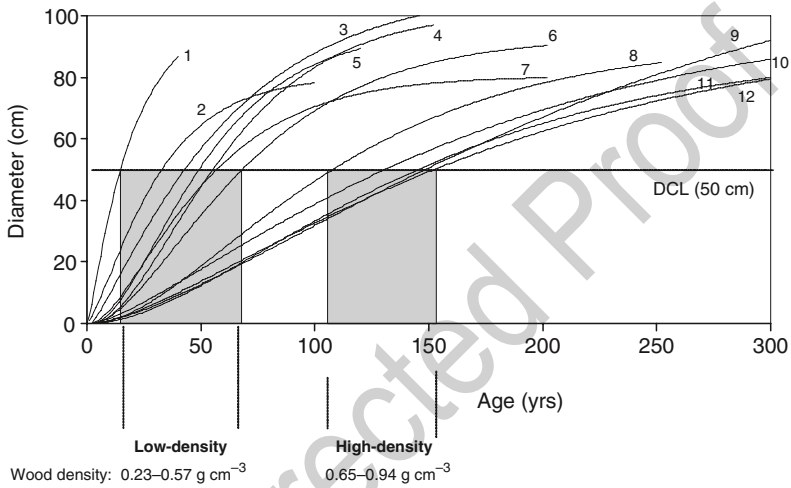


Fig. 21.4 Mean cumulative diameter growth curves of 12 low-density and high-density timber species from the Central Amazonian várzea floodplain forests (1 *Ficus insipida*, 2 *Pseudobombax munguba*, 3 *Luehea cymulosa*, 4 *Ilex inudata*, 5 *Macrolobium acaciifolium*, 6 *Albizia subdimidiata*, 7 *Sloanea terniflora*, 8 *Pouteria elegans*, 9 *Piranhea trifoliata*, 10 *Chrysophyllum argenteum*, 11 *Tabebuia barbata*, 12 *Eschweilera albiflora*). A diameter cutting limit (DCL) of 50 cm is indicated (Schöngart 2008)

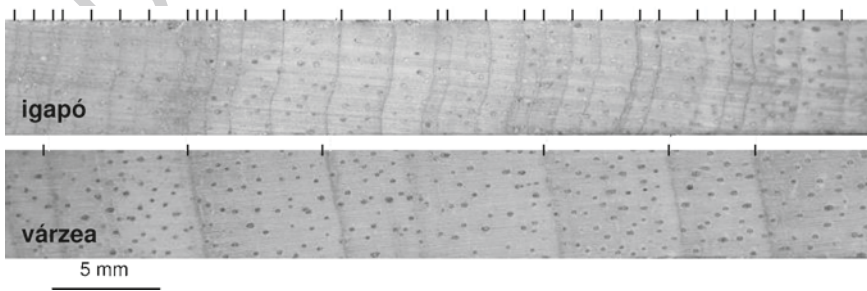


Fig. 21.5 Wood growth of the same species differs significantly in central Amazonian floodplains under contrasting nutrient status as shown by tree-ring series of *Macrolobium acaciifolium* from samples of the igapó (nutrient-poor) and the várzea (nutrient-rich) (Schöngart et al. 2005)

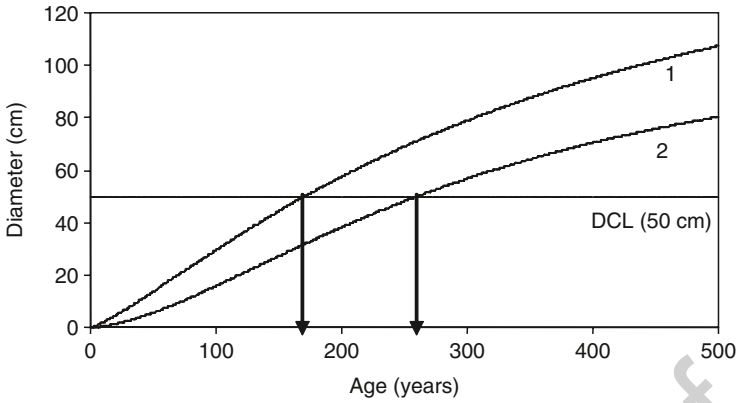


Fig. 21.6 Cumulative diameter growth curves of the low-density timber species *Macrolobium acaciifolium* (1) and the high-density timber species *Calophyllum brasiliense* (2) from the black-water floodplain forests (igapó) of Central Amazonia. The diameter cutting limit (DCL) of 50 cm is indicated

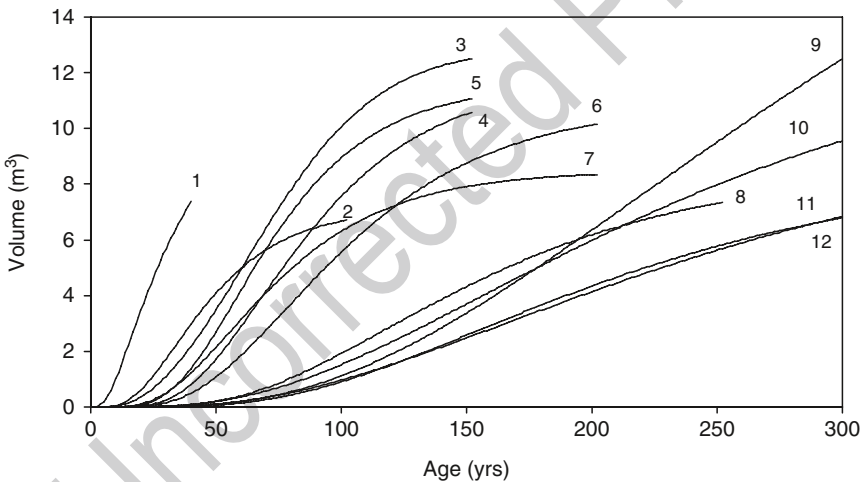


Fig. 21.7 Cumulative mean volume growth curves of 12 low-density and high-density timber species from the Central Amazonian várzea floodplain forests (1 *Ficus insipida*, 2 *Pseudobombax munguba*, 3 *Luehea cymulosa*, 4 *Ilex inundata*, 5 *Macrolobium acaciifolium*, 6 *Albizia subdimidiata*, 7 *Sloanea terniflora*, 8 *Pouteria elegans*, 9 *Piranhea trifoliata*, 10 *Chrysophyllum argenteum*, 11 *Tabebuia barbata*, 12 *Eschweilera albiflora*) (Schöngart 2003; Schöngart et al. 2007)

215 Because of the higher diameter and height increments the volume growth of
 216 low-density tree species is much faster than that of high-density species in the
 217 várzea. For example, the first group produces a volume of 6 m³ within 70–100 years,
 218 while the high-density timber species need between 200 and 260 years (Fig. 21.7).
 219 For selective logging, it is important to know at which age and diameter a tree
 220 reaches its growth optimum. The simulation of the diameter (Fig. 21.4) and volume

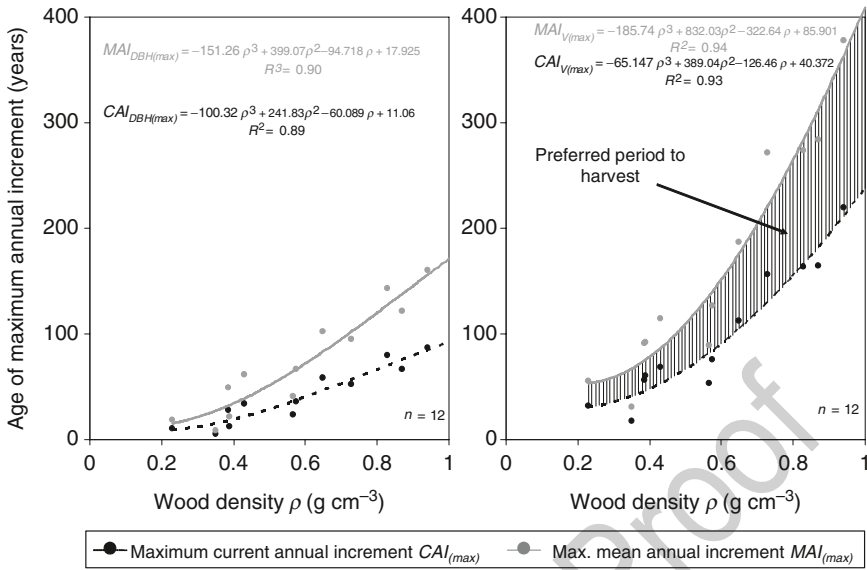


Fig. 21.8 Maximum current and mean annual increment rates in diameter (left) and volume (right) as a function of specific wood density. The hatched area indicates the preferred period for harvest (Schöngart 2003, 2008)

(Fig. 21.7) growth permits the definition of the culmination points of the current and mean annual increments for diameter and volume (Fig. 21.8). Interestingly, the ages of the trees at the maximum current and mean increment rates of diameter and volume correlate significantly with wood density (ρ). The relationship between ρ and the age at the maximum current and mean annual increments in diameter and volume can be described by polynomial functions. These explain 89–90% of the variability between diameter increment and ρ and 93–94% of the variability between volume increment and ρ ($p < 0.001$). As usual, the diameter increment culminates much earlier than the volume increment, while with increasing ρ , the current and mean volume increments culminate at higher tree ages. Also the time difference between the maximum current and mean increment becomes longer with increasing ρ . From the model in Fig. 21.8, the preferred age of harvest lies between the ages of maximum current and mean annual volume increment (Fig. 21.3). It can also be estimated for other várzea timber species as a function of ρ . In addition, their MLDs can be defined as diameter at the age of the maximum current volume increment. For most species, the MLDs as derived from growth model simulation are greater than a DCL of 50 cm established by IN n°5 (Table 21.1).

In the várzea, felling cycles derived from the growth models are 3–14 years for low-density tree species and 22–32 years for high-density trees (Table 21.1). The felling cycle of timber species in the várzea correlates significantly with the specific wood density ($r = 0.95$, $p < 0.01$). In the nutrient-poor igapó, the estimated felling cycles are much higher, e.g., 37 years (*M. acaciifolium*) and 53 years (*C. brasiliense*). The period to reach the same MLD of 55 cm varies between 17 years for *F. insipida*

Table 21.1 Minimum logging diameter (MLD) and felling cycles derived from growth models for low-density and high-density timber species in the nutrient-rich (várzea) and nutrient-poor (igapó) central Amazonian floodplains

	Timber species	Wood density g cm ⁻³	MLD (cm)	Period to reach MLD (years)	Felling cycle (years)
t1.3	VÁRZEA				
t1.4	Low-density tree species				
t1.5	<i>Ficus insipida</i>	0.35	55	17.0±3.6	3.3 (2.4–3.7)
t1.6	<i>Pseudobombax munguba</i>	0.23	47	39.5±2.4	8.2 (7.9–8.9)
t1.7	<i>Ilex inundata</i>	0.38	59	61.0±9.7	10.5 (8.7–12.0)
t1.8	<i>Macarolobium acacifolium</i>	0.43	62	67.0±5.6	10.5 (9.9–11.7)
t1.9	<i>Albizia subdimidiata</i>	0.57	49	53.5±7.1	10.5 (9.5–12.4)
t1.10	<i>Luehea cymulosa</i>	0.39	61	68.5±11.7	11.0 (9.3–13.1)
t1.11	<i>Sloanea terniflora</i>	0.57	58	82.0±9.1	13.9 (12.6–15.7)
t1.12	High-density tree species				
t1.13	<i>Pouteria elegans</i>	0.65	54	120.0±21.8	21.5 (18.2–26.3)
t1.14	<i>Chrysophyllum argenteum</i>	0.73	58	144.0±22.4	24.1 (21.0–28.7)
t1.15	<i>Eschweilera albiflora</i>	0.83	53	164.5±44.6	30.9 (22.6–39.5)
t1.16	<i>Tabeaiba barbata</i>	0.87	54	168.5±19.8	30.6 (27.5–34.9)
t1.17	<i>Piranhca trifoliata</i>	0.94	70	227.0±23.5	32.1 (29.1–35.8)
t1.18	IGAPÓ				
t1.19	Low-density timber species				
t1.20	<i>Macarolobium acacifolium</i>	0.39	83	326.0±4.5	39.3 (38.6–40.0)
t1.21	High-density timber species				
t1.22	<i>Calophyllum brasiliense</i>	0.66	55	293.0±44.0	52.7 (50.8–54.2)

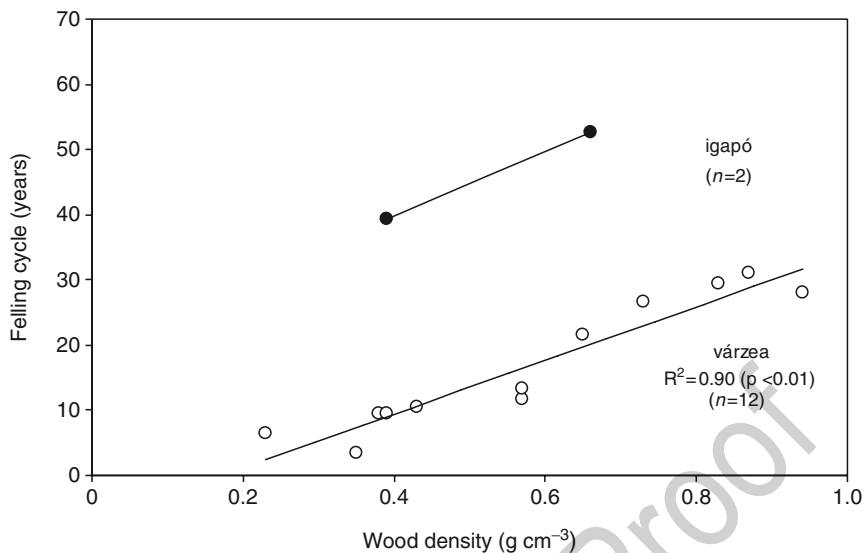


Fig. 21.9 Defined felling cycles of 12 timber species from the nutrient-rich várzea and two species from the nutrient-poor igapó floodplain forest in Central Amazonia as a function of the felling cycles established by Brazilian forest legislation (IBAMA, Normative Instruction IN n°5, 11 December 2006)

in the várzea and 288 years for *C. brasiliense* in the igapó, which is almost a 17-fold difference (Fig. 21.9).

21.3.2 Management Potential of Central Amazonian Floodplain Forests

The sustainable use of timber stocks in the nutrient-poor igapó is, under current management options, not practicable due to the low increment rates of the tree species, as shown for *C. brasiliense* and *M. acaciifolium* (Fig. 21.6). Fonseca Jr. et al. (2009) show for *T. barbata* and *V. guianensis* the same finding which have significant lower lifetime increment rates in diameter in the igapó than in the várzea under similar flooding conditions due to the lower nutrient content (Furch 1997, 2000) (Fig. 21.10). Stadler (2007) reported that aboveground wood biomass production of old-growth forests is much lower in the igapó than in the várzea. The igapó forests are especially vulnerable to inadequate timber management due to the slow dynamical processes reflected by the significantly lower diameter increment when compared to the várzea. Floodplain forests of the igapó should be therefore excluded from timber resource management and permanently protected as habitats for their highly diverse and partially endemic flora and fauna. However, the igapó floodplain forests have a potential for the development of ecotourism and management of ornamental fishes (Chao and Prang 1997; Junk et al. 2007; Faria 2005).

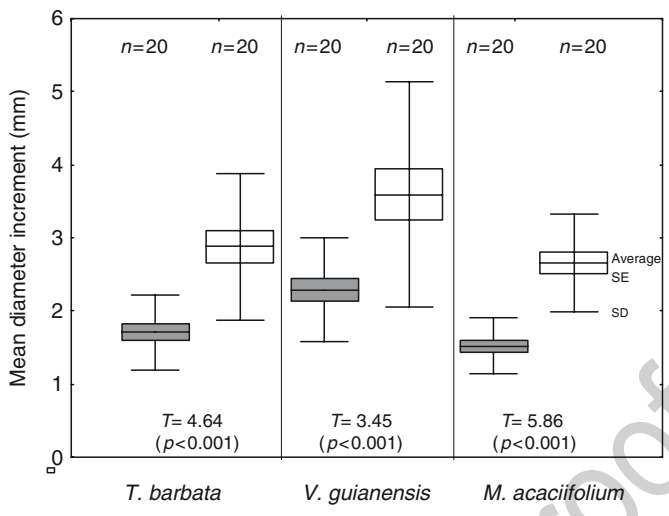


Fig. 21.10 Mean diameter increment of a tree species differs significantly between igapó (grey boxes) and várzea (white boxes) due to the nutrient availability as shown for *Tabebuia barbata*, *Vaitaiera guianensis* and *Macrolobium acaciifolium* indicated by two sample tests (data: Schöngart et al. 2005; Fonseca et al. 2009). Box with mean and standard error; whiskers indicate standard deviation

263 Generally, the conditions for sustainable and integrated forest management and
 264 conservation are more favourable in the várzea. It is a dynamic system with highly
 265 productive forest ecosystems (Schöngart et al., this volume b), has plenty of com-
 266 mercial timber species (Wittmann and Oliveira-Wittmann, this volume) and timber
 267 harvesting is characterized by low costs (Schöngart et al., this volume b). The annu-
 268 ally regular flood-pulse deposits sufficient nutrients to maintain long-term fertility
 269 and utility of floodplain soils (Furch 1997, 2000). This favours the development of
 270 a integrated sustainable forest management. However, the derived MLDs and fell-
 271 ing cycles indicate that the currently practised forest management in the várzea
 272 cannot be sustainable, because it applies only one fixed DCL and felling cycle to
 273 harvest a high number of tree species, which vary in lifetime growth rates, tree ages
 274 and reproduction strategies. The management in the várzea requires therefore a
 275 species-specific management.

276 **21.3.3 Management of Low-Density Timber Species in the Early**
 277 **Forest Succession of the Várzea**

278 Forests of the early succession in the várzea (early secondary and late secondary
 279 stages) are species poor and have uniform age and architectural structures
 280 (Terborgh and Petren 1991; Worbes 1997; Wittmann et al. 2002b; Schöngart 2003;

Wittmann et al., this volume). They are dominated by fast-growing tree species with low wood densities, such as *F. insipida*, *P. munguba*, *I. inundata*, and *L. cymulosa*. Structural analyses of the timber species indicated very high timber stocks, with a total of 67 trees ha⁻¹ above the DCL of 50 cm, representing a stem volume of 139 m³ ha⁻¹ (Schöngart 2003). Due to the similarities in the growth patterns of the trees, a management concept for the early successional stages of this species group can be devised in which the aim is to produce large quantities of high-quality timber for plywood and veneer (Worbes et al. 2001; Schöngart 2003). By contrast, the high stem-volume stocks of 50-year-old late secondary stage trees cannot be managed by a selective system with a felling cycle of 25 years. After selective logging of 5 trees ha⁻¹, the majority of the low-density timbers will have died at the end of the following felling cycle due to the relatively short life-span of these tree species (Worbes et al. 1992; Schöngart 2008).

A principle of sustainable management is that the yield of a timber species renews the harvested volume within the prospected period of the following harvest. This depends on the increment rates, but also on the successful regeneration and establishment of the particular timber species in order to renew regrowth and in-growth in the lower size classes. It can be assumed that a harvest level of maximally 5 trees ha⁻¹ would probably not create the favourable light conditions needed on the forest floor for the successful regeneration of low-density timbers. The majority of the tree species regenerating in the early forest succession of floodplain forests are light-demanding pioneers or long-living pioneer tree species (Worbes et al. 1992; Wittmann and Junk 2003; Wittmann et al., this volume). This is shown by an analysis of the abundance distributions of timber species in 10-cm diameter classes (Hartshorn 1980; Swaine and Whitmore 1988) in four different successional stages in relation to relative photosynthetically active radiation (*rPAR*) on the forest floor (Wittmann 2001) (Fig. 21.11). The low-density timbers indicate changing patterns of diameter distributions with decreasing *rPAR*. In the 20-year-old secondary stage with 19.4% *rPAR* the low-density tree species *I. inundata*, *L. cymulosa*, and *P. munguba* have a reverse J-shaped diameter distribution (decreasing abundance with increasing diameter), indicating that these tree species still regenerate and successfully establish in the stand. In the following 50-year-old early successional stage, the population structure of these tree species changes considerably as solar radiation on the forest floor declines to 9.6% *rPAR*. The highest abundances of these three species were observed in the middle diameter classes, whereas regeneration was absent. In the case of *P. munguba*, a large number of trees are recorded in the lowest diameter class mainly occurring in gaps (Ziburski 1991), but the abrupt decline to the next diameter class indicates that these young trees do not establish successfully at this stage. With declining *rPAR* in the 125-year-old and 240-year-old late successional stages, these low-density species appear only in small abundances of different size classes, indicating that they regenerate only sporadically in these stands, probably after the creation of larger gaps (Hartshorn 1980). For *F. insipida*, the dominating timber species in the early secondary stage, no regeneration was observed (Schöngart et al. 2007) (Fig. 21.7). This finding can be traced back to the insufficient light conditions on the forest floor (Wittmann and Junk 2003). A polycyclic system is thus

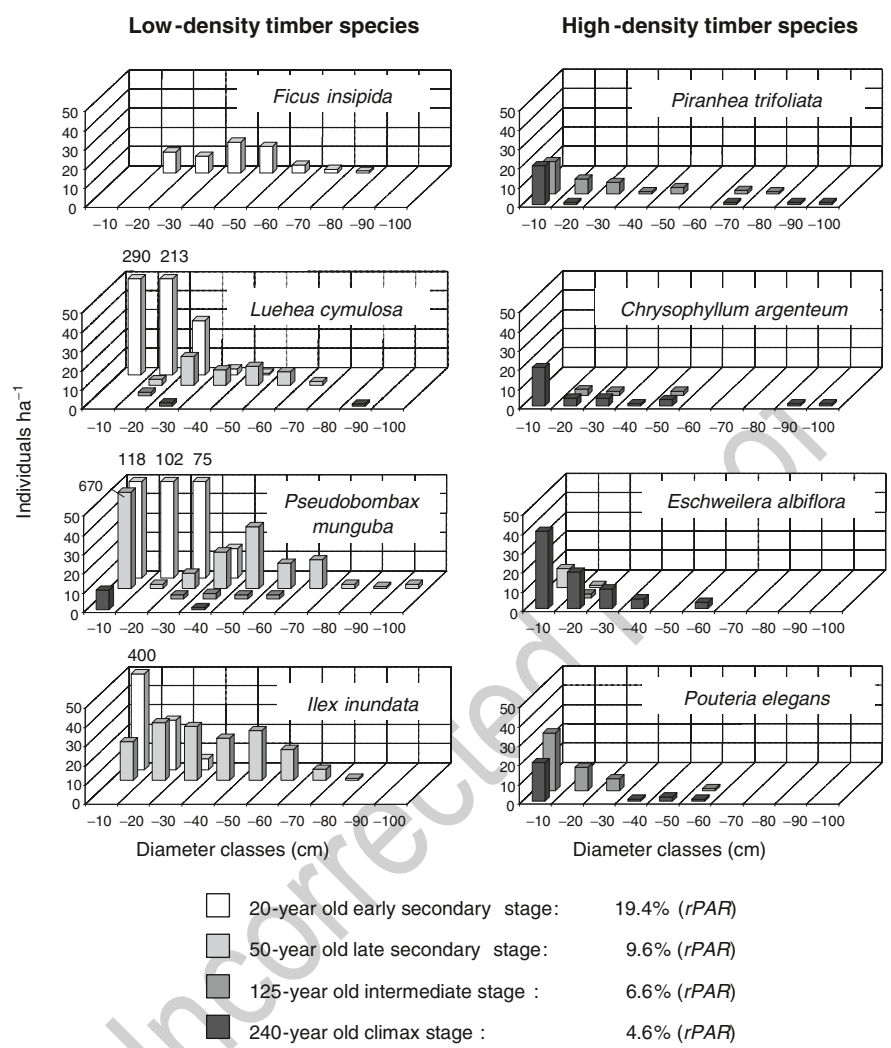


Fig. 21.11 Population structure (abundance for 10-cm diameter classes) of the low-density timber species (*left*) and high-density timber species (*right*) of four different successional stages (Schöngart 2008). Data for mean, minimum and maximum relative photosynthetically active radiation (*rPAR*) are obtained from Wittmann (2001)

326 economically and ecologically inappropriate to manage the timber resources of these
 327 fast-growing low-density timber species.

328 The management of these shade-intolerant/light-demanding pioneers in young
 329 successional stages of the Amazonian floodplain forests (Salo et al. 1986; Terborgh
 330 et al. 1997; Wittmann et al. 2004) requires a monocyclic silvicultural system
 331 (Shelterwood Systems) (Lamprecht 1989; Dawkins and Philip 1998; Whitmore
 332 1993) (Fig. 21.12). Monocyclic systems support a uniform crop of trees from the
 333 young regeneration phase and allow both heavy harvesting and broad silvicultural

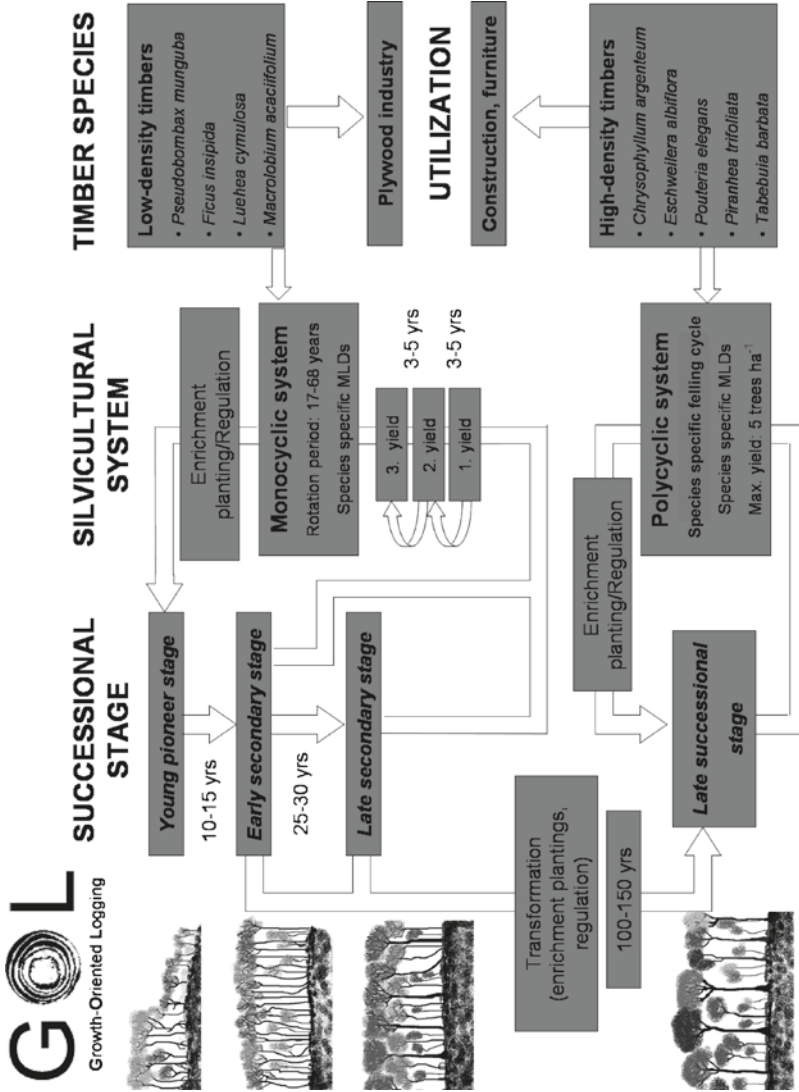


Fig. 21.12 Forest management concept for Central Amazonian floodplain forests of the low várzea, differentiated for low-density (monocyclic system) and high-density (polycyclic system) tree species (Schöngart 2008)

334 treatments. A new even-aged crop is established by applying preparatory and
335 establishment cuttings to achieve natural regeneration (i.e., seedlings and saplings)
336 of the desired trees. At an appropriate time, the overstorey of all marketable stems
337 is removed in one or more harvestings. The period between the establishment of the
338 seedlings and the harvest of the mature trees is defined as the rotation period (in
339 contrast to the felling cycle). The advantage of this system is the high economic
340 efficiency and immediate cash flow, but problems arise in terms of nutrient removal,
341 the risks of soil erosion and the need for often intensive silvicultural work, such as
342 beating-up or weeding/cleaning, and later tending and thinning (Lamprecht 1989;
343 Bruenig 1996). A well known monocyclic system is, for instance, the Malaysian
344 Uniform System which became introduced in lowland dipterocarp forests in 1948
345 by Wyatt-Smith (1963). It consists of felling the mature crop of all trees above 45
346 cm diameter, poison girdling all defective relics and non-commercial species down
347 to 5 cm diameter and releasing established seedlings.

348 The rotation period of a monocyclic system for low-density timber species in the
349 early successional stages of the várzea floodplains can be defined as the time inter-
350 val between establishments of the trees until the maximum current volume incre-
351 ment is reached, if this is the desired time of harvesting the main crop (Fig. 21.8,
352 Table 21.1). For *F. insipida*, which, as noted above, dominates in the early second-
353 ary stage, the rotation period is 17 years whereas for timber species in the late
354 secondary stage it is 30–64 years. In monocyclic systems clear-cuts should be
355 avoided, because young successional stages are mostly located close to river marg-
356 ins, where they have an important ecological functions to protect the ground
357 against soil erosion (Schöngart et al. 2007) and possibly to maintain biologically
358 healthy conditions in the water body. A modified monocyclic system could entail
359 the logging of all trees with diameter over the species-specific MLD (Table 21.1),
360 thus creating large gaps in the stand that favour the regeneration of light-demanding
361 tree species. The enlargement of these gaps could be repeated in two or three 3- to
362 5-year intervals, corresponding to the mean passage of time through 10-cm diam-
363 eter classes until the previous stand is completely removed and substituted by a new
364 stand, which has grown up during that period (Fig. 21.12). In this phase, enrichment
365 plantings could be carried out to improve regeneration and increase the abundance
366 of timber species if their natural regeneration is absent.

367 Another option is to transform stands of the early forest succession, either
368 directly or after one or more rotation periods, into intermediate and climax stages
369 made up of high-density timber species. This corresponds to the natural succession
370 dynamics of low-várzea forests (Salo et al. 1986; Terborgh and Petren 1991;
371 Worbes et al. 1992; Wittmann et al. 2002b; Wittmann et al., this volume). As forest
372 succession (primary succession) initiates on newly created areas by the sedimenta-
373 tion processes of white-water rivers, the newly established areas compensate for
374 those transformed to late successional forests. Silvicultural treatments such as
375 enrichment plantings and regulation of the natural forest regeneration of occurring
376 timber species may be viable, but costly options which need further research. Also,
377 in a later step, the pruning of selected future crop trees might be a silvicultural
378 option to increase the wood quality.

The high tolerance against prolonged flooding and the enormous growth potential of low-density species indicate their great potential for reforestation of degraded floodplain areas, such as those traditionally used for agriculture and pasture but subsequently abandoned (Junk et al., this volume a). The planting of species in enrichment plantations or agroforestry systems either as monocultures on small areas or as mixed stands can help to decrease the pressure on the few remaining areas of intact floodplain forests, especially in the high várzea. An additional benefit to be gained is the relatively rapid improvement of the economic situation of the local riverine population. First experiments of reforestation with mixed stands with varying silviculture treatments are actually performed in the MSDR.

21.3.4 Management of High-Density Timber Species in the Late Forest Successions of the Várzea

High-density timber species, such as *T. barbata*, *P. trifoliata*, and *C. argenteum*, dominate old-growth forests of the low várzea, which are characterized by an uneven-age structure (Worbes et al. 1992; Schöngart et al. 2003). This species group achieves timber stocks of 57–70 m³ ha⁻¹ and 57–59% of this stem volume comprises trees of DCL >50 cm (Schöngart 2003). These timbers are mainly utilized for furniture, veneer, home construction, and ship-building (Worbes et al. 2001; Wittmann and Oliveira-Wittmann, this volume). Therefore, the aim of forest management in such stands is the production of high-quality timber with high wood densities. High-density tree species of commercial interest have similarities in wood growth (Schöngart 2008). Wood densities of the above-mentioned species are in the range of 0.72–0.94 g cm⁻³ and life spans are between 200 and 400 years (Worbes et al. 1992; Schöngart 2003, 2008). The cumulative diameter growth curves indicate that trees of this species group need periods of 100–150 years to surpass a DCL of 50 cm (Fig. 21.4). The current diameter increment culminates in trees 60–90 years of age, while current volume increments reach their maximum in trees 160–230 years of age (Fig. 21.8).

The differences in felling cycles with respect to tree species (Table 21.1, Fig. 21.9) show clearly that a polycyclic system based on a fixed MLD and felling cycle tends to over- or under-harvest some of these species. Under current management practices, the timber stocks of high-density woods in the várzea are over-exploited, as is the case for the high-density timber species *P. trifoliata*, which dominates late successional stages in low-várzea forests (Worbes et al. 1992). In a late successional stage (Schöngart 2003), 29 trees >10 cm diameter were recorded in a 1-ha plot. A simulation of selective harvesting under current management options, as practised in the MSDR (Schöngart et al., this volume a), produced a yield of 9.2 m³ ha⁻¹ stem volume from three trees >50 cm (Fig. 21.13). For the remaining 26 trees, in-growth was projected using the species-specific growth model (Fig. 21.4) for a felling cycle of 25 years (prospective analysis) (Brienen and Zuidema 2006b). For this period, the model predicted a low

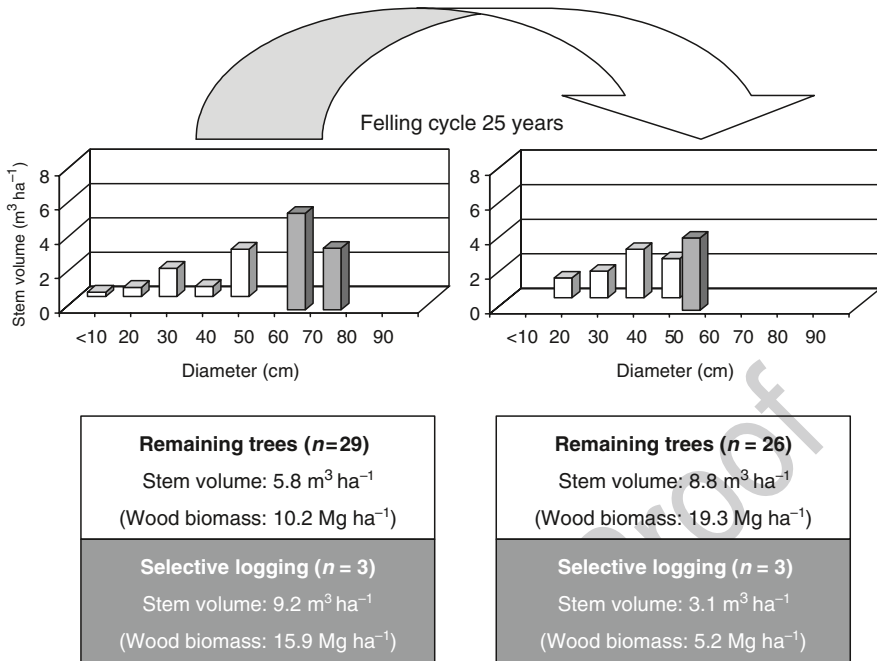


Fig. 21.13 Simulation of selective logging (polycyclic system) of the high-density timber species *Piranha trifoliata* in a mature low-várzea forest under currently practised forest management criteria (felling cycle of 25 years; diameter cutting limit of 50 cm). Data on population structure and stem volume are obtained by Schöngart (2003). The ingrowths of the remaining trees were projected by the specific growth model (Fig. 21.4)

420 recuperation of the initially harvested volume, and a stem volume of only 3.1 m³
 421 ha⁻¹ could be forecasted for the next harvest (n=3 trees). To achieve a sustainable
 422 yield of *P. trifoliata* under current management options, a felling cycle of
 423 60 years needs to be applied, which makes forest management for this tree species
 424 economically unviable. Predictions of in-growth for one felling cycle still need
 425 improvement, including information on the species-specific mortality rates in dif-
 426 ferent diameter classes, recruitment rates, and the reactions of the residual trees
 427 after selective logging, which are monitored in permanent sample plots. However,
 428 the prospective analysis (Fig. 21.13) clearly indicated that current management
 429 practises are unsustainable and lead in the specific case to an overlogging of the
 430 timber stocks of *P. trifoliata* because the potentially most vigorous trees are
 431 removed before they reach their optimum volume growth. The IN n° 5 enables also
 432 a management option in the várzea with felling cycles of 10 years and a low peri-
 433 odic yields of 10 m³ ha⁻¹ of commercial volume (MLD >50 cm) restricted to 3
 434 trees ha⁻¹ independent from the tree species. It is obvious that a management
 435 adopting these measures would lead to a dramatic decline of the timber stocks of
 436 *P. trifoliata* with probably also negative effects on genetic diversity and demo-
 437 graphic structures of the species. The increase of the diameter limit of felling from

50 to 70 cm produces a higher sustainable long-term increment of *P. trifoliata*, because the high predicted volume increment rates of residual trees in the medium diameter classes (50–70 cm) renews the harvested volume within an estimated felling cycle of 32 years (Table 21.1).

In contrast to the low-density species of the early successional stages, the high-density timber species *P. trifoliata*, *C. argenteum*, *E. albiflora*, and *P. elegans* usually exhibit a J-reverse distribution pattern, despite the relatively low light intensities of 4.6–6.6 *rPAR* (Fig. 21.11). In humid tropical forests, as elsewhere, this pattern is characteristic for shade-tolerant tree species (Hartshorn 1980; Swaine and Whitmore 1988). Therefore, polycyclic selective systems are appropriate to manage the timber resources and to maintain the uneven-age stand structure of these várzea tree species communities (a.o., Whitmore 1993). Selective logging should concentrate on individual trees above the species-specific MLD, which varies from 53 to 70 cm (Table 21.1) applying felling cycles of 21–32 years for high-density timber species (Fig. 21.12).

Silvicultural treatments, e.g., thinning to increase diameter increment rates (Finegan et al. 1999; Nebel et al. 2001e; Kammesheidt et al. 2003; Carvalho et al. 2004), that lead to shortened felling cycles cannot be recommended for high-density tree species. Worbes et al. (2001) reported differences in the wood growth patterns of *T. barbata* growing in young successional stages versus old-growth forests. The mean passage time for 10-cm diameter classes of *T. barbata* in young successional stages is twice as fast as in old-growth forests. Nonetheless, this results in significantly lower wood densities ($0.65 \pm 0.07 \text{ g cm}^{-3}$) than obtained in old-growth forests made up of stands of trees over 200 years old ($0.84 \pm 0.10 \text{ g cm}^{-3}$) (Fig. 18.5 in Schöngart et al., this volume b). The decrease in wood density and the associated changes in the mechanical-physical wood properties due to accelerated diameter growth could have negative consequences on the potential use of high-density timbers in shortened felling cycles. Similar observations have been made and are reported for *Swietenia macrophylla* (Mahogany): trees from forest plantations have much lower wood densities, as a consequence of the higher sapwood portion, than trees from natural forests (Mayhew and Newton 1998). Selective logging should be therefore restricted to a maximum of 5 trees ha^{-1} (Dykstra and Heinrich 1996; Vidal et al. 1997, 2002; Gerwing 2002). RIL within a sustainable forest management system will limit residual stand damages and minimize the costs and expenses of logging and skidding (Johns et al. 1996; Boltz et al. 2001; Holmes et al. 2002). Low-density tree species such as *P. munguba* and *L. cymulosa*, which occur sporadically in these stands, can be harvested to float sinkable logs of high-density timbers for skidding during the aquatic phase (Albernaz and Ayres 1999; Schöngart et al., this volume a).

21.4 Discussion and Conclusions

The high species richness and diversity that characterizes tropical forests, together with methodological problems in determining tree ages and lifetime growth rates, has resulted in a lack of growth models for commercial tree species. Most studies

479 monitor tree growth in permanent observation plots by repeated diameter
480 measurements (Clark and Clark 1999; Finegan et al. 1999; Nebel et al. 2001e;
481 Valle et al. 2006) or dendrometer bands (Silva et al. 2002) for some years. Based
482 on the diameter increments maximum allowable yields are estimated according to
483 growth models (Vanclay 1994; Alder and Silva 2000; Sist et al. 2003). However,
484 the majority of growth models evaluate volume increment at the stand level (Dauber
485 et al. 2005; Neeff and Santos 2005; Valle et al. 2006), but this approach fails to
486 provide criteria for the species-specific management of timber stocks. Other mod-
487 els evaluate the diameter growth rates of trees of different size classes within a
488 species to project tree growth over the total life span of the species (Lieberman and
489 Lieberman 1985; Korning and Balslev 1994; Terborgh et al. 1997; Clark and Clark
490 1999; Nebel 2001; Sokpon and Biaoou 2002). This method is likewise limited due
491 to the relative short period during which diameter growth is monitored (Condit
492 1995) and to the low density of commercial species especially trees of larger size
493 in permanent sample plots (Clark and Clark 1996). The resulting diameter growth
494 trajectories are based on simplifications and assumptions, which can result in unre-
495 alistic long-term growth data and inaccurate estimations for the different tree spe-
496 cies. Lifetime trajectories of tree species projected by diameter growth rates of
497 different size classes based on data from permanent sample plots also frequently
498 underestimate the growth rates of future canopy trees, thus overestimating tree age.
499 Nebel et al. (2001b), for instance, determined diameter growth of the low-density
500 timber species *Maquira coriacea* in the Peruvian várzea based on 432 trees of dif-
501 ferent size classes during a 4-year period. The annual diameter growth rates
502 recorded for the size classes <1 cm ($n = 15$), 1–5 cm ($n = 115$), and 5–10 cm ($n = 67$)
503 were 0.02, 0.21, and 0.27 cm, respectively, or 88 years on average to reach a diam-
504 eter of 10 cm. However, most of these trees will not reach harvestable sizes; more-
505 over, due to the extremely low diameter increment of the seedlings and saplings, the
506 tree age of *M. coriacea* at a diameter of 10 cm was overestimated. For *M. coriacea*,
507 which has a wood density of 0.47 g cm⁻³ (Worbes et al. 2001), the growth models
508 (Figs. 21.4 and 21.8) indicated that trees with an age of 88 years are already of a
509 harvestable size.

510 Other studies have evaluated stand growth and development for a period of 240–
511 400 years by using process-oriented forest growth models, for example, for Southeast
512 Asian dipterocarp lowland forests (Huth and Ditzer 2000; Huth et al. 2005) or tropical
513 forests in Venezuela (Kammesheidt et al. 2001). These models are based on carbon
514 balances of individual trees from different crown layers, as determined by the main
515 physiological processes (photosynthesis, respiration) (Bossel and Krieger 1991;
516 Jansen and Martin 1995) and by allometric functions relating aboveground biomass,
517 tree height, stem diameter, and crown parameters. However, estimations of maximum
518 tree ages were based on assumptions and the effect of increasing atmospheric tem-
519 perature and CO₂ concentrations (IPCC 2007) while their feedback on photosynthetic
520 and respiration rates was not considered (Cox et al. 2000). This calls into question the
521 suitability of these models to predict stand development of dipterocarp lowland forest
522 for the next 240–400 years (Huth and Ditzer 2000; Huth et al. 2005). These models
523 also are not able to define species-specific management options.

In contrast to other methods of modelling growth, tree-ring analysis has many advantages (Brienen and Zuidema 2006a, b) as it yields direct values for tree ages and lifetime growth rates of individual trees based on retrospective analysis. In tree-ring analysis, emergent trees that are successfully established in the canopy are sampled. This approach provides diameter growth data representing realistic growth trajectories for harvestable trees. Thus, tree ages determined by dendrochronology are much lower than those extrapolated from diameter growth trajectories derived from the short-term data of permanent sample plots, which result in tree ages of up to 1,000 years for central Amazonian tree species (Laurance et al. 2004).

The use of tree-ring data to define management options for tropical timber species is not new. From 1855 to 1862, in the British colony of Burma (today Myanmar), the German-born Botanist, Dietrich Brandis, later Sir Dietrich Brandis, developed and applied a specific management plan for teak (*Tectona grandis* (Verbenaceae) (Bruenig 1996). From stand inventories performed along transects (linear taxation) and ring counting of stumps, Brandis (1898) estimated felling cycles of 24 years (mean passage time through a size class) and a MLD of four cubits (~58.8 cm) to promote the sustainable use of teak stocks (Hesmer 1975; Dawkins and Philip 1998). Since then, controversial discussions in the literature about the significance of the occurrence of annual, periodic or episodic tree rings in the wood of tropical tree species (Worbes and Junk 1999; Worbes and Fichtler, this volume) have severely limited the application of dendrochronological methods to model tree growth in the tropics. Simulations of diameter growth curves based on tree-ring data so far exist only for some tree species in Cameroon (Worbes et al. 2003), Zimbabwe (Stahle et al. 1999), Tanzania (Schwartz et al. 2002), Venezuela (Worbes 1999), Bolivia (Brienen and Zuidema 2006a, b, 2007), and the central Amazonian floodplains (Worbes 1994; Worbes et al. 2001; Schöngart 2003, 2008; Schöngart et al. 2007; Fonseca Júnior et al. 2009). These studies have shown that dendrochronology can be used to construct simple growth models based on the lifetime growth rates of harvestable trees and is therefore an important tool for developing management concepts to increase the level of sustainability in tropical forests. Tree rings are evident for many tropical tree species of different ecosystems (summaries in Worbes 1995, 2002). The growth trajectory for a particular timber species can be considered as a general representation of the growth dynamics of that species under certain site conditions (climate, hydrology, edaphical conditions, successional stage). Accordingly, growth models can be easily established by tree-ring analysis for different site conditions whereas data from permanent plots are important in determining mortality rates for different size classes of trees as well as recruitment, logging damage, and the reaction of the residual trees after logging (Condit 1995, Nebel et al. 2001e, Kammesheidt et al. 2003, Carvalho et al. 2004).

Ecologically compatible and sustainable management of tropical forests, as of any other production forests generally, requires species-specific and site-specific management systems, rules and regulations. The same holds true generally and worldwide for tropical polycyclic management systems that operate with only one felling cycle for several timber species (Table 21.2).

t2.1 **Table 21.2** Sustainable forest management projects with polycyclic systems (selection
 t2.2 management system) in tropical non-flooded (terra firme) and floodplain forests (Adapted from
 t2.3 Worbes et al. 2001)

t2.4 Polycyclic system	Project size (ha)	Yield (m ³ ha ⁻¹)	Felling cycle (years)	Yield (m ³ ha ⁻¹ year ⁻¹)
t2.6 PT. ITCI (terra firme) t2.7 Kalimantan, Indonesia	601,750	57	35	1.6
t2.8 North Queensland (terra firme) t2.9 Australia	160,000	20	40	0.5
t2.10 TSS t2.11 Nigeria (terra firme)	90,000	35	50	0.7
t2.12 Celos t2.13 Suriname (terra firme)	20,000	30	25	1.2
t2.14 Mil Madeireira t2.15 Brazil (terra firme)	>400,000	35–40	25	1.4–1.6
t2.16 Gethal t2.17 Brazil (terra firme)	71,000	21–151	30	2.8 (0.7–5.0)
t2.18 Gethal t2.19 Brazil (várzea)	43,000	37–78	30	1.7 (1.2–2.6)
t2.20 MSDR, Brazil	20,000	38	25	1.2

569 Achieving sustainable yields requires the species- and site-specific management
 570 of timber resources (van Gardingen et al. 2006; Sebbenn et al. 2008), in which the
 571 different growth features of low- and high-density timber species and the varying
 572 site conditions are considered. The GOL concept for the low várzea (Fig. 21.12) is
 573 adapted to the natural dynamics of the successional forest and offers an approach
 574 to ecological sustainability based on the population structures and wood increments
 575 of low- and high-density tree species. The application of modified monocyclic
 576 systems to early forest succession and of polycyclic selection systems to old-
 577 growth forests preserves the multiple ecological functions of these forest ecosys-
 578 tems while at the same time supporting both the growing riverine populations and
 579 the expanding timber and plywood industries of Amazonia. Sustainable forest man-
 580 agement in the low várzea can thus be seen as a mean to decrease the pressure on
 581 timber species populations of high-várzea sites. In contrast to high-várzea forests,
 582 low-várzea forests have a large proportion of endemic tree species (Wittmann et al.,
 583 this volume) and are characterized by their high floristic similarity over large geo-
 584 graphic distances due to long-distance dispersal by currents and fishes (Wittmann
 585 et al. 2006a). Concepts like the one formulated by GOL offer a powerful tool to
 586 promote the sustainable forest management of timber resources not only for other
 587 forest ecosystems in Amazonia but also for other tropical regions.

588 Nevertheless, felling cycles or rotation periods only guarantee the sustainable use
 589 of timber resources if the harvested species recruit. Little information is available on
 590 the germination, growth, and establishment of seedlings and saplings or their
 591 relation to external abiotic (flooding, light conditions, water and nutrient supply) and
 592 biotic factors (seed banks, inter-specific and intra-specific competition, herbivory)
 593 (Oliveira-Wittmann et al., this volume). Costs-benefit analyses are necessary to
 594 evaluate silvicultural improvements, such as enrichment plantings, thinning to

regulate recruitment and competition, as well as the pruning to increase stem 595
qualities (Lamprecht 1989; Mesquita 2000). This would promote development of an 596
appropriate silvicultural strategy – one that is based on scientific data – to increase 597
the sustainability of tropical forests through their management. Future studies 598
should test the concepts formulated by GOL against conventional management sys- 599
tems (IN n°5) and unmanaged forests (control) focusing on the population dynamics 600
of timber species. Immediate efforts is crucial to obtain realistic estimations of tree 601
ages, increment rates, volume production, population structure and regeneration 602
processes of commercial tree species growing under varying edaphic, hydrologic, 603
and climatic conditions. The participation of the riverine population in this phase is 604
essential to analyse the time and cost demands in the different activities (forest 605
inventure, logging, skidding, etc.) and calculate the income (wood quality, wood 606
prices). This allows performing cost-benefit analyses which are a powerful tool to 607
evaluate social and economic aspects of the sustainability of different management 608
options. Public policies, represented by the IBAMA, Institute of Environmental 609
Protection of the Amazonas State (IPAAM) and Secretary for Environment and 610
Sustainable Development of the Amazonas State (SDS) and other stakeholders such 611
as NGOs, municipalities and timber industries should participate from the beginning 612
to monitor and validate new management concepts. This increases the possibility of 613
a step-wise implementation of adaptive management in paractise and forest legisla- 614
tion to rationally approach sustainable management and conservation. This guaran- 615
tees the welfare of the involved local populations and maintains the ecosystem's 616
multiple services and is a long-term ecological and socio-economic viability of the 617
management of timber resources in the central Amazonian várzea floodplains. 618

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Abstract	The Sustainable Development Reserve (SDR) is a novel category of protected area, corresponding to IUCN (The World Conservation Union) category VI – an area containing predominantly unmodified natural systems, managed to ensure long-term protection and maintenance of biological diversity, while also providing a sustainable flow of natural products and services to meet community needs.	

Chapter 22 1
Protected Areas in the Amazonian Várzea 2
and their Role in its Conservation: The Case 3
of Mamirauá Sustainable Development Reserve 4
(MSDR) 5

[AU1] **Helder Lima de Queiroz and Nelissa Peralta** 6

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22.1 Introduction 7

The Sustainable Development Reserve (SDR) is a novel category of protected area, corresponding to IUCN (The World Conservation Union) category VI – an area containing predominantly unmodified natural systems, managed to ensure long-term protection and maintenance of biological diversity, while also providing a sustainable flow of natural products and services to meet community needs.

First of its kind, the Mamirauá Sustainable Development Reserve (MSDR) is located in the floodplains of central Amazonia, alongside the Solimões River. The remarkable importance of the várzea ecosystem was essential to the establishment of this protected area in the heart of the Amazon basin. Besides a rich biodiversity, the area is home to many rare, endangered or threatened species that have been drastically reduced in numbers elsewhere in the Amazon. The Reserve is also the address to some of the most innovative conservation experiments in Brazil.

The national impact of the management developed at Mamirauá was due to the fact that the reserve not only provided improved levels of protection to local biodiversity, but also achieved this by means of a strong alliance with the local population

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23 for more than 15 years. This alliance was based on the empowerment of locals (by
 24 their involvement and participation in all levels of the decision making processes),
 25 and based on the assumption that adequate management of sustainable use of bio-
 26 diversity could promote a better quality of human life in natural environments
 27 (Queiroz 2005b; Queiroz and Peralta 2006).

28 The conception of this new model of protected area, its development, challenges
 29 and outcomes are described in this chapter. The use and management of natural
 30 resources in Mamirauá's várzea are discussed; their historic threats as well as the
 31 answers to those threats in terms of the creation of the new model of conservation
 32 and sustainable use of natural resources. Moreover, this chapter intends to discuss
 33 the importance of protected areas, particularly those associated with the perma-
 34 nence of traditional Amazonian riverine populations, in the conservation of this
 35 particular environment. In all aspects, the case of MSDR, its history, its conserva-
 36 tion model, its failures and achievements enable an important perspective into the
 37 protected areas issue in this important and threatened environment.

38 22.2 Localization of the Area

39 The MSDR is located at the confluence of the Solimões and Japurá Rivers and the
 40 Auatí-Paraná, a branch of the Solimões draining into the middle course of the Japurá
 41 (Fig. 22.1). Mean water level fluctuations in the MSDR are about 11.4 m (Schöngart
 42 et al. 2005). When floodwaters are at their highest point, virtually all lands of
 43 MSDR, or 1,124,000 ha, are completely submerged, and only the highest parts of the
 44 forest canopy can be seen above the water line (Sociedade Civil Mamirauá 1996). [AU2]
 45 The flood pulse is mono-modal, with high predictability and high amplitude (Junk
 46 1997b). It defines the whole biology of the aquatic terrestrial transition zone, which
 47 is mostly covered by different types of floodplain forest (Wittmann et al. 2002b).

48 The MSDR is the largest Brazilian protected area devoted to the conservation of
 49 the biodiversity of floodplain forests, and one of the few functional protected areas

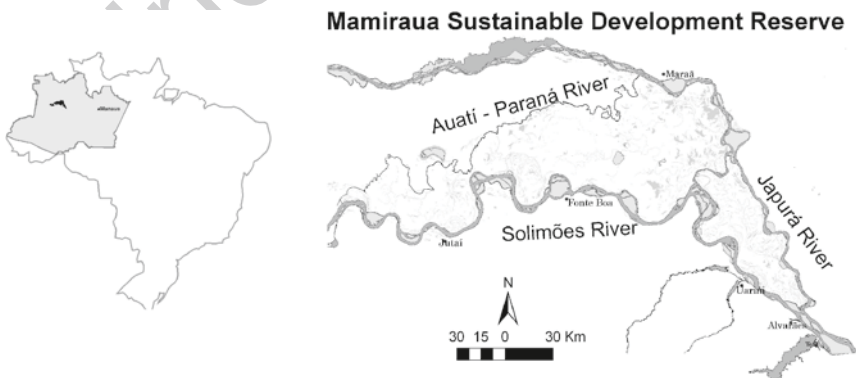


Fig. 22.1 Localization of Mamirauá Sustainable Development Reserve in Brazil

conserving the várzea forests in Brazil. Other reserves protecting várzea are 50
 Piagaçu-Purus Sustainable Development Reserve, Resex (*Reserva Extrativista*) 51
 Auatí-Paraná, Resex Unini, and Jutai-Solimões Ecological Station. 52

22.3 Biodiversity in the MSDR 53

The geomorphology of MSDR has provided a large number of aquatic habitats 54
 inside this protected area. They vary from the open water habitats such as rivers, 55
 and river branches (*paranãs*), streams (or channels) and lakes, to other perennial 56
 habitats such as backwater areas, or temporary ones such as water holes, pools of 57
 water in the forest floor and in the sands or mud of the beaches. 58

Differences in the elevation of terrain, and consequently, the duration of 59
 flooding, lead to the development of distinct terrestrial habitats during the low 60
 water season, with different vegetation structures and compositions in the várzea 61
 ecosystem (Ayres 1993). According to the protected area's management plan, about 62
 10.2% of the area is covered by permanent water bodies, and out of the remaining 63
 89.8%, 44.3% comprises low and high *restingas* (flooded forests located in higher 64
 levees), 31.3% is made of *chavascal* (flooded shrubby vegetation located in lower 65
 areas, Wittmann et al., this volume), and 14.2% is formed by other plant communi- 66
 ties (palm groves, grasslands, beaches and cleared lands and gardens) (Sociedade 67
 Civil Mamirauá 1996). Other habitat classifications have been put forward, 68
 Wittmann et al. (2002b), for example created a new classification system for veg- 69
 etation in várzeas based on aerial photography and satellite imagery, describing 70
 two main habitats – low and high várzeas (Wittmann et al., this volume). 71

The fauna found in Mamirauá shows some endemic species. There are also some high 72
 biodiversity figures in some specific taxonomic groups of the Reserve, such as in the fish 73
 fauna; which is more diverse than the adjacent black or white-water river sections. 74
 Mamirauá Reserve was created specially to protect the famous white uakari, *Cacajao* 75
calvus calvus, the only neo-tropical primate with a very short tail, covered in whitish fur 76
 and with a bald red face. Almost the entire range of distribution of this primate is located 77
 inside Mamirauá Reserve. Other endemic and very important primate species from 78
 Mamirauá is *Saimiri vanzolinii* the black-headed squirrel monkey. Other threatened spe- 79
 cies are also present, like the black giant caiman, *Melanosuchus niger*, the Amazon 80
 manatee, *Trichechus inunguis*, the jaguar *Panthera onca*, or the giant bonny tongue fish 81
Arapaima gigas. They are all very abundant in Mamirauá, although some of them are 82
 rare in many other parts of the Amazon (Queiroz and Fernandes 2001). 83

About 340 bird species are found in Mamirauá (Brangham 2000). The avian 84
 fauna of Mamirauá is placed within that of the High Amazon Province, in the 85
 domain of forests in environments with an aquatic influence. It can be said that this 86
 fauna represents the whole of the avian fauna of the várzea of the Solimões sector. 87

To date, about 340 fish species have been recorded in the MSDR and in the imme- 88
 diately adjacent bodies of water. There is little doubt that Mamirauá has an exception- 89
 ally diverse fish fauna. This is the greatest number of species ever registered for a 90

91 várzea environment. The reason for this diversity is probably the range of aquatic
92 habitats available and the wide environmental fluctuations that characterize the
93 hydrologic regime (Queiroz and Crampton 1999).

94 **22.4 History of Human Occupation and Use of Natural** 95 **Resources in Mamirauá**

96 In comparison to other areas in the Amazon, várzeas have always been considered
97 rich in fish and forest resources, and fertile soils (Ayres et al. 1996; Junk et al. 2000). [AU3]
98 This is due to the annual deposit of nutrients, which make várzeas very productive
99 ecosystems, which in turn allow for intense human occupation and exploitation of
100 natural resources. Social reproduction in the várzea is based in a way of life that is
101 intrinsically dependent on nature and its resources. Domestic production and con-
102 sumption, migration, and income are influenced by the availability of resources,
103 and by the water level variation. Modern human population in the várzea of middle
104 Solimões still has a deep interaction with the environment (Lima-Ayres 1992; Ohly
105 2000b; Alencar 2002).

106 Most of the population in Mamirauá is connected to floodplain environments.
107 Consequently, subsistence is contrastingly different from terra firme areas, and is
108 based on a multi-task seasonal calendar, where activities associated to fisheries,
109 hunting, timber extraction and agriculture are combined in accordance to the sea-
110 sonal hydrologic pulse of inundation. People living in the flooded forests are
111 involved in a large number of traditional management systems, and have a diverse
112 knowledge of traditional techniques for sustainable use of natural resources
113 (Queiroz and Peralta 2006).

114 In order to understand the importance of the Mamirauá várzea, it is helpful to look
115 at patterns of human occupation and use of natural resources in the area over the
116 years. Human occupation of the várzea in the middle Solimões River has been both
117 intense and sparse, depending on the period of time in question. Social factors have
118 determined patterns of occupation (Lima and Alencar 2000), although, environmental
119 aspects have had some influence. Land tenure, kinship, and economic, political and
120 religious systems, are the most influential features of social organization that deter-
121 mined patterns of human settlement in the várzea at the area of Mamirauá.

122 The use of natural resources in the várzea has been registered since the first
123 Spanish expeditions that went down the Amazon River in the mid-sixteenth cen-
124 tury, when the Amazonian várzea surprised first travelers with a large population in
125 settlements with hundreds and even thousands of inhabitants who occupied the
126 islands and uplands *restingas* (Lima and Alencar 2000; Ohly 2000b). Due to the
127 productivity of agriculture, hunting and fishing in várzea, this environment could
128 support much denser populations than in terra firme forests, which explains the
129 high demographic concentration and the dimensions of indigenous settlements
130 observed by the first travelers (Porro 1996). All this indicates a complex pattern of
131 occupation, with intensive use of natural resources.

During colonial times, most of the indigenous population that inhabited the várzea ecosystem at the time of the first European expeditions was decimated. By the end of the seventeenth century the Amazonian várzea was depopulated and infested with diseases brought by the white man (Porro 1996). Conflicts between the Spanish and Portuguese crowns over the control of the area resulted in wars, epidemics, and slavery, which reduced drastically the Amerindian population, with the most devastating effects over peoples inhabiting the margins of main rivers, such as *Omagua*, *Aisuari* and *Yurimagua* in the middle Solimões (Lima and Alencar 2000). Very few settlements were established in the Solimões várzea during the eighteenth and nineteenth centuries, and during this period, the exploitation of natural resources was carried out through expeditions from the urban colonial settlements toward rural areas in search of market-value commodities (*drogas do sertão*). But by that time, the Mamirauá area was already exploited by a small settlement founded by Spanish priests in the lower Tefé River, which would later become the town of Tefé (or Ega, during the eighteenth century).

In the beginning of the twentieth century, when the rubber economy dominated the Amazon, the occupation of várzea was limited since this ecosystem did not contain natural populations of *Hevea brasiliensis*. But most rubber tapers were attracted to the vicinity of Mamirauá, to exploit rubber in the middle Japurá River, north of the várzea area of the middle Solimões River. With the decline of the rubber economy, the growth of the demand for várzea products (like fish and timber) and the subsequent expansion of rural commerce in the 1920s, more settlements were established in the middle Solimões várzea. Most of these were based in areas dominated by the traders called patrons – who exchanged the várzea natural products with basic commodities – through what is called the *aviamento* system, a patron-client relationship based on debt bondage. Some of these settlements can be found still today, and some of the families of old times patrons are well known in the middle Solimões area.

From the 1960s, with the first signs of depletion of natural resources in the várzea, most patrons migrated to urban centres, and settlements dependent on this system of trade declined or even became extinct. Most inhabitants also migrated to cities and major towns, such as Manaus, Tefé and Coari. Encouraged by the local catholic institutions, the remainder of the population created new communities – a “term that connotes not only the settlement itself, but also implies a type of social organization where there is communal responsibility for the political decisions that affect the life of its inhabitants” (Lima and Alencar 2000). This type of social organization has been recognized as legitimate, and adopted by governmental and non-governmental institutions since the 1980s.

At present, more than 20,000 people of roughly 140 communities inhabit or use about 60–70% of Mamirauá várzea, and the social organization promoted by the local institutions from the Catholic Church, and endorsed by Mamirauá, is still in place. We will discuss further on in more depth the importance of the social movement of preservation, and its implication to the consolidation of protected areas of sustainable use, promoted by the local Catholic Church.

177 **22.5 The Sustainable Development Reserve Model**

178 Mamirauá Reserve was created back in 1984 as an Ecological Station by the
179 Federal Government, aiming the protection of the white uakari, one of the most
180 threatened primate species in the Amazon. This act was a result of a proposal made
181 by biologist José Márcio Ayres to the Brazilian environmental authorities. However,
182 this protected area had a very short life, and before it was lost in the middle of
183 administrative changes in the government at the end of the 1980s, it was turned into
184 an Amazonas State Ecological Station in 1990 (Ayres et al. 1996). Nevertheless,
185 Ecological Stations are protected areas that are devoted solely to protection, envi-
186 ronmental education and scientific research, and this category was not in accord-
187 dance to the traditional occupation of the area and the economic activities of the
188 inhabitants of the area (Queiroz 1994). Mainly to bring the situation of the manage-
189 ment of the protected area to more realistic levels, it was proposed its transforma-
190 tion into a new category created by the Amazonas State government, the SDR.

191 The impact of this new category of protected area in Brazil was considerable,
192 and Márcio Ayres, his group and their proposals had a very positive impact in the
193 National System of Protected Areas (SNUC). This system, approved by the
194 Brazilian Congress in 2000, brought to the Federal level the category of SDR.
195 Nowadays this category is well distributed in the Amazon, and also in other
196 Biomes, such as the Atlantic Forest (*Mata Atlântica*).

197 **22.5.1 Participatory Management**

198 The SDR model is based on the permanence of local populations in the protected
199 area and on the development of a solid scientific basis for natural resource manage-
200 ment. These two fundamental pillars, when acting in conjunction, create favorable
201 conditions for the social acceptance of management rules based on conservation
202 principles.

203 Before the transformation of the Ecological Station into SDR, an ample array of
204 scientific studies was produced in order to serve as base for the elaboration of the
205 management plan (Queiroz 2005a). This research program lasted for three years,
206 minimum amount of time considered necessary to obtain sufficient information for
207 the first management plan proposal, which was discussed with the local population
208 throughout 1995 and finally approved by the government in 1996. Scientific
209 research programs in the reserve continue and some of the results are referred to in
210 different chapters of this book (e.g., Wittmann et al., this volume, Oliveira-
211 Wittmann, this volume, Schöngart et al., this volume a).

212 The sustainable development model is implemented through the creation and
213 approval of norms and regulations for the use of natural resources, including the
214 zoning system. This zoning system, with its norms and regulations, was a result of
215 a long process involving the population in its elaboration and negotiation, and cul-
216 minating in a good level of appropriation and acceptance.

Integrated and participatory management of the protected area is consolidated in a management plan that contains the norms of use. Although indispensable, a scientifically based and well-accepted management plan is not a guarantee for effective conservation. The guarantee of an everlasting involvement and formation of a clear commitment of local populations toward conservation is only achieved through the establishment of a clear correlation between conservation and improved standards of living – accomplished both with generation of income, better health and education, and productive and technological enhancement - factors that combined may result in local sustainable development. Once this correlation is established, there is a reduction of human pressure on natural resources, especially on those species mostly impacted. The reduction, regulation, and limitation of this human pressure result in improved levels of biodiversity conservation, which are the main goals of the protected area.

Participatory management has taken place due both to the strategies developed by the leaderships, and to somewhat favorable social conditions, which albeit appeared adverse at first, in the long run contributed to the establishment and success of the initiative. As Lima (1999) argues “the involvement of the population in the establishment of the MSDR was facilitated by the precedence of the movement for the preservation of lakes, since the reserve responded to their [local people’s] need for legal support for the lake preservation movement”. The social movement for the preservation of lakes was instigated by catholic institutions, and was consolidated in the 1980s. The existence of this movement prior to the creation of the MSDR was critical to its implementation afterward. As occurred in other areas, the partnership between the social and environmental movements was a key to the implementation of MSDR and the protection of its várzea.

According to Reis (2003), the main motivation for the movement of preservation of lakes was the preoccupation of the communities with their own subsistence, which had been threatened by predatory fishing, intensified with the introduction of new fishing technologies in the 1970s, such as nylon gillnets and boats equipped with Styrofoam boxes to preserve the catch. These local institutions encouraged people to protect their livelihoods by identifying lakes into different categories (reproduction and subsistence) and protecting their territory of traditional use.

The MSDR has endorsed the social institutions established in partnership with the church. Participation at Mamirauá occurs through community and leaderships meetings, where most of the decisions regarding the management of natural resources are taken. Community organization is based on the idea that decisions over common-pool resources should be taken democratically, since they affect everyone. The social organization structure promoted by the church since the 1960s was based on this premise. Each community has elected leaders, who besides intermediating decision making inside their own communities, are also their representatives in other forums. In Mamirauá, communities are formed and organized based on strong kinship ties, thus many decisions are consensual results of negotiations between different interests. Besides community-level, there are three main forums for decision-making: sector meetings, the general assembly, and the deliberative council.

262 The MSDR is divided into political sectors, which are groups of nearby communities
263 that manage common resources. A lot of management decisions that only affect one
264 sector are dealt in sector meetings that occur every 2 months. Communities aggregated
265 into sectors discuss many management aspects such as zoning, protection and surveil-
266 lance of the sector. The representatives gathered in sector meetings discuss and decide
267 about the most important management actions for that particular sector, and provide a
268 very effective mean of local community participation.

269 Another forum for decision-making is the general assembly, when elected repre-
270 sentatives of each community meet once a year to discuss different issues in the
271 management of the protected area with other local institutions. Only community
272 representatives have the right to vote, although other participants may take part in the
273 discussions. The general assembly was the most important decision-making forum of
274 the protected area, where disputes were resolved and resolutions were taken.

275 In the year 2000, however, federal legislation (SNUC) determined that SDRs
276 should be managed through a deliberative council, composed of representatives
277 of the public sector and of civil society, including inhabitants of the protected
278 area. Mamirauá deliberative council is presided by CEUC (*Centro Estadual de*
279 *Unidades de Conservação*), the governmental institution responsible for the man-
280 agement of the area, and has representatives of the Brazilian Institute of
281 Environment and Renewable Natural Resources (IBAMA), the Amazonas State
282 University (UEA), local government, armed forces, fisher's union, Amerindian
283 population, and local population. While in the previous decision making system
284 of assemblies the decision was reached by vote of the representatives of the vil-
285 lages, in this current system the decision is reached by the vote of representatives
286 of the villages and representatives of other social groups mentioned above. The
287 implications in this new system of participation in the decision making process
288 are yet to be determined.

289 Different levels and forums of discussion allow for legitimating and appro-
290 priation of decisions, and enhance local population's ability to control and
291 manage their own resources. Disputes and conflicts that arise due to the existe-
292 nce of many different intra and inter community interests are dealt with in
293 other forums like sector meetings, general assembly, and ultimately in the
294 deliberative council.

295 Involvement and participation are also important in other levels. There is
296 always the need for accordance or approval by the local representatives for any
297 activity carried out in the areas of a particular village or group of villages.
298 Scientific research, visitation, guarding, and management in itself have to be
299 approved by locals or their representatives, who also are directly involved in
300 those activities. This system of involvement and participation, together with a
301 continued service of environmental education and circulation of relevant infor-
302 mation, grant the improvement of representatives through time, the high quality
303 of discussions and deliberation, and a good level of commitment of local popula-
304 tion with conservation of the protected areas (Queiroz 2005b; Queiroz and
305 Peralta 2006).

Governance of the reserves in such a participatory system is based on an effective alliance with locals. This alliance assumes that the involvement of members of local villages in all activities can be assured if those members have a clear perspective of the benefits derived from the protection of the areas, the conservation of local biodiversity and the sustainable use of local natural resources. This is probably the factor that raises more constituencies among local villages, gathering local political support and ensuring that a large part of the local population will contribute to the enforcement of rules and regulations previously agreed.

22.5.2 Zoning System

In Mamirauá, the zoning system was based mainly on the use of fish resources, the main type of natural resource exploited. The system proposed for evaluation originated from two main sources. One was the result of biological and social research, aiming to determine the distribution of occurrence of main species, and their traditional patterns of use by human populations (Sociedade Civil Mamirauá 1996). Research generated a series of maps where distribution of species and their use patterns were registered. It was imperative to identify how local communities historically distributed and utilized land and resources, so as to elaborate an equivalent system integrating local interests and scientific information. This traditional system was represented through the application of participatory mapping, which also served to identify areas of conflict. A process of negotiation was carried out to integrate the interests of different communities and produce a system of use that was truly implemented by local populations.

The other base for the zoning system was the system of use proposed by the movement for the preservation of lakes – the social movement promoted by the local Catholic Church. This church-based system divided the lakes into two main categories: (1) Maintenance lakes were directed at fishing for subsistence and (2) procreation lakes were preserved to guarantee the reproduction and increase of fish stocks. Despite the fact that this zoning system was not based on strong scientific evidence, and did not ensure protection and reproduction of natural stocks, the local population benefited from this system gathering experience in dealing with preservation strategies such as this, and introducing the issue of resource preservation and conservation in the communities. Thus the social movement for the preservation of lakes offered an important foundation for Mamirauá zoning system with different categories of use. These categories were adapted and transformed, to match their biological and managerial destination.

Mamirauá zoning system is basically composed of two main large zones: A zone for sustainable use, and a zone for total preservation (Fig. 22.2). The latter was created in order to protect genetic resources, acting as a source of stocks for adjacent areas, where sustainable use of natural resources is allowed. In total preservation zones no human activities are permitted besides research, monitoring and surveillance. In areas of sustainable use, resources are available for local



Fig. 22.2 Zoning System of Mamirauá Sustainable Development Reserve

347 people, but their use must be regulated by the norms of the management plan.
 348 In addition to these two main zones, there are also special management zones,
 349 areas where the use of a specific resource has to be regulated (Sociedade Civil
 350 Mamirauá 1996).

22.5.3 Norms for the Use of Natural Resources

351

The same biological research that generated information regarding spatial distribution of occurrence of species and their traditional use also provided important information on appropriate use practices. Such information was based on the biological characteristics of species studied, especially in relevant aspects of population dynamics (like recruiting, either by birth or migration, and mortality, either natural or induced by use). Therefore, important aspects like the reproduction of resources and their regeneration and resilience capacities were always considered, when known. These aspects were fundamental in generating management recommendations for key species like *pirarucus* (*A. gigas*), *tambaquis* (*Colossoma macropomum*), the Curimatidae and Prochilodontidae fish families, caimans, manatees, and also many important tree species (Schöngart, this volume; Schöngart et al. this volume a). Studies on hunting and agriculture, which were more related to the use of species, were also fundamental for understanding the spheres of action of local communities (Sociedade Civil Mamiirauá 1996). They also investigated technologies employed in the use of biodiversity and estimated their environmental impacts.

Researchers suggested norms based on these studies, which were then evaluated and debated with local leaderships. These norms established use restrictions by limiting effort and production – creating or reinforcing areas of protection or prohibition of use, establishing minimum sizes for capture, limiting the sex to be removed, creating limitations on the employment of some technologies, etc. These norms aimed at an ecologically sustainable use of resources, following the principle that an animal would only be exploited after it had the opportunity to reproduce.

The zoning system and norms of use were approved by the local population in voting sessions of the General Assembly, and were ratified by the Institute of Environmental Protection of the Amazonas State (IPAAM).

22.5.4 Economic Alternatives

378

Although the management plan considered the traditional use of natural resources by local communities, in some cases new norms of use and access were implemented. These new restrictions could cause socioeconomic impacts on local communities. Thus, some economic alternatives based on the results of scientific research were proposed as compensatory measures. These economic alternatives are either traditional or non-traditional productive activities with low environmental impacts. The objectives of these activities were: (a) to value the products of local biodiversity in the market, (b) to aggregate value to those products, (c) to avoid the decrease of local income due to the compliance to norms and restrictions of the management plans, (d) to promote a direct correlation between generation of income and conservation, with ample educational and demonstrative implications,

390 and (e) to raise income, whenever possible, promoting the welfare of local
391 communities.

392 These economic alternatives ally traditional practices of production to new ones,
393 such as diversification of species exploited (reducing pressure), commercialization
394 of products in new markets, economic management and access to credit. These
395 initiatives involved complex activities, such as the organization of producers,
396 training human resources, implementation of infrastructure adequate to production,
397 development of systems of market information to commercialize products (Viana
398 et al. 2004).

399 Natural resource management programs in Mamirauá act in three different
400 spheres: At the economic sphere, with generation of income; at the sociopoliti-
401 cal sphere, by creating systems of natural resource management that integrate
402 access to resources with participation of locals in its protection; and at the eco-
403 logical sphere, aiming to promote better conservation levels for renewable natu-
404 ral resources.

405 The implemented natural resources management systems were developed from
406 traditional practices allied to low impact techniques based on scientific research. A
407 monitoring system was built and is used in order to evaluate effectiveness of man-
408 agement models and practices. In some cases, these economic alternatives represent
409 the adaptation or re-structure of traditional activities, such as fishing, timber exploi-
410 tation, and agriculture. In other cases, new economic activities are introduced like
411 ecotourism (Peralta 2005) and exploitation of non-wood forest products (NWFPs)
412 (Wittmann and Oliveira Wittmann, this volume).

413 One important innovation of the implementation of economic alternatives inside
414 a protected area is the creation of a direct correlation between conservation and
415 generation of economic benefits for local residents. This connection is part of a
416 broader conservation strategy that includes other actions, such as systems of control
417 and surveillance, political strengthening of local groups and leaderships, and envi-
418 ronmental education and activities that promote community health. The promotion
419 of a clear correlation between conservation and generation of income has been the
420 main approach through which the model of conservation has been applied. An
421 example of this is the regulation of access to economic benefits from the conserva-
422 tion of biodiversity. The implementation of these economic alternatives resulted in
423 discussions about the regulation of access to resources. In fisheries management,
424 for example, commercial exploitation is today carried out through associations,
425 whose members have annual quotas, established according to their performance in
426 relation to some pre-determined criteria, such as participation in courses and meet-
427 ings promoted by the associations, participation in the community surveillance and
428 protection system, and their compliance to the management rules. Although each
429 member has access to a minimum quota for commercialization, the possibility of
430 raising this quota encourages fishermen to support conservation initiatives (Viana
431 et al. 2007).

432 Another example of this effect was produced by those communities and associa-
433 tions involved in the development of ecotourism inside Mamirauá. The profits
434 derived from this activity are divided among the communities that participated in

the initiative. Access to these monetary resources by the communities was also regulated. Direct economic benefits, like services and sale of products to the lodge, go to those who respect management rules (Peralta 2005). Besides, each community receives part of the profits according to their performance in the sustainable management of that area, and on the level of participation in conservation. It is important to note that communities themselves elaborated and regulated the system of access to natural resources.

Generation of benefits through the sustainable use of resources has promoted more local support and better levels of conservation than other more traditional methods of biodiversity protection, and it is probably one of the most important strategies for conservation of the Amazon today. The economic alternatives consolidated in the MSDR so far are fisheries management, forest management, ecotourism, and handicrafts production. The management of other resources, like ornamental fish, caimans and terrestrial wildlife are now under study and planning.

Most of the conservation targets present in Mamirauá were under intense pressure due to unsustainable use. For some natural resources this threat was documented by monitoring the levels and intensity of traditional use of natural resources in the reserves. In doing so, the need for intervention and implementation of sustainable measures was clear to all social actors involved. The kills of game animals, the catch of most important fish species, and all timber extraction in the area are examples of time series of data built with the participation or collaboration of local residents as for instance the monitoring of the *pirarucu* fishery from 1993 to 2006 (Fig. 22.3).

Before the implementation of this particular management system, more than 70% of all *pirarucus* produced in the MSDR under the monitoring network were

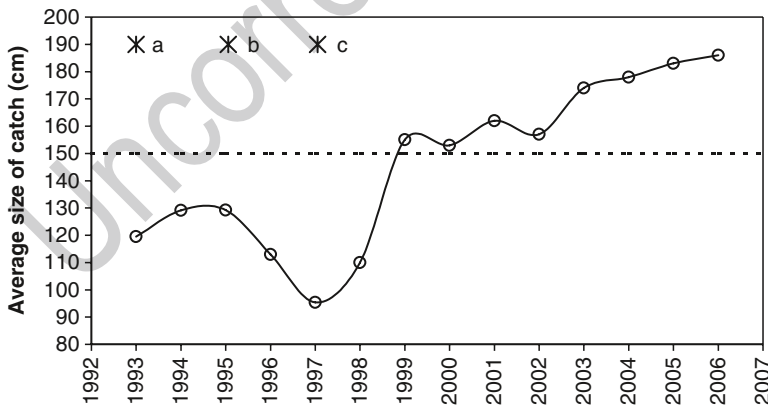


Fig. 22.3 Average size (total length in cm) of *pirarucus* caught from 1993 to 2006 at Jarauá sector, MSDR, represented by the open circles. The dotted line represents the minimum catch size of the specimen established in the current legislation. Marks represent important moments in the management history. **a:** In 1993 starts the campaign of public awareness and environmental education. **b:** In 1996 the management plan gets published with regulations for sustainable use of *pirarucus*. **c:** In 1998 begins the productive management system of *pirarucus* fisheries in the MSDR.

459 below the minimum size of catch established at the time by the IBAMA, which is
460 150 cm of total length. This evidence of bad traditional management and its conse-
461 quences was crucial to draw the attention of local social actors, especially the
462 fishermen inside the reserve, and led the way to the agreements about new regula-
463 tions and modifications in the behavior of local fishermen. The need for large-scale
464 change was evident, and the best way to promote this was engaging local social
465 actors in management of resources. Promoting best practices of sustainable use in
466 pilot management systems was an idea that followed the publication of Mamirauá
467 Reserve Management Plan, in 1995/96. Consequently, in 1998, after a series of
468 initial studies (Queiroz 1997; Queiroz and Sardinha 1999; Queiroz 2000) added by
469 further studies (Castello 2004, 2007; Viana et al. 2004), the most important pilots
470 of management systems were put in place. In that year, the promotion of sustainable
471 fisheries of *pirarucus* started.

472 Data has shown that this management system has been a success so far. The
473 populations of managed resources present good demographic parameters, the pro-
474 duction has been increasing and the producers were able to reach better markets,
475 and get better prices for their products (Viana et al. 2007). After a few years it was
476 clear to all local associations that all those involved in management systems were
477 better off.

478 Nevertheless, it needs to be emphasized that the pattern of natural resources use
479 did not change immediately after the implementation of actions of public awareness
480 and environmental education (1992/93), neither after the discussions with local
481 leadership for the agreement upon new regulations for protected area use, and pub-
482 lication of the management plan. Change did occur only immediately after the
483 beginning of the productive management and when the financial results of the new
484 trade were obtained after 1998 (Fig. 22.3).

485 Something similar happened to the management system of timber (Pires et al.
486 2001). As it is largely recognized, illegal logging in the Amazonian várzeas is one
487 of the most important threats to these forests, since more than 60% of the timber
488 exploited by the industry in the region comes from várzeas (Klenke and Ohly 1993;
489 Higuchi et al. 1994; Schöngart et al., this volume a). Even after a program of aware-
490 ness and environmental education (focusing also on loggers) was put into place in
491 1993, illegal logging continued in Mamirauá (Albernaz and Ayres 1999). Despite
492 local producers and local communities agreement on the need to stop unsustainable
493 exploitation of timber (including threatened or rare species), it was only when the
494 productive management of logging started, two years afterwards (in 1998) that
495 illegal timber extraction was really reduced inside the protected area (Fig. 22.4).

496 In the case of the management of timber resources, the effectiveness of the pro-
497 tection was obtained after two major groups of measures. At first, awareness and
498 education proved to be very effective, but a reasonably high number of illegal log-
499 gers were still operating inside the area. Secondly, when the productive manage-
500 ment was put in place, almost all the illegal logging was abolished inside the
501 protected areas. It is expected that the same effect will be accomplished in relation
502 to NWFPs, and also to ornamental fish and game animals, when their respective
503 management systems will be put in place in the near future.

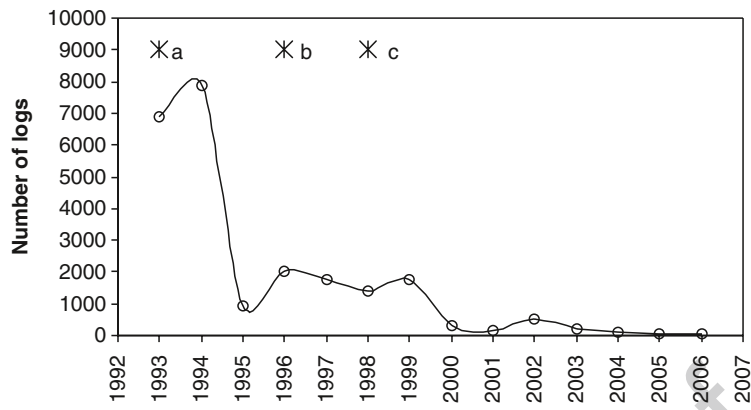


Fig. 22.4 Number of logs removed from MSDR between 1993 and 2006. Marks represent important moments in the timber management history. **a:** In 1993 starts the campaign of public awareness and environmental education in regard of illegal timber extraction. **b:** In 1996 the management plan gets published with regulations on logging inside the protected area. **c:** In 1998 begins the productive management system of timber extraction at the Reserve (Modified from Pires 2004)

Nevertheless, abolishment of illegal logging still does not guarantee an ecologically sustainable use of the timber resources. After scientific research was carried out in the MSDR through a partnership between the Mamirauá Institute for Sustainable Development (IDSM), National Institute for Amazon Research (INPA) and Max-Planck Institute for Limnology (MPIL), a scientific database was created to subsidize forest management. The studies focused on the successional dynamics of floodplain forests (Wittmann et al. 2002a, b, 2004; Wittmann and Junk 2003; Schöngart 2003; Wittmann et al., this volume). Furthermore, individual growth rates for many commercially important tree species of Mamirauá have been determined by tree-ring analysis and as the basis for modeling growth parameters (Schöngart et al. 2005, 2007; Schöngart, 2008; Schöngart, this volume; Schöngart et al., this volume b). This led to the determination of optimal minimum logging diameters and felling cycles that differed strongly from the values indicated by the Brazilian forest legislation (felling cycle of 25 years, diameter cutting limit of 45 cm). This shows that scientific parameters need to be found to guarantee a sustainable management, protecting the forest ecosystems and their multiple functions and at the same time providing resources for the local human populations improving their standard of living (Schöngart, this volume, Schöngart et al. this volume a).

22.6 Improvements in the Quality of Life 522

There are many different ways to represent the improvement of the quality of life in the areas of natural resources management of Mamirauá. The idea of “quality of life” itself is enormously difficult to define and quantify, and a great deal of indexes

526 and indicators have been created to describe it. Here we choose to represent this in
527 a few socio-economic indicators only, for the purpose to demonstrate how Mamirauá
528 became a reserve that provides a better quality of living for its resident population.

529 Income generation has increased a great deal in the area. In general terms, local
530 households improved their income in almost 110% in only a decade (1994–2004).
531 For those households directly involved in the managed fisheries of *pirarucus*, this
532 improvement was much higher (Fig. 22.5). Elevation of income has had impacts on
533 the improvement of health conditions and education levels.

534 Despite the fact that “quality of life” can be measured by different indicators, the
535 improvement in income generation has impacted many other aspects of social life,
536 like health and education of the villages inside Mamirauá. Although the increase in
537 income generation is considerable, the other social, cultural, political and economic
538 indicators were also important sources of attraction towards the management sys-
539 tems for all the marginal communities around Mamirauá. Maybe one of the more
540 important impacts of the improvement in income of locals in the reserve (as a con-
541 sequence of productive management of natural resources) is that infant mortality
542 was reduced almost four times during the last 15 years (Fig. 22.6). Infant mortality
543 is here measured as the number of one year old infants, or younger, deceased for
544 each group of thousand children born alive. During the period when this indicator
545 was monitored, there was a yearly 20% decrease.

546 Nowadays, many local associations found outside the MSDR request the expan-
547 sion of the systems of management, and most communities in the vicinity of the
548 reserve are also interested in implementing such systems, in similar basis. It is a
549 large improvement in the relationships with the people of the reserve and the people
550 living around them. These relations went from suspicion, in the first year after the
551 creation of Mamirauá, back in 1990, to participation, involvement, and agreement,
552 during the period of 1997 to 2004, to finally attraction, in the last 4 years or so.

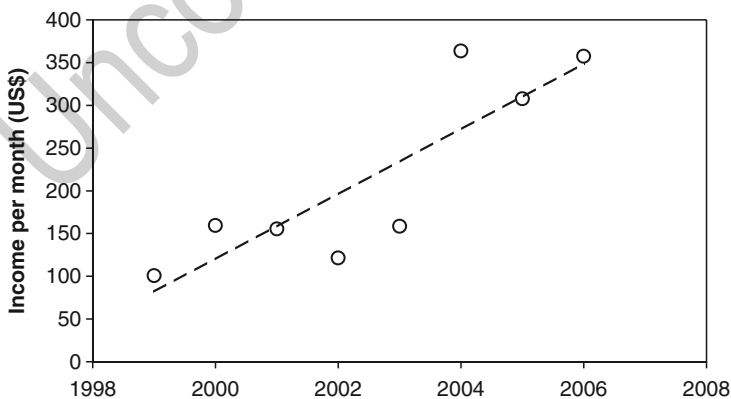


Fig. 22.5 Income (in US\$) per capita per month of fishermen involved in the management systems of *pirarucu* fisheries at Mamirauá, from 1999 to 2006 (data with data modified from Viana et al. 2007)

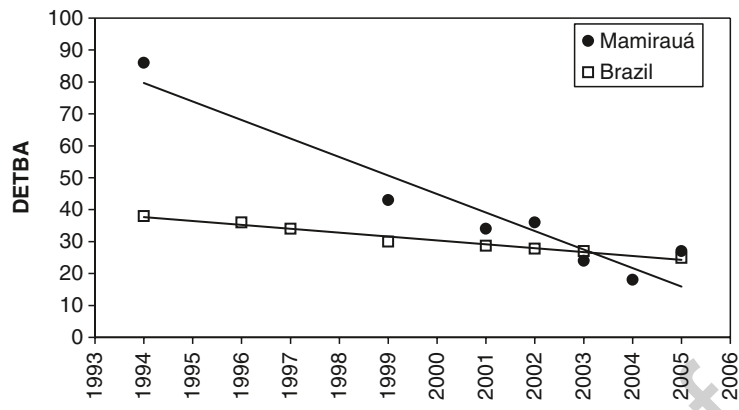


Fig. 22.6 Infant mortality (measured as the number of deaths for each thousand born alive, DETBA) at Mamirauá and in Brazil

[AU4]

The success of management systems implemented in Mamirauá has drawn 553
attention to this model of protected area. Up to date, 15 new SDRs have been 554
created only in the Brazilian Amazon (ISA 2008). Though, the abilities and commit- 555
ment to replicate the management models based on scientific and traditional 556
knowledge have yet to be demonstrated. One example of this is the replication of 557
pirarucu management experience. Other institutions established management sys- 558
tems in the várzea floodplains close to MSDR to promote *pirarucu* fisheries. It was 559
supposedly a replication of the original system, based on the same principles and 560
with the same objectives implemented in Mamirauá. However, attributes of the 561
original system, that is, efforts directed to enhance the organization of the local 562
associations, a careful annual survey for stock assessment, and a comprehensive 563
monitoring system failed to be arranged adequately. Nevertheless, this and similar 564
inadequate initiatives of replication have received official permits to fish large 565
amounts of animals during the last three years. Consequently, local organizations 566
involved were not capable to extract the annual permitted quota, trade is not based 567
in the principles of benefit sharing and there is no guarantee that these stocks are 568
adequately managed, and are under a considerable risk of collapse in the near 569
future. It is clear that the replication of management systems has to be carefully 570
planned and implemented. Nevertheless, lack of appropriate regulation and lack of 571
commitment to comply with available regulation, and the absence of strong links 572
with the local communities are the main sources of risk to these unregulated man- 573
agement systems based on the participation of locals, which may ultimately 574
threaten successful management systems implemented in vast areas. 575

Clearly, the legal framework to support sustainable use of natural resources inside 576
protected areas, and participatory management of natural resources as a whole need 577
more clarification and regulation by the Brazilian authorities. Perhaps most of the 578
problems identified so far, and briefly described above, could benefit from clear 579
official regulation. In addition to that, availability of strong and comprehensive data 580

581 on the biology of the natural resources to be exploited, as well as information on
582 social and economic aspects of management is crucial to the success of the system
583 implemented. Other important aspect for in-depth research is the carrying capacity
584 of different types of natural environments (with and without deep disturbances).

585 **22.7 Conclusions**

586 In the past 5 years, the monitoring systems implemented at Mamirauá have detected the
587 recovery of the populations of natural resources, which were declining in previous
588 years. A substantial decrease in the conversion of habitats was also observed in the last
589 16 years. Forested areas are no longer used for agriculture, only secondary forest. In the
590 same period, some vertebrates rarely seen before, such as wild cats, manatees and river
591 turtles are now more regularly sighted. These species have in common low reproduction
592 rates, long periods for maturation, and vulnerability to human pressure. Their recovery
593 suggests that protection measures implemented at Mamirauá are succeeding.

594 All the positive environmental and social impacts of Mamirauá described above
595 suggest that protected areas can be viable tools for the protection and conservation of
596 Brazilian várzeas. Since it is a highly populated ecosystem, the Amazonian flooded
597 forests are under intense human pressure. Depletion of natural resources tends to be
598 followed by biodiversity losses, and finally a large and wide degradation of the physi-
599 cal structure of the environment. Establishing effective protection in strategic portions
600 of flooded areas is vital for recovery of most stocks of natural resources.

601 Nonetheless, it is not easy to create and implement protected areas in várzeas,
602 and there are constraints to be considered. As a densely populated environment,
603 várzeas demand costly implementation of a protected area system. The conserva-
604 tion of this ecosystem also demands important action outside protected areas.
605 Successful and insightful experiences may provide a handful of best practices for
606 sustainable use of natural resources by local traditional population, despite being
607 inside a protected area or not. Large scale strategies for Amazonian conservation
608 necessarily call for involvement and participation of local traditional populations
609 living outside protected areas (Ayres et al. 2005). This is particularly relevant in
610 respect of várzea conservation.

611 The success of conservation strategies in the Brazilian Amazon is definitely
612 dependent on the capacity to involve local population in the management of
613 resources effectively (inside and outside protected areas), together with the creation
614 of protected areas. Local residents and other groups with cultural and economic
615 bonds to the area must be mobilized in order to promote sustainable use and conser-
616 vation. The protected areas should not be seen as islands of protection disconnected
617 from human social activities. Only when social factors are considered intrinsically
618 in conservation planning, the probabilities of success may be increased.

Author Queries

Chapter No.: 22 0001170111

Queries	Details Required	Author's Response
AU1	Please provide authors' affiliations.	
AU2	Sociedade Civil Mimirauá 1996 not in Reference list. Please check.	
AU3	Please fix if it is 2000a or b here and in further occurrences.	
AU4	ISA 2008 not in Reference list. Please check.	

Uncorrected Proof

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Abstract

The floodplains along the Amazon River and its large whitewater tributaries cover about 200,000 km², including river channels and floodplain lakes. Undisturbed, the floodplain forest would cover about 60% of central Amazonia. At the low-water level, about 25% of the region is covered by permanent water bodies and 15% by natural grassland. The actual area covered by water and by grassland varies considerably depending on the minimum water level in the respective year. The high percentage of floodplain forest points to its importance in the ecosystem. For human settlers who first reached the area about 12,000 years BP, abundant fish and game animals and fertile soils provided good living conditions. However, European immigrants developed different strategies to exploit the várzea and its high natural productivity, often at the expense of the floodplain forest. After World War II, increasing efforts were made to study Amazonian ecosystems, including the large river floodplains (Junk and Piedade 2004). The accumulated knowledge on the ecology of the várzea has been summarized in several books (Sioli 1984; Goulding et al. 1996; Junk 1997a, 2000a; Smith 1999). Unfortunately, even after 350 years of European occupation and after half a century of modern research, which provided a sound scientific basis regarding the ecology of the várzea, a fundamental understanding of the structures, functions, and processes of the várzea has hardly reached the conscience of many politicians and planners.

Chapter 23 1
The Role of Floodplain Forests in an Integrated 2
Sustainable Management Concept 3
of the Natural Resources of the Central 4
Amazonian Várzea 5

[AU1] **Wolfgang J Junk, Maria Teresa Fernandez Piedade, Florian Wittmann,** 6
and Jochen Schöngart 7

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23.1 Introduction 8

The floodplains along the Amazon River and its large whitewater tributaries cover 9
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[AU2]

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25 a sound scientific basis regarding the ecology of the várzea, a fundamental under-
26 standing of the structures, functions, and processes of the várzea has hardly reached
27 the conscience of many politicians and planners.

28 This chapter provides a short introduction to both the history of human occupation
29 of the várzea and its ecology. Special attention is given to the prediction of floods
30 and droughts, which provides a basis for the efficiency of the different management
31 systems. The current state of knowledge regarding fishery, fish culture, agriculture,
32 cattle- and buffalo-ranching, as well as forestry in the várzea is summarized.
33 Specific sections are devoted to the biodiversity and the carbon cycle, and the possible
34 impacts of climate change on the várzea and its management. We also point
35 out recent developments and problems and offer suggestions – taking into account
36 new scientific discoveries – that can improve systems designed to manage the
37 várzea while improving the quality of life of the local population.

38 **23.2 History of Human Occupation of the Amazon River** 39 **Floodplain**

40 The Amazon floodplain, locally called várzea, was colonized by Paleo-Indians
41 about 12,000 years ago, as shown by artifacts discovered at Caverna da Pedera
42 Pintada at Monte Alegre, near the city of Santarem at the lower Amazon River
43 (Roosevelt 1999). The fish bones and large shell middens that accumulated about
44 8,000 years ago indicate the importance of aquatic resources to the várzea's inhabit-
45 ants. The highly productive floodplain of the Amazon River consistently had the
46 highest human population density in the entire region (Meggers 1984). Roosevelt
47 (1999) postulated that indigenous kingdoms at the lower Amazon consisted of
48 many thousands of people living in settlements of many square kilometers at the
49 highest locations of the várzea or at strategic points nearby.

50 The high fertility of the várzea's soils and water result in high primary and second-
51 ary production during the aquatic and terrestrial phases and allows the sustainable use
52 of natural resources at quantitatively and qualitatively high levels. The predictable
53 periodic inundation provides a dry period for the production of terrestrial crops and a
54 flood period for aquatic ones. About 4,000 years ago, horticulturists planted cassava,
55 and about 2,000 years ago maize and tropical beans were cultivated. Native rice spe-
56 cies were first collected and, later, planted in suitable floodplain lakes. Abundant
57 mussels and snails, fishes, turtles, caimans, water fowl, and aquatic mammals pro-
58 vided animal protein throughout the year. The factors limiting human settlements in
59 the várzea were probably the small number of high-lying areas for settlement, inter-
60 tribal rivalries, and parasites and diseases that thrive in areas of high human density.

61 The first Europeans traveling along the Amazon River observed large settle-
62 ments along the River's shores, with luxurious home-gardens and plentiful food.
63 According to Denevan (1976), pre-Columbian population density in the non-flooded
64 upland, locally called terra firme, reached about 1.2 people per square kilometer,
65 but in the várzea it was as high as 28 people per square kilometer (average 14.6 people).

Soon after the arrival of the Europeans, tribal structures disintegrated, and imported diseases and slave raids decimated the local population within two centuries. Export-oriented, unsustainable exploitation of the area's natural resources replaced the sustainable subsistence systems of the Amazonian Indians. For instance, European style management of the abundant river turtles and manatees by a post-Columbian population that was much smaller than the pre-Columbian one led, in two centuries, to the near-extinction of these animal populations. Already in 1895, Verissimo blamed the destruction of the stocks of manatees and turtles on the European settlers and predicted the near destruction of the giant osteoglossid fish pirarucu (*Arapaima gigas*). Goeldi (1904) protested the destruction of white herons and red ibises at the lower Amazon and Marajó Island, which was due to the demand for the feathers of these shorebirds in Europe and North America. After World War II, valuable timber resources became increasingly exploited and large parts of the floodplain forest at the lower Amazon River were destroyed for jute plantations and cattle-ranching. In the 1940s, black caiman (*Melanosuchus niger*), and in the 1950s spectacled caiman (*Caiman crocodilus*) were overexploited because of their skins. The formerly abundant populations of these reptiles were dramatically reduced and are today protected.

In addition to environmental concerns, socio-economic and juristic problems challenge the sustainable use of the várzea. Many studies have described the socio-economic conditions of the riverine population, the land-use systems in place in the area, and the distribution of responsibilities in the resident families and communities (Noda et al. 2000; Lima 2005). Of special interest is the regulation of land ownership, which remains very complex and contradictory. The rivers and their floodplains belong to the government. However, despite the fact that there is no official documentation of land ownership, private properties are recognized or contested by the local population and can be bought or sold on a real-estate market. This situation has led to uncertainty and conflicts regarding land ownership and the rights to use the várzea's resources. Hence, there is a growing interest to resolve these questions by issuing documents that regulate land ownership in order to facilitate access to benefits such as rural credits. McGrath and Gama (2005) provided a detailed analysis of the problems related to land ownership. The legal basis for the use of the várzea's resources was analyzed by Vieira (2000) and Surgik (2005), that of land ownership by Treccani (2005) and Benatti (2005).

[AU3]

23.3 Ecological Characterization of the Várzea and Igapó Based on Management Considerations

The terms *várzea* and *igapó* are used by the Amazonian population to describe periodically flooded areas. They are also used in the scientific literature and were first defined by Sioli (1956), based on limnochemical parameters, and later confirmed by Irmiler (1977), with studies on benthic invertebrates, and Prance (1979), with floristic inventories. Várzeas are the floodplains accompanying nutrient-rich whitewater rivers, igapós the floodplains of nutrient-poor blackwater and clearwater rivers (Junk and

108 Piedade, this volume). The low fertility of its water and sediments makes the igapó of
109 blackwater rivers unsuitable for agriculture, cattle-ranching, and forest culture. Fish
110 biomass is about one fifth of that of the várzea (Saint-Paul et al. 2000). The nutrient
111 status of clearwater river floodplains is better but inferior to that of whitewater rivers
112 (Furch 1997, 2000; Furch and Junk 1997a). Considering the high biodiversity of the
113 igapó forest, the most suitable management of the igapó is by extensive fishery, eco-
114 tourism, and the sustainable extraction of non-timber products. Only the várzea has
115 the economic potential to support fishery, agriculture, ranching, and forest culture.

116 The várzea and igapó are pulsating systems, i.e., they alternate between a ter-
117 restrial and an aquatic phase. The conceptual considerations regarding pulsating
118 systems are described by the flood pulse concept (FPC) (Junk et al. 1989), which
119 has been recently rediscussed and updated (Junk and Bayley 2008; Junk and
120 Wantzen 2004; Junk 2005). The flood pulse of both the várzea and the igapó is
121 monomodal, predictable, and of high amplitude (Fig. 23.1). This favors the adapta-
122 tion of plants and animals to the change between the aquatic and the terrestrial
123 phase and allows sufficient time for organisms to make use of the floodplain's
124 resources. For example, fish migrate during rising and high waters into the flooded
125 forest to feed on fruit, seeds, terrestrial insects, and terrestrial detritus but also on
126 phytoplankton, periphyton, aquatic macrophytes, zooplankton, and aquatic insects
127 produced in the floodplain. At low water, fish migrate back into permanent water
128 bodies and river channels, and terrestrial plants and animals occupy the floodplain
129 (Fig. 23.2). There is an intense exchange of nutrients and energy between the rivers
130 and their floodplains. Flood pulsation increases and maintains habitat and species
131 diversity but also results in heavy losses within the plant and animal populations.
132 Organisms react with different strategies, including high reproduction rates, rapid
133 growth, and early maturity, to compensate for these losses. In the nutrient-rich
134 várzea, this behavior leads to high levels of primary and secondary production,
135 whose products can be used by humans. For details see Junk (1997a).

136 Its recognition of the events associated with rising and falling water levels sup-
137 ports the FPC's use as the scientific basis for broader concepts dealing with the
138 sustainable management of the várzea. The multiple use concept (Junk 2000a)

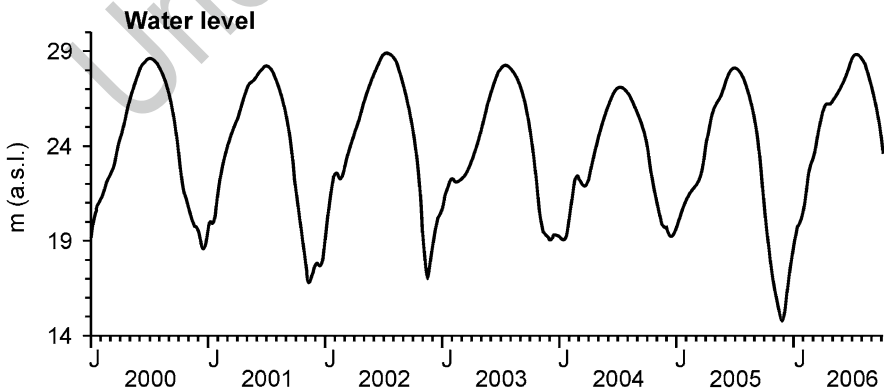


Fig. 23.1 Water-level fluctuations of the Negro River at Manaus. Data provided by the Manaus harbor authorities

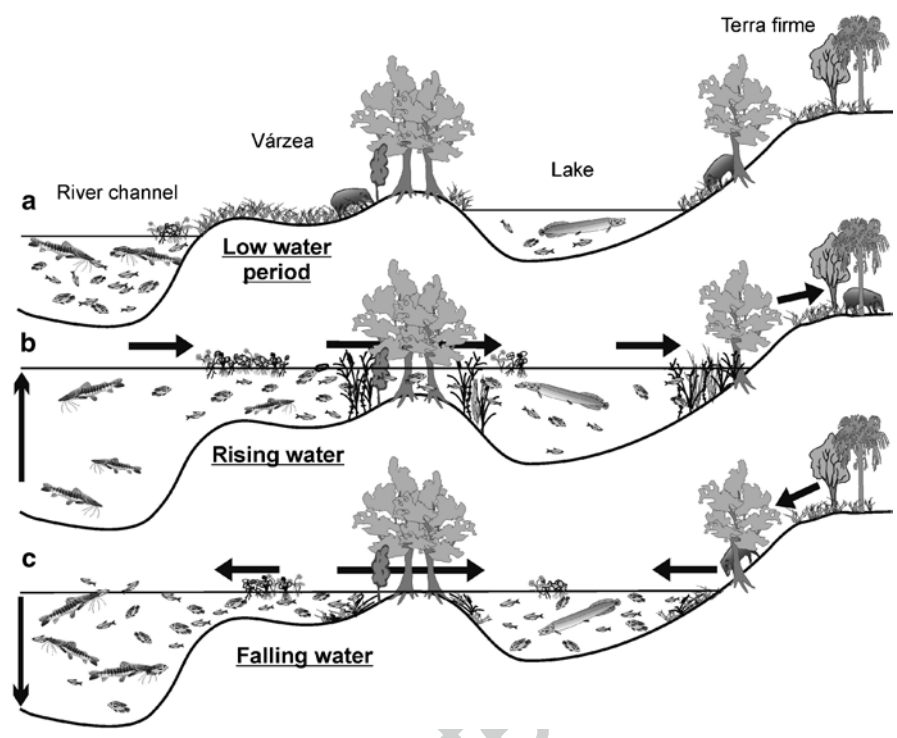


Fig. 23.2 Migrations of fish and terrestrial mammals between the river channel, floodplain lakes, floodplain, and upland at different water-level stages

concludes that the high productivity of the várzea during the aquatic and terrestrial 139
 phases can be best used by recognizing the complex interactions between the two. 140
 Large-scale changes in hydrology, e.g., by dikes to prevent flooding, will negatively 141
 affect productivity and thereby change plant and animal communities. Destruction 142
 of the floodplain forest reduces the availability of food for many commercially 143
 important fish species. Agrotoxics used by farmers during the dry period poison 144
 aquatic organisms, including fish and their larvae, at rising water levels. Optimization 145
 of the economic outcome of the different management options is required instead 146
 of maximization of the economic outcome of a single option, for instance by avoiding 147
 agricultural and cattle-ranching activities that may be prejudicial for fishery. 148

23.4 A New Model for Water-Level Prediction 149
as a Prerequisite for Efficient Resource 150
Management of the Várzea 151

All activities in the várzea are related to the water level. Although the flood pulse 152
 is predictable in its timing and height, there are variations of several meters in its 153
 amplitude (Fig. 23.1). This natural variability regulates the várzea's plant and 154

155 animal populations and contributes to the high biodiversity and productivity of
156 the system (Intermediate Disturbance Hypothesis; Connell 1978). For manage-
157 ment purposes, however, it creates serious problems. High floods destroy crops
158 and may kill livestock; low floods inhibit the extraction of timber from the flood-
159 plain, and very low water levels hinder navigation as well as the transport of
160 goods and result in large kills of fishes and other aquatic animals. A precise fore-
161 cast of the hydrograph is essential for the riverine population to adapt their activi-
162 ties accordingly and to minimize losses. Since 1989, monthly forecasts of the
163 maximum water level have been made from March to May by the Serviço
164 Geológico do Brazil (CPRM). The hydrological models are based on statistical
165 analyses of hydrological data sets.

166 Recently, a new method was proposed that may complement the CPRM
167 (Serviço Geológico) forecasts (Schöngart and Junk 2007). This method incor-
168 porates the fact that rainfall in the Amazon basin is influenced by El Niño and
169 La Niña events, which can be predicted by sea-surface temperature (SST)
170 anomalies of the tropical Pacific Ocean. High temperatures indicate El Niño
171 years, with low rainfall in the Amazon basin and low flood levels, and low
172 temperatures La Niña years, with high rainfall in the basin and high floods
173 (Schöngart et al. 2004). Temperatures correlate well with the high-water level
174 (Fig. 23.3). The forecasted and observed maximum water levels of the last 5
175 years are given in Fig. 23.4.

176 From 1950 to 2005 the minimum water level at the harbour of Manaus shows
177 a significant correlation with monthly SST anomalies in the tropical North
178 Atlantic (TNA, 05°–20° N/60°–30°W). The correlation between minimum water
179 level and monthly SST anomalies in the TNA is evident for 11 consecutive
180 months before the appearance of the minimum water level (Schöngart et al.,
181 submitted). Warm SSTs in the TNA are also the source of tropical cyclones and
182 hurricanes. Thus, there is a significant relationship between the minimum water
183 levels in Manaus and the accumulated cyclone energy (ACE) index (Trenberth
184 2005), since both are related to the increased SST in the TNA. In years in which
185 the ACE is above normal (median>117%), the water level in Central Amazonia
186 is 155 cm below the minimum water level of other years. Tropical cyclones and
187 hurricanes probably shift large amounts of humidity from the TNA to the
188 Caribbean Sea and Gulf of Mexico, leading to severe droughts in Amazonia
189 (Table 23.1).

190 **23.5 The Potential of Fisheries and Fish Culture**

191 **23.5.1 Fisheries**

192 Inland fishery plays an essential role in providing high-quality animal protein at
193 relatively low cost to the population. Estimates of the mean amount of fish consumed
194 by rural floodplain communities vary between 370 g day⁻¹ (Cerdeira et al. 1997)

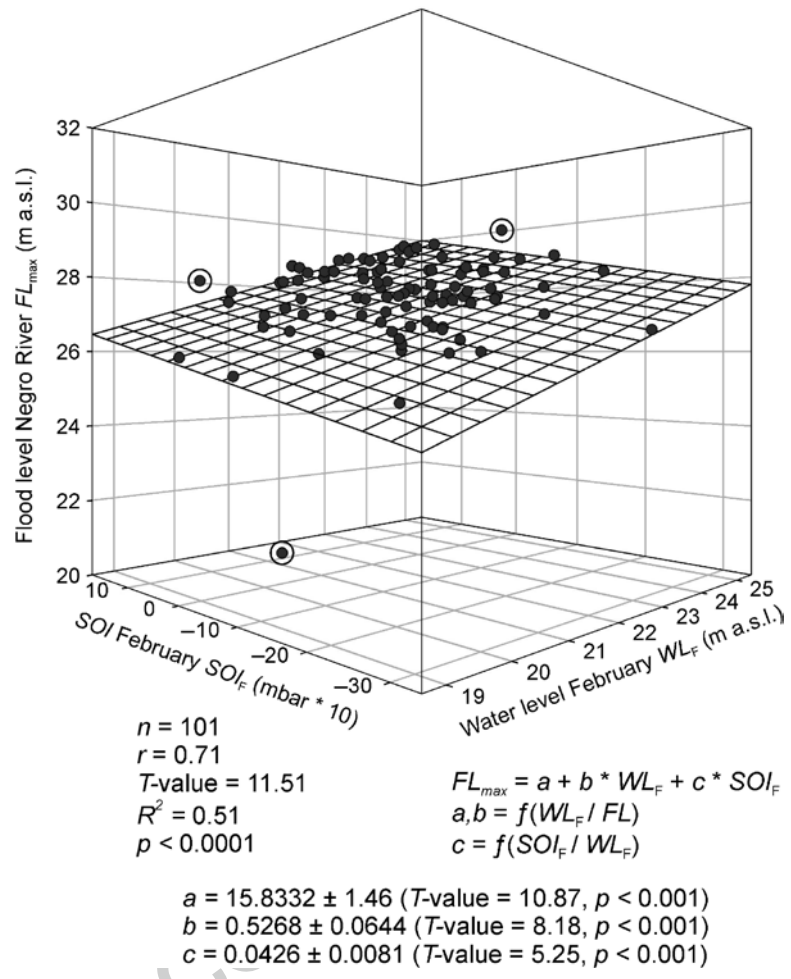


Fig. 23.3 Multiple regression model to forecast the maximum water level of the Negro River (Manaus) using the mean water level and southern oscillation index (SOI) for February during the period 1903 to 2004 (101 years). The model explains 51% of the variability of the parameters; only in 3 years (3% of the cases) does the model fail to predict the maximum flood level. The maximum water level is forecast by applying a simple model that uses the relationships between the mean water level in February and the maximum water level (parameters *a* and *b*) and the February SOI and the maximum water level (parameter *c*). Parameters and the standard errors are indicated (Schöngart and Junk 2007). Figure 23.4 in annex

and 400–800 g day⁻¹ (Batista et al. 1998; Fabr e and Alonso 1998) and by urban 195
 populations between 50 and 194 g day⁻¹ (Shrimpton et al. 1979; Smith 1979; Santos 196
 1986/87). The Amazon basin has an inland fishery potential of about 900,000 t year⁻¹ 197
 (Bayley and Petrere 1989), with inland fishery production recently estimated to be 198
 425,000 t (Bayley 1998). Of this amount, 79% is consumed in Brazil and 20% in 199
 Peru. These numbers indicate that the fishery potential of Amazonia is not fully 200

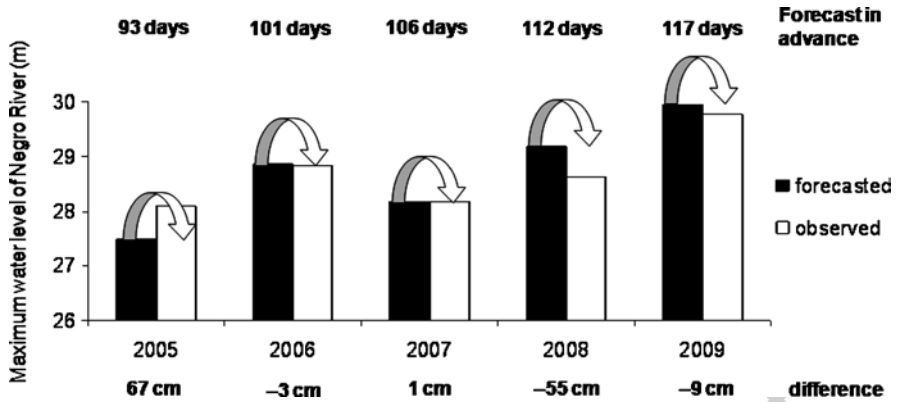


Fig. 23.4 Comparison between forecasted and observed maximum water levels of the Negro River at the port of Manaus from 2005 to 2009. The time span and difference between forecast and occurrence of the maximum water level are indicated

t1.1 **Table 23.1** Correlation of the minimum water level of the Negro River near Manaus and the
t1.2 accumulated cyclone energy (ACE) index

t1.3	1950–2005	ACE >117% (n=24)	Other years (n=32)	T-Statistics
t1.4	Minimum water	17.04±1.75	18.59±1.89	t=3.19 (p<0.01)
t1.5	level (m asl)			

201 exploited. More than half of the catch is captured by artisanal fishermen and
202 riverine communities for their own consumption. About 20% of the Amazonian
203 population lives in the várzea. The easy access to fish, fruit, and carbohydrates
204 avoids nutritional deficiencies. A portion of the region’s production is sold either at
205 small local markets or to professional fishermen and shipowners, who bring the fish
206 to urban centers. While about 200 species are captured, only 6–12 species make up
207 more than 80% of what is sold at the markets of major cities (Barthem and Fabrè
208 2004).

209 In the 1970s, an increasing number of fishing boats together with inadequate
210 fishery legislation led to conflicts between riverine communities and professional
211 fishermen, which, in Brazil, could not be resolved by centralized fishery manage-
212 ment. Therefore, by the early 1990s, the Federal Brazilian Environmental Agency
213 (IBAMA) opted to decentralize participative management of the fishery (Fisher
214 et al. 1992; McGrath et al. 1994, 1999; IBAMA 1994, 1997; Ruffino 1996; Isaac
215 et al. 1998), transferring some of the responsibilities and rights to local communi-
216 ties, which assisted in controlling the lakes in their territories and were granted
217 fishing rights in some of the lakes. The fish caught in those lakes can be used for
218 local consumption or sold to professional fishermen (*reserva de lagos, acordos de*
219 *pesca*). As a result of these benefits, communities began to protect their lakes. The
220 overall impact of this approach on the local fish stocks and the fishery has not been
221 evaluated yet; however, positive results are expected for the stocks of sedentary
222 species. Migratory species may be less affected while the impact on stocks of large

catfish, which migrate between the estuary and the headwaters of the Amazon River system, can be neglected.

Another approach was the delineation of reserves for sustainable management, such as in Mamirauá, where local communities, under the auspice of IBAMA and assisted by scientists, develop and test sustainable management methods. Experiments with the sustainable management of local stocks of pirarucu (*Arapaima gigas*) yielded encouraging results, and the method is now being applied also by other communities (Viana et al. 2003). In a multi-species fishery, this type of management of a large predatory species is based on the production of a small amount of a single highly prized species instead of a large amount of many lesser-prized species. This option is only possible in remote areas with comparatively low human population densities.

23.5.2 Fish Culture

Fish culture does not have a long tradition in Amazonia. The Indians stored live fish in tanks (Acuña 1865) but fish culture was not practiced, probably because it was obviated by the abundance of fish in rivers and lakes. The first experiments with fish culture were carried out in Belém, in 1920, by Rudolpho von Ihering, and continued by Pedro de Azevedo in the Brazilian Northeast (Ihering and Azevedo 1934, 1936). Today, 17 species are cultivated in the Brazilian Amazon, three of them exotics: *Cyprinus carpio*, *Oreochromis niloticus*, and *Tilapia* sp.. More than 4,300 culturists, 2,500 of them in Acre, raise fish on a total area of about 3,000 ha (Val et al. 2000). About 60% use extensive methods, only 1.8% practice intensive fish culture. Mean fish production in the state of Amazonas is currently 4.5 t year⁻¹. Tambaqui (*Colossoma macropomum*) and matrinchã (*Brycon melanopterus*) are cultivated successfully in tanks near Manaus and fed with pellets. They are sold when fishery supplies are low and prices are high. Tambaqui, pirarucu, and matrinchã are also produced in Colombia, Peru, Venezuela, and Bolívia. During the last few years, catfish (*Pseudoplatystoma* spp.) have been cultivated successfully in the state of Mato Grosso.

Despite the technological gains, fish culture in Amazonia is still in its beginning stages. A lack of research, insufficient technical assistance, high production costs, and difficult access to bank credits are among the limiting factors (Saraiva 2003). The availability of large amounts of clean water in most of the basin favors the development of fish culture, but large fluctuations in water availability during the annual cycle poses technical challenges for tank construction, such as excess water during the rainy season, a water shortage during the dry season, and large water-level fluctuations in large rivers and floodplain lakes. The danger of the escape of exotic species is reduced by the successful breeding of native species. However, established methods have been recently threatened by rapid advances in hybridization technologies. Hybrids often have faster growth rates than their parent species and are thus of particular interest for aquaculture. The negative side effects are that

264 they may escape into nature and establish viable populations that compete with
265 natural ones, or that they will cross-breed with specimen from natural populations,
266 thus diminishing genetic diversity. Thus, hybrid cultivation in Amazonian fish culture
267 requires intensive research aimed at avoiding these problems, e.g., by the produc-
268 tion of mono-sex hybrids or triploids.

269 It may be argued that fish culture on a major scale is economically not viable, as
270 long as there is productive fishery for the same species. However, stocks of highly
271 valuable species are, at least regionally, over-fished and prices are increasing; in
272 addition, fish production is highly seasonal, which leads periodically to low supplies.
273 Fishery is concentrated mainly along the large whitewater rivers whereas new urban
274 centers develop along the new highways, far away from the landing sites of fishing
275 vessels. Here, fish culture has the advantage of low transport costs from producer
276 to consumer.

277 Today, fish culture in Amazonia remains a complementary activity to fishery,
278 providing high-quality fish at reasonable prices during the entire year. Over the
279 long run, some species, such as tambaqui, pirarucu, and large catfish, have export
280 potential, but this requires large-scale production at low cost throughout the year.
281 This can, however, be achieved, as shown by Vietnam, which in two decades
282 established a catfish (*Pangasius pangasius*) culture industry whose current annual
283 production is more than 1 million tons, with a considerable portion being
284 exported. The várzea plays a minor role in fish culture not only because of direct
285 competition with regional fishery but also because of fluctuations in the water
286 level of large bodies of water, which create serious technological problems.
287 Nonetheless, the availability of cheap fish as food for highly prized carnivorous
288 species, such as pirarucu and large catfish, may provide opportunities in specially
289 adapted lakes.

290 23.6 The Role of Agriculture

291 Agriculture has economic potential only in the várzea, because of its relatively high
292 soil fertility and the renewal of nutrients during floods. The area of the várzea,
293 including lakes and river channels, is estimated to be about 200,000 km² (Junk
294 1997b). However, only about 5% is suitable for agriculture because these plots
295 fulfill the following conditions. (1) They are situated along river channels and lake
296 shores with permanent connections to the main river channel, allowing the transport
297 of agricultural products by boat to markets. (2) They are out of the water for a mean
298 of 9 months per year, which provides sufficient time for planting; this area corre-
299 sponds to the *várzea alta* (Wittmann et al., this volume). While watermelons and
300 certain types of beans (*feijão de praia*) need less cultivation time, farmers cannot
301 rely solely on these crops. (3) They are close to urban centers that offer markets for
302 the products. The different production systems have been analyzed by several
303 authors (Oliveira et al. 2000; Gutjahr 2000; Bueno et al. 2000; Hund and Ohly
304 2000; Noda et al. 2000; Lima and Saragoussi 2000; Junk et al. 2000b).

[AU4]

[AU5]

The major problems of agriculture in the várzea can be summarized as follows. 305

1. The period of plantation and harvesting is determined by the hydrological cycle, which is not in synchrony with the natural plantation cycle. The highest water level is reached about 3 weeks after the beginning of the dry season. Since the growth period of crops coincides with the dry season, when there is a water deficit in the soils, expensive irrigation is required for many crops. 306-310
2. When the river rises quickly, farmers may lose a portion of their crops. 311
3. Very high floods can lead to the loss of those perennial crops that are scarcely flood tolerant and are therefore planted on the highest levees, such as bananas, manioc, and papaya. 312-314
4. The concentration of production to within a specific period may result in an excess of products at the market and thus to a decrease in prices. 315-316
5. Várzea soils are very heterogeneous in structure because of small-scale changes in the sedimentation pattern. This limits the potential level of mechanization and the establishment of large monocultures. 317-319
6. There are severe deficits in infrastructure, such as transport, schools, hospitals, and a reliable supply of electricity. 320-321
7. There are periods of heavy insect molestation, e.g., mosquitoes, and horseflies, lead to extensive losses. 322-323

An economic analysis of the agrarian production systems of the várzea identified two different approaches. Traditional systems are low-profit subsistence systems in which diversified production minimizes the risks. These systems still contain many elements of the “caboclo culture,” considered by Parker (1989) to be a biological, cultural, and historical link to the floodplain Indians of post-contact Amazonia. Such elements are, for instance, the maintenance of species-diverse home-gardens and the practice of mutual aid systems, such as the preparation of cassava flour, the clearing of new land for farming, large-scale fishing and hunting operations, the construction and maintenance of community infrastructure, and mutual assistance in the case of diseases, accidents, travel, etc. (Noda et al. 2000). 324-333

Modern systems are labor-intensive and specialized, produce for local markets and compensate higher risks with higher profits, as shown in Table 23.2. Mutual aid is substituted by the regular payment of farm workers. Specialization directed at vegetable and fruit production is associated with the highest labor and land productivity, but the products are perishable. Production is feasible only near urban centers and the losses are high. During the last several years, efforts have been made to overcome the periodicity of the productive cycle. One such approach to maintain production during the high-water season is the planting of vegetables on the highest levees in wooden cages mounted on posts, to protect the crops from flooding. These efforts should be assisted by the government with on-farm research to overcome technical problems because: (1) even on small plots the várzea can sustainably produce enough to meet a considerable part of the local demand for fruit and vegetables and (2) they allows many people to remain in rural areas, because of the high demand for labor, rather than migrate to the over-crowded cities. Furthermore, well-targeted marketing campaigns can be used to revive interest in several local high-quality products that have 334-348

t2.1 **Table 23.2** Comparison of the land and labor productivity associated with different production
 t2.2 systems of the central Amazonian várzea (Modified from Junk et al. 2000b)

t2.3		Land	Labor	Gross farm	
t2.4		productivity	productivity	income	
t2.5		US\$ ha⁻¹	US\$ man⁻¹ day⁻¹	US\$ year⁻¹	
t2.6	Arable farming ^a				
t2.7	Staple-crop farming	424	2.32	1,781	
t2.8	Vegetable farming:				
t2.9	(mixed farming)	Low income	468	2.24	1,639
t2.10		Medium income	883	4.59	3,890
t2.11		High income	1,130	7.62	6,890
t2.11	Vegetables				
t2.12	(intensive)	Tomatoes	1,680	16.80	
t2.13		Cucumber	1,300	12.20	
t2.14		Lettuce	3,050	19.20	
t2.15	Fruits				
t2.16		Papaya	1,896	8.50	
t2.17		Passionfruit	1,846	8.00	
t2.18		Banana	916	8.00	
t2.19	Other field crops				
t2.20		Watermelon	430	16.00	
t2.21		Jute	480	1.80	
t2.22	Animal farming ^a				
t2.23	Cattle-ranching				
t2.24	(extensive)	Beef	33.8	4.90	
t2.25		Cheese	30.6	5.56	
t2.26	(intensive)	Milk	59.7	6.97	
t2.27	Water-buffalo ranching				
t2.28	(extensive)	Meat	32.9	11.25	
t2.29	Forestry^c				
t2.30	Selective logging		15 – 57 ^e		
t2.31	Forest culture ^c		79 – 237 ^e		
t2.32	Fishery^d				
t2.33	Actual		338		
t2.34	Potential		675		

t2.35 ^aJunk et al. 2000b

t2.36 ^bGutjahr 1996

t2.37 ^cDetails in Table 23.3

t2.38 ^dTheoretical production of comestible fish 90 g m⁻² year⁻¹ (Bayley 1983) with a market value of
 t2.39 US\$ 1 kg⁻¹; present use: 50% (Junk et al. 2000b). Cost for fishing effort: 25%.

t2.40 ^eBased on an exchange rate of 1 US\$ = 1.80 BR\$

349 disappeared from the market because of low acceptance, such as *taioaba* (*Colocasia* sp.)
 350 and *ariá* (*Calathea allouia*) (Bueno et al. 2000). These products can be reintroduced
 351 in the food offered not only to local people but also to tourists.

352 An over-reliance on specific crops can negatively affect biodiversity in the várzea.
 353 For example, in the middle of the last century, large areas were deforested for the
 354 cultivation of the fiber crops jute (*Corchorus capsularis* L. [Tiliaceae]) and, to a lesser
 355 extent, mallow (*Urena lobata* L. [Malvaceae]) (Homma 1998). When the boom

ended, in the 1980s, these areas were abandoned and subsequently became colonized 356
 first by large perennial grasses (*Echinochloa polystachya*, *Paspalum fasciculatum*) 357
 and later by a species-poor secondary forest that today represents the main forest 358
 cover of the lower Amazon várzea. This experience supports the need to protect at 359
 least part of the várzea alta because of its importance for biodiversity (see below). 360

23.7 The Impact of Cattle- and Buffalo-Ranching 361

In central Amazonia, cattle-ranching started at the end of the eighteenth century near 362
 Manaus to provide beef and milk for the population of the military post Barra do Rio 363
 Negro, later named Manaus. At the end of the nineteenth century, cattle-ranching was 364
 introduced in the várzea near Manaus and was carried out by immigrants from the dry 365
 northeastern part of Brazil. The traditional roots of cattle-ranching are detectable 366
 today in many areas of the várzea (Sternberg 1998). At the beginning of the twentieth 367
 century, most of the animals still came from natural pastures at the Branco River but 368
 two thirds of the imported dried meat was of Argentinean origin. In the 1890s, water 369
 buffalo were imported in the Amazon delta, a practice that spread slowly upriver. 370
 Today, small herds are found in the floodplains of most tributaries (Ohly 2000b). 371

Cattle- and buffalo-ranching are important economic activities in the várzea. 372
 Like all other natural and human activities in the region, they are strongly influenced 373
 by the hydrological cycle. The natural food offer for cattle and buffalo is limited 374
 because the várzea is a forested floodplain. All areas lying higher than 22 m (measured 375
 at Manaus harbor), corresponding to a mean flood period of up to 8 months 376
 per year, are covered by floodplain forest. Natural pastures grow only at the lowest 377
 parts of the floodplain, and as floating meadows in lakes and channels of the flood- 378
 plain. To keep the animals in the floodplain for longer periods, the rancher has to 379
 remove forest to provide pasture for animals at higher-lying areas. This negatively 380
 affects the stocks of the many frugivorous fish species, as well as silviculture and 381
 biodiversity, because many plant and animal species are closely related to the forest. 382
 Furthermore, the ranchers partially compete with farmers, who also require 383
 high-lying areas and produce much more per unit area and labor force. Even so, the 384
 rancher is continuously confronted with the dilemma of having too much pasture 385
 during low-water periods and too many cattle during high-water periods. 386
 The major problems of cattle-ranching can be summarized as follows: 387

1. Periodicity in the supply of pasture. 388
2. The risks of losses during high-water periods. 389
3. The lack of an efficient veterinary system. 390
4. Extensive production systems with low productivity. 391
5. Competition for space with agriculture and forestry and, thus, negative impacts 392
 on fish stocks. 393
6. Negative impacts on biodiversity because of large-scale destruction of the floodplain 394
 forest. Despite these problems, animal-ranching in the várzea continues to increase 395
 because the demand for meat is high and the price for the producer is stable and 396

397 attractive. Land productivity is low, but land is relatively inexpensive and animal
398 production needs a small labor force. This development will increase conflicts with
399 other stakeholders, mainly small landholders and subsistence farmers.

400 In order to minimize the risks and over-development of cattle- and buffalo-ranching,
401 the following measures should be taken (Pisarz 1995; Ohly 2000a; Ohly and Hund
402 2000; Hopf and Münchow 2000):

- 403 1. Ranching in areas near urban centers should be restricted to favor farmers who
404 produce perishable goods for the local market. Fencing should be obligatory to
405 avoid conflicts with other stakeholders.
- 406 2. Increases in beef production should be obtained by intensification rather than by
407 the expansion of ranch size, e.g., by better-adapted and specialized breeding
408 stocks for milk and meat as well as improvements in reproduction rates, animal
409 health (including the establishment of an efficient veterinary system), pasture
410 utilization (by rotational grazing and adequate stocking rates), the management
411 abilities of ranchers and farm personnel, and slaughtering, processing, and mar-
412 keting facilities.
- 413 3. Forests growing below the 25-m water level (measured at Manaus harbor) should
414 be protected from transformation into pastures, because the utility of such pas-
415 tures is low but the environmental impact of forest destruction is severe.
- 416 4. Water buffaloes should be kept only in small numbers and under human control
417 to avoid environmental destruction.
- 418 5. Alternative, economically viable feeding systems during the high-water period
419 should be developed to reduce weight losses by the animals, e.g. crop residues,
420 fodder from trees, and seeds from trees.

421 23.8 The Potential of Forestry

422 If we define forestry as the sustainable management of a forest for timber production,
423 forestry in the várzea is in its infancy. The classic home-gardens of the riverine popu-
424 lation can be considered traditional agroforestry systems (Lima and Saragoussi 2000;
425 Santos et al. 2004). Preliminary experiments with *Schizolobium amazonicum*
426 (*Paricarana*) for plywood and cellulose production are ongoing in eastern Amazonia.
427 Timber extraction by an expanding timber and plywood industry is of great economic
428 importance (Higuchi et al. 1994; Uhl et al. 1998). Compared with non-flooded fore-
429 sts, the costs of selective logging, skidding, and timber transport in várzea forests are
430 low because the timber is removed by boats and shipped to sawmills during the
431 aquatic phases (Barros and Uhl 1995). Thus, between 60% and 90% of the local and
432 regional markets in the western Amazon basin are still provided with timber from the
433 várzea (Kvist and Nebel 2001; Worbes et al. 2001). From about 900 tree species
434 (Wittmann et al. 2006a), only slightly more than 40 timber species are used (Parolin
435 2000; Kvist et al. 2001; Worbes et al. 2001). Species with low wood densities (0.20–
436 0.60 g cm⁻³) have mainly been commercialized for plywood production while those

with high wood densities ($0.60\text{--}1.00\text{ g cm}^{-3}$) are used for the construction of houses, ships, and furniture (Albernaz and Ayres 1999; Parolin 2000; Worbes et al. 2001). Nonetheless, only a few timber species are of commercial interest, such as *Ceiba pentandra*, *Virola surinamensis*, *Calophyllum brasiliense* and *Cedrela odorata*. However, due to unsustainable logging practices and a lack of information about the growth rates and regeneration, these species quickly disappeared from local and regional markets (Higuchi et al. 1994) and were subsequently replaced by alternative timber species, such as *Hura crepitans*, *Couroupita subsessilis*, *Ocotea cymbarum*, and *Sterculia elata* (Albernaz and Ayres 1999; Worbes et al. 2001).

A prerequisite for management models in tropical forests is the development of a method to determine the age and growth rate of the trees. In várzeas and igapós, the flood pulse reduces the wood increment during floods, such that annual tree rings of varying width form according to the length of the terrestrial phase. These can be counted and used for growth rate studies (Worbes 1989; Worbes and Junk 1989; Schöngart et al. 2002, 2004), allowing the determination of realistic growth and timber-production rates. Sustainable management systems of várzea forests are now under development and they are being tested in the Mamirauá Sustainable Development Reserve (MSDR), founded in 1990 and comprising 11,240 km² of várzea floodplains. The MSDR is part of a network of community-based local management systems that have been established in response to the results of socio-economic and bio-ecological studies, including those on fishery, agriculture, agro-forestry, ecotourism, and forestry (Sociedade Civil Mamirauá 1996; Ayres et al. 1998). The forest management program “Community Based Forest Management” (*Manejo Florestal Comunitário*), established in 1998, is a polycyclic selection system (Lamprecht 1986; De Graaf et al. 2003) in which the trees have a minimum logging diameter (MLD) of 45 cm, a cutting cycle of 25 years, and a maximum yield of 5 trees ha⁻¹, based on legal restrictions and the normative instructions established by the Brazilian Federal Environmental Institute (IBAMA). Commercial timber species facing extinction, such as *C. odorata*, *C. brasiliense*, *C. pentandra*, *Platymiscium ulei*, *Xylopia frutescens*, and *V. surinamensis*, are excluded from forest management and are protected. The most important timber species logged in the year 2003 were those with comparatively low wood densities (*H. crepitans*, *C. subsessilis*, *Maquira coriacea*, and *Ficus insipida*), but also included some species with higher wood densities (*O. cymbarum*, *Calycophyllum spruceanum*, and *Piranhea trifoliata*). Wood prices at the riverbank for softwood species were US\$ 7.90–11.40 m⁻³, and for hardwood species US\$ 15–20 m⁻³ (year 2003).

Growth curves from 12 low- and high-density timber species of the várzea were constructed in accordance with the sequences of tree rings (Schöngart 2003, 2008; Schöngart et al. 2007). In the várzea, low-density tree species surpass the MLD of 45 cm much faster than high-density species (Fig. 23.5). For all species, however, the MLDs defined by the growth models are greater than 45 cm, varying between 47 and 70 cm. The cutting cycles between the tree species vary almost tenfold, between 3 and 32 years. If current forest management practices are continued, the timber stocks of high-density woods in the várzea will be over-exploited, whereas the growth potential of low-density woods in várzea floodplain forests is not used efficiently.

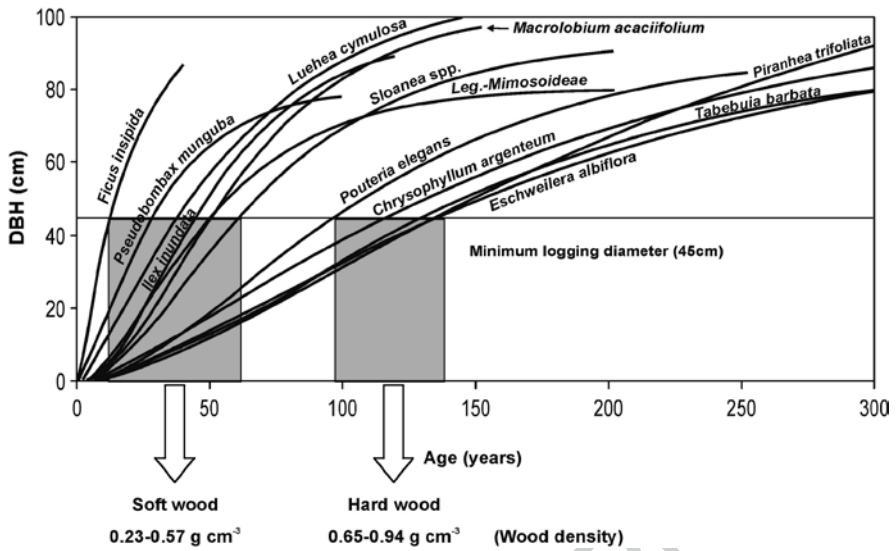


Fig. 23.5 Growth curves showing the mean cumulative diameters of 12 timber species of várzea forests. The trees are classified as low- and high-density species (Schöngart 2003). The minimum logging diameter (MLD) of 45 cm is indicated

482 Sustainable management of tropical forests requires data on species- and site-specific
 483 growth rates, tree age, and regeneration processes. To achieve a higher level of sus-
 484 tainability, Schöngart (2008) developed a management concept based on the timber
 485 stocks and growth rates of the different successional stages in the várzea. This
 486 Growth-Oriented Logging (GOL) concept is adapted to the forest's natural suc-
 487 cessional dynamics and allows for a higher degree of sustainability in tropical forest
 488 management, considering both the population structure and the wood increments of
 489 low- and high-density tree species. The development of similar concepts will pro-
 490 vide a powerful tool to promote sustainable management of timber resources in
 491 other forest ecosystems in Amazonia and in other tropical regions.

492 The sustainable use of timber stocks in the nutrient-poor igapó is, under the cur-
 493 rent management options, not practicable due to the low increment rates of its tree
 494 species (Schöngart et al. 2005; Stadler 2007; Fonseca Júnior et al. 2009). Therefore,
 495 floodplain forests of the igapó should be excluded from forest management and,
 496 instead, permanently protected.

497 23.9 The Impact of Different Management 498 Options on Biodiversity

499 The maintenance of biodiversity is a subject of worldwide interest and is becoming
 500 increasingly important in Brazilian politics. Floodplains are of specific importance
 501 because they harbor aquatic, terrestrial, and amphibious species in addition to periodic

visitors from adjacent deep-water and terrestrial habitats. Furthermore, they serve as resting sites on the flyways of many long-distance migratory bird species.

Detailed species lists of the many plant and animal groups are not available because there are no complete inventories. It is widely assumed that many species have yet to be described, mainly those belonging to terrestrial and aquatic invertebrates, bacteria, and fungi. Even in well-studied groups, such as fish, new species are discovered frequently. Our list of trees of the floodplain forest comprises more than 900 species (Wittmann et al., this volume), that of herbaceous plants about 400 species (Junk and Piedade 1993). We estimate about 600 fish species in the main channel and in the várzea near Manaus, and about 400 species of birds. The species list of the MSDR indicates 30 species of mammals, 34 species each for reptiles and amphibians, 348 species of birds, and 343 species of fish (Bannermann 2001).

But what do these numbers mean in the context of Amazonian biodiversity and what affects species diversity in the várzea? Junk (2000b) provided a theoretical approach to the development and maintenance of biodiversity in neotropical river floodplains. He pointed out the importance of the flood pulse, which leads to increased habitat diversity and habitat and community dynamics. The change between aquatic and terrestrial phases is a heavy stress factor that reduces the species number of strictly terrestrial groups, e.g., spiders and termites (Höfer 1997; Martius 1997), but also leads to adaptations and the development of endemic species, e.g., tiger beetles and pseudoscorpions (Adis 1997). These flood-adapted ecotypes increase genetic diversity (Ferreira et al., this volume).

Large rivers and their adjacent floodplains are corridors that are used actively or passively by organisms as dispersal routes (Fig. 23.6). This hinders speciation because of the lack of genetic isolation. Henderson et al. (1998) postulated that speciation occurs mainly in the headwaters and that species trickle downriver, where they become established or eliminated. This explains the rather great uniformity of phytoplankton, zooplankton, aquatic insects, aquatic macrophytes, and fish

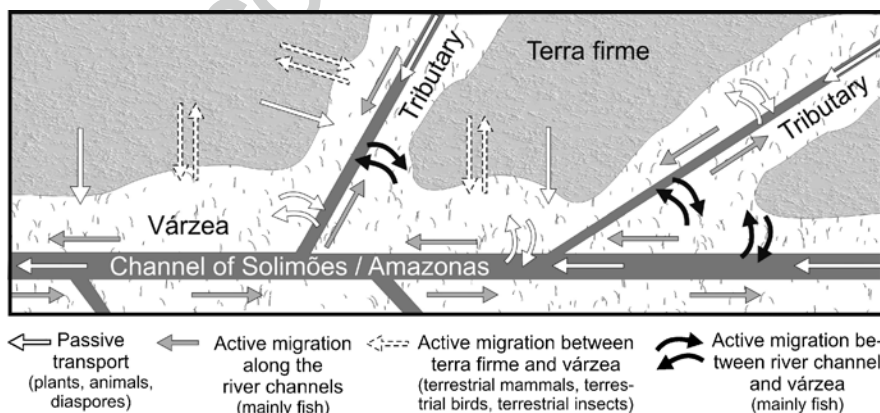


Fig. 23.6 Migration pathways and dispersal routes of organisms along the Amazon River system and between the rivers, their floodplains and the upland

530 over long stretches of Amazonian rivers, as described by Goulding et al. (1988) for
531 fish of the Negro River and as observed by Junk and Piedade (1997) for aquatic
532 macrophytes. Changes occur only when environmental conditions change, e.g., a
533 decrease in the flood amplitude at the lower Amazon River increases the number of
534 aquatic macrophyte species rooted in the sediment and the number of bivalves that
535 can colonize the lake sediments because of a sufficient oxygen supply (Junk, personal [AU6]
536 observation).

537 There is also a lateral immigration of terrestrial organisms from the adjacent
538 upland, as shown by Wittmann et al. (this volume) for trees of the floodplain forest.
539 Despite the high and prolonged inundations, várzea forests are the most species-
540 rich floodplain forests worldwide. The composition of tree species varies considerably
541 along the river course at the high várzea – which is flooded to a height of only up
542 to 3 m, corresponding to less than 50 days year⁻¹ – because in the adjacent upland
543 many species that have slightly flood-tolerant ecotypes colonize these areas.
544 Approximately one-third of the approximately 900 tree species recorded in várzea
545 forests across the Amazon basin also occur in upland forests (Wittmann et al.
546 2006a). Of the tree species common to both ecosystems, approximately 70% are
547 restricted to the high várzea. In várzea forests, these species show comparatively
548 low abundances, but they increase species diversity within the high várzea expo-
549 nentially. By contrast, low-várzea forests (mean inundation > 3 m in height) are less
550 diverse, and species similarity can be high over large spatial distances (Fig. 23.7).
551 The dominance of widely distributed low-várzea tree species is explained by the
552 longitudinal connectivity of forest communities via seed dispersal by the rivers.
553 Moreover, it reflects the selection pressure in response to the exceptional environ-
554 mental conditions in highly flooded sites, which lead to a restricted number of
555 highly flood-tolerant tree species.

556 Of overwhelming importance for the development and maintenance of biodiver-
557 sity is the floodplain forest. Besides adding a large number of tree species to the
558 species list, it offers specific habitats for many types of animals. The relationship
559 between the forest and populations of fish (Gottsberger 1978; Goulding 1980), birds
560 (Petermann 1997), and monkeys (Ayres 1993) has been well-studied. A very large
561 number of terrestrial invertebrates live permanently in the canopy or migrate periodi-
562 cally to the crown or the stem to escape the floods (Adis 1997). The maintenance of
563 the floodplain forest is therefore a key factor in preserving biodiversity.

564 **23.10 Management Options and the Carbon Cycle** 565 **in a Changing Global Climate**

566 Generally, the conditions for sustainable and integrated forest management and con-
567 servation are more favorable in the várzea than in the terra firme, as the former
568 consists of highly productive forest ecosystems, has plenty of commercial timber
569 species, and timber harvesting is simple and its costs are low (Schöngart et al. 2007).
570 The rapid depletion of nutrient stocks in the soils following the removal of large

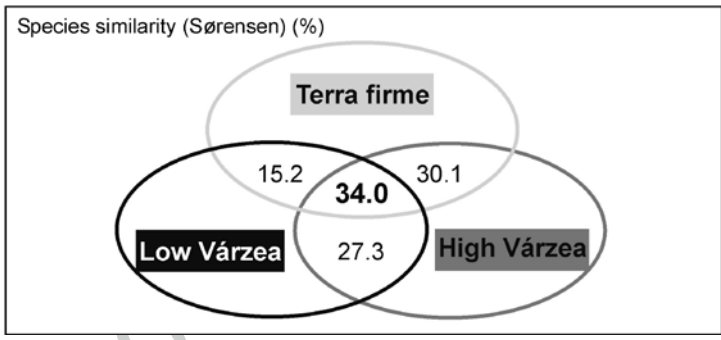
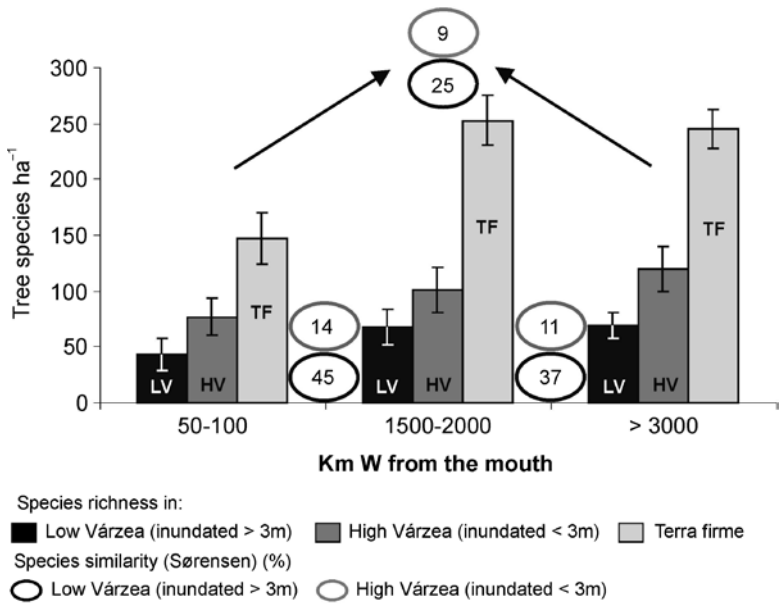


Fig. 23.7 Above: Tree species richness (species ha⁻¹) in low-várzea forests (LV), high-várzea forests (HV), and terra firme (TF) forests in the eastern, central, and western Amazon basin; and species similarity (circles, Sørensen 1948 fehlt !!!) between LV and HV of the three regions (for details, see Wittmann et al. 2006a). Below: Overall tree species similarity (Sørensen 1948 fehlt!!) (n= 918 várzea tree species) between low-várzea forests, high-várzea forests, and terra firme forests of the Amazon basin (Wittmann et al. 2006a; data for terra firme forests are from Oliveira and Mori 1999; Ribeiro et al. 1999; Pitman et al. 2001; Duque et al. 2002)

amounts of wood biomass, as reported for timber exploitation in Amazonian terra firme forests (Martinelli et al. 2000), is not a problem in várzea forests. The annually regular sediment load deposits sufficient nutrients to maintain both long-term fertility and the utility of floodplain soils (Furch 1997, 2000). Várzea floodplain forests are among the most productive tropical forest ecosystems. The volume increments of mature várzea forests are in the range of 10.1–16.2 m³ ha⁻¹ year⁻¹, and those of young successional stages are even higher, 43.7–51.9 m³ ha⁻¹ year⁻¹ (Schöngart 2003).

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578 There are two options for timber management in the várzea: (1) the management
579 of timber species in native floodplain forests such as carried out in the MSDR, in
580 which a polycyclic (selection) system is applied to community forest management,
581 and (2) reforestation of degraded floodplain areas with timber species in monocul-
582 tures, mixed cultures, or agroforest systems. The community forest management
583 approach operates with a 25-year felling cycle, allowing the extraction of 4.57–5
584 trees ha⁻¹, corresponding to 0.55–2.37 m³ ha⁻¹ year⁻¹ (0.16–0.67 mg C ha⁻¹ year⁻¹).
585 The annual gross income is between US\$ 15.42 and US\$ 57.07 ha⁻¹. In terms of the
586 productivity of várzea floodplain forests, these annual amounts of extracted volume
587 or wood biomass can be annually renewed; nevertheless, there are concerns regarding
588 the sustainability of this type of timber management (Schöngart 2008). Reforestation
589 with fast-growing low-density tree species may locally reduce exploitation pressure
590 on undisturbed forests, maintaining their ecological functions including climate
591 control, biodiversity conservation, and watershed protection. Reforestation of
592 deforested and degraded areas is likely to provide Brazil with credits from interna-
593 tional carbon markets, within the framework of the Kyoto Protocol and decisions
594 in the follow-up meetings of the United Nation Framework Convention of Climate
595 Change (UNFCCC). The former specifically considers the emissions from sources
596 and the removal by sinks that result from direct human-induced land-use change as
597 well as forest-related activities (deforestation, reforestation, and afforestation)
598 undertaken since 1990 (Binkley et al. 2002; Silver et al. 2004). Reforestation acts
599 as a carbon sink since it results in the build-up of carbon stocks in the newly estab-
600 lished biomass. When commercial harvests are accompanied by reforestation, the
601 effect of C-losses by land-clearing is offset, over the long term, by C-sequestration
602 and the accumulation of carbon stocks in the regenerating forest and by C-storage
603 in long-lived wood and paper products. The GOL concept for sustainable timber
604 production in the várzea and the reforestation of degraded and deforested areas
605 together constitute a powerful instrument allowing community-based management
606 to generate carbon credits in the future.

607 Fast-growing low-density tree species such as *F. insipida* (Schöngart et al. 2007)
608 are of particular interest in terms of their potential for the reforestation of degraded
609 areas. The lack of data on reforestation in Amazonian floodplains makes it difficult
610 to estimate an economic value of timber production in plantation forests. Table 23.3
611 provides rough estimates for four commercial tree species of the várzea floodplain,
612 two low-density tree species (*F. insipida* and *M. acaciifolium*) and two high-density
613 tree species (*O. cymbarum* and *C. odorata*). Based on the relationships between
614 diameter and crown area (Schöngart 2003), species-specific tree density ha⁻¹ was
615 estimated considering the MLD of a species (Rosa 2008; Schöngart 2008).
616 Relationships between diameter and stem height as well as stem height and form
617 factor (Schöngart 2003) were used to estimate stem volumes per hectare for the four
618 species and the results were then multiplied by the current wood prices (Schöngart
619 et al., this volume a) in order to roughly estimate the gross income per hectare and
620 year. The estimated annual gross income was found to vary three-fold among tree
621 species, between US\$ 237 ha⁻¹ (*F. insipida*) and US\$ 79 ha⁻¹ (*M. acaciifolium*);
622 however, these values are more than four times higher than those gained from

community forest management. Timber management in plantations has an even higher estimated economic value than cattle-ranching, but is still lower than that of agriculture (Junk et al. 2000b). The relatively long rotation periods, estimated to be between 17 and 63 years, are problematic for the establishment of management reserves such as the MSDR, but these predictions need to be confirmed by long-term studies, since the growth patterns of tree species in natural successional stages and in plantations vary considerably with respect to the different light regimes, soil conditions, and silvicultural treatments. Similarly, further studies combined with cost-benefit analyses are necessary to evaluate plantings on degraded areas and the effects of silvicultural treatments in improving wood growth and wood quality.

Many studies have shown that SSTs in the tropical Pacific basin and tropical North Atlantic influence both water-level fluctuations and discharge in the catchments of the Amazon's rivers (Marengo 1992; Coe et al. 2002; Foley et al. 2002; Schöngart et al. 2004; Ronchail et al. 2005). The El Niño-Southern Oscillation (ENSO) causes large-scale precipitation anomalies in the Amazon basin, which results in high flood levels of the Amazon River during La Niña events (cold ENSO phases) and low flood levels during El Niño events (warm ENSO phases) (Schöngart and Junk 2007). These interannual climate variations strongly impact tree growth in Central Amazonian floodplain forests (Schöngart et al. 2002, 2004, 2005). The predicted increase in SSTs in the tropical Pacific and Atlantic (IPCC 2007) are likely to lead to increased periods of drought (Malhi et al. 2008) and to lower floodings in the Central Amazonian floodplain forests (Schöngart and Junk 2007), thus affecting forest dynamics and the carbon cycle in the AGWB of floodplain forests.

23.11 Discussion and Conclusions

The complexity of Amazonian ecosystems and their tremendous biodiversity have allowed politicians, planners, and scientists to claim that there is not enough knowledge available for the elaboration of scientifically based development schemes. This erroneous opinion has led to programs that ignore already available scientific knowledge, and has resulted in costly and inefficient development projects that function on the basis of trial and error, without scientific underpinnings and with few lessons learned from failures.

There is no doubt that our knowledge on Amazonia is insufficient and that increased efforts have to be undertaken to provide the information required by modern Brazilian society for the sustainable use of Amazonian ecosystems. That said, there is also no doubt that during the last several decades our knowledge about the ecology of Amazonian ecosystems has increased considerably. At this writing, there are about 5,000 publications on different aspects of Amazonian floodplains. Many of them address very specific problems but there are also many reviews of the state-of-the-art for the different fields of interest. Scientific concepts, such as the flood pulse concept (Junk et al. 1989), the concept of decentralized participative

664 management (Fisher et al. 1992; McGrath et al. 1994; IBAMA 1994, 1997; Ruffino
665 1996), and the multiple use concept (Junk 2000a), have been developed in
666 Amazonia or with special reference to the conditions there. At a global scale, the
667 central Amazon floodplain is the best-studied floodplain in the tropics, despite the
668 fact that the density of its human population is relatively low and modern research,
669 which was initiated about a century ago, accelerated only after World War II (Junk
670 and Piedade 2004).

671 So, what exactly is the problem? In our opinion, it is the separation between
672 science and development. Basic ecological research is considered as an academic
673 exercise without applicable results. Planners avoid including scientists in develop-
674 ment projects because of the fear that their technological approaches will be
675 restricted and that they will be blamed for the failures. Scientists, on the other hand,
676 too often restrict themselves to descriptions of problems that are already suffi-
677 ciently known and to criticizing development schemes without offering proposals
678 for scientifically sound alternatives.

679 What, then, is the solution? We strongly believe that it lies in the willingness of
680 politicians and planners to include the scientific community in the planning and
681 execution of development projects and the agreement by high-level scientists to
682 participate in these projects and to share the responsibility for their success and
683 failures. "Learning by doing" can be a viable practical approach but it requires that
684 the lessons learned be thoroughly analyzed scientifically. Scientists must be willing
685 to submit their hypotheses to the test of practical viability. The third important
686 stakeholder group that must be included in this approach is the local population, as
687 sustainable management of natural resources cannot be achieved without the active
688 participation of local communities.

689 The approach laid out by Decentralized Participative Management is new for
690 Amazonia, whose natural resources were, until the 1990s, mostly under the juris-
691 diction of the central Brazilian government. The potential of Decentralized
692 Participative Management has by far not yet been exploited and should also include
693 other stakeholders. This would be an important step to achieve the goals of the
694 multiple use concept, which requires optimizing the output of a combination of
695 different management systems instead of maximizing the output of a single one.

696 Analyses of the production capacity of the different management systems and
697 their environmental impacts on the várzea indicate that fishery has the highest pro-
698 duction and the lowest environmental costs. Furthermore, there are many people
699 directly and indirectly involved in activities related to fishery. Therefore, the sus-
700 tainable management of fishery resources should have highest priority, and the
701 activities of other stakeholders should be restricted when the impact on fish stocks
702 becomes negative. The sustainable management of floodplain forests is another
703 "várzea-friendly" activity. As summarized by Junk et al., (this volume b),
704 Amazonian floodplain forests are very diverse and highly adapted forests, with high
705 productive potential in the fertile várzea. However, these forests require specific
706 management methods, many of which remain to be tested in practice.

707 Subsistence agriculture in combination with subsistence fishery provides living
708 conditions for many people in the várzea, although the economic return is relatively

Table 23.3 Estimation of gross income and carbon sequestration for plantation forests in the várzea, referencing two low-density (*Ficus insipida*, *Macarobium acacifolium*) and two high-density (*Cedrela odorata*, *Ocotea cymbarum*) timber species, based on estimated rotation periods, minimum logging diameters (MLD), estimated tree densities, basal areas, volumes, and actual wood prices

Tree species	MLD (cm) ^a	Rotation period (yrs) ^b	Density (trees ha ⁻¹) ^c	Basal area (m ² ha ⁻¹) ^d	Stem volume (m ³ ha ⁻¹) ^e	Wood price (US\$ m ³) ^f	Gross income (US\$ ha ⁻¹ rotation period ⁻¹)	Annual gross income (US\$ ha ⁻¹ year ⁻¹) ^g	Accumulated carbon in AGBW (Mg C ha ⁻¹) ^h	Mean C-sequestration rate (Mg C ha ⁻¹ year ⁻¹) ⁱ
<i>F. insipida</i>	55	17	110	26.1	196	20.55	4,024	236.73	59.2	3.5
<i>M. acacifolium</i>	49	54	131	24.7	178	23.89	4,251	78.72	72.5	1.3
<i>C. odorata</i>	38	45	196	21.7	144	66.67	9,579	212.87	67.5	1.5
<i>O. cymbarum</i>	53	63	115	25.7	191	34.44	6,570	118.26	109.9	1.7

^aData for minimum logging diameter (MLD) from (Rosa 2008; Schöngart 2008)

^bData for rotation period (time to reach MLD) from (Rosa 2008; Schöngart 2008)

^cTree density estimated by the relationship between diameter and crown area (10,000 m²/crown area) (Schöngart 2003)

^dStand's basal area calculated by the basal area of the MLD multiplied by the tree density

^eStem volume estimated by tree density multiplied by the basal area of the MLD, stem height (derived from the linear relationship between diameter and stem height), and form factor (calculated by a non-linear regression model relating stem height with the form factor) (Schöngart 2003)

^fWood prices indicated by Schöngart et al., (this volume a) calculated based on an exchange rate of 1 US\$ = 1.80 R\$.

^gAnnual gross income estimated by dividing the gross income per hectare by the number of years of the rotation period

^hEstimated by the equation: AGBW = 0.0509 × ρ × H × DBH², where AGBW is the aboveground coarse wood biomass, ρ is wood density, H is tree height, and DBH is diameter at breast height (Chave et al. 2005). Wood densities obtained by Schöngart (2003) and Wittmann et al. (2006b). Carbon content is 45% of the AGBW for fast-growing low-density tree species and 50% for slow-growing high-density tree species (Clark et al. 2001; Elias and Potvin 2003)

ⁱEstimated C-sequestration in AGBW during the rotation period

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709 small. Agriculture directed at fruits and vegetables has a high production potential
710 and economic return, but technologies and marketing have to be improved.
711 Agriculture is labor intensive and thus retains many people within the várzea who
712 would otherwise migrate to the cities. Because of the production of perishable
713 goods, agriculture should be concentrated in areas located near urban centers.
714 Agriculture destroys the floodplain forest of the species-rich high várzea and desta-
715 bilizes the várzea in general by reducing the established system of protection
716 against river currents during floods. Nonetheless, the area that can be exploited by
717 farmers is relatively small such that there is no need to limit smallholder
718 agriculture.

719 Animal-ranching occupies much larger areas and is expanding because ranchers
720 are economically strong, land is relatively inexpensive, prices for meat are high,
721 and the ranches need only a small labor force. However, land productivity is rela-
722 tively low and the environmental costs are high, as large areas of valuable flood-
723 plain forest are destroyed to establish natural and artificial pastures. Animal-ranching
724 competes with agriculture and forestry and negatively affects fishery. To increase
725 production, ranchers should invest in intensifying production instead of amplifying
726 the size of their ranches. Ranch size near urban centers should be restricted in favor
727 of farming systems.

728 The biodiversity of the várzea is strongly related to its habitat diversity, which,
729 accordingly, must be maintained by the different management systems. A key habi-
730 tat is the floodplain forests, since, in addition to many tree species, they harbor
731 numerous terrestrial invertebrates at the forest floor and in the canopy, and closely
732 interact with many species of fish, birds, and mammals. Preservation and sustainable
733 management of the floodplain forest is the greatest challenge in várzea protection,
734 because centuries are required to restore a species-rich mature floodplain forest.

735 To improve the productivity of the different production systems, demonstration
736 projects are required that transfer scientific knowledge into practice and which
737 combine scientific experimental design with practice-oriented execution. This
738 should be done with the close cooperation of scientific institutions, farmers, fisher-
739 men, cattle-ranchers, foresters, other stakeholders, and the State Government. Key
740 aspects should be economic viability, environmental impact, and socio-economic
741 acceptance. This would increase the land and labor productivity of both farming
742 and animal-ranching and would justify improvements in the infrastructure that
743 would also benefit the várzea population.

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AU4	Oliveira et al. 2000 not in Reference list. Please check.	
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Abstract

Amazonian floodplain forests have called the attention of scientists since the time of the expeditions of natural historians, because access to the central Amazon basin was possible only by the rivers and naturalists were impressed by the vast and deeply flooded forests. More detailed taxonomic studies started in Brazil at the end of the nineteenth century (Junk and Piedade, this volume). Since the 1960s, many studies were performed on limnology, fish and fisheries, general use of the várzea, the natural history of floodplain forests, and socio-economic aspects of the riverine population. These studies have been summarized in several books and proceedings (Sioli 1984; Ayres 1993, Goulding 1980; Goulding et al. 1996; Junk et al. 1997; Sternberg 1998; Smith 1999; Padoch et al. 1999; Junk et al. 2000a; and others). Detailed studies on biodiversity, primary production, ecophysiology and sustainable management started only a few decades ago. The results of these studies are presented in this book.

Chapter 24 1
Ecophysiology, Biodiversity and Sustainable 2
Management of Central Amazonian Floodplain 3
Forests: A Synthesis 4

Wolfgang J Junk, Maria T.F. Piedade, Pia Parolin, Florian Wittmann, 5
and Jochen Schöngart 6

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24.1 Introduction 7

Amazonian floodplain forests have called the attention of scientists since the time of 8
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17 Smith 1999; Padoch et al. 1999; Junk et al. 2000a; and others). Detailed studies on
18 biodiversity, primary production, ecophysiology and sustainable management started
19 only a few decades ago. The results of these studies are presented in this book.

20 Aim of this synthesis chapter is to summarize the information provided in the
21 individual chapters about central Amazon floodplain forests, to discuss the major
22 findings in a comprehensive approach, to call attention to major gaps, to point to
23 the economic potential of the sustainable management of the forests for the local
24 population, and to discuss actual and future threats including impacts of future
25 regional and global climate change.

26 24.2 Age and Evolution of Amazonian Floodplain Forests

27 The Amazon basin is a very old depression, which existed already in the Pre-
28 Cambrium period on the Gondwana continent. When South America separated
29 from Africa in the Early Cretaceous period, about 110 million years ago, the basin
30 became closed in the West by the uprising Andes. The paleo-Amazon drained west-
31 ward to a large depression which extended along the eastern side of the Early Andes
32 and was connected in the North to the paleo-Caribbean Sea. In the following periods
33 several marine transgressions occurred in the Late Cretaceous (83–67 Ma), the
34 Early Tertiary (61–60 Ma), and the Late Tertiary (11.8–10 Ma) periods, as indicated
35 by marine sediments. They alternated with periods in which freshwater swamps and
36 lakes prevailed. Large freshwater lakes were formed in the Tertiary period (Lago
37 Pozo in the Middle Eocene–Early Oligocene, 43–30 Ma; and Lago Pebas in the
38 Late Tertiary, 20–11.8 Ma). They were filled with sediments of riverine origin from
39 the Andes and the shields of Central Brazil and the Guianas. In the Late Miocene
40 (8 Ma), the connection to the Caribbean Sea and the Orinoco basin was closed by
41 the Vaupes Arch. The Amazon River opened its way to the Atlantic Ocean by
42 breaching the Purus Arch, and the modern Amazon drainage system incised large
43 valleys and floodplains in the soft sediments (Lundberg et al. 1998).

44 During the entire period, the area remained near the equator and we can assume a
45 hot and humid climate. During periods of marine transgressions, freshwater habitats
46 became separated from each other favoring speciation of aquatic and palustric organ-
47 isms by genetic separation. In periods of extended freshwater swamps and lakes, the
48 species conquered large areas and new habitats until the next marine transgression
49 separated the populations again. The large number of fruit-feeding and seed dispersing
50 fishes (ichthyochory) point to the co-evolution of floodplain forests and fishes. Fossils
51 indicate that over the course of the last 13.5 million years or longer, fish such as tam-
52 baqui (*Colossoma macropomum*), which apparently has not changed its diet of fruits
53 and seeds (Lundberg et al. 1998; Lundberg et al. 1998), have persisted.

54 During Quaternary times periodic oscillations in global climate led to alternating
55 glacial and interglacial periods which resulted in changes in the water level of
56 the oceans worldwide (Irion et al., this volume). These changes affected the lower
57 course of the Amazon River by increasing the slope during marine low water periods

(Irión et al., this volume). Dramatic hydrologic changes started approximately 900,000 to 600,000 years ago during the so-called Mid Pleistocene Revolution (Berger and Wefer 1992). From this time on sea level changes reached 100 m and more, and affected the floodplains along the lower courses of all large Amazonian rivers until 3,500 km inside the continent. During marine low water periods, the rivers excavated deep valleys, which they filled up with sediments during the following interglacial high sea levels. Parts of the old sediments remained and form the Pleistocene várzeas. These areas can be found at the today's high water level or they reach up to 20 m or more above it. The height of some Pleistocene várzeas in western Amazonia is in part explained also by a slow raise of the area by tectonic activity. The fluvial origin of the Pleistocene várzeas can be shown by geomorphologic features characteristic for river floodplains, such as ridges and swales, but also by mineralogical and chemical composition of the sediments, which show much larger similarity to the recent river sediments than to the surrounding tertiary soils (Irión et al., this volume).

During the last glacial period, the sea level was about 130 m lower and the slope of the Amazon river several times larger than today. This had a dramatic impact on the hydraulic geometry of the Amazon River and its large tributaries. There is a controversial discussion about the paleo climate in Amazonia during the last glacial period. Several authors postulate a dryer and cooler climate and the retreat of the Amazon rain forest to a few forested areas interspersed in savannah vegetation (refuge theory) summarized by Haffer and Prance (2001). Other authors reject this theory, summarized in Colinvaux et al. (2001). Studies of Irión et al. (this volume) on a 50 m sediment core of the mouth bay of the Tapajós River also do not support this assumption. Considering an increased slope of 130 m to the Atlantic Ocean and a similar discharge than today, we postulate that the Amazon River changed its behavior from interglacial meandering to glacial braiding with high current velocity and strong erosive forces. At that time, the floodplain surface of the Amazon River near Manaus was about 40 m lower (Irión et al., this volume). Fluvial-morphologic units were subjected to a much higher dynamic than today and probably had turnover periods of a few decades to centuries in comparison to today's turnover periods of centuries to millennia. We assume that therefore much larger areas were covered by pioneer forests or early successional stages than today, but there were certainly sufficiently large areas available with turnover periods of several centuries to allow the development of mature floodplain forests dominated by the respective set of species. Today's large number of flood adapted trees point to low extinction rates during long geologic periods.

24.3 Extension, Distribution and Classification of Wetland Forests

Estimates about the extent of wetlands in Amazonia vary considerably. The highest number was given by Klinge et al. (1990) and Junk (1993) who related about 1 million square kilometers to large river floodplains and large interfluvial wetlands and another

99 one million square kilometers to narrow stripes of riparian wetlands along streams and
100 low order rivers. The first number has now been confirmed by the analysis of remote
101 sensing data (Melack and Hess, this volume). Extended wetlands occur in the upper
102 Madeira River, the Negro River, the Araguaia River, and along the Amazon River and
103 its white-water tributaries Purús, Juruá and Japurá. According to these authors, about
104 80% of the flooded area is covered by flood tolerant forest and shrubland. Our studies
105 show that most of the wetlands along low order rivers are covered by riparian forest.
106 If Junk's estimate of 1 million square kilometers of riparian wetlands holds true, the
107 total area of forest subjected to periodic water logging or long term flooding increases
108 to about 1.8 million square kilometers, corresponding to one fourth of the Amazon
109 basin and 35% of the central Amazonian rain forest area of about 4.6 million square
110 kilometres. The remaining 200,000 square kilometres belong to riparian forests in the
111 *cerrado* belts. This estimate changes dramatically the view on the Amazon rain forest,
112 which has been described largely as non flooded, *terra firme* forest. Flooding or water
113 logging of the soil has to be considered an environmental factor that affects 40% of the
114 forests in the Amazon basin, with far reaching consequences for the physiology of the
115 trees and edaphic processes, which affect the entire biome including the atmosphere.
116 This aspect has been neglected so far in ecological studies concerning the role of the
117 Amazon rain forest in the global climate change debate, as well as the impact of
118 regional climate change scenarios on Amazonian wetlands and their vegetation.

119 Amazonian wetlands occur in great heterogeneity. A classification system is still
120 missing, but urgently needed (1) for a better comparability of the results of wetland
121 studies, (2) for the elaboration of research projects to close major gaps in wetland
122 research, and (3) for the establishment of a national wetland policy to sustainably
123 manage and protect wetlands and their resources, including biodiversity. First
124 attempts to elaborate such a classification are ongoing in the State of Amazonas
125 (Junk and Piedade 2005) and the Pantanal (Nunes da Cunha C and Junk, in press).
126 These classification efforts base on hydrological and hydrochemical parameters, as
127 did Prance (1979), who elaborated the first classification system for Amazonian
128 wetland forests. We consider this approach very useful and have adopted it with
129 minor modifications (Junk and Piedade, this volume; Table 24.1).

130 As Wittmann et al. (this volume) have shown, species composition in floodplain
131 forests varies considerably according to the position on the flooding gradient but
132 also along the river axes and between river basins. Therefore the major classifica-
133 tion units in Table 24.1 will be subdivided in future in different subunits according
134 to species composition, as soon as enough regional data are available.

135 **24.4 Evolution, Species Diversity and the Tree Species** 136 **Colonization Concept**

137 **24.4.1 *Tree Species Diversity***

138 Despite consisting of partially highly adapted and many endemic tree species,
139 Amazonian floodplain forests are the most-species rich floodplain forests worldwide

Table 24.1 Key to the principle types of Amazonian forests subject to inundation, according to Prance (1979), modified	t1.1
Periodically inundated forests	t1.2
Flooded by regular annual cycles of rivers	t1.3
White-water	t1.4
Black-water and clear-water	1. Seasonal várzea t1.5
Flooded by tidal movements	2. Seasonal igapó t1.6
Saltwater	t1.7
Freshwater backup	3. Mangrove t1.8
Flooded by irregular rainfall (flash floods)	4. Tidal várzea t1.9
Long-term inundated forests^a	5. Riparian forests along low-order rivers ^a t1.10
White-water	6. Várzea swamp forest, várzea chavascal ^a t1.11
Black-water and clear-water	7. Igapó swamp forest, igapó chavascal ^a t1.12
^a Our modifications	t1.13
	t1.14

(Wittmann et al., this volume). The importance of increased habitat diversity and isolation of subpopulations by river dynamics for speciation has already be pointed out by Salo et al. (1986) for sub-Andean western Amazonia where geologic activity and river dynamics are much higher than in central Amazonia. Flooding and the hydro-ecologic connectivity of the vast Amazonian river system allow for ecological processes and predictable aggregations of tree species over huge geographic distances. Nonetheless, with an increasing species diversity from eastern to western Amazonia, tree species diversity variations and oligarchies in Amazonian floodplains seem to follow environmental gradients and rules similar to those of Amazonian terra firme. This demonstrates the existence of intense ecological interactions and species migrations between both ecosystems (Wittmann et al., this volume).

Low-várzea forests are richer in endemic tree species than high-várzea forests, where continuous species migrations between flooded areas and the non-flooded uplands are most probable to occur (Wittmann et al., this volume). Together with the evidence that high-várzea forests are floristically more similar to the uplands than low-várzea forests Wittmann et al. (this volume) proposed a Tree Species Colonization Concept for Amazonian floodplain forests (Fig. 24.1).

The concept implies that flooding and the associated hydro-geomorphologic dynamism of the Amazonian rivers act as a natural regime of disturbance on tree species establishment and distribution, thus providing extreme environmental conditions, which directly influence on speciation processes throughout the Amazon basin without requiring geographic or tectonic barriers. Therefore, periodic floods combined with the related hydro-geomorphologic dynamism of the rivers maybe one of the most important environmental triggers for speciation (Ferreira et al., this volume; Wittmann et al., this volume), and thus one of the main reasons for the exceptional high tree species diversity within the Amazon basin. There are some evidences that large part of recent equatorial upland forests were influenced by floods during one or several periods of landscape evolution, especially during Pleistocene and Holocene warm periods, when the sea-level was comparatively high (Irion et al., this volume). On the other hand, constantly migrating river-channels especially of the Amazonian white-water rivers affected large part of western equatorial Amazonia,

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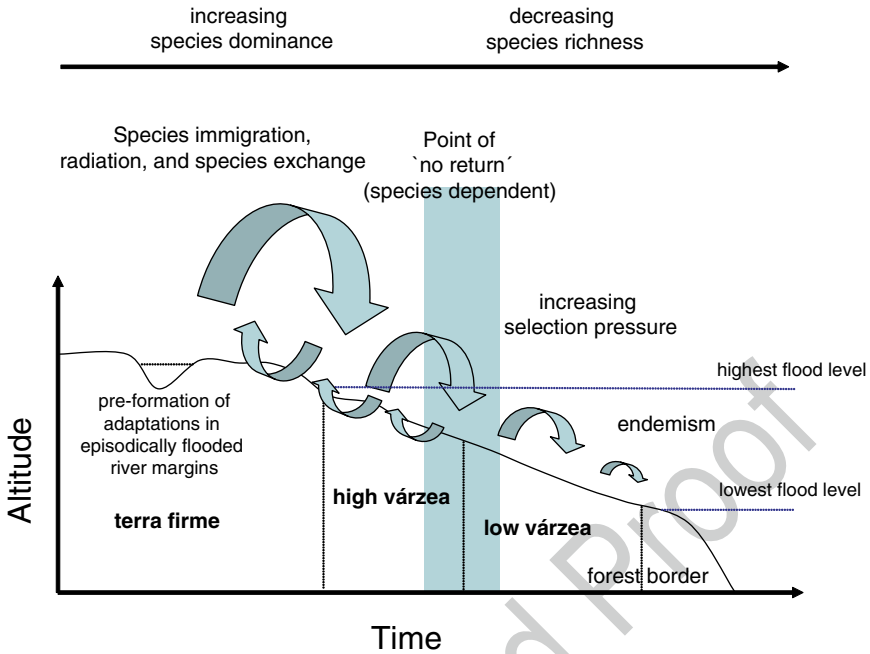


Fig. 24.1 Species Colonization Concept in várzea floodplains

171 and defined physical and chemical soil characteristics also within the substrates of
 172 recent uplands. Studying the flora of recent upland and floodplain forests thus pro-
 173 vides data and evidences about landscape evolution, and allows for the creation of
 174 speciation and species distribution models in both the past and under future climate
 175 change. In this context, our knowledge about species migrations and the ecological
 176 interactions at the aquatic terrestrial transition zone (ATTZ; Junk et al. 1989) is
 177 extremely scarce. More comparative floristic inventories in both floodplain and terra
 178 firme forests are needed to fulfill this gap of knowledge in order to allow for reliable
 179 interpretations of the evolution of the Amazonian flora.

180 **24.4.2 Floodplain Forests as Habitats for Associated**
 181 **Animal Species**

182 The Amazonian floodplain forests provide important habitats for a large variety of
 183 animals. Best studied are the importance of the forests as food source for the fishes
 184 and the dispersal mechanisms of seeds (ichthyochory) (Parolin et al., this volume
 185 b; Goulding 1980). Large scale forest destruction will severely affect local fishery,
 186 because many commercially important fish species rely on fruit and seeds from the
 187 forest. Two monkey species, the White Uakari (*Cacajao calvus calvus*) and *Saimiri*
 188 *vanzolini* are endemic to the várzea forests. In a study on birds of the Marchantaria

Island in the Amazon near Manaus, Petermann (1997) registered about 210 species. 189
 Some of them are restricted to forest patches, many using scrub communities on 190
 lake sides and sand bars. Many wading birds use trees for resting at night and nesting. 191
 Petermann attributes the low number of forest bird species at Marchantaria island 192
 to the patchy distribution of forested areas, strong human disturbance and isolation 193
 of the island in the middle of the main channel of the Amazon River. This points to 194
 the importance of large, undisturbed forest areas for bird species diversity in 195
 Amazonian floodplains (Queiroz and Peralta, this volume). 196

Of specific importance is the floodplain forest for species diversity of terrestrial inver- 197
 tebrates. Adis (1997) differentiates between terricolous and arboricolous species. 198
 Arboricolous species live mostly on the tree trunks or in the canopy. But many terricolous 199
 species also use the trees to escape flooding during the high water period. Periodic flood- 200
 ing reduces invertebrate species numbers in Amazonian floodplains in comparison to 201
 non-flooded habitats, but creates many specific survival strategies and endemic species. 202

An analysis of beetle communities in the canopies of different forest types 203
 shows lower species diversity in the floodplains in comparison to terra firme forests 204
 but high site specific variability between different floodplain forest types. The 205
 authors relate these findings to greater tree species diversity in the terra firme, dif- 206
 ferences in tree species composition in the floodplain forests, and flood stress (Adis 207
 et al., this volume). The authors postulate that local deforestation will result in the 208
 loss of many unique restricted beetle species. This statement holds certainly true for 209
 terrestrial invertebrates in general. 210

24.5 Community Structure and Succession 211

Species distribution, diversity, and forest succession in Amazonian várzea forests is 212
 partially well-described. Abiotic variables, such as flood height and duration, sediment- 213
 ation rates, distance from the main-river channels, soil texture, and solar radiation on the 214
 forest floor, but also biotic variables, including species richness, stand density, stand 215
 architecture, mean wood density, and increment and growth rates of trees, are variables 216
 that change during forest succession and interact with each other. Therefore, many 217
 várzea tree species can easily be classified as pioneer, secondary, or late-successional 218
 species, and the rules of forest succession allow for a certain predictability of forest 219
 type establishment and species diversity (Wittmann et al., this volume; Fig. 24.2). 220

However, the alluvial dynamism continuously changes in spatial and temporal 221
 scales. The time scale for the development of the different várzea forest types range 222
 from a few years in pioneer stages near the highly dynamic river banks to several 223
 centuries or even millennia in low-dynamic backwater depressions and high-várzea 224
 forests. Combined with continuous channel migrations of the white-water rivers, 225
 the alluvial landscape is characterized by a small-scale mosaic of different forest 226
 types. This complicates the rapid assessment of tree species richness in várzea 227
 forests at larger scales, and often implies the need for very detailed floristic inven- 228
 tories to secure an adequate and sustainable management of the várzea landscape. 229

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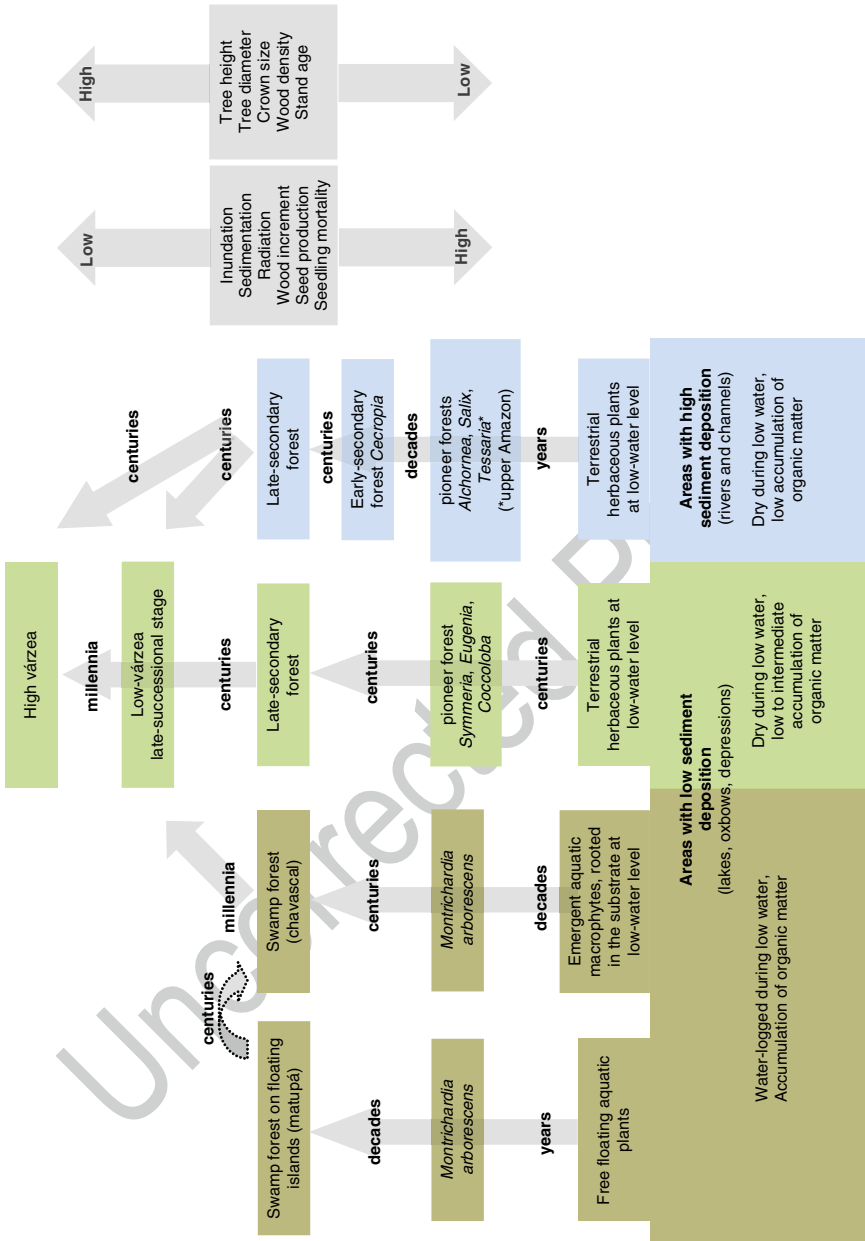


Fig. 24.2 Schematic model of forest succession in Amazonian várzea

230 There is, on the other hand, a gap of knowledge about species composition and
 231 diversity, forest structure, and succession in Amazonian igapó. The existing data
 232 suggest that igapó forests are characterized by a distinct flora that shows low floristic

similarities to other Amazonian ecosystems, including the várzea (Wittmann et al., 233
 this volume). Due to the generally low sediment load of Amazonian black-water 234
 rivers, igapó forests are characterized by the long-term stability of periodically 235
 flooded habitats. Combined with the paucity of nutrients, forest succession in 236
 Amazonian igapó occurs in longer time-scales than in Amazonian várzea, and trees 237
 are characterized by reduced growth rates (Schöngart et al., this volume b), which 238
 possibly induce higher maximum tree ages than those reported for várzea trees 239
 (Schöngart et al. 2005). This directly influences the community structure of 240
 Amazonian igapó forests, and is an important trait for the management of forest 241
 resources. There is an urgent need for floristic inventories and ecological studies in 242
 Amazonian igapó, in order to create the basic knowledge about species composition, 243
 diversity variations, and tree growth behaviour in dependence of the abiotic 244
 environment. 245

24.6 Adaptations to Periodic Flooding 246

24.6.1 Morphological, Physiological and Phenological Adaptations 247
 248

Terrestrial and aquatic phases occur under tropical temperature and light conditions 249
 that are throughout the entire year optimal for plant growth and development, 250
 implying the need for adaptations of trees to long term water-logging and shallow 251
 flooding. Trees do not persist in a dormant state, but grow vigorously during most 252
 of the year, including the aquatic period. The flooding period of Amazonian flood- 253
 plains does not correspond to a temperate winter ('physiological winter' *sensu* 254
 Gessner 1968) implying reductions of growth and metabolic activity to complete 255
 dormancy as observed for trees of temperate forests in the period of unfavorable 256
 growth conditions. 257

Although in Amazonian floodplains the terrestrial phase is the main growth 258
 period for tree species, at high water the periods of limited growth last only few 259
 weeks, and new leaf flush, flowering, and fruiting occur in most trees while flooded 260
 (Parolin et al., this volume c). This requires a number of adaptations which allow 261
 growth despite waterlogging or submergence (Fig. 24.3). 262

Adaptations to flooding in plants are usually considered as either tolerance adap- 263
 tations or else avoidance mechanisms (Crawford 2003). In the former, metabolic 264
 adaptations have been found which allow some plants to endure anaerobic condi- 265
 tions for a length of time sufficient to overcome the period of oxygen deprivation 266
 caused by flooding. In the latter, aerenchyma and other structures facilitate aeration 267
 of the inundated root. Both these aspects of flooding are by no means mutually 268
 exclusive as shown by many Amazonian floodplain tree species. 269

In some species, the severe physiological stress caused by anoxic conditions in 270
 the root zone is indicated by a reduction of the transpiring surfaces via leaf shedding. 271

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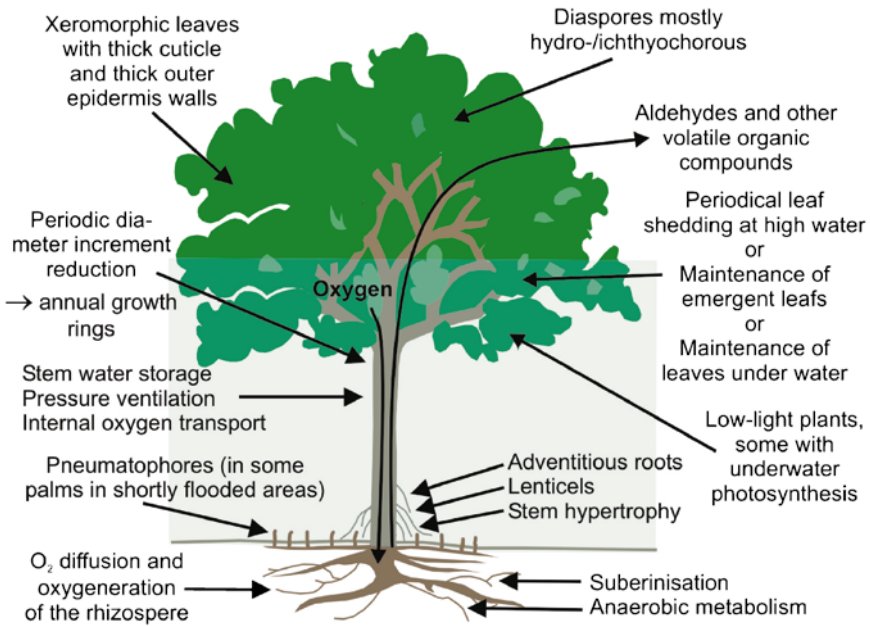


Fig. 24.3 Schematic presentation of morphologic, physiologic and phenologic adaptations of central Amazonian trees to periodic flooding

272 In other species, the diurnal patterns of crown sap flow (a surrogate for transpiration)
 273 are influenced by the size of the stem water store that acts as internal water reservoir
 274 during the day and is refilled during the night. Individuals having larger internal
 275 water storage capacity, e.g. *Pseudobombax munguba* maintain maximum or near
 276 maximum transpiration rates for a longer period of time (Horna, et al., this volume).
 277 Water limitation does not lead directly to drought damage on leaves but may indi-
 278 rectly trigger leaf-shedding e.g. by hormone signals. Reduction in diameter incre-
 279 ment of the stem during the flood period (ring formation, Worbes and Fichtler, this
 280 volume) points to the flood stress for tree growth.

281 Since trees which have an active sap flow have a need for adequate supplies of
 282 carbohydrate also in the flooded period, a set of metabolic adaptations are required
 283 for survival and growth despite flooding (Horna et al., this volume). Among these
 284 metabolic adaptations we find a large amount of starch for energy supply in the
 285 roots of *Eugenia inundata*, a decrease of respiration and a switch to anaerobic path-
 286 ways as shown for *Astrocaryum jauari* and *Macrolebium acaciifolium*.

287 A primary morphological plant strategy in response to flooding is the develop-
 288 ment of air spaces in the roots and stems which allow diffusion of oxygen from the
 289 aerial portions of the plant into the roots (Jackson and Armstrong 1999). Thus the
 290 roots do not have to depend on getting oxygen from the soil. Yet, different trees
 291 evolved different strategies to cope with the periodical flooding. Soil inundation
 292 usually inhibits root formation and branching, and growth of existing roots and
 293 mycorrhizae (Kozlowski 1997). This is not the case in Amazonian floodplains,

where tree roots grow below water and mycorrhizae are not affected (Meyer and Junk, this volume; Haase and Rättsch, this volume). 294
295

The different permeability of root types, which is determined by their morpho- 296
anatomy and degree of suberization, results in three main strategies described by 297
De Simone et al. (2002b, 2003) and Haase and Rättsch (this volume). 298

- 1 No suberization and strong radial oxygen loss (ROL): Well oxygenated aeren- 299
chymatous adventitious roots which are able to build up a several millimeters 300
thick oxygenated layer around the whole roots, suggesting a mechanism of 301
detoxifying reduced phytotoxins by ROL. This is the case in the fast-growing 302
pioneer *Salix martiana*. 303
- 2 Weak suberization and limited ROL: Deposition of suberin in radial (Casparian 304
bands) and tangential cell walls of the exodermis equips the root with a hydro- 305
phobic barrier that contributes to the plant's overall resistance. In this way, 306
exchange between root and rhizosphere is not completely inhibited, enabling the 307
loss of toxic ethanol, but also the entry of reduced phytotoxic compounds into 308
the roots. 309
- 3 Strong suberization and no ROL: a heavily suberized exodermis starting imme- 310
diately behind the root tip limits radial oxygen loss (ROL) from the root to the 311
rhizosphere in oxygen-depleted soils and inhibits the entry of toxic substances 312
and infection by microbial pathogens but also inhibits release of ethanol, e.g. in 313
Tabernaemontana juruana. 314

Root aeration, respectively the production of toxic ethanol by alcoholic fermentation 315
in the roots may lead to the emission of considerable amounts of ethanol, acetalde- 316
hyde and acetic acid from the canopy of the floodplain forest. Experiments with 2–3 317
years old tree seedlings of four floodplain tree species under greenhouse conditions 318
showed no emission of these substances under non-flooded conditions (Rottenberger 319
et al. 2008). Flooding of roots resulted in the emission of ethanol and acetaldehyde 320
in all species while emissions of acetic acid occurred only by the species exhibiting 321
the highest ethanol and acetaldehyde emission rates. All three compounds showed a 322
similar diurnal emission profile, each displaying an emission maximum in the 323
morning, followed by a decline in the evening. This concurrent behaviour supports 324
the conclusion, that ethanol is transported from the roots to the leaves with the 325
transpiration stream and finally partly converted to acetaldehyde and acetic acid by 326
enzymatic processes. Emission rates substantially varied among tree species, with 327
maxima differing by up to two orders of magnitude ($3\text{--}200\text{ nmol m}^{-2}\text{ min}^{-1}$ for 328
ethanol and $5\text{--}500\text{ nmol m}^{-2}\text{ min}^{-1}$ for acetaldehyde). Acetic acid emissions reached 329
 $12\text{ nmol m}^{-2}\text{ min}^{-1}$. The observed differences in emission rates between the tree 330
species are explained by root adaptive strategies to tolerate long term flooding. 331
Species which develop morphological root structures allowing for enhanced root 332
aeration produced less ethanol and showed much lower emissions compared to spe- 333
cies which lack gas transporting systems, and respond to flooding with substantially 334
enhanced fermentation rates. Considering the large areas covered by floodplain for- 335
ests, emissions of ethanol, acetaldehyde and acetic acid from the canopy may play a 336
significant role in Amazonian air chemistry at least during flood periods. 337

338 In contrast to the manifold adaptations at the root level, astonishingly the
339 morpho-anatomy of leaves (Waldhoff and Parolin, this volume) does not show a
340 close relationship between leaf parameters and the periodicity of flooding. The
341 measured variations, e.g. in leaf mass and size, are not understood as adaptations
342 but rather as genetically fixed characteristics of the tree genera which immigrated
343 from the terra firme. For example, the xeromorphic leaf structure found in the
344 floodplain species (Waldhoff and Parolin, this volume) is typical for trees of tropical
345 forests in general. Xeromorphy helps to cope with insufficient water supply to the
346 tree crowns during the aquatic phase, and with periods of drought occurring occa-
347 sionally in the terrestrial phase. Apparently, the leaves which are not shed and
348 maintain their functions despite prolonged submergence do not require different or
349 additional morphological traits. The development of densely packed stacks in the
350 chloroplasts and the low chlorophyll a/b ratio point to high photosynthetic effi-
351 ciency under low light conditions, enabling the plants to maintain photosynthesis at
352 low levels under water (Waldhoff and Parolin, this volume). The same is true for
353 leaf shedding which may not be a strategy against water loss but rather an endoge-
354 neously triggered rudiment related to the species' origin. Stem succulent trees of
355 the Malvaceae family (former Bombacaceae) for example originate in semi-arid
356 environments, drought avoidance being enhanced by leaf shedding. This behaviour
357 may have facilitated immigration into the floodplains (Kubitzki 1989), by overcom- [AU2]
358 ing first flood stress to water uptake by the fine root system.

359 A new development in flooding ecology is the unravelling of the molecular regula-
360 tion of hormonally controlled processes. The expression of an ethylene receptor gene
361 in *Rumex palustris* was highlighted by Blom (1999) and it may be expected that
362 Amazonian floodplain trees exhibit similar genes. When we look at the physiological
363 performance of the trees, it becomes evident that mechanisms which have not been
364 described yet must be acting which enable the plants to survive in this ecosystem.

365 **24.6.2 Phylogenetic Development of Adaptations**

366 Flooding stress is a strong driver of adaptive evolution (Jackson and Colmer 2005).
367 The regularity of the recurrence of flooding, i.e. the predictability of the flood pulse
368 (*sensu* Junk et al. 1989), enhances the evolution of specific adaptive traits and may
369 have led to the large variety of species which are able to successfully colonize,
370 establish and dominate the floodplains. Morphological adaptations may be rem-
371 nants of pre-adaptations from the non-flooded terra firme species where floodplain
372 trees originate from. The degree of flood tolerance may also depend on the time
373 taken to colonize the floodplains. Some species have the potential for the develop-
374 ment of adaptive traits – as revealed in waterlogging experiments with seedlings
375 (Haase and Rättsch, this volume) – but do not show them in the field in average
376 years. For example, under natural conditions in the floodplains, adventitious roots,
377 lenticels, or stem hypertrophy were observed only in few individuals probably due
378 to the constant change in water level. Although not frequently encountered in the
379 field, their function may be important in years with flooding anomalies.

Recent genetic studies emphasize the continuous adaptation to different habitats as driving force initiating diversification (Ferreira et al., this volume). The genetic separation of individuals of *Himatanthus succuba* in geographically and ecologically continuous environments shows that terra firme vs. floodplains could act as speciation sites. Seedlings growing in the várzea all survived a prolonged period of waterlogging, whereas 30% of the seedlings from the terra firme died when subjected to waterlogging. With complete submergence, in the várzea population 30% of the seedlings had died after 120 days, in the terra firme population after 90 days mortality was 100%.

The várzea forest thus can be regarded as an environment capable of promoting recurrent adaptive changes in plants, which enhances metabolic adjustments and morphoanatomical modifications. The feature which favors the action of natural selection in these environments is the flood pulse. The terra firme acts as a pre-selective environment providing habitats with periodically waterlogged soil conditions. Flooding intensities are longer and higher on the lower levels in the flooding gradient so that the flood pulse causes a species zonation along the flooding gradient. These conditions could promote population isolation and act as barriers to gene flow between individuals of the same species that live in these two ecosystems. In this way, the flood pulse can be seen as driver for speciation as postulated by the Species Colonization Concept (Fig. 24.1; Wittmann et al., this volume).

24.6.3 Seeds and Seedlings: Chemical Composition, Dispersal and Fate

High resource allocation to seeds may reflect the need for fast initial seedling growth. Seedlings which are able to protrude the highest possible portion above the water surface before the next flood period have higher survival chances than seedlings which soon get fully submerged. In the Amazon floodplain, the time before the next flooded period is limited to few months a year and survival rates of the seedlings will be higher if a certain height can be achieved before the onset of flooding. Thus, the need for rapid height growth may have selected for species with larger seeds which enable seedlings to be less dependent on soil nutrients. This however was not found in nutrient-rich várzea, where species growing at high and low elevations did not show any differences in seed mass. Significantly higher seed masses were found only in nutrient-poor blackwater floodplains, on sites with short periods of flooding, i.e. on high levels in the flooding gradient in igapó. In várzea, nutrient reserves are available from the environment and the need to supply the seedling with nutrients from the parental tree is small. This is not the case in igapó, where the environment provides very little nutrients and the seed resources which are particularly important for early growth of seedlings have to be supplied by the parental tree. Only at high levels in the flood gradient fast height growth is an important survival strategy, which on low levels and a water column of many meters is not efficient. Investigating the growth behaviour of seedlings from 19 várzea tree species, Oliveira Wittmann (2007) confirmed this hypothesis showing that some high-várzea species were characterized by height increments of more than 1 m during a period of less than 180 d.

422 Further research on the growth behaviour of floodplain tree species is needed to
423 interpret different growth strategies as adaptation on flooding and/or other environ-
424 mental factors.

425 A second explanation for the high energy reserves of seeds might be linked to
426 the close relationship between seeds and fishes. Most Amazonian floodplain fruits
427 eaten by fish have a high fat and protein content, so that the caloric value and delivered
428 energy are high (Waldhoff et al. 1996; Parolin et al., this volume b). The costly
429 allocation of energy reserves to the seeds makes sense in the light of long-distance
430 dispersal, and even more when considering that fish can also transport seeds upriver
431 against the water current. Long-distance dispersal plays an imminent role especially
432 because the biota of Amazonian floodplains is less shaped by in situ speciation and
433 radiation, but more by an equilibrium of immigration and extinction (Wittmann
434 et al., this volume). This stands in contrast to most island and continental biotas and
435 vegetational patterns, where the contrary is normal: the biota are mostly shaped by
436 in situ speciation rather than an equilibrium of immigration and extinction (Price
437 and Elliot-Fisk 2004).

438 As a first step to establishment, seed dispersal mechanisms play a crucial role,
439 and are frequently linked to the abundant water in form of hydro- and ichthyochory
440 (Parolin et al., this volume b). However, many animals involved in seed dispersal
441 are also seed predators, and the efficiency of dispersal mechanisms has not been
442 measured. Therefore the mere interpretation of the diaspore structure and the potential
443 distribution mechanisms may result in misleading conclusions. Today, many of the
444 tree species of the várzea forests are the most widely distributed in Amazonia,
445 partially because of the persistence of floodplain forests along river systems during
446 very long geological periods (Junk and Piedade, this volume) and partly because of
447 the ease of diaspore dispersal by water and fish.

448 Many floodplain tree species produce diaspores during the aquatic phases
449 (Parolin et al., this volume c; Wittmann et al., this volume). The diaspores may float
450 during variable periods on the water surface or sink to river and lake bottoms. The
451 contact of the diaspores with the river water is controversially discussed in litera-
452 ture. While some authors interpret the contact with the water surface as to be the
453 most important factor breaking seed dormancy, other authors argue that submer-
454 gence prevents the seeds from oxygen supply that is necessary for respiration and
455 to initiate germination (Oliveira Wittmann et al., this volume). In Amazonian
456 várzea forests, viability of seeds that are in contact with the river water varies
457 between 48 h (*Salix martiana*) to up to 5 months (*Piranhea trifoliata*). Germination
458 experiments indicate that some várzea tree species show faster germination and
459 higher germination rates when subjected to experimental flooding (Oliveira
460 Wittmann et al., this volume). But our knowledge about the different germination
461 strategies is extremely scarce and more germination experiments are necessary.

462 In contrast to the environmental conditions in Amazonian terra firme where seedling
463 establishment is mainly keyed to the light-demand of tree species (i.e., Bazzaz and
464 Pickett 1980; Denslow 1980; Whitmore 1989), seedling establishment in Amazonian
465 floodplain forests is primarily determined by the flood pulse (Junk et al. 1989).
466 Seedlings establish during the terrestrial phases and often must cope with full and

prolonged submersion in the early life stages. Despite hypoxic conditions below 467
 water, In black and white water they are deprived of light for many months due to 468
 low water transparency and suffer hypoxic or even anoxic conditions in soil and water. 469
 However, mortality rates in 459 seedlings of the várzea tree species *Eschweilera* 470
ovalifolia and *Vitex cymosa* that were monitored before and after an aquatic phase in 471
 a low-várzea forests near Manaus (mean inundation depth 6.5 m, corresponding to 472
 210 days year⁻¹) amounted to only 2.5% and 33%, respectively (Oliveira Wittmann 473
 et al., this volume), values that were surpassed by the establishment of new individu- 474
 als of the same species during the following terrestrial phase. 475

Tree seedling establishment and mortality in várzea forests depend on forest 476
 succession, which is strongly interrelated to flooding (Wittmann et al., this vol- 477
 ume). Most várzea tree species are well-adapted to very small ecological ampli- 478
 tudes and habitats, and forest succession implies that for most várzea species the 479
 optimal range of conditions are present only during a restricted period within the 480
 successional sere. Many of the trees do not successfully compete when regenerating 481
 at the same site as the parent trees. Despite the high impact of flooding, establish- 482
 ment of overall-dispersing early-successional species occurs frequently. Seedling 483
 densities in early-successional stages can amount to more than 2,000 individuals m⁻² 484
 (Oliveira Wittmann et al., this volume). However, mortality rates in early- 485
 successional species amount to at least 99.98% (Wittmann et al., this volume). The 486
 proceeding forest succession and decreasing impact of flooding lead to an increased 487
 number of tree species with low but more efficient reproduction strategies. Seedling 488
 densities in late-successional forests are low, but so are mortality rates. 489

24.7 Photosynthesis, Primary Production, Biomass and Timber Production 490
 491

24.7.1 Photosynthesis 492

Photosynthetic activities of Amazonian floodplain species change in the annual 493
 cycle, and the whole physiological apparatus is perfectly well adapted to the regular 494
 flood pulse. Under waterlogged conditions, most species show a reduction of mean 495
 CO₂-uptake in aerial leaves ranging from 10% (early successional *Cecropia latiloba*, 496
Senna reticulata) to 20–50% (late successional *Nectandra amazonum*, *Crateva* 497
benthami, *Tabebuia barbata*, *Vitex cymosa*) lower CO₂-uptake than in the terrestrial 498
 phase (Parolin et al. 2004; Parolin et al., this volume a). CO₂-uptake rises again 499
 before the end of the flooded phase and remains high throughout the terrestrial 500
 phase (Parolin 2000). Single measurements – in contrast to average values of the 501
 complete aquatic period – show that photosynthetic activity during waterlogging 502
 could reach the same or even higher values than in the terrestrial phase in almost 503
 all analysed species (Parolin 2000). Waterlogged adults or seedlings of *Senna reticulata* 504
 often showed higher assimilation rates than non-flooded individuals: in a flooding 505

[AU3]

[AU4]

506 experiment, waterlogged seedlings had an average assimilation rate which was 15
507 % higher than that of the well-watered control (Parolin 2001c). *Senna reticulata*,
508 flooded by a water column of 4 m with only few leaves appearing above the water
509 surface showed assimilation rates of up to $25 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$, which represent the
510 highest photosynthetic activity measured in waterlogged Amazonian floodplain
511 trees (Parolin 2001c). In several species, the influence of drought appeared to be by
512 far more harmful than that of waterlogging or even submergence in terms of
513 growth, photosynthetic performance and vitality after stress end (Waldhoff et al.
514 1998). In fact, drought may represent more of an impairment to survival than flooding
515 to the local vegetation (Keel and Prance 1979; Scarano et al. 1994). This gains an
516 increasing importance given the climatic changes which are predicted for the future
517 in the Amazon basin (Malhi et al. 2008). Seedling recruitment and photosynthetic
518 activity may become affected by increasing drought events and this may result in
519 productivity changes and shifts of species composition.

520 **24.7.2 Primary Production, Carbon Stock and Carbon Cycle**

521 The high nutrient stocks in the alluvial soils (Furch 2000) and the periodic nutrient
522 input by floods result in a high productivity of the várzea. A critical nutrient may be
523 nitrogen, however the legume trees, which occur in large species and individual
524 numbers, compensate possible nitrogen deficits by nitrogen fixation, which adds
525 $17\text{--}20 \text{ kg N ha}^{-1} \text{ year}^{-1}$ to the budget (Kern et al., this volume). Várzea forests are
526 among the most productive tropical forest ecosystems worldwide with estimated
527 aboveground net primary productions of $6.6\text{--}15.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (Schöngart et al.,
528 this volume b). But carbon stocks and fluxes in aboveground coarse wood biomass
529 (AGWB) differ considerably among floodplain forest types. Young successional
530 stages have low carbon stocks in the AGWB, but high net carbon sequestration rates,
531 while old-growth várzea forests have high C-stocks in the AGWB, but almost no net
532 carbon sequestration. The carbon stock in the AGWB of the entire várzea forest
533 ecosystem, however, is more or less balanced, since the carbon sequestered during
534 the first 50–100 years of primary succession is lost by natural tree mortality and forest
535 destruction due to lateral erosion by the river and channel migration.

536 The carbon cycle in the AGWB of várzea forests differs considerably in
537 comparison to the non-flooded terra firme forests. Central Amazonian várzea forests
538 have C-storages in the AGWB with up to 120 Mg C ha^{-1} , while terra firme
539 forests stocks about $116.0\text{--}195.5 \text{ Mg C ha}^{-1}$ (Chambers et al. 2001). C-sequestration
540 rates in the AGWB of várzea forests vary from $8.5 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ in the early
541 successional stages to $2.7 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ in old-growth forests. In the terra firme
542 old-growth forests the C-sequestration in the AGWB is about $2.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$.
543 This results in a two to three times lower mean carbon residence time in the várzea
544 (higher C-turnover) when compared to non-flooded terra firme forests, characterizing
545 the high dynamical processes of this ecosystem. But also the interannual short-term
546 C-sequestration in the central Amazonian várzea forests differs from adjacent terra

firme forests due to a displacement of two to three months between the growth 547
 rhythms of trees in both ecosystems with consequences in their function as short-term 548
 climate-induced carbon sinks and sources (Schöngart et al. 2002, this chapter b). 549
 The growth rhythms of trees in the terra firme are mainly controlled by the seasonal 550
 precipitation, while in the várzea forests these are mainly triggered by the flood-pulse. 551

The El Niño-Southern Oscillation originating from the equatorial Pacific associ- 552
 ates both, the interannual variation in precipitation and flooding patterns in central 553
 Amazonia. It causes exceptional droughts during the rainy season in the Amazon 554
 leading to climate-induced C-releases from large regions of the terra firme to the 555
 atmosphere (Prentice and Lloyd 1998; Foley et al. 2002). During these events, how- 556
 ever, parts of the várzea forests can be considered as C-sinks, because the flood- 557
 pulse is weakened and the extension of the vegetation period results in higher 558
 increment rates and thus higher C-sequestration rates (Schöngart et al. 2004). This 559
 duality of biogeochemical sinks and sources in adjacent forest ecosystems is not 560
 considered in existing estimates of carbon fluxes based on biogeochemical models, 561
 measurements of gas fluxes or accumulation of carbon in vegetation and soils in the 562
 Amazon basin. However, data on C-storage and C-sequestration available for flood- 563
 plain forests still remain underrepresented considering their wide geographic distri- 564
 bution and different forest types as a result of varying climatic, edaphic and 565
 hydrologic factors. Especially for the igapó along black-water and clear-water rivers 566
 only very few estimates are available (Malhi et al. 2004; Stadtler 2007). These stud- 567
 ies characterize the igapó forests as ecosystems with C-stocks in the AGWB in the 568
 range of várzea forests, but much lower C-sequestration rates and lower C-turnover. 569
 Tree-ring studies comparing tree growth of three species occurring in both systems 570
 under similar hydrological conditions confirmed the significant lower tree growth in 571
 the igapó compared to the várzea (Schöngart et al. 2005; Fonseca Júnior 2007). 572
 Therefore igapó forest ecosystems, especially those along nutrient-poor black-water 573
 rivers, should be excluded from forest management activities and permanently pro- 574
 tected by the creation of large conservation units (Schöngart, this volume). 575

24.8 Actual Use and Management Options 576

24.8.1 Traditional and Modern Management Options 577
of the Várzea 578

The várzea has been used and settled by a human population for centuries conducting 579
 agriculture, pasture, fishing, hunting, and the extraction of timber and non-timber 580
 products as a function of water-level fluctuations (Junk et al., in press). Commercial 581
 fishing occurs mainly during the low-water period, when fishes are concentrated in 582
 the remaining, often isolated water bodies. 583

Planting of crops is performed at the beginning of the terrestrial phase and the 584
 harvest at their end. Logging starts before the water reaches the forests and the timber 585

586 is skidded and transported during the flooded period. In the Mamirauá Sustainable
587 Development Reserve (MSDR), about 70% of the domestic income of an average
588 household comes from fishery (Schöngart et al., this volume a) and consequently
589 the income is high during the terrestrial phase and low during the high water period
590 when economic activities are mainly restricted to timber extraction (Fig. 24.4).

591 Management plans involving local communities have been successfully devel-
592 oped, tested and implemented in the MSDR based on a large number of environ-
593 mental, biological-ecological and socio-economic studies (Queiroz and Peralta, this
594 volume). The community-based fishing of the giant pirarucu (*Arapaima gigas*), for
595 instance, resulted in increasing fish populations and increasing incomes for the
596 involved riverine population during the last ten years (Castello 2007).

597 Modern crop farming, animal ranching, fisheries and their impact on the várzea
598 ecosystem have been studied near Manaus (Junk et al. 2000a). The following table
599 indicates land and labor productivity of the different production systems (Junk et al.
600 2000b). Data on the land and labor productivity of the different production systems
601 and calculations of timber productivity are presented in Junk et al. (this volume a)
602 on sustainable management. An environmental impact analysis indicates cattle and
603 water buffalo ranching as most detrimental for the environment because it destroys
604 in large scale the floodplain forest for the establishment of natural and artificial
605 pastures. Land productivity is low but compensated by relatively high labor produc-
606 tivity, resulting from a very low number of herdsmen employed by the ranchers.
607 Negative impact is severe on fishery, habitat diversity and stability, and biodiversity.
608 In contrast, the impact of selective logging is considered low when sustainability is

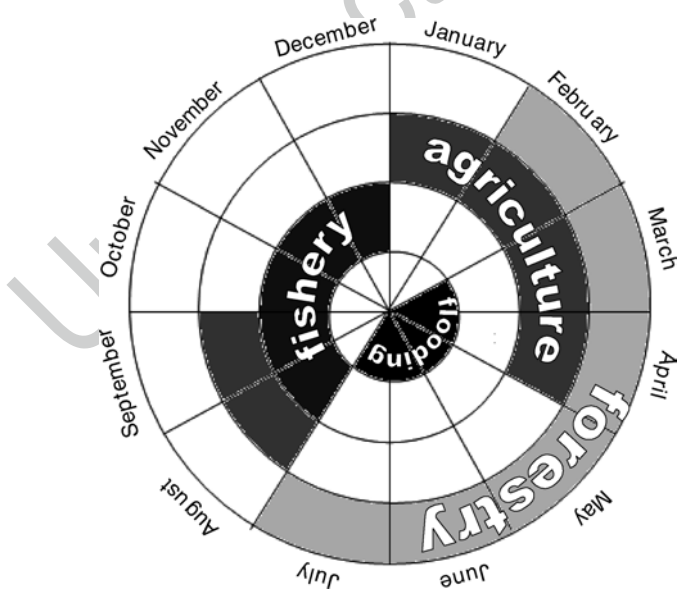


Fig. 24.4 Annual cycle of economic activities of riparian people in the Mamirauá Sustainable Development Reserve related to the seasonal variation of the water level

guaranteed by adapted management methods, because it little affects fisheries and other environmental services (Junk et al., this volume a).

24.8.2 Management of Várzea Resources and Water Level Prediction

The timing of flooding and drought dramatically affect the exploitation of the natural várzea resources. The temporal pattern of the water level is more or less predictable. High water levels in Central Amazonia occur mostly in the 2nd half of June, while the low water levels appear in the 2nd half of October/1st half of November (Irion et al. 1997). However, the height of the minimum and maximum levels varies considerably from one year to the other. Recently developed models to forecast low and high water levels based on tropical Pacific and Atlantic sea surface temperatures (SSTs) (Schöngart and Junk 2007; Schöngart et al., submitted) are powerful instruments to increase the efficiency of planning and executing of the economic activities. In years of low maximum water levels, for instance, the high várzea does not inundate and harvested logs can not be skidded and get rotten causing economical damages for the riverine people and ecological damages on the forest ecosystem. Forecast models, however, allow predicting the maximum flood level already 100 days before its occurrence (Schöngart and Junk 2007) and areas for timber extraction can be selected according to the forecasted water level thus avoiding economic and ecological damages (Fig. 24.5).

Change in precipitation is probably the most critical deterrent in the climate fate of the Amazon. The extreme low water level in many regions of the Amazon basin in the year 2005 raised the question among scientists whether this phenomenon can be explained by the natural climate variability or if it is a result of the human-induced climate change and/or the consequence of increasing deforestation in the tropics. But due to a missing network of long-term climate records in the Amazon basin this question can hardly be answered. Even the century-long hydrological record at the harbor of Manaus, reflecting mean precipitation conditions in the watersheds of the Negro and Solimões rivers of about 3 Mio. km², does not indicate if exceptional low water levels or high flooding of the main stem of the Amazon River are the result of man made changes in vegetation cover, and if they still are in the range of their natural climate variability or already a result global climate change (Schöngart and Junk 2007).

24.8.3 Traditional Use of Timber and Non-Timber Forest Products

Timber exploitation concentrates on a few species mainly from the high-várzea forests, which stores the most part of timber species, and which only cover approximately

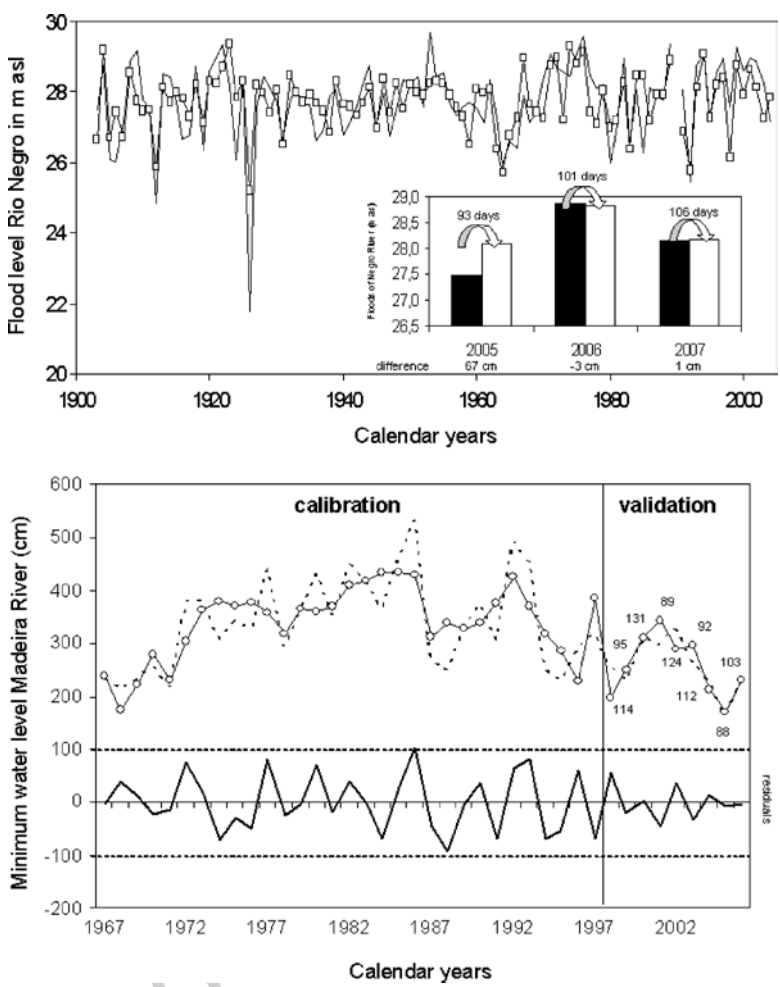


Fig. 24.5 Comparison between the observed (black line) and predicted (dotted line) maximum flood levels of the Negro River (Manaus) for the period 1903–2004 (Schöngart and Junk 2007). The forecasted maximum levels of the Negro River from 2005 to 2007, the difference between forecast (black bars) and observation (white bars) is indicated in the small figure (above). Comparison between observed (black line) and forecasted minimum water levels (dotted line) of the Madeira River at Porto Velho for the period of calibration (1967–1997) and validation (1998–2006). Numbers indicate the period between forecasted and observed minimum water levels in days (below) (Schöngart et al., submitted)

646 10–15% of the floodplain (Wittmann and Oliveira Wittmann, this volume). Easy
 647 easy access combined with the low cost of timber harvesting, processing, and transport
 648 led to the overexploitation of many floodplain trees soon after the intense immigra-
 649 tions associated with the rubber boom (1850–1920) (Santos 1980). Although the
 650 area covered by floodplain forests is smaller than the accounted for by Amazonian
 651 terra firme, about 70–75% of the wood exploited in Amazonia before the mid-1970s

originated from the floodplains, because most of Amazonian settlements are located along or close to Amazonian white-water rivers. In the Brazilian Amazon, wood production in floodplains contributes US\$ 120 million to the Amazonian gross product and currently directly generates about 30,000 jobs (Bentes-Gama et al. 2002). Most timber species are locally used for house construction, carpentry, furniture, and boat, houseboat, and canoe construction (Wittmann and Oliveira Wittmann, this volume).

The use of floodplain forests has been unsustainable and often illegal, over most decades of the twentieth century. Tree species such as *Ceiba pentandra*, *Virola surinamensis*, *Cedrela odorata*, *Calophyllum brasiliense* and others have been intensively harvested for few decades without any information on tree ages, growth rates, germination and seedling establishment and growth. Due to the decline of the species population these tree species almost disappeared from the local and regional markets and have been substituted by tree species with similar wood characteristics such as *Hura crepitans*, *Ocotea cymbarum*, *Calycophyllum spruceanum* and *Maquira coriacea*. But also for these species information on tree growth and regeneration does rarely exist. If intensive harvest on these species continues they may have similar destinies as the earlier generation of timber species in the várzea (Schöngart et al., this volume a).

An increased timber extraction from the várzea forests and the competition between forest management and other land-use options (agriculture, pasture, settlement) requires strategies and concepts for the long-term conservation of the floodplain forests. In this context, a large number of participatory community-based forest management, and forest management on small scales (private properties < 500 ha), have been established in recent years in the MSDR and within the frame of large development programs such as PPG7-Projects Pro-Manejo and Pro-Várzea. In the Amazonas state > 600 management plans for small-scale private properties and community-based forest managements have been implemented, mainly in várzea floodplains along the Solimões, Amazonas, Juruá, and Madeira rivers (Schöngart et al., this volume a). Most of these projects promote selection harvest combined with reduced impact logging as sustainable forest management. Due to the legalization of a controlled timber extraction wood prices increased up to ten times within a decade in the central Amazonian region. The traditional community-based forest management, established in 2000, experienced an over 200% increase of wood prices due to the legalization of the timber extraction and political structuring of the local people by creating local associations. In the MSDR, it improved significantly the financial status of the involved associations especially during the flooded period when the income of an average household is very low (Schöngart et al., this volume a). But these technical and logistical improvements for timber extraction are not sufficient to provide a sustainable management of the timber resources, as shown later.

Besides timber, the economic potential of non-timber forest products (NTFP) in Amazonian floodplain forests is exceptionally high, because nearly all stems present in forest inventories can be useful to the inhabitants (Phillips et al. 1994). In addition, their role as a buffer in times of food shortage makes NTFP a critical component in the food security of rural populations (Lipper 2000). While in the western

697 Amazonian floodplains up to 87% of all tree species present in forest inventories
698 are useful to the floodplain inhabitants, approximately 53% of all tree species provide
699 NTFP in central Amazonian floodplains (Wittmann and Oliveira-Wittmann, this
700 volume). Many NTFP are of subsistence or indirect values to the inhabitants, and
701 their value thus difficult to measure. Phytomedical products and edible fruits are
702 among the most important use categories of NTFP in Amazonian floodplains, but
703 a variety of other uses can be of huge local or even regional importance, such as
704 fruits used as fish bait, fruits and wood for handicrafts, palm-heart extraction, latex
705 and resins for fishing and hunting poisons, fibres for tying and braiding, oil, fuel,
706 dyes, containers, or construction material in general (Wittmann and Oliveira-
707 Wittmann, this volume).

708 Ethnobotanical inventories about the uses of NTFP in floodplains are practically
709 absent within the Brazilian part of the Amazon basin, and their economically
710 importance including possible variations between the Amazonian flooded ecosys-
711 tems and along the river system remains widely unknown. Most information about
712 the use of forest resources originates from the Amerindian population, which may
713 differ substantially from the use of colonialists. While the Net Present Value (NPV)
714 of timber depends on the regional, national, and international timber markets, and
715 thus can easily be quantified, much remains to be learned about the economic value
716 of NTFP. The value of many NTFP to the local inhabitants may be indirect and thus
717 difficult to measure. Additionally, the NPV of phytomedical and phytocosmetical
718 products is mostly unknown and/or undervalued by extractors, thus depriving
719 inhabitants of a fair economic return. However, an increasing effort in ethnobotanical
720 inventories could not only be important for the improvement of communally sus-
721 tainable forest management plans, but it also would provide essential information
722 for authorities about how to supply the rural population during periods with cata-
723 strophically low or high water levels.

724 ***24.8.4 Growth-Oriented Logging (GOL), a New Forest*** 725 ***Management Concept for Timber Production***

726 The long-term success of forest management in the várzea and other multi-species
727 forest ecosystems requires information on species-specific and site-specific growth
728 rates to determine sustainable harvesting volumes and cutting cycles. However, the
729 current Brazilian forest legislation considers only one cutting cycle and one mini-
730 mum logging diameter (MLD) to manage a high variety of timber species of different
731 forest types. In the várzea, there is the risk of overexploitation of slow-growing
732 timber species, while the fast-growing timber species with low wood densities are
733 not efficiently used (Schöngart, this volume). The new concept “Growth-Oriented
734 Logging – GOL” developed by Schöngart (this volume), has been created as an aid
735 to improve the forest management in the MSDR and central Amazonian várzea.
736 GOL is based on species-specific and site-specific management criteria, such as
737 MLDs and felling cycles derived from growth models based on tree-ring analysis,

which is unique for tropical silviculture (Fig. 24.6). Due to the occurrence of annual rings in tree species of many tropical regions (Worbes and Fichtler, this volume), such growth models and concepts can be established also for other timber species and forest types.

However, felling cycles or rotation periods only guarantee a sustainable use of the timber resources, if the harvested species continue to recruit. Little information is available on germination, growth, and establishment of seedlings and saplings as well as their relationship to external abiotic (flooding, light conditions, water and nutrient supply) and biotic factors (seed banks, inter-specific and intra-specific competition, herbivory) (Piedade et al., this volume). Further studies should therefore focus on the germination, growth, and mortality rates of seedlings of timber species and their relationship to environmental factors. Cost-benefit analyses are necessary to evaluate silvicultural improvements, such as enrichment plantings and thinning to regulate recruitment and competition as well as removing of branches to increase stem quality. Together with data on tree species distribution patterns in dependence of abiotic variables (i.e., inundation, soil characteristics, solar radiation at time of plant establishment, (Wittmann et al., this volume), these data serve for successful reforestation on degraded and deforested site under optimal conditions, thus lowering the risks of failure.

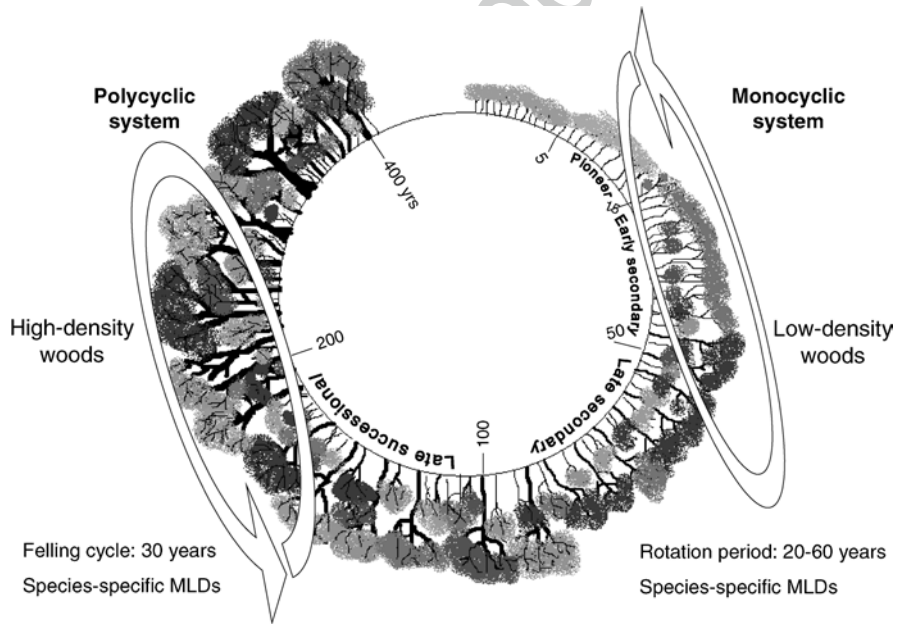


Fig. 24.6 GOL – Growth Oriented Logging: a silvicultural concept based on growth models derived from tree-ring analysis. The sustainable use of fast growing low-density woods in early and late secondary stages is achieved by monocyclic systems and that of slow growing high-density woods in late successional stages by polycyclic, selective systems (Schöngart, this volume)

757 **24.9 Threats and Possible Impacts of Land-Use and Climate**
758 **Change on Central Amazonian Floodplain Forests**

759 Scenarios of Soares-Filho et al. (2006) indicate increasing deforestation in the
760 Amazon basin driven by the expansion of soybean, sugarcane, cattle industries and
761 major infrastructure programs such as paving and construction of roads, hydroelectric
762 dams, ports, pipelines and waterways. Removal of the forest cover in the catchment
763 area of the large rivers, such as the Madeira and Tocantins Rivers probably leads to
764 earlier and more pronounced discharges due to the higher surface water runoff, as
765 Costa et al. (2003) showed it for the Tocantins River basin in Brazil with a 25%
766 increase in river discharge coincident with expanding agriculture in the catchment
767 area but no major change in precipitation. Between 17 Pg C and 33 Pg C will be
768 released by land use changes in the Amazon basin to the atmosphere until 2050
769 depending if recent deforestation trends will continue or if the Brazilian environ-
770 mental legislation will restrict and decline deforestation across the Amazon basin
771 (Soares-Filho et al. 2006). Despite the C-emissions, the release of NO_x , aerosols
772 and black carbon particle to the atmosphere by biomass burning has significant
773 impacts of the oxidation processes, the atmospheric composition and the formation
774 of droplets (Andreae et al. 2004; Oliveira et al. 2007) with serious effects on water
775 balance, formation and lifetime of clouds as well as local and regional precipitation
776 patterns and hydrological cycles. Severe droughts provoked by increased SST
777 anomalies in the tropical Atlantic and Pacific (El Niño) cause climate-induced CO_2 -
778 releases on large areas of the intact Amazonian terra firme (Prentice and Lloyd
779 1998; Tian et al. 1998; Foley et al. 2002) and especially in regions experiencing
780 forest fragmentation with increased vulnerability to large-scale fires (Nepstad et al.
781 1999; Laurance and Williamson 2001; Cochrane 2003). Especially for these areas
782 new climate scenarios predict an increased drought probability for the future (Malhi
783 et al. 2008). These processes increase the release of huge amounts of CO_2 and other
784 greenhouse gases, which feed back and accelerate climate changes (IPCC 2007).

785 Under this aspect the construction of hydroelectric dams and an industrial water-
786 way as it is planned in for instance for the Madeira River by the Brazilian government
787 within large infrastructure programs (Brazilian Growth Acceleration Program –
788 PAC, Initiative for the Integration of Regional Infrastructure in South America -
789 IIRSA) is very problematic. The establishment of several hydroelectric dams in the
790 upper Paraná River affected its floodplains only within two decades characterized
791 by a significantly declined amplitude of the monomodal flood-pulse leading to a
792 decrease of its seasonal dynamic, loss of sediments retained by the dams causing a
793 decreased connectivity and oligotrophication as well as an increased transparency
794 of the water (Agostinho et al. 2007). These dramatic changes have severe impacts
795 of the functioning of the floodplain ecosystem and its biodiversity favoring the
796 invasion of alien species and causing extinction of other species.

797 Such experiences can be transferred to the floodplains of the Amazonian rivers
798 where human populations depend on their natural resources to carry out agriculture,
799 pasture, fishing and hunting, as well as the extraction of timber and non-timber

products in relation to the flood-pulse. Due to the construction of hydroelectric 800
dams nutrient-rich sediments will be retained in the artificial basins also favoring 801
the accumulation of toxic materials like mercury due to the gold mining activities 802
(Padovani et al. 1995). The increase of the water surface area in the artificial basins 803
leads to extended water evaporation and the dams hinder the migration of many 804
commercially important fish species which must reach the catchments for their 805
reproductive cycle (Junk et al. 1997). These negative ecological and socio-economical 806
impacts get more severe in the background of possible lower future water dis- 807
charges in the large watershed caused by increasing SSTs in the tropical Northern 808
Atlantic and tropical Pacific (Schöngart et al. submitted). 809

Global climate change models are not yet sufficiently precise to make predictions 810
for the Amazon region for the next century (IPCC 2007; Marengo 2006). There is 811
general agreement that the coastal areas will become affected by a sea-level rise of 812
20–40 cm. This will lead to a shift of the mangroves further inland, when suitable 813
areas are available, and also affect the floodplains at the lower course of the Amazon 814
river. A reduced river slope will lead to increased sediment deposition in the lower 815
Amazon River valley. However, floodplain forests are dynamic systems and species 816
composition and distribution will adapt to changing sediment deposition and flood 817
stress. After the last glacial maximum, the sea-level raised about 100m in 10,000 818
years corresponding to a mean increase of 1m per century. Even higher rates of 1.6m 819
per century were found for the last interglacial period (Rohling et al. 2008). 820

The temperature increase in the central Amazonian lowlands may reach about 821
4–6°C (IPCC 2007; Malhi et al. 2008). Its impact on the floodplain forest is hard 822
to be evaluated and will become detectable only after many decades, because the 823
reactions of the many tree species to increased temperatures are not sufficiently 824
understood. The Hadley Center climate model coupled to a dynamic vegetation and 825
carbon cycle model indicates during the next few decades a dramatic decrease 826
in carbon stored in central Amazonian soils and vegetation leading from rain forest 827
cover to a savannah vegetation. We consider such predictions as unrealistic because 828
of the precarious data base. They are also politically dangerous, because they coun- 829
teract all efforts to protect the rain forest, and may even be used to favor deforestation 830
and soy bean and sugar cane plantations. 831

Temperature increase may have strong impacts in the high Andes and will lead to 832
accelerated melting of glaciers (IPCC 2007), affecting the discharge pattern of the 833
upper Amazon River and its large tributaries with Andean headwaters. In Central 834
Amazonia these effects will probably be in part compensated by the impact of the 835
different discharge curves of the large tributaries. Until today, no changes in the 836
hydrology of the Amazon River can be detected. Extreme floods related to La Niña 837
episodes such as in the years 1971/72, 1974/76, and 1999 or droughts associated 838
with increased SSTs in the tropical North Atlantic as observed in 2005, respectively, 839
are in the natural range of pluriannual hydrological cycles as shown by a 200 years 840
proxy, based on a tree ring analyses, calibrated for the last 100 years by the hydro- 841
logical data of the Manaus Harbour Authority (Schöngart et al. 2004; Fig. 24.7). 842

The predictions about precipitation changes are not yet clear, but a decrease of 843
precipitation in the southern and northern Cerrado belts is probable. Precipitation 844

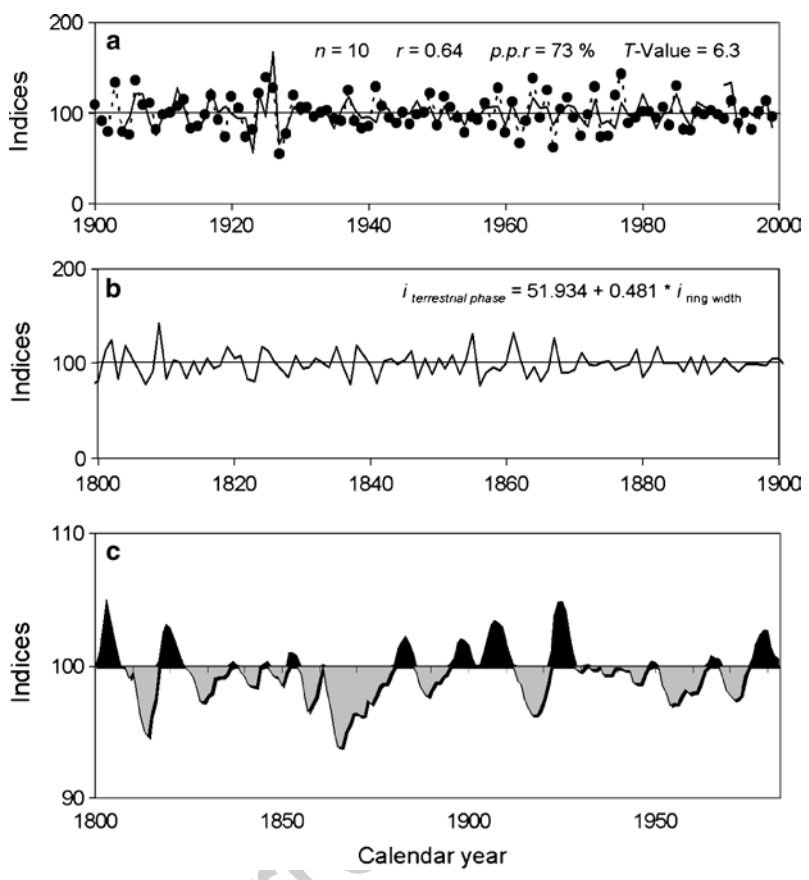


Fig. 24.7 Indexed ring-width chronology *Piranhea trifoliata* (dotted curve) and deseasonalized time series of the duration of the non-flooded period (black curve) derived from the daily recorded water-level at the port of Manaus. The correlation between the two curves is significant ($p.p.r$ is the percentage of parallel run between the two curves). Based on a linear regression model the flood patterns were reconstructed for the nineteenth century (Schöngart et al. 2004)

845 amounts in the forested parts of Amazonia may continue at the same level but
 846 differences between dry and rainy season may increase, increasing the drought
 847 stress for the trees during the dry season. Global climate simulation models indicate
 848 increasing SSTs in the tropical ocean sectors for the forthcoming decades. This
 849 may cause more frequent lower maximum floods related to positive SST in the
 850 tropical Pacific (Schöngart and Junk 2007) and probably more frequent and severe
 851 droughts in the Amazonian floodplains associated with increased SSTs in the tropical
 852 North Atlantic (Schöngart et al. submitted). This points to water availability as the
 853 strongest stress factor in Amazonia.

854 Studies of Nepstadt et al. (2001) show that already today, large parts of the terra
 855 firme rainforest in eastern Amazonian are vulnerable to fire during strong El Niño
 856 periods. Abundant charcoal in terra firme, caatinga and igapó soils near San Carlos

de Rio Negro suggest that fire has been in the mid- to late-Holocene a disturbance factor (Sanfort Jr. et al. 1985). Our observations in the igapós of the tributaries of the middle Negro River show that these forests are very vulnerable to fire at low water, too. They grow on sandy soils with a low water retention capacity, and have a superficial root system, to avoid anoxic conditions during the flood period. These forests suffer flood stress during flood periods and a heavy edaphic drought stress during strong El Niño periods, which makes them vulnerable to wild fires, as shown by several burned areas delineated on one side by the river channel and on the other by intact upland forest. In the 1920s, the bishop of Barcelos at the middle Negro River reported large fires in the area. Such occurrences are reported for the severe drought during 1925–1927 associated with the strong El Niño phenomenon of 1925/26 (Schöngart et al. 2004) when a full-year drought occurred in the Rio Negro catchment area, with many forest fires lasting for over a month and extremely low river-water levels that impeded river travel (Sternberg 1987). This event is well documented in a report by the Salesian bishop to the Vatican (Sombroek 2001) and also by other historical documents for the Caroni River, a tributary of the Orinoco in the Venezuela (Williams et al. 2005).

24.10 Conclusions

After a period of taxonomic studies at the beginning of the twentieth century, Amazonian floodplain forests were let at the sideline of research despite its large economic importance for timber supply in the region. Only in the last decades researchers in Iquitos and Manaus started intensive studies on ecophysiology, primary production, biodiversity and sustainable management. With more than 1,000 confirmed species these studies substantiate the high species diversity. They also show that the várzea forests can be sub-divided in different types and successional stages, which are related to the position of the forest on the flooding gradient. Igapós require additional studies for general statements on species and community diversity. A large number of morphological, anatomical, physiological and phenological adaptations are combined by the trees of várzea and igapó in different strategies to cope with flooding. This supports the postulation of the flood pulse concept (Junk et al. 1989) that indicates hydrology as the major driver in river-floodplain systems. However, phenological behavior often does not fit to the flood pulse periodicity and points to other drivers, e.g. evolutionary traits related to species origin in dryland habitats.

The large number of highly adapted tree species is the result of the existence of large river floodplains and wetlands in South America throughout long geologic time periods without major extinction periods. Strong hydrodynamics led to high habitat diversity and habitat dynamics favoring the co-existence of many species (Intermediate Disturbance Hypothesis, Connell 1978). But it is also the result of the permanent trickling-in of species from the highly diverse upland forest, first to the higher parts of the floodplain and later from there to the deeply flooded lower parts

898 (Species Colonization Concept, Wittmann et al., this volume). Lateral and longitudinal
899 genetic exchange plays an essential role in the development and maintenance of
900 species diversity in the Amazon river floodplain. This holds true also for other species
901 groups, such as fishes, birds, mammals and invertebrates, which live in the flood-
902 plain forests and depend on them. Additional genetic studies are required to clarify
903 origin and relationship of the species and better explain speciation processes.

904 The fertile alluvial soils and the periodic flooding of white-water river flood-
905 plains provide the nutrient basis for high productivity despite intensive flood stress,
906 which surpasses the productivity of central Amazonian upland forests by a factor
907 1.5 to 2 and that of the nutrient-poor igapó by a factor 2 to 2.5. Igapós grow on
908 nutrient-poor soils and have no potential for sustainable timber production, but
909 várzeas belong to the very few areas in central Amazonia, which can be used with-
910 out risk of nutrient depletion. Growth Oriented Logging (GOL) (Schöngart, this
911 volume), provides the conceptional basis for sustainable forest culture with fast
912 growing soft-wood species in areas covered by early successional stages and
913 selected timber extraction of slow-growing hardwood species in advanced succes-
914 sional stages, without losing diversity, when substitution of the logged specimen is
915 guaranteed by natural rejuvenation or plantation of saplings.

916 This concept has to be tested in praxis urgently, because the studies show
917 increasing forest degradation by unsustainable logging methods and large scale
918 forest destruction by cattle ranching (Junk et al. 2000b). Exploitation of floodplain
919 forests spread from the urban centers to remote areas even along the lower courses
920 of the large tributaries. Today, most forests along the main stem of the lower
921 Amazon River are heavily degraded or substituted by grassland. Large areas are
922 covered by a species poor secondary forest that grows on abandoned jute planta-
923 tions, and former pastures. Forests are under permanent pressure by cattle and
924 water buffaloes which negatively affect natural regrowth by trampling and feeding
925 on fruits and saplings Crop plantations little affect total forest area because they
926 occupy only relatively small areas on the highest levees, mainly near urban centers
927 which provide a market for the products.

928 Balancing the predicted impacts of global climate change and the impact of
929 other human activities on Central Amazonian floodplain forests and their biodiver-
930 sity we can state that serious risks arise, if sustainable management practices are
931 not introduced in environmental policy in the next future and if its implementation
932 is not seriously controlled. Floodplain forests on sandy soils at some tributaries of
933 the Negro River and on shallowly flooded interfluvial wetlands may suffer increased
934 fire stress during El Niño periods and periods of extreme low water levels.
935 Vörösmarty et al. (2000) state that rising water demands will greatly outweigh
936 greenhouse warming in defining the state of global water systems to 2025. We state
937 that unsustainable use will greatly outweigh greenhouse warming in defining the
938 state of central Amazonian floodplain forests to the end of the twenty-first
939 century.

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AU2	Please fix if it is Kubitzki 1989a, b or c.	
AU3	Please fix if it is Parolin et al. 2004a or b.	
AU4	Please fix if it is Parolin 2000a, b, c or d here and in further occurances.	

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Abstract

Long lasting inundations affect the physicochemical conditions in the soil, with oxygen deficiency in the rhizosphere and resulting stresses (Haase and Rättsch this volume) which have a strong influence on the whole metabolism of the trees. Continuous investigations of the rhizosphere are extremely difficult and hardly feasible for the entire yearly cycle in adult trees due to the high periodic water level fluctuations. Therefore other parameters have to be taken as indicators for the reactions of the trees to waterlogging. Clear indicators of the condition of a tree are its assimilation organs (Medina 1984). Several parameters can be easily measured directly on the living leaves, such as size and mass, water, chlorophyll and nitrogen contents, and anatomical characteristics for example of the surface structure, cuticle, parenchyma and stomata. Investigations from Parolin (2002c), indicate for Amazonian floodplain trees a periodicity in physiological leaf traits which changes with leaf phenology and consequently with leaf age. The phenological behaviour is linked to the flooding periodicity (Wittmann and Parolin 1999; Schöngart et al. 2002), and typical regular changes occur during the annual cycle. Many species shed their leaves in the first weeks to months of waterlogging or submergence, but the waterlogged trees resprout new leaves several weeks to months before the end of the high water period. Other species maintain all their leaves, also when completely submerged. Under experimental conditions, saplings were even able to produce new leaves under water (Waldhoff and Furch 2002; Waldhoff 2003) but in the field measurements to this respect are lacking.

Chapter 9 1
Morphology and Anatomy of Leaves 2

[AU1] **Danielle Waldhoff and Pia Parolin** 3

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9.1 Introduction 4

Long lasting inundations affect the physicochemical conditions in the soil, with oxygen 5
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20 or submergence, but the waterlogged trees resprout new leaves several weeks to
21 months before the end of the high water period. Other species maintain all their leaves,
22 also when completely submerged. Under experimental conditions, saplings were even
23 able to produce new leaves under water (Waldhoff and Furch 2002; Waldhoff 2003)
24 but in the field measurements to this respect are lacking.

25 The different parameters defining leaves may change in specific recurring pat-
26 terns during the annual cycle. Since photosynthesis and the leaves' conditions are
27 crucial for the energy balance of the trees, it is supposed that these parameters make
28 statements possible about the physiological condition of the trees in situ.

29 Another striking feature when observing the leaves of Amazonian floodplain
30 trees is that in many species at least some of the leaves are not shed when sub-
31 merged, e.g. *Tabernaemontana juruana* (Fig. 9.1). Not only, but these leaves retain
32 their structure and functional capability throughout the submerged period which
33 can last as long as 7 months and leaves then can be in complete darkness for several
34 weeks. Surprisingly, some of the plants do not display scotomorphogenesis induced
35 by the lack of light during the flood periods (Fernandes-Corrêa and Furch 1992):
36 their habitus, inner structures, metabolism and movements with respect to the ambi-
37 ent environment – called photomorphogenesis in light – are not optimized or
38 changed with respect to the long period of darkness under water.

39 Thus, the aim of this chapter is to describe the leaf characteristics of Amazonian
40 floodplain trees, to analyse the reactions to flooding of parameters related to the

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Fig. 9.1 Submerged *Tabernaemontana juruana* in Manacapuru Lake (Parolin, August 1994)

assimilation organs and to discuss the variation in response to flooding. In the 41
 whole chapter we deal with leaves which were not newly developed under water 42
 but which were already present at the start of the flooding event. 43

9.2 Leaf Lifespan and Age 44

Leaf age appears to play a major role for changes of leaf characteristics in the annual 45
 cycle. Leaf lifespan varies between the species, ranging from few months in *Senna* 46
reticulata to probably 2 years in *Nectandra amazonum* (Fig. 9.2) or even more (up to 47
 5 years; Waldhoff, pers. comm.) in *Symmeria paniculata*. Most species have leaf 48
 lifespans of about 1 year. New leaves are commonly flushed towards the end of the 49
 flooded period, and leaf senescence occurs almost exclusively in the first waterlogged 50
 months. Therefore average leaf age is higher in the aquatic than in the terrestrial 51
 period, and might be responsible for higher average specific leaf mass. It was especially 52
 high in the months prior to leaf shedding. The same was due concerning leaf 53
 water content, which in new leaves was higher than in adult and senescent leaves. 54

9.3 Xeromorphism 55

The leaves of Amazonian floodplain trees exhibit traits which are generally considered 56
 as xeromorph (Medina 1983; Roth 1984; Bolh ar-Nordenkampf and Draxler 1993; 57
 Waldhoff et al. 2002; Waldhoff 2003): large epidermal cells (*Hevea spruceana*, 58

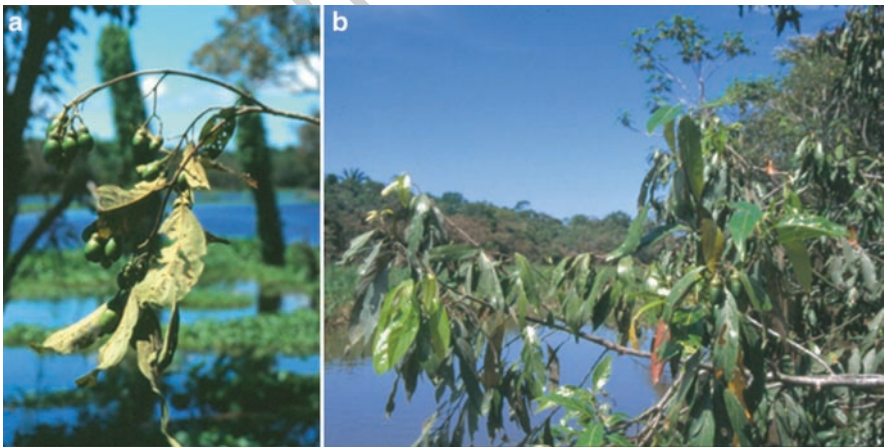


Fig. 9.2 Branch of *Nectandra amazonum*: Leaf shedding and replacement occurs continuously, but a period with clearly senescent leaves (a) and fruit maturation dominates in the beginning of the aquatic period, whereas new leaves are flushed (b) at the highest water peak and towards the end of the aquatic phase

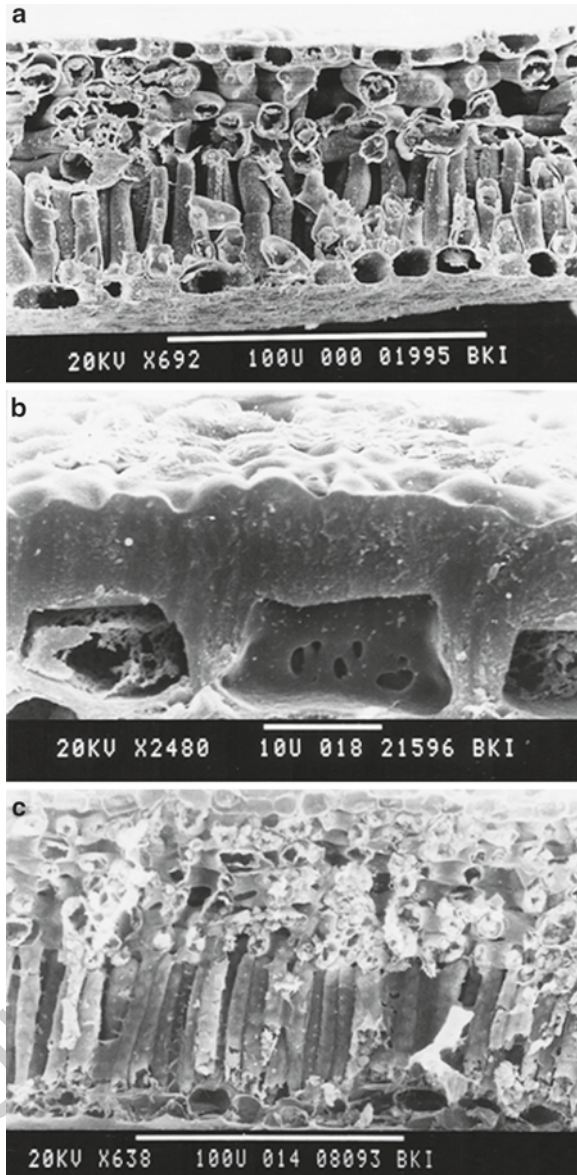


Fig. 9.3 Leaf anatomy: (a) *Eugenia inundata* cross section with large epidermal cells; (b) *Rheedia brasiliensis* thick outer epidermis walls; (c) *Senna reticulata* compact spongy parenchyma with only few and small intercellular spaces

59 *Eugenia inundata*, Fig. 9.3a), thick outer epidermis walls (*Rheedia brasiliensis*
 60 Fig. 9.3b, *Himatanthus sucuiba*), thick cuticle (*Eschweilera tenuifolia*, *Simaba guianensis*),
 61 compact spongy parenchyma with only few and small intercellular spaces (*Senna reticulata*

Fig. 9.3c, *Licania apetalata*), sunken stomata (*Vitex cymosa*, *Pouteria glomerata*), 62
 and transcurrent vascular bundles with a strong sclerenchymatous bundle sheath 63
 (*Nectandra amazonum*, *Eugenia inundata*). 64

Xeromorphic characters may be associated to high efficiency mechanisms for 65
 nutrient cycling that compensates for low soil nutrient contents (Medina 1984) 66
 which is surely not the case in nutrient-rich Amazonian white-water floodplains. 67
 Xeromorphic characters also can be a result of defense responses against herbi- 68
 vores. Pressure of herbivores is severe in tropical systems, and supposedly also in 69
 the floodplains (Turner 1994). 70

Xeromorphism can also be a response to drought (Medina 1983; Medina et al. 71
 1990). Xeromorphic characters of all leaf types indicate that the trees experience 72
 drought stress in their floodplain habitats, independent of leaf-fall behaviour. 73
 This at a first glance is astonishing, because the trees grow during several months 74
 in flooded or waterlogged soils and during the remaining time drought stress seems 75
 to be moderate because of a high groundwater table in the floodplain and/or 76
 sporadic rainfall. However, the significance of xeromorphism as an adaptation to 77
 drought and/or nutrient deficiency in central Amazonian floodplains remains elusive. 78
 Xeromorphic leaves are reported to be a general feature in tropical forests (Roth 1984). 79
 Worbes (1986, 1997) reported on water deficit in the canopy of central Amazonian 80
 floodplain forests during the inundation period similar to the one found in trees on 81
 terra firme during the dry season. 82

[AU2] The xeromorphic leaf structure may represent a pre-adaptation resulting from the 83
 dry habitats most tree species originate from (Kubitzki 1989). It helps to cope with 84
 insufficient water supply to the tree crowns during the aquatic phase which is caused 85
 by a decrease of root functioning due to waterlogging and submergence. It also is an 86
 adaptation against the periods of drought which occur occasionally in the terrestrial 87
 phase. Secretory canals in leaves of *Rheedia brasiliensis* and *Hevea spruceana* rep- 88
 resent peculiarities of the families, Clusiaceae and Euphorbiaceae, respectively, and 89
 do not seem to be related to xeromorphism (Roth 1984; Waldhoff and Furch 2002). 90

9.4 Anatomy of Leaves 91

When analysing cell sizes in different leaf components (Table 9.1) Waldhoff and Furch 92
 (2002) found that several species that keep submerged leaves showed a very thick 93
 cuticula and outer wall on the upper leaf side (e.g. *Eschweilera tenuifolia*, *Rheedia* 94
brasiliensis). On the contrary, other species that shed submerged leaves showed an 95
 upper epidermis with a thin outer wall/cuticula (e.g. *Senna reticulata*, *Simaba guian-* 96
ensis, *Vitex cymosa*). Others presented either medium (*Licania apetalata*, *Nectandra* 97
amazonum) or thick (*Eugenia inundata*, *Hevea spruceana*, *v. sucuuba*, *Pouteria glomerata*) 98
 cuticula and outer walls. The outer walls and cuticula of the lower epidermis tended to 99
 be rather thin in all analysed species. With the exception of *Pouteria glomerata* all species 100
 showed medium, large or even very large upper epidermis cells, long palisade parenchyma 101
 cells, and medium to small spongy parenchyma cells. 102

Table 9.1 Cell size in different leaf components (all measures in μm). Epidermis cells, width \times length, small: $<10 \times 5$, medium: $>10 \times 5$, large: $>15 \times 10$, very large: $>30 \times 15$. Thickness of cuticula including outer cell wall, thin: <2 , medium: >2 , thick: >3 , very thick: >9 . Length of palisade parenchyma cells, small: <30 , medium: >30 , long: >40 , very long: >70 . Width of spongy parenchyma cells, small: <10 , medium: >10 , large: >15 (From Waldhoff and Furch 2002; Waldhoff 2003)

	Species	Epidermis cell size		Outer wall – cuticula		Palisade parenchyma cell size	Spongy parenchyma cell size
		ue	le	ue	le		
t1.1		Large	Large	Medium	Thick	Medium	Medium
t1.2	<i>Aldina latifolia</i>	Small	Small	Medium	Medium	Long/small	Medium
t1.3	<i>Alchornea</i> sp.	Large	Small	Thick	Thin	Medium/small	Medium
t1.4	<i>Alibertia</i> sp.	Small	Small	Thick	Thick	Medium	Small
t1.11	<i>Bacris bidentata</i>	Medium+	Medium	Thick	Medium	Not existing	Medium
t1.12	<i>Bacris maraja</i>	Medium	Medium	Thick	Thick	Very long/small	Small
t1.13	<i>Calliandra amazonica</i>	Large	Small	Medium	Thick	Small	Small
t1.14	<i>Cratva benthami</i>	Large	*	Thin	*	*	*
t1.15	<i>Cecropia latiloba</i>	Medium	Medium	Thin	Thin	Small	Small
t1.16	<i>Cassia leiandra</i>	Large	Medium	Thick	Medium	Medium/small	Not existing
t1.17	<i>Couepia paraensis</i>	Large	Medium	Thick	Thin	Medium	Medium
t1.18	<i>Eugenia inundata</i>	Large	Small	Very thick	Thick	Long/small/small	Medium
t1.19	<i>Eschweilera tenuifolia</i>	Medium	Small	Thick	Thin	Very long	Medium
t1.20	<i>Hevea spruceana</i>	Very large	Large	Thick	Thin		Medium
t1.21	<i>Himatantus sucuba</i>	Large	Large	Thick	Thin		Medium
t1.22	<i>Ilex inundata</i>	Medium	Small	Thick	Thick	Very long/small	Small
t1.23	<i>Licania apetala</i>	Large	(Papilla)	Medium	(Papilla)	Long/small/small	Medium
t1.24	<i>Macrobolium</i>	Large	Medium	Thick	Thin	*	Medium
t1.25	<i>acacifolium</i>						
t1.26	<i>Maprounea guianensis</i>	Medium	Large	Thick	Thin	Long	Small
t1.27	<i>Mouriri guianensis</i>	Small	Small	Thick	Thin	Small	Large
t1.28	<i>Nectandra amazonum</i>	Large	Large	Medium	Medium	Long/small/small	Not existing
t1.29	<i>Nectandra</i> sp.	Large	Large	Thick	Thick	Medium/small	Large
t1.30	<i>Ouratea hexasperma</i>	Large	Medium	Very thick	Medium	Very long	Medium

t1.31	<i>Psidium acutangulum</i>	Large +	Small	Thick	Thin	Medium/small	Medium
t1.32	<i>Pouteria glomerata</i>	Small	Small	Thick	Medium	Medium	Small
t1.33	<i>Pseudobombax munguba</i>	Large	Medium	Thin	Medium	Long/small	Small
t1.34	<i>Quinia rhytidopus</i>	Medium	Small	Thick	Thin	Medium	Medium
t1.35	<i>Rheedia brasiliensis</i>	Large	Large	Very thick	Thick	Medium/small	Medium
t1.36	<i>Simaba guianensis</i>	Large	Small	Thin	Thick	Medium	Small
t1.37	<i>Salix humboldtiana</i>	Medium+	Medium	Thin	Thin	Small/small etc.	Not existing
t1.38	<i>Senna reticulata</i>	Medium	Medium	Thin	Thin	Long	Medium
t1.39	<i>Tabebuia barbata</i>	Medium+	Large	Thin	Thin	Long-very long	Medium
t1.40	<i>Tabernaemontana</i>	Large	Large	Thick	Thick	Small	Large
t1.41	<i>juarana</i>						
t1.42	<i>Tovomita macrophylla</i>	Large	Large	Thick	Thick	Small	Small
t1.43	<i>Vitex cymosa</i>	Large	Large	Thin	Thin	Long/small/small	Not existing

t1.44 le, lower epidermis; ue, upper epidermis; *, missing data; cells not visible (see text).

103 All species that shed submerged leaves showed only one layer of palisade
104 parenchyma except for *Vitex cymosa*. Those that do not shed submerged leaves
105 showed more than one layer of palisade parenchyma at the lower leaf side, with the
106 exception of *Pouteria glomerata* (Table 9.2). In leaves with multiple palisade paren-
107 chyma layers cell length decreased towards the inner layers (Table 9.1).

108 The compactness of the spongy parenchyma ranged from loose in *Rheedia*
109 *brasiliensis* and *Simaba guianensis*, regular in *Eugenia inundata*, and compact to
110 very compact in other species (Table 9.2). The spongy parenchyma was completely
111 missing in *Couepia paraensis*, *Nectandra amazonum*, *Salix martiana* and *Vitex cymosa*
112 (Waldhoff 2003). Neither the spongy parenchyma was associated with leaf-fall behaviour
113 or fate of submerged leaves nor the extension of the vascular bundles as well as the
114 form of the sclerenchymatous sheath (Waldhoff 2003). Both the extension of the
115 vascular bundles and the form of the sclerenchymatous sheath varied between spe-
116 cies in different combinations (Table 9.2) (Waldhoff and Furch 2002).

117 9.5 Stomata

118 Stomatal density at the lower leaf side of 34 analysed tree species varied between
119 25 and 2,339 mm⁻² (Table 9.3) and did not differ significantly between species that
120 keep or shed submerged leaves (Waldhoff 2003). Species with higher stomatal
121 densities tended to show small epidermal cells (e.g. *Mouriri guianensis*, *Ouratea*
122 *hexasperma*, *Quiinia rhytidopus*) and vice versa (e.g. *Acmanthera latifolia*,
123 *Tabernaemontana juruana*, *Tovomita macrophylla*). Stomatal densities were apparently
124 not associated with a certain type of leaf-fall behaviour, which corresponds with the
125 literature on the relation of stomatal density with xeromorphism (Wilkinson 1979;
126 Roth 1984; Bolh ar-Nordenkampf and Draxler 1993; Cao 2000; Dong and Zhang
127 2000). While hypostomatic leaves represent the usual pattern among dicotyledonous
128 trees, additional stomata at the upper leaf side may have emerged as an adaptation
129 to dry habitats in some species (Bolh ar-Nordenkampf and Draxler 1993), e.g.
130 *Rheedia brasiliensis* (Fig. 9.4a), *Bactris maraj a*, *Pouteria glomerata*, and *Psidium*
131 *acutangulum* (Fig. 9.5). Amphistomatic leaves are commonly found in members of
132 the family Caesalpinaceae (Roth 1984; Metcalfe and Chalk 1950).

133 Most of the analysed species had sunken stomata at the lower side of the leaf (Fig. 9.4b;
134 Waldhoff 2003), some even had stomata that are not visible because they are buried in a
135 cavity or pit-like hole, sunken between waxy elevation or cuticular folds (Table 9.3).

136 Waldhoff et al. (2002), Fernandes-Corr ea and Furch (1992), and Schl uter and Furch
137 (1992) also described sunken stomata in several tree species that do not shed submerged
138 leaves. The latter two studies ascribed this structure to a postulated function they called
139 “reverse plastron respiration” which would enable a “plastron photosynthesis”.

140 Sunken stomata are common in xeromorphic leaves (Roth 1984; Bolh ar-
141 Nordenkampf and Draxler 1993). On the other hand Fahn and Cutler (1992) reported
142 that only 34% of xeromorphic species (35 dicotyledons, 33 monocotyledons,
143 3 gymnosperms) from arid and semi-arid environments possess sunken stomata.

Table 9.2 Parenchyma characteristics (From Waldhoff and Furch 2002; Waldhoff 2003)

	Species	No. of layers of palisade parenchyma	Compactness of spongy parenchyma	Canals	Vascular bundles	
					Extension	Sclerenchyma
t2.1	<i>Aldina latifolia</i>	1	Very compact		Some transcurrent	Weekly developed
t2.2	<i>Alchornea</i> sp.	1 up, 1 low	Very compact		Some transcurrent	Weekly developed
t2.3	<i>Alibertia</i> sp.	2	Compact		Not transcurrent	Weekly developed
t2.4	<i>Bactris bidentata</i>	1	Compact		Not transcurrent	Sheath surrounding the bundle, fibres
t2.5	<i>Bactris maraja</i>	Not existing	Compact		Not transcurrent	Sheath surrounding the bundle, fibres
t2.6	<i>Calliandra amazonica</i>	1 up, 1 low	Loose		Not transcurrent	Weekly developed
t2.7	<i>Cratava benthami</i>	1-2	Loose		Not transcurrent	No sclerenchyma
t2.8	<i>Cecropia latiloba</i>	*	*		*	*
t2.9	<i>Cassia leiandra</i>	1	Compact		Transcurrent	Strong sheath surrounding the bundle
t2.10	<i>Couepia paraensis</i>	4	-		Transcurrent	Capping bundles on both sites
t2.11	<i>Eugenia inundata</i>	1	Regular		Transcurrent	Capping bundles on both sites
t2.12	<i>Eschweilera tenuifolia</i>	1 up, 1 low	Very compact		Mostly transcurrent	Sheath surrounding the bundle
t2.13	<i>Hevea spruceana</i>	1	Compact	Laticiferous	Not transcurrent	Weekly developed
t2.14	<i>Himatanthus sucuba</i>	*	*		*	*
t2.15	<i>Ilex inundata</i>	2	Regular		Not transcurrent	Capping bundles on one site
t2.16	<i>Licania apetala</i>	2	Very compact		Not transcurrent	Strong sheath surrounding the bundle
t2.17	<i>Macarobium acaciifolium</i>	*	Regular		*	*
t2.18	<i>Maprounea guianensis</i>	1	Regular		Transcurrent	Strong sheath surrounding the bundle
t2.19	<i>Mouriri guianensis</i>	1	Regular		Not transcurrent	Strong sheath surrounding the bundle
t2.20						
t2.21						
t2.22						
t2.23						
t2.24						
t2.25						
t2.26						
t2.27						
t2.28						
t2.29						

(continued)

Table 9.2 (continued)

Species	No. of layers of palisade parenchyma	Compactness of spongy parenchyma	Canals	Vascular bundles	
				Extension	Sclerenchyma
<i>Nectandra amazonum</i>	2 up, 1 low	Not existing		Transcurrent	Capping bundles on both sites
<i>Nectandra</i> sp.	1 up, 1 low	Compact		Transcurrent	Capping bundles on both sites
<i>Ouratea hexasperma</i>	1	Very compact		Not transcurrent	Capping bundles on both sites
<i>Psidium acutangulum</i>	1-3	Compact		Not transcurrent	Sheath surrounding the bundle
<i>Pouteria glomerata</i>	1	Very compact		*	*
<i>Pseudobombax munguba</i>	2	Loose		Transcurrent	Capping bundles on both sites
<i>Quiinia rhytidopus</i>	1	Regular		*	*
<i>Rheedea brasiliensis</i>	2	Loose	Resin	Mostly transcurrent	Strong sheath surrounding the bundle
<i>Simaba guianensis</i>	1	Very loose		Not transcurrent	Weekly developed
<i>Salix humboldtiana</i>	5-6	Not existing	Oil cells	Transcurrent	Weekly developed
<i>Senna reticulata</i>	1	Compact		Transcurrent	Capping bundles on both sites
<i>Tabebuia barbata</i>	1	Regular		Transcurrent	Capping bundles on both sites
<i>Tabernaemontana juruana</i>	1	Loose		Not transcurrent	Weekly developed
<i>Tovomita macrophylla</i>	1-2	Regular		Not transcurrent	Weekly developed
<i>Vitex cynosa</i>	2-3	Not existing		Transcurrent	Capping bundles on both sites

t2.30 up, upper side of leaf; low, lower side of leaf; *, missing data.

Table 9.3 Density and form of stomata (from Waldhoff and Furch 2002; Waldhoff 2003) t3.1

Species	Density (number mm ⁻²)		Form	
	ue	le		
<i>Aldina latifolia</i>		25	Sunken in thick cuticula	t3.3
<i>Alchornea</i> sp.	309	233	Not sunken	t3.4
<i>Alibertia</i> sp.		696	Not sunken	t3.5
<i>Bactris bidentula</i>		nv	Completely sunken in cuticular folds	t3.6
<i>Bactris maraja</i>	63	248	Sunken	t3.7
<i>Calliandra amazonica</i>		643	Sunken in thick cuticula	t3.8
<i>Crateva benthami</i>		582	Not sunken	t3.9
<i>Cecropia latiloba</i>	69	?	Not sunken	t3.10
<i>Cassia leiandra</i>		814	Sunken	t3.11
<i>Couepia paraensis</i>		nv	Sunken in cuticular folds, hidden by hairs	t3.12 t3.13
<i>Eugenia inundata</i>		620	Sunken in cavity formed by the raised stomatal rim	t3.14 t3.15
<i>Eschweilera tenuifolia</i>		nv	Sunken in very thick cuticula	t3.16
<i>Hevea spruceana</i>		369	Sunken	t3.17
<i>Himatanthus sucuuba</i>		675	Sunken, with raised stomatal rim	t3.18
<i>Ilex inundata</i>		601	Sunken with raised stomatal rim	t3.19
<i>Licania apetala</i>		nv	Sunken in deep pit formed by papillose subsidiary cells	t3.20 t3.21
<i>Macrolobium acaciifolium</i>	nv	nv	le: sunken between elevations of wax	t3.22 t3.23
<i>Maprounea guianensis</i>		nv	Sunken in cuticular folds	t3.24
<i>Mouriri guianensis</i>		1,952	Sunken in holes formed by cuticular folds	t3.25
<i>Nectandra amazonum</i>		1,188	Sunken	t3.26
<i>Nectandra</i> sp.		318	Sunken in cuticula	t3.27
<i>Oureatea hexasperma</i>		913	Sunken in cavity formed by the raised stomatal rim	t3.28 t3.29
<i>Psidium acutangulum</i>	149	837	Sunken in cavity formed by the raised stomatal rim	t3.30 t3.31
<i>Pouteria glomerata</i>	177	449	ue: not sunken, le: sunken with raised stomatal rim and long, narrow aperture	t3.32 t3.33 t3.34
<i>Pseudobombax munguba</i>	nv	284	Sunken with raised stomatal rim	t3.35 t3.36
<i>Quiinia rhytidopus</i>		2,339	Sunken in deep pit formed by papillose subsidiary cells	t3.37 t3.38
<i>Rheedia brasiliensis</i>	nv	178	Sunken in pit formed by very thick cuticula	t3.39 t3.40
<i>Simaba guianensis</i>		4	Sunken	t3.41
<i>Salix humboldtiana</i>	393	343	Sunken with raised stomatal rim	t3.42
<i>Senna reticulata</i>	141	84	Sunken	t3.43
<i>Tabebuia barbata</i>		287	Sunken with raised stomatal rim	t3.44
<i>Tabernaemontana juruana</i>		716	Not sunken	t3.45 t3.46
<i>Tovomita macrophylla</i>		201	Not sunken	t3.47
<i>Vitex cymosa</i>		176	Sunken in cavity formed by the raised stomatal rim	t3.48 t3.49

le, lower epidermis; nv, not visible; ue, upper epidermis t3.50

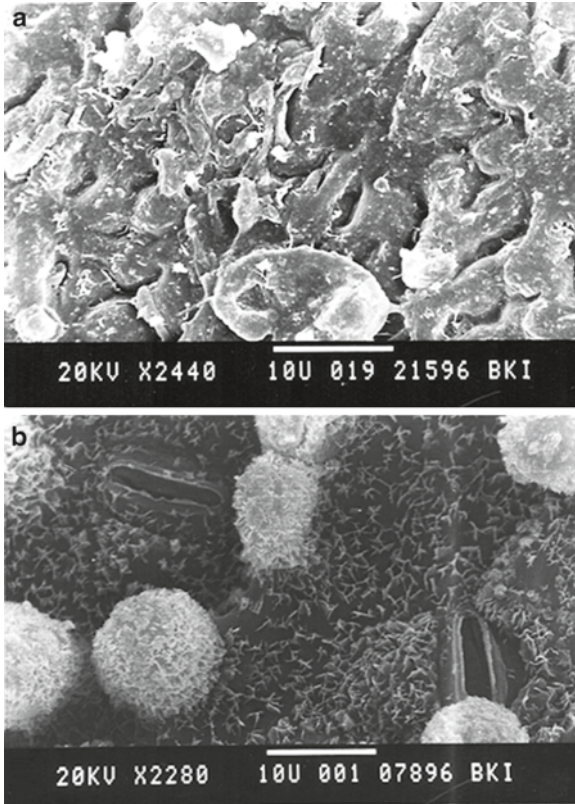


Fig. 9.4 *Rheedia brasiliensis* stomata on the upper leaf side (a); sunken stomata on the lower side of the leaf in *Cassia leiandra*, with wax crystals (b)

144 Lindorf (1993) studied 17 tree species from Venezuelan tropical rainforests and
145 found no species with sunken stomata. From this perspective the presence of
146 sunken stomata in 27 out of 34 species studied seems remarkable.

147 9.6 Surface Structures

148 Glandular and non-glandular hairs were found in leaves from several species studied
149 in the floodplain forests, e.g. *Cassia leiandra*, *Nectandra amazonum*, and *Pouteria*
150 *glomerata* (Fig. 9.6, Table 9.4; Waldhoff and Furch 2002; Waldhoff 2003).
151 The lower leaf surface of *Licania apetala*, *Senna reticulata*, *Cassia leiandra*, and
152 *Quinia shytidopus* is covered with papillae (Fig. 9.6a). Roth (1984) reported that
153 both hair types and papillae are scarce in the humid tropics.

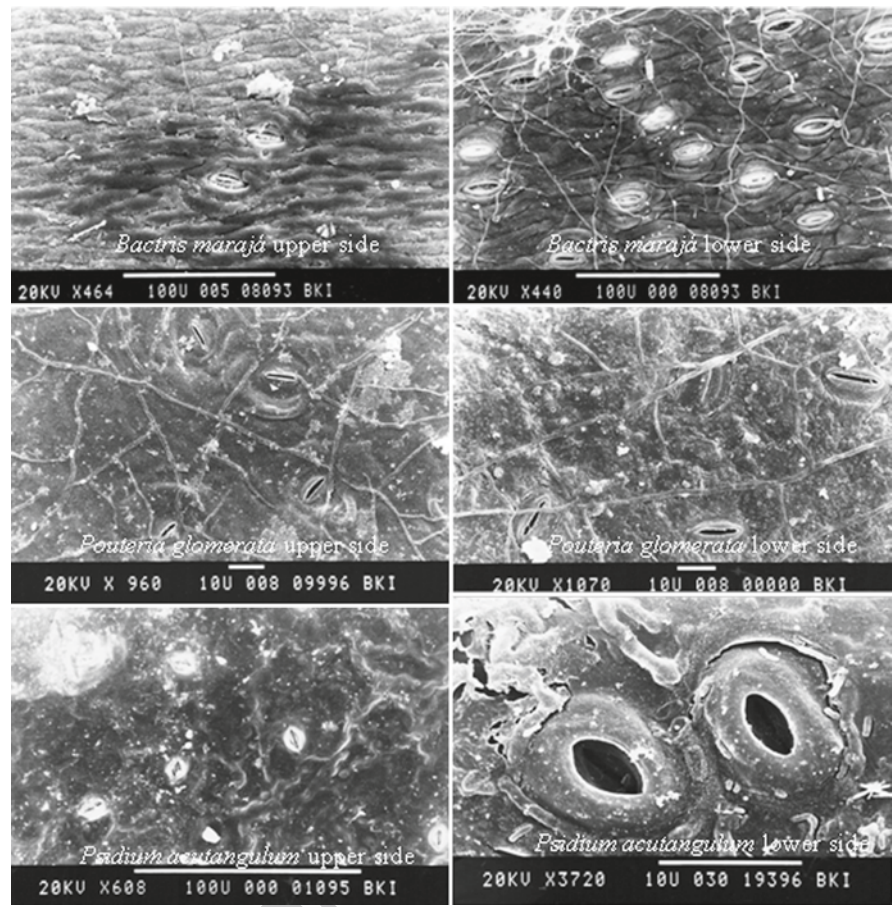


Fig. 9.5 Upper (left) and lower (right) leaf side of *Bactris marajá*, *Pouteria glomerata*, and *Psidium acutangulum*

Ten analysed species exhibited wax deposits (Fig. 9.7), twenty showed cuticular ornamentations, mostly on the lower leaf side (see Table 9.4). These ornamentations are reported to be quite common in leaves of trees from tropical rainforests (Roth 1984). These have been interpreted in the literature as assisting water to channel off the leaf surface (Barthlott 1990; Carpenter 1994). The sculpturing of *Hevea spruceana* is very similar to that of *Hevea brasiliensis* from terra firme uplands (Wilkinson 1979; Sena Gomes and Kozlowski 1988).

In analogy to the sunken stomata ascribed to the postulated function called “reverse plastron respiration” mentioned above which would enable a “plastron photosynthesis” the existence of wax layers may be interpreted as an adaptation to avoid water influx in submerged leaves (Fernandes-Corrêa and Furch 1992; Schlüter and Furch 1992).

[AU3,4]

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166 **9.7 Chloroplasts**

167 In the palm *Bactris bidentula*, palisade parenchyma cells are densely filled with
 168 chloroplasts (Waldhoff 2003). Such a high density of chloroplasts in palisade
 169 parenchyma had not been described hitherto. It might be helpful for a possible
 170 photosynthesis under water when light is the limiting factor (Furch et al. 1985).
 171 Although light can be an important limiting factor under water, presumably CO₂ is
 172 much more limiting (Mommer and Visser 2005), but no studies are available to this
 173 respect in Amazonian floodplain trees.

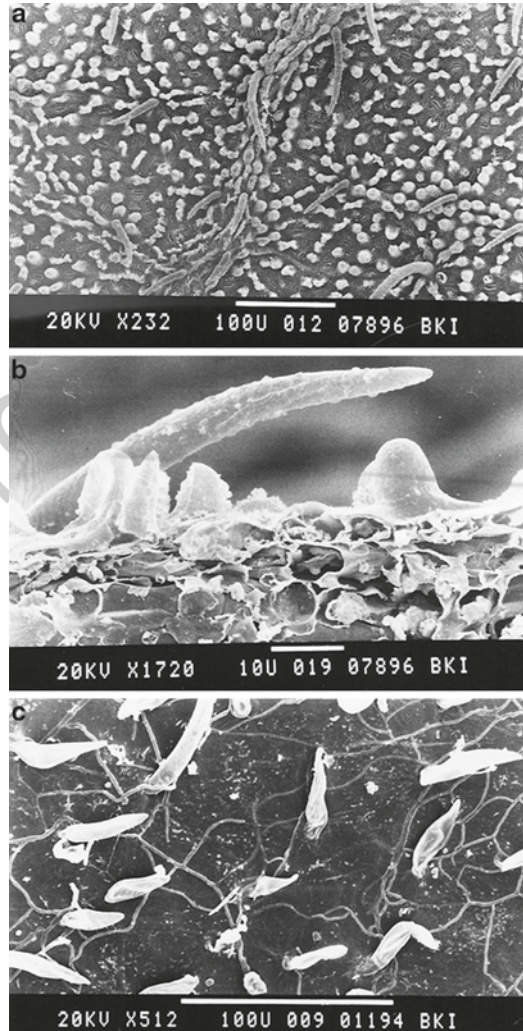


Fig. 9.6 Leaf surface structures: hairs and papillae (a, cross section b) on lower leaf surface of *Cassia leiandra*, hairs on upper (c) and lower (d) leaf side of *Nectandra amazonum*, and lower leaf side (e) of *Pouteria glomerata*

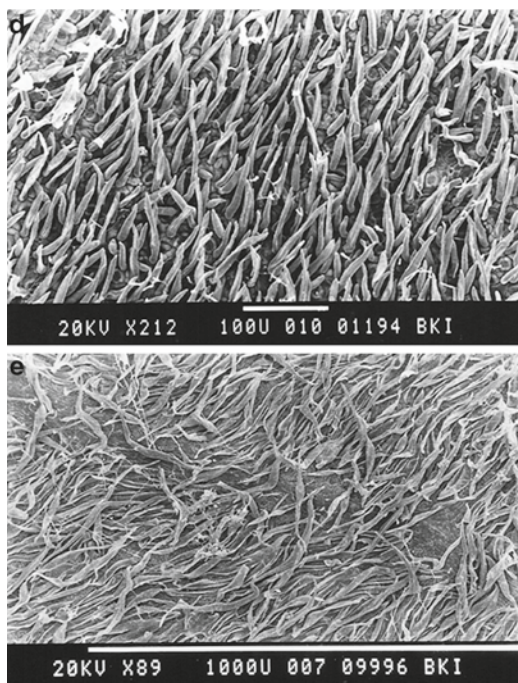


Fig. 9.6 (continued)

Transmission electron microscope (TEM) analyses of leaves from *Symmeria* 174
paniculata at 1 m depth showed that short-term submergence did not affect neither 175
chloroplast shape nor the interior structures of chloroplasts with thylakoids, stacks, 176
and starch grains (Waldhoff et al. 2002). The leaves have big epidermis cells with 177
thick outer walls followed by the first row of palisade parenchyma, which show 178
chloroplasts along the cell walls filled with stroma and grana thylakoid-forming 179
stacks and starch grains (Fig. 9.8). These stacks are responsible for the tolerance of 180
extreme low light in this species. On the other hand, chloroplast shape and starch 181
content may change with long-term submergence as was found in *Laetia corymbu-* 182
losa and *Pouteria glomerata* (Waldhoff et al. 2002). 183

9.8 Specific Leaf Mass

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Specific leaf mass was higher in waterlogged months in many species, e.g. *Cecropia* 185
latiloba, *Nectandra amazonum*, *Senna reticulata*, *Tabebuia barbata*, and *Vitex* 186
cymosa, in adult trees in the field as well as in seedlings under experimental conditions 187

Table 9.4 Occurrence and characteristics of epidermal and cuticular structures: hairs, papillae, wax layer, and cuticular ornamentations (From Waldhoff and Furch 2002; Waldhoff 2003)

	Species	Hairs		Papillae	Wax layer	Cuticular ornamentation
		Not glandular	Glandular			
t4.1	<i>Aldina latifolia</i>	le				le: rough surface with irregular elevations
t4.2						
t4.3						
t4.4	<i>Alchornea</i> sp.					ue: radiating striae around stomata
t4.5	<i>Alibertia</i> sp.					le: rough surface
t4.6	<i>Bactris bidentata</i>				le	ue, le: the whole surface is structured by many cuticular folds
t4.7						
t4.8						
t4.9						
t4.10						
t4.11	<i>Bactris maraja</i>	le				ue, le: the whole surface is structured by many cuticular folds
t4.12						
t4.13						
t4.14	<i>Calliandra amazonica</i>	ue				ue, le: the whole surface is structured by many cuticular folds
t4.15	<i>Crateva benthami</i>					
t4.16						
t4.17						
t4.18	<i>Cecropia latiloba</i>	ue; le: filamentous hairs	ue			
t4.19						
t4.20	<i>Cassia leiandra</i>	le		le: simple, corn-like	ue, le: upright scales	
t4.21						
t4.22	<i>Couepia paraensis</i>	le				le: cuticular folds; ue: very large cuticular folds
t4.23						
t4.24	<i>Eugenia inundata</i>		ue, le: glandular scales			le: concentric rings of striae around stomata and radiating striae around concentric rings
t4.25						ue: striae random and very dense
t4.26						
t4.27						
t4.28						
t4.29	<i>Eschweilera tenuifolia</i>		ue, le: glandular scales			
t4.30						

t4.31	<i>Hevea spruceana</i>		le	ue, le: reticulum of crests and buttressed ridges around stomata
t4.32				le: concentric rings of striae around stomata
t4.33				le: concentric rings of striae around the stoma
t4.34	<i>Himatanthus sucuuba</i>			
t4.35			ue	
t4.36	<i>Ilex inundata</i>			
t4.37				
t4.38	<i>Licania apetala</i>			le: with dense papillose hairs
t4.39				
t4.40	<i>Macrolobium</i>			ue: many elevations
t4.41	<i>acaciifolium</i>			
t4.42	<i>Maprounea gutanensis</i>			le: dense network of radiating striae around the stoma and between them
t4.43				le: dense network of cuticular folds
t4.44				
t4.45	<i>Mouriri gutanensis</i>			
t4.46				
t4.47	<i>Nectandra amazonum</i>			le: rods of wax
t4.48	<i>Nectandra</i> sp.			
t4.49	<i>Ouratea hexasperma</i>			le: elevations formed by cuticula
t4.50	<i>Psidium acutangulum</i>		le	ue, le: cuticula forms puzzle like structures
t4.51				
t4.52	<i>Pouteria glomerata</i>			le: dense and complex network of undulate striae
t4.53				
t4.54	<i>Pseudobombax munguba</i>			le: concentric rings of striae around the stoma, and radiating striae around concentric rings
t4.55				
t4.56				

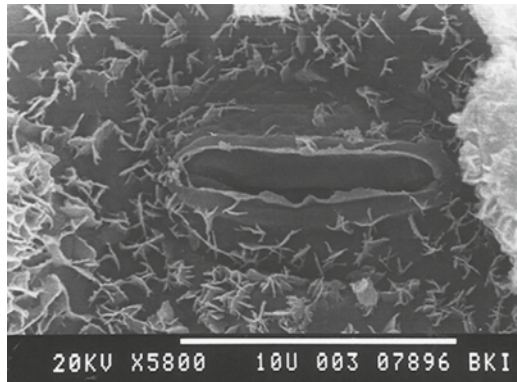
(continued)

Table 9.4 (continued)

Species	Hairs		Papillae	Wax layer	Cuticular ornamentation
	Not glandular	Glandular			
<i>Quinia rhytidopus</i>			le: with dense papillose hairs		
<i>Rheedia brasiliensis</i>		le			le: concentric rings of striae around stomata and radiating striae around concentric rings
<i>Simaba guianensis</i>		ue, le glandular scales			le: concentric rings of striae around stomata and radiating striae around concentric rings, ue: striae random and very dense
<i>Salix humboldtiana</i>					le: concentric rings of striae around the stoma, and radiating striae around concentric rings
<i>Senna reticulata</i>	ue, le		ue, le: simple, cone-like scales		
<i>Tabebuia barbata</i>		le			le: radiating striae around stomata
<i>Tabernaemontana juruana</i>					
<i>Tovomita macrophylla</i>					
<i>Vitex cymosa</i>	le	le, flattened glandular scales			ue: dense network of cuticular elevations le: rough surface of bulbous-like elevations

14.57 ue, upper epidermis; le, lower epidermis

Fig. 9.7 Leaf surface structures: wax crystals and stoma on lower leaf surface of *Cassia leiandra*



(Parolin 2002d). Specific leaf mass in the non-flooded period varied between 188
 48.8 gm^{-2} for the pioneer *Senna reticulata* and 118.9 gm^{-2} for the evergreen non- 189
 pioneer *Nectandra amazonum* (Table 9.5). In waterlogged months, specific leaf 190
 mass in an average was 5–33% higher than in non-flooded months. Only *Crateva* 191
benthami had significantly lower specific leaf mass with waterlogging. This was 192
 due to the fact that the new leaves – which were mainly produced in the aquatic 193
 period – had higher specific leaf mass than older leaves. In *Cecropia latiloba*, 194
Crateva benthami, *Tabebuia barbata* and *Vitex cymosa* there was a constant 195
 increase of specific leaf mass in the first months after leaf expansion, which occurs 196
 in the last months of the flooded period. 197

9.9 Leaf Size 198

The size of single leaves varied between few cm^2 for *Salix* and more than 2,380 cm^2 199
 for *Cecropia latiloba* (Table 9.5). The pioneer *Senna reticulata* and two deciduous 200
 non-pioneers (*Crateva benthami*, *Tabebuia barbata*) had highly significant reduc- 201
 tions of leaf area (25–37%) in the aquatic period, compared to the terrestrial period 202
 (Table 9.5). *Cecropia latiloba* and *Nectandra amazonum* produced leaves with a 203
 more or less constant size throughout the year. 204

Reductions of leaf size were caused by leaf senescence and a subsequent loss of 205
 leaflets. Only in *Senna reticulata* leaf size reduction was a direct response to water 206
 stress: in waterlogged months, the newly produced leaves and leaflets were smaller 207
 than in the terrestrial period (Parolin 2001c) (Fig. 9.9). Data in this study indicate 208
 a periodicity in several leaf traits which changes parallel to the flooding periodicity, 209
 but which is determined primarily by leaf age and senescence and only indirectly 210
 by flooding. The timing of the changes of specific leaf mass and leaf size was similar 211
 between species and was concentrated in the aquatic period, but the degree of 212
 changes differed among the species. Leaves of pioneer and non-pioneer species, 213

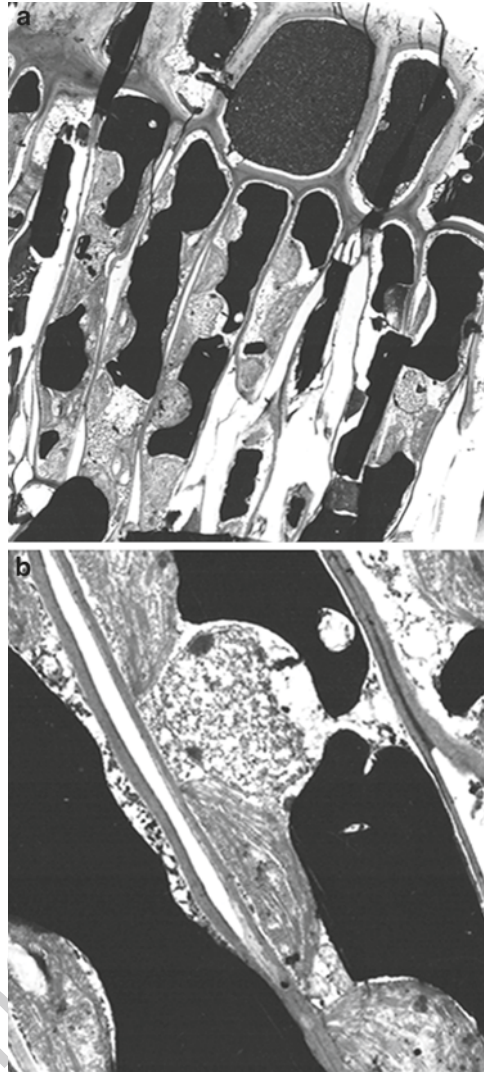


Fig. 9.8 Cross-sections from a leaf of *Symmeria paniculata* submerged at 1m depth: (a) Epidermis cells (upper row) and palisade parenchyma (lower row; arrow: starch grain); (b) chloroplast (upper organelle) and nucleus (middle organelle) from palisade parenchyma cell (transmission electron microscopy photographs, from Waldhoff et al. 2002)

214 and leaves of deciduous and evergreen species did not show a uniform trend, characteristic
215 for certain growth strategies, as response to flooding. Apparently differences were
216 closely linked to leaf age and cannot be considered as adaptive to the changing
217 hydricological conditions.

t5.1 **Table 9.5** Specific leaf mass and leaf area of six species in the non-flooded and waterlogged months (From Parolin
 t5.2 2002c): minimum and maximum measured values, average of the measurements in the terrestrial phase, average of the
 t5.3 measurements in the aquatic phase, with standard deviations, difference between terrestrial (= 100%) and aquatic
 t5.4 phase

		Specific leaf mass			
		Min-max (gm ⁻²)	Terrestrial phase (gm ⁻²)	Aquatic phase (gm ⁻²)	Difference (%)
t5.5	Species				
t5.6	<i>Cecropia latiloba</i>	43.8–112.7	74.6 ± 16	78.0 ± 17	4.6
t5.7	<i>Senna reticulata</i>	25.3–86.7	48.8 ± 11	64.8 ± 12	32.7
t5.8	<i>Nectandra amazonum</i>	95.0–163.9	118.9 ± 14	140.1 ± 17	17.7
t5.9	<i>Cratava benthami</i>	38.2–126.9	94.3 ± 24	80.5 ± 28	-14.6
t5.10	<i>Tabebuia barbata</i>	33.4–133.5	76.3 ± 19	96.5 ± 23	26.4
t5.11	<i>Vitex cymosa</i>	50.8–143.4	83.3 ± 19	106.9 ± 20	28.4
t5.12	Leaf area				
t5.13	Min-max (cm ²)		Terrestrial phase (cm ²)	Aquatic phase (cm ²)	Difference (%)
t5.14	<i>Cecropia latiloba</i>	605–2,380	1,051.9 ± 113	1,090.3 ± 122	3.7
t5.15	<i>Senna reticulata</i>	660–1,588	805.4 ± 218	504.3 ± 262	-37.0
t5.16	<i>Nectandra amazonum</i>	12–101	42.0 ± 12	52.3 ± 18	24.6
t5.17	<i>Cratava benthami</i>	49–531	209.0 ± 81	131.7 ± 47	-37.4
t5.18	<i>Tabebuia barbata</i>	89–670	371.1 ± 105	278.9 ± 122	-24.9
t5.19	<i>Vitex cymosa</i>	88–663	262.1 ± 133	232.9 ± 93	11.1

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Fig. 9.9 *Senna reticulata* with different leaf size in non-waterlogged (control) and waterlogged conditions



218 9.10 Leaf Water Content

219 Leaf water content varies between 49% and 74% (Parolin 2002c). Evergreen pioneer
 220 species had the highest water contents, and evergreen non-pioneer *Nectandra amazonum*
 221 the lowest (Table 9.6). In the flooded period, leaf water content was lower in all analysed
 222 species, probably as a result of new leaf expansion during this time. While differences
 223 were neglectable in *Cecropia latiloba* and *Nectandra amazonum*, where leaf water
 224 content was rather constant throughout the year, it changed significantly in the
 225 deciduous species and in the pioneer *Senna reticulata*. In all species, the new leaves
 226 had higher water contents than the adult and senescent leaves in the subsequent
 227 months. The absolute highest water contents were measured in newly developed
 228 leaves during the flooded period, but overall means were lower in this period.

229 9.11 Discussion and Conclusions

230 Most measured parameters and their changes in the annual cycle do not reflect the
 231 extreme environmental conditions to which trees in Amazonian floodplains are sub-
 232 jected. The hydrological conditions in the floodplains are unfavourable for tree growth
 233 for several months every year, as indicated by regular growth reductions in the wood

Table 9.6 Leaf water content of six species in the non-flooded and waterlogged months (from Parolin 2002c): 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, and statistical probability p

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

*p ≥ 0.05; **p ≥ 0.01; ***p ≥ 0.001; n.s. not significant

(Worbes 1989). A relationship between leaf parameters and flooding periodicity was not found in the study species, and the measured variations, e.g. in leaf mass and size, are not understood as adaptations against flooding. If we take for example leaf size, we find that it 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 and Vermeij 1976). The reduction of the transpirational surface, i.e. leaf size, in periods of unfavorable hydric conditions could be an adaptation to the reduced tree water status induced by flooding (Borchert 1994a). 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* (Parolin 2001c). Since this species constantly produces new leaves, the production of smaller leaves under unfavourable conditions can be seen as adaptation against waterlogging. In other species, leaf production was not as fast as in *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 et 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 in old leaves.

Concluding, leaf parameters make statements possible about the physiological condition of the trees in situ but the reactions to flooding are not as astonishing as could have been expected given the extreme flooding conditions the trees are subjected to. Most parameters indicate that the assimilation organs perform perfectly well despite the long periods of waterlogging or complete submergence in darkness. The high diversity of species is reflected in a high diversity of life strategies (evergreen/deciduous, fast-/slow-growing, high/low annual wood increments, high/low wood specific gravity, etc.) to cope with flooding, and leaf types differ to a certain extent (perhaps also due to taxonomic differences). However, the reactions of the leaves' functions are not as manifold as the extreme environment could suggest.

267 Leaf anatomy is not particularly divergent between species. Common to most species
268 are a xeromorphic character, large upper epidermis cells, long palisade parenchyma
269 cells, small spongy parenchyma cells, sunken stomata, hairs and wax layers on the
270 leaf surface.

271 Amazonian floodplains show all characteristics of extreme sites. A very long
272 uninterrupted period of flooding with a high amplitude, rapid changes of water level,
273 anoxic conditions in the rhizosphere, high sedimentation in várzea, lack of nutrients
274 in sediment-poor igapó, high mechanical stress and even drought lead to difficult
275 conditions for growth of all organisms living in this ecosystem. Nevertheless, the
276 high diversity of species and life strategies may result from the fact that this
277 extreme site has only a reduced number of factors representing stress for the trees,
278 and the regular disturbances may even represent a driving force for resistance and
279 adaptive evolution. The high complexity of the system and the short but regular
280 occurrence of factors enhancing tree growth allow the formation of highly diverse
281 survival strategies. The species are seldom highly specialized – most have high
282 ecological amplitudes. In these floodplains, specialization is low enough to allow
283 the trees to react to changing environmental conditions, and is high enough to allow
284 a high diversity along the hydric and edaphic gradient.

Author Queries

Chapter No.: 9 0001170098

Queries	Details Required	Author's Response
AU1	Please provide affiliations.	
AU2	Please specify a, b or c in Kubitzki (1989).	
AU3	'Barthlott 1990' is cited in text but not given in the reference list. Please provide details in the list.	
AU4	'Carpenter 1994' is cited in text but not given in the reference list. Please provide details in the list.	

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